

**THE BIOLOGY, ECOLOGY AND CONSERVATION OF  
FOUR FLUFFTAIL SPECIES, *SAROTHRURA* (AVES: RALLIDAE)**

by

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B

**Frontispiece** A: adult male Buffspotted Flufftail at a feeding station, Scotston, Underberg, October 1991.  
B: adult male (left) and immature male (in submissive pose) Redchested Flufftail, Zimbabwe, April 1992.

## ABSTRACT

The distribution, status, biology and ecology of four flufftail species were investigated in South Africa and Zimbabwe. The Redchedest Flufftail is a successful and widely distributed species, occupying a wide range of dense vegetation, from seasonally wet grassland and sedges to permanently shallowly flooded reedbeds. It colonizes artificially created wetland patches and occupies very small patches of suitable habitat. Redchedest Flufftails maintain a permanent pair bond and are permanently territorial and entirely sedentary. Their habitat is relatively stable but unpredictable catastrophic events such as burning may force temporary emigration in winter or spring. Displaced birds move a short distance, occupy often marginally suitable habitat and recolonize burned areas as soon as vegetation cover becomes adequate. Periodic burning improves habitat quality, and recommendations are formulated for the management of wetland habitats by burning. The size of the winter territory is larger than the minimum required for survival and provides an insurance against forced emigration, while immatures often share parental territories in winter.

The Striped Flufftail's grassland habitats in Natal are decreasing and its numbers are declining. Striped Flufftails are sedentary in low-altitude grassland habitats, but in high-altitude sourveld the decrease in invertebrate food forces emigration in April-June, when the birds move to unknown wintering destinations (movements are possibly altitudinal). Return time to unburned vegetation is dependent upon invertebrate food availability. Return time to burned vegetation is governed by the development of suitable cover, which may occur too late in the breeding season to permit occupation. The species is well adapted to frequent burning of its habitats, which serves to maintain suitable fire-climax grassland, but is also adapted to post-fire-climax vegetation types.

The Whitewing Flufftail is rare but its occurrence was regularly noted during the summer at four sites in Natal and the Transvaal. Habitat preferences and movement patterns were clarified, as was the bird's ecological segregation from the Redchedest Flufftail. No conclusive evidence was found for breeding in South Africa and it is suggested that lack of suitable breeding habitat (possibly as a result of its being occupied by breeding Redchedest Flufftails) may account for this. Some aspects of the bird's behaviour and calling were investigated. In view of this bird's threatened status and the continuing destruction of its wetland habitats, further surveys are urgently required to clarify the bird's status and the full extent of suitable habitat in South Africa, while a captive breeding programme is recommended to study breeding behaviour.

The Buffspotted Flufftail inhabits a wide variety of forested and bushed habitats, and in Natal is a successful colonist of exotic vegetation in gardens. Its breeding biology, territorial and aggressive behaviour, and feeding ecology, were investigated in detail. It has regular seasonal movements in

Natal, probably both altitudinal and coastal, although birds may remain throughout the year in areas where conditions are suitable. Seasonal departures are correlated with decreasing invertebrate food availability, while return time is largely governed by food availability, although cover development in exotic vegetation delayed recolonization at one site. The pair bond and the territory are maintained throughout the breeding season, and possibly throughout the year under suitable conditions. Adult mortality is probably high and the species' breeding strategy emphasises fecundity, this being achieved by a large clutch size, a very restricted period of parental care and rapid re-nesting. Juvenile mortality is high. The plumage, behavioural and vocal development of the young were studied in detail.

**PREFACE**

The experimental work described in this thesis was carried out in the Department of Zoology and Entomology, University of Natal, Pietermaritzburg, from September 1988 to January 1993, under the supervision of Professor G. L. Maclean.

These studies represent original work by the author and have not been submitted in any form to another university. Where use was made of the work of others it has been duly acknowledged in the text.

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The Southern African Bird Atlas Project provided data on flufftails and other rallids, and allowed me to use their mapping system to present some distributional data. James Harrison was particularly helpful in response to all my requests for information. Dr Terry Oatley supplied information on flufftails from the Southern African Bird Ringing Scheme and the Nest Record Scheme while Guy Gibbon provided wetland bird calls for analysis. The vegetation and altitude maps of Natal (Figs. 2.2 and 2.3) are taken from Cyrus & Robson (1980) and are reproduced with the permission of the authors and the publisher. I am also grateful to the authors for permission to use their mapping system in the presentation of my distributional data for flufftail species.

Rainfall and temperature data for Bromley, Zimbabwe, were provided by the Meteorological Office, Harare, and those for South African sites by the University of Natal's Computer Centre for Water Research, Ukuzinga Research Farm, Cedara Agricultural College, the South African Sugar Association's Mt Edgecombe Research Station, Durban Municipality, the Allerton Veterinary

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## CONTENTS

ABSTRACT . . . . .	ii
PREFACE . . . . .	iv
ACKNOWLEDGEMENTS . . . . .	v
LIST OF FIGURES . . . . .	xix
LIST OF TABLES . . . . .	xxvi
LIST OF PLATES . . . . .	xxix
CHAPTER 1. INTRODUCTION . . . . .	1
1.1    The family Rallidae and the genus <i>Sarothrura</i> . . . . .	1
1.2    A literature survey of the study species . . . . .	3
1.2.1 <i>Sarothrura elegans</i> (A. Smith). Buffspotted Flufftail . . . . .	3
1.2.1.1    Distribution and status . . . . .	3
1.2.1.2    Habitat . . . . .	4
1.2.1.3    Behaviour, food and predation . . . . .	5
1.2.1.4    Voice . . . . .	6
1.2.1.5    Breeding and moult . . . . .	8
1.2.1.6    Movements . . . . .	9
1.2.2 <i>Sarothrura rufa</i> (Vieillot). Redchested Fluftail . . . . .	11
1.2.2.1    Distribution and status . . . . .	11
1.2.2.2    Habitat . . . . .	12
1.2.2.3    Behaviour, food and predation . . . . .	13
1.2.2.4    Voice . . . . .	14
1.2.2.5    Breeding and moult . . . . .	15
1.2.2.6    Movements . . . . .	17
1.2.3 <i>Sarothrura affinis</i> (Smith). Striped Flufftail . . . . .	17
1.2.3.1    Distribution and status . . . . .	17
1.2.3.2    Habitat . . . . .	18
1.2.3.3    Behaviour, food and predation . . . . .	19
1.2.3.4    Voice . . . . .	19
1.2.3.5    Breeding . . . . .	20
1.2.3.6    Movements . . . . .	20
1.2.4 <i>Sarothrura ayresi</i> (Gurney). Whitewinged Flufftail . . . . .	20
1.2.4.1    Systematics and nomenclature . . . . .	20
1.2.4.2    Distribution and status . . . . .	21
1.2.4.3    Habitat . . . . .	23
1.2.4.4    Behaviour, food and predation . . . . .	23
1.2.4.5    Voice . . . . .	24
1.2.4.6    Breeding . . . . .	24
1.2.4.7    Movements . . . . .	26
1.3    Aims of the study . . . . .	26
1.3.1    Overall conservation objectives . . . . .	26
1.3.2    General research objectives . . . . .	27

<b>CHAPTER 2. SURVEY AREAS AND STUDY SITES . . . . .</b>	<b>29</b>
2.1    Introduction and survey areas . . . . .	29
2.2    The study sites: location, topography, vegetation, climate and management . . . . .	29
2.2.1    Bromley, Zimbabwe . . . . .	33
2.2.1.1    Climate and weather . . . . .	33
2.2.1.2    Vegetation . . . . .	33
2.2.1.3    Use and management . . . . .	37
2.2.2    Dullstroom, near Belfast, Transvaal . . . . .	37
2.2.2.1    Climate and weather . . . . .	37
2.2.2.2    Vegetation . . . . .	37
2.2.2.3    Use and management . . . . .	40
2.2.3    Wakkerstroom Vlei, Transvaal . . . . .	40
2.2.3.1    Climate and weather . . . . .	41
2.2.3.2    Vegetation . . . . .	41
2.2.3.3    Use and management . . . . .	41
2.2.4    Karkloof Forest, near Howick, Natal . . . . .	43
2.2.4.1    Climate and weather . . . . .	43
2.2.4.2    Vegetation . . . . .	43
2.2.4.3    Management . . . . .	44
2.2.5    Gartmore Farm, Karkloof Valley, Howick, Natal . . . . .	44
2.2.5.1    Climate and weather . . . . .	44
2.2.5.2    Vegetation . . . . .	48
2.2.5.3    Use and management . . . . .	48
2.2.6    Ferncliffe Forest, Pietermaritzburg, Natal . . . . .	50
2.2.6.1    Climate and weather . . . . .	50
2.2.6.2    Vegetation . . . . .	53
2.2.7    Allerton, Pietermaritzburg, Natal . . . . .	53
2.2.7.1    Climate and weather . . . . .	55
2.2.7.2    Vegetation . . . . .	55
2.2.7.3    Use and management . . . . .	58
2.2.8    Bisley Valley, Pietermaritzburg, Natal . . . . .	58
2.2.8.1    Climate and weather . . . . .	58
2.2.8.2    Vegetation . . . . .	61
2.2.8.3    Management . . . . .	61
2.2.9    Danville Park Reserve, Durban North, Natal . . . . .	61
2.2.9.1    Climate and weather . . . . .	62
2.2.9.2    Vegetation . . . . .	62
2.2.9.3    Management . . . . .	67
2.2.10    Scotston Farm, Underberg, Natal . . . . .	67
2.2.10.1    Climate and weather . . . . .	69
2.2.10.2    Vegetation . . . . .	69
2.2.11    Vernon Crookes Nature Reserve, Umzinto, Natal . . . . .	69
2.2.11.1    Climate and weather . . . . .	72
2.2.11.2    Vegetation . . . . .	72

2.2.11.3 Grazing and management . . . . .	76
2.2.12 Franklin Vlei, East Griqualand, Natal . . . . .	76
2.2.12.1 Climate and weather . . . . .	76
2.2.12.2 Vegetation . . . . .	78
2.2.12.3 Use and management . . . . .	78
2.2.13 Mt Currie Nature Reserve, Kokstad, East Griqualand, Natal .	78
2.2.13.1 Climate and weather . . . . .	80
2.2.13.2 Vegetation . . . . .	86
2.2.13.3 Use and management . . . . .	88
2.2.14 Penny Park, near Kokstad, East Griqualand, Natal . . . . .	89
2.2.14.1 Climate and weather . . . . .	89
2.2.14.2 Vegetation . . . . .	91
2.2.14.3 Use and management . . . . .	91
<b>CHAPTER 3. GENERAL METHODS . . . . .</b>	<b>92</b>
3.1 The location and observation of flufftails . . . . .	92
3.2 Definitions of home range and territory . . . . .	93
3.3 Radio tracking for studies of territory size, behaviour and movements . . . . .	95
3.4 Censusing and territorial mapping using call counts and taped playback . . . . .	96
3.5 Estimating populations from census data . . . . .	101
3.6 Vegetation sampling . . . . .	102
3.6.1 Measurements of vegetation cover . . . . .	102
3.6.1.1 Grassland . . . . .	103
3.6.1.2 Wetland . . . . .	103
3.6.1.3 Forest . . . . .	105
3.6.2 Measurements of vegetation height . . . . .	106
3.6.3 Other measurements of wetland vegetation regrowth . . . . .	107
3.6.3.1 Light within the reedbed . . . . .	107
3.6.3.2 Number of leaves . . . . .	108
3.7 Invertebrate sampling . . . . .	108
3.7.1 Grassland . . . . .	109
3.7.2 Wetland . . . . .	110
3.7.3 Forest . . . . .	111
3.8 Trapping flufftails . . . . .	112
3.8.1 Buffspotted Flufftail . . . . .	112
3.8.2 Redcheasted Flufftail . . . . .	113
3.8.3 Striped Flufftail . . . . .	114
3.8.4 Whitewinged Flufftail . . . . .	114
3.9 Recording biometric and other data from trapped flufftails .	114
3.10 Marking flufftails . . . . .	115
3.11 Collecting of general data from other sources . . . . .	115

<b>CHAPTER 4. THE DISTRIBUTION, STATUS, GENERAL BIOLOGY AND BEHAVIOUR OF THE REDCHESTED FLUFFTAIL . . . . .</b>	<b>117</b>
4.1    Introduction . . . . .	117
4.2    Survey areas, study sites and study aviaries . . . . .	119
4.3    Methods . . . . .	120
4.3.1    Surveys, censusing and territorial mapping . . . . .	120
4.3.2    Territorial behaviour . . . . .	120
4.3.3    General behaviour . . . . .	122
4.3.4    Feeding and energy requirements . . . . .	122
4.3.5    Vocalizations . . . . .	123
4.3.6    Breeding . . . . .	124
4.4    Results . . . . .	124
4.4.1    Distribution and status . . . . .	124
4.4.2    Habitat . . . . .	127
4.4.3    Seasonal variations in permanent habitat type and extent .	130
4.4.4    General behaviour . . . . .	131
4.4.4.1    Activity patterns and characteristic behaviour . . . . .	131
4.4.4.2    The pair bond . . . . .	132
4.4.4.3    Comfort activities . . . . .	133
4.4.4.4    Flight . . . . .	135
4.4.4.5    Play and inquisitiveness . . . . .	135
4.4.5    Territoriality and aggressive behaviour . . . . .	137
4.4.5.1    Territoriality . . . . .	137
4.4.5.2    Aggressive behaviour . . . . .	143
4.4.6    Feeding methods, food and energy requirements . . . . .	151
4.4.7    Other feeding-related behaviour . . . . .	156
4.4.8    Vocalizations and calling patterns . . . . .	156
4.4.9    Breeding season . . . . .	163
4.4.10    Breeding . . . . .	165
4.4.10.1    Courtship and mating . . . . .	165
4.4.10.2    Nest-building, laying, incubation and hatching . . . . .	167
4.4.10.3    Development and care of the young . . . . .	168
4.4.10.4    Breeding success and survival . . . . .	169
4.4.11    Dispersal of young birds . . . . .	169
4.4.12    Predation and mortality . . . . .	172
4.5    Discussion . . . . .	173
4.5.1    Distribution, status and habitat . . . . .	173
4.5.2    General behaviour . . . . .	174
4.5.3    Territoriality . . . . .	176
4.5.4    Vocalizations and calling patterns . . . . .	179
4.5.5    Breeding seasons . . . . .	180
4.5.6    Predation . . . . .	180

<b>CHAPTER 5. PERMANENT TERRITORIES AND SEASONAL MOVEMENTS: THE EFFECTS OF SEASONAL HABITAT CHANGES ON THE REDCHESTED FLUFFTAIL . . .</b>	182
5.1    Introduction . . . . .	182
5.2    Study areas . . . . .	183
5.3    Methods . . . . .	183
5.3.1    Definition of habitat types . . . . .	183
5.3.2    Territorial mapping and censusing . . . . .	184
5.3.3    Behaviour and movements in response to burning . . . . .	186
5.4    Results . . . . .	187
5.4.1    The permanence of territories . . . . .	187
5.4.2    The influence of habitat type on territory size . . . . .	187
5.4.3    Seasonal variations in territory size . . . . .	190
5.4.4    The causes and effects of nonbreeding territory size reductions . . . . .	192
5.4.5    Conditions enabling Redchested Flufftails to tolerate severe winter and spring habitat modifications . . . . .	198
5.4.6    Behaviour in response to burning . . . . .	200
5.4.7    Temporary nonbreeding territories and winter/spring movements . . . . .	201
5.4.8    Post-burn territory extensions, displacement and sharing .	204
5.5    Discussion . . . . .	205
5.5.1    Territory size and habitat types . . . . .	205
5.5.2    Behaviour in response to burning . . . . .	207
5.5.3    Comparative effects of burning on sympatric rallids of dense wetland vegetation . . . . .	207
5.5.4    The hazards of enforced movements and the possible effects of recolonization timing on breeding . . . . .	208
5.5.5    Neighbour recognition, post-burn displacement and territory sharing . . . . .	209
5.5.6    Permanent territories . . . . .	210
5.5.7    Territoriality in the Black Crake and the African Rail .	212
5.5.8    Immatures and floaters . . . . .	212
<b>CHAPTER 6. SOME EFFECTS OF BURNING AND MOWING ON THE WETLAND HABITATS AND DISPERSION OF THE REDCHESTED FLUFFTAIL IN NATAL . . .</b>	214
6.1    Introduction . . . . .	214
6.2    Study sites . . . . .	217
6.3    Methods . . . . .	218
6.4    Results . . . . .	221
6.4.1    The effects of burning and mowing on vegetation regrowth and recolonization times . . . . .	221
6.4.1.1    Allerton, Pietermaritzburg . . . . .	222
6.4.1.2    Gartmore, Howick . . . . .	226
6.4.1.3    Mt Currie, Kokstad . . . . .	229

6.4.1.4 Relationships between return time and habitat variables . . . . .	233
6.4.2 The effects of burning and mowing on habitat quality and the dispersion and territory sizes of Redchested Flufftails . . . . .	242
6.4.2.1 Allerton, Pietermaritzburg . . . . .	242
6.4.2.2 Gartmore, Howick . . . . .	248
6.4.2.3 Mt Currie, Kokstad . . . . .	260
6.4.3 The effects of burning and mowing on invertebrate availability . . . . .	271
6.4.4 Substrate conditions at recolonization time . . . . .	273
6.5 Discussion . . . . .	273
6.5.1 Vegetation regrowth and reoccupation times . . . . .	273
6.5.2 Relationships between return time and habitat variables . . . . .	276
6.5.3 Dispersion, territory size and habitat quality . . . . .	277
6.5.4 Partial and complete burns . . . . .	279
6.5.5 Food availability . . . . .	279
6.6 Conclusion: burning wetlands to maintain optimal habitat for Redchested Flufftails . . . . .	280
<b>CHAPTER 7. THE DISTRIBUTION, STATUS AND GENERAL BIOLOGY OF THE STRIPED FLUFFTAIL IN SOUTH AFRICA . . . . .</b>	
7.1 Introduction . . . . .	282
7.2 Survey area and study sites . . . . .	283
7.3 Methods . . . . .	283
7.3.1 Surveys . . . . .	283
7.3.2 Collection of data from other sources . . . . .	284
7.3.3 Censusing and territorial mapping . . . . .	284
7.3.4 Mapping home range . . . . .	285
7.3.5 Habitat preferences, movements, vocalizations, territorial behaviour and breeding . . . . .	285
7.3.6 Measurements of the effects of burning on vegetation structure and food availability . . . . .	288
7.4 Results . . . . .	289
7.4.1 Distribution, status and habitat . . . . .	289
7.4.1.1 Natal and Transkei . . . . .	289
7.4.1.2 Transvaal and Cape Provinces . . . . .	298
7.4.2 Vocalizations and calling patterns . . . . .	300
7.4.3 Aggressive behaviour . . . . .	304
7.4.4 Breeding seasons and breeding behaviour . . . . .	306
7.4.5 Habitat preferences at the Mt Currie Reserve study site . . . . .	308
7.4.6 Territories and dispersion at Mt Currie . . . . .	316
7.4.7 The effects of burning on vegetation structure at Mt Currie . . . . .	316
7.4.8 The effects of burning on invertebrate food availability . . . . .	323

7.4.9	Relationships between occurrence patterns and (a) habitat quality, (b) the availability of cover and food, (c) burning . . . . .	330
7.4.10	Post-breeding dispersal . . . . .	335
7.4.11	Feeding methods and food . . . . .	336
7.4.12	Predation, mortality and population size . . . . .	338
7.5	Discussion . . . . .	340
7.5.1	Distribution, status and habitat . . . . .	340
7.5.2	Migratory status . . . . .	343
7.5.3	Habitat preferences at the Mt Currie Reserve study site . . . . .	344
7.5.4	Territories and dispersion at Mt Currie . . . . .	345
7.5.5	Burning, vegetation structure and invertebrates at Mt Currie . . . . .	346
7.5.6	Other considerations regarding occurrence patterns at Mt Currie . . . . .	350
7.5.7	Responses of other birds to grassland burning . . . . .	350
<b>CHAPTER 8. THE BIOLOGY, ECOLOGY AND CONSERVATION OF THE WHITEWINGED FLUFFTAIL . . . . .</b>		352
8.1	Introduction . . . . .	352
8.2	Survey areas and study sites . . . . .	355
8.3	Methods . . . . .	356
8.4	Results . . . . .	357
8.4.1	Distribution and status . . . . .	357
8.4.2	Habitat preferences . . . . .	360
8.4.2.1	Dullstroom, Transvaal . . . . .	363
8.4.2.2	Wakkerstroom, Transvaal . . . . .	364
8.4.2.3	Franklin, Natal . . . . .	366
8.4.2.4	Penny Park, Natal . . . . .	368
8.4.2.5	Other wetland areas surveyed in Natal and the Transvaal . . . . .	369
8.4.3	Seasonality and pattern of occurrence . . . . .	372
8.4.4	Voice . . . . .	374
8.4.5	General behaviour . . . . .	389
8.4.6	Breeding . . . . .	392
8.5	Discussion . . . . .	394
8.5.1	Distribution and status . . . . .	394
8.5.2	Habitat preferences . . . . .	394
8.5.3	Pattern of occurrence and migratory status . . . . .	399
8.5.4	Behaviour: calling, territoriality and breeding . . . . .	400
8.6	Conclusions and recommendations for further study . . . . .	403

<b>CHAPTER 9. SOME ASPECTS OF THE BIOLOGY AND ECOLOGY OF THE BUFFSPOTTED FLUFFTAIL . . . . .</b>	<b>405</b>
9.1    Introduction . . . . .	405
9.2    Study sites and survey areas . . . . .	406
9.3    Methods . . . . .	407
9.3.1    Surveys and territorial mapping . . . . .	407
9.3.2    Periods of occurrence and movements . . . . .	407
9.3.3    Behaviour and breeding . . . . .	408
9.3.4    Food, feeding ecology and energy requirements . . . . .	409
9.3.5    Vocalizations . . . . .	409
9.3.6    Moult and plumage development . . . . .	410
9.4    Results . . . . .	410
9.4.1    Distribution and status . . . . .	410
9.4.2    Habitat . . . . .	413
9.4.3    Occurrence patterns and movements . . . . .	415
9.4.3.1    Long-term study sites . . . . .	415
9.4.3.2    Other visual and sound records . . . . .	417
9.4.3.3    Casualties . . . . .	419
9.4.4    General behaviour . . . . .	421
9.4.4.1    Activity patterns and characteristic behaviour . . . . .	421
9.4.4.2    The pair bond . . . . .	428
9.4.4.3    Comfort activities . . . . .	428
9.4.4.4    Flight . . . . .	429
9.4.4.5    Play and inquisitiveness . . . . .	431
9.4.5    Territoriality and aggressive behaviour . . . . .	431
9.4.5.1    Territory size . . . . .	431
9.4.5.2    Territorial behaviour . . . . .	432
9.4.5.3    Aggressive behaviour . . . . .	441
9.4.6    Feeding methods, food and energy requirements . . . . .	444
9.4.7    Other feeding-related behaviour . . . . .	456
9.4.8    Vocalizations and calling patterns . . . . .	456
9.4.9    Breeding season . . . . .	464
9.4.10    Breeding . . . . .	467
9.4.10.1    Courtship and mating . . . . .	467
9.4.10.2    Nest and nest-building . . . . .	470
9.4.10.3    Laying, incubation and hatching . . . . .	474
9.4.10.4    Development and care of the young . . . . .	476
9.4.10.4.1    Introduction . . . . .	476
9.4.10.4.2    Growth and plumage development . . . . .	476
9.4.10.4.3    Development of vocalizations . . . . .	482
9.4.10.4.4    Behavioural development . . . . .	493
9.4.10.4.5    Parental behaviour . . . . .	495
9.4.10.4.6    Breeding success and survival . . . . .	496
9.4.11    Dispersal of young birds . . . . .	498
9.4.12    Predation and mortality . . . . .	500

9.4.13 Moult . . . . .	501
9.5 Discussion . . . . .	502
9.5.1 Distribution, status and habitat . . . . .	502
9.5.2 Movements . . . . .	503
9.5.3 General behaviour . . . . .	504
9.5.4 Territoriality . . . . .	505
9.5.5 Vocalizations and calling patterns . . . . .	505
9.5.6 Development and rejection of the young . . . . .	507
<b>CHAPTER 10. THE SEASONAL OCCURRENCE OF THE BUFFSPOTTED FLUFFTAIL IN NATAL IN RELATION TO VEGETATION COVER AND THE AVAILABILITY OF INVERTEBRATE FOOD . . . . .</b> 508	
10.1 Introduction . . . . .	508
10.2 Study sites . . . . .	508
10.3 Methods . . . . .	509
10.4 Results . . . . .	510
10.4.1 Vegetation cover . . . . .	510
10.4.1.1 Danville Park . . . . .	510
10.4.1.2 Bisley Valley . . . . .	512
10.4.1.3 Ferncliffe Forest . . . . .	514
10.4.1.4 Scotston Farm . . . . .	514
10.4.1.5 Comparisons between the four sites . . . . .	517
10.4.2 Invertebrate abundance and diversity . . . . .	520
10.4.2.1 Potential food items . . . . .	520
10.4.2.2 Danville Park . . . . .	520
10.4.2.3 Bisley Valley . . . . .	523
10.4.2.4 Ferncliffe Forest . . . . .	523
10.4.2.5 Scotston Farm . . . . .	525
10.4.3 Flufftail occurrence patterns . . . . .	525
10.5 Discussion . . . . .	526
10.5.1 Danville Park . . . . .	526
10.5.2 Bisley Valley . . . . .	526
10.5.3 Ferncliffe Forest . . . . .	527
10.5.4 Scotston Farm . . . . .	527
10.5.5 Conclusions . . . . .	528
<b>CHAPTER 11. CONCLUSION . . . . .</b> 531	
11.1 Introduction . . . . .	531
11.2 Conservation of flufftails and their habitats . . . . .	531
11.2.1 The Redchested Flufftail, sympatric wetland rallids and their habitats . . . . .	531
11.2.2 The Striped Flufftail and its grassland habitats . . . . .	533
11.2.3 The Whitewinged Flufftail . . . . .	535
11.3 Flufftail life histories . . . . .	536
11.3.1 The Whitespotted Flufftail . . . . .	537

11.3.2	The Redchested Flufftail . . . . .	537
11.3.3	The Buffspotted Flufftail . . . . .	539
11.3.4	The Streakybreasted Flufftail . . . . .	540
11.3.5	Discussion . . . . .	540
<b>REFERENCES</b>	. . . . .	542

## LIST OF FIGURES

<b>Fig. 2.1</b>	Map of Natal and KwaZulu showing quarter-degree squares, grid references and place names . . . . .	30
<b>Fig. 2.2</b>	Altitude map of Natal and KwaZulu . . . . .	31
<b>Fig. 2.3</b>	Vegetation map of Natal and KwaZulu . . . . .	32
<b>Fig. 2.4</b>	Bromley, Zimbabwe: long-term mean precipitation and maximum/minimum temperatures . . . . .	34
<b>Fig. 2.5</b>	Wakkerstroom and Dullstroom, Transvaal: long-term mean precipitation and maximum/minimum temperatures . . . . .	39
<b>Fig. 2.6</b>	Map of the Gartmore Farm study site, Howick, Natal . . . . .	45
<b>Fig. 2.7</b>	Precipitation at Gartmore: (A) 1988-1989; (B) 1989-1990 . . . . .	46
<b>Fig. 2.8</b>	Precipitation at Gartmore: (A) 1990-1991; (B) 1991-1992 . . . . .	47
<b>Fig. 2.9</b>	Temperature ranges at some study sites . . . . .	49
<b>Fig. 2.10</b>	Ferncliffe Forest, Pietermaritzburg, Natal: long-term mean precipitation and maximum/minimum temperatures . . . . .	51
<b>Fig. 2.11</b>	Precipitation and temperatures at Ferncliffe: (A) 1990-1991; (B) 1991-1992 . . . . .	52
<b>Fig. 2.12</b>	Map of the Allerton study site, Pietermaritzburg, Natal . . . . .	54
<b>Fig. 2.13</b>	Precipitation at Allerton: (A) 1988-1989; (B) 1989-1990 . . . . .	56
<b>Fig. 2.14</b>	Precipitation at Allerton: (A) 1990-1991; (B) 1991-1992 . . . . .	57
<b>Fig. 2.15</b>	Bisley Valley, Pietermaritzburg, Natal: long-term mean precipitation and maximum/minimum temperatures . . . . .	59
<b>Fig. 2.16</b>	Precipitation and temperatures at Bisley Valley: (A) 1990-1991; (B) 1991-1992 . . . . .	60
<b>Fig. 2.17</b>	Map of the Danville Park study site, Durban, Natal . . . . .	63
<b>Fig. 2.18</b>	Danville: long-term mean precipitation and maximum/minimum temperatures . . . . .	64
<b>Fig. 2.19</b>	Precipitation and temperatures at Danville: (A) 1988-1989; (B) 1989-1990 . . . . .	65
<b>Fig. 2.20</b>	Precipitation and temperatures at Danville: (A) 1990-1991; (B) 1991-1992 . . . . .	66
<b>Fig. 2.21</b>	Map of the Scotston Farm study site, Underberg, Natal . . . . .	68
<b>Fig. 2.22</b>	Scotston: long-term mean precipitation and maximum/minimum temperatures . . . . .	70
<b>Fig. 2.23</b>	Precipitation and temperatures at Scotston: (A) 1990-1991; (B) 1991-1992 . . . . .	71
<b>Fig. 2.24</b>	Vernon Crookes Nature Reserve, Umzinto, Natal: long-term mean precipitation and maximum/minimum temperatures . . . . .	73
<b>Fig. 2.25</b>	Precipitation and temperatures at Vernon Crookes: (A) 1988-1989; (B) 1989-1990 . . . . .	74
<b>Fig. 2.26</b>	Precipitation and temperatures at Vernon Crookes: (A) 1990-1991; (B) 1991-1992 . . . . .	75
<b>Fig. 2.27</b>	Franklin, East Griqualand, Natal: long-term mean precipitation and maximum/minimum temperatures . . . . .	77

<b>Fig. 2.28</b>	Map of Mt Currie Nature Reserve, Kokstad, Natal . . . . .	79
<b>Fig. 2.29</b>	Mount Currie: long-term mean precipitation and maximum/minimum temperatures . . . . .	82
<b>Fig. 2.30</b>	Precipitation and temperatures at Mt Currie: (A) 1988-1989; (B) 1989-1990 . . . . .	83
<b>Fig. 2.31</b>	Precipitation and temperatures at Mt Currie: (A) 1990-1991; (B) 1991-1992 . . . . .	84
<b>Fig. 2.32</b>	Map of the wetland at Mt Currie Reserve . . . . .	87
<b>Fig. 4.1</b>	Natal distribution map for the Redchested Flufftail (monthly data by quarter-degree square): (A) data from this study; (B) atlas scheme data . . . . .	125
<b>Fig. 4.2</b>	A-C: frequency distribution of Redchested Flufftail activities by hour of the day . . . . .	134
<b>Fig. 4.3</b>	Reactions of adult Redchested Flufftails to models and mirrors throughout the year . . . . .	138
<b>Fig. 4.4</b>	Reactions of adult and immature Black Crakes to models, mirrors and taped playback throughout the year . . . . .	140
<b>Fig. 4.5</b>	Reactions of adult and immature African Rails to taped playback throughout the year . . . . .	141
<b>Fig. 4.6</b>	Hourly variation in consumption of mealworms by captive Redchested Flufftails . . . . .	155
<b>Fig. 4.7</b>	Variation in consumption of mealworms by captive Redchested Flufftails by period of the day . . . . .	155
<b>Fig. 4.8</b>	Calling patterns of adult male Redchested Flufftails: (A) hoots; (B) territorial calls . . . . .	160
<b>Fig. 4.9</b>	Calling patterns of male (A) and female (B) Redchested Flufftails . . . . .	161
<b>Fig. 4.10</b>	Occurrence and calling pattern of immature Redchested Flufftails within parental territories . . . . .	162
<b>Fig. 4.11</b>	Mean monthly maximum temperatures at three study sites . .	181
<b>Fig. 4.12</b>	Mean monthly minimum temperatures at three study sites, with Redchested Flufftail breeding periods . . . . .	181
<b>Fig. 5.1</b>	Frequency distribution of summer (A) and winter (B) Redchested Flufftail territory sizes . . . . .	188
<b>Fig. 5.2</b>	Variation in summer (A) and winter (B) Redchested Flufftail territory sizes with Flooding Type . . . . .	191
<b>Fig. 5.3</b>	Frequency distribution of percentage changes in Redchested Flufftail territory areas during the nonbreeding season . .	193
<b>Fig. 5.4</b>	Frequency distribution of Type B events (A) causing nonbreeding-season size reductions in Redchested Flufftail territories and (B) causing territories to be vacated . . .	194
<b>Fig. 5.5</b>	Frequency distribution of nonbreeding-season size reductions in Redchested Flufftail territories, and their effects . .	195

<b>Fig. 5.6</b>	A-E: frequency distribution of nonbreeding-season size reductions in Redchested Flufftail territories, by Flooding Type . . . . .	196
<b>Fig. 6.1</b>	Increase in height of burned and cut <i>Cyperus/Mariscus</i> sedge beds on different substrates at Allerton . . . . .	223
<b>Fig. 6.2</b>	Increase in cover in burned and cut <i>Cyperus/Mariscus</i> sedge beds on different substrates at Allerton . . . . .	223
<b>Fig. 6.3</b>	Increase in leaf numbers in burned and cut <i>Cyperus/Mariscus</i> sedge beds on different substrates at Allerton . . . . .	224
<b>Fig. 6.4</b>	Increase in height of burned mixed sedge and hygrophilous grassland on different substrates at Gartmore . . . . .	227
<b>Fig. 6.5</b>	Increase in cover in burned mixed sedge and hygrophilous grassland on different substrates at Gartmore . . . . .	227
<b>Fig. 6.6</b>	Increase in canopy cover in burned <i>Carex acutiformis</i> and <i>Typha capensis</i> beds on different substrates at Mt Currie .	230
<b>Fig. 6.7</b>	Increase in ground cover in burned <i>Carex acutiformis</i> and <i>Typha capensis</i> beds on different substrates at Mt Currie .	230
<b>Fig. 6.8</b>	Increase in height of burned <i>Carex acutiformis</i> and <i>Typha capensis</i> beds on different substrates at Mt Currie .	231
<b>Fig. 6.9</b>	Redchested Flufftail: variation in return date with vegetation type, for dated returns to burned vegetation .	236
<b>Fig. 6.10</b>	Redchested Flufftail: variation in return date with substrate saturation, for dated returns to burned vegetation . . . . .	236
<b>Fig. 6.11</b>	Redchested Flufftail: interval plot of the relationship between return date after a burn and substrate saturation .	238
<b>Fig. 6.12</b>	Redchested Flufftail: variation in return month with vegetation type, for estimated returns to burned vegetation . . . . .	238
<b>Fig. 6.13</b>	Redchested Flufftail: variation in return month with substrate saturation, for estimated returns to burned vegetation . . . . .	240
<b>Fig. 6.14</b>	Redchested Flufftail: variation in return month with vegetation type/substrate saturation group, for estimated returns to burned vegetation . . . . .	240
<b>Fig. 6.15</b>	Redchested Flufftail territories, Allerton, January 1989 .	243
<b>Fig. 6.16</b>	Extent of the September 1989 burn at Allerton, and the post-burn position of the affected Redchested Flufftail territories . . . . .	243
<b>Fig. 6.17</b>	Redchested Flufftail territories, Allerton, January 1990 .	247
<b>Fig. 6.18</b>	Extent of the August 1990 burn at Allerton, and the post-burn position of all Redchested Flufftail territories . . .	247
<b>Fig. 6.19</b>	Redchested Flufftail: variation in mean territory size between summer and winter territories at Allerton . . . .	249

<b>Fig. 6.20</b>	Redchested Flufftail: variation in mean territory size at Allerton with burning treatment . . . . .	249
<b>Fig. 6.21</b>	Redchested Flufftail territories, Gartmore, January 1989 .	253
<b>Fig. 6.22</b>	Redchested Flufftail territories, Gartmore, July 1989 . . .	253
<b>Fig. 6.23</b>	Redchested Flufftail territories at Gartmore after late-1989 burning and mowing . . . . .	254
<b>Fig. 6.24</b>	Redchested Flufftail territories, Gartmore, January 1990 .	254
<b>Fig. 6.25</b>	Redchested Flufftail territories, Gartmore, July 1990 . . .	256
<b>Fig. 6.26</b>	Redchested Flufftail territories, Gartmore, January 1991 .	256
<b>Fig. 6.27</b>	Redchested Flufftail territories, Gartmore, July 1991 . . .	257
<b>Fig. 6.28</b>	Redchested Flufftail territories, Gartmore, January 1992 .	257
<b>Fig. 6.29</b>	Redchested Flufftail: variation in mean territory size with burning treatment at Gartmore . . . . .	259
<b>Fig. 6.30</b>	Redchested Flufftail: generalized linear model of proportions of habitat used at Gartmore each year . . . . .	259
<b>Fig. 6.31</b>	Redchested Flufftail territories, Mt Currie, January 1989 .	262
<b>Fig. 6.32</b>	Redchested Flufftail territories, Mt Currie, January 1990 .	263
<b>Fig. 6.33</b>	Redchested Flufftail territories, Mt Currie, January 1991 .	265
<b>Fig. 6.34</b>	Redchested Flufftail territories, Mt Currie, January 1991, after the severe hailstorm of 18 January . . . . .	266
<b>Fig. 6.35</b>	Redchested Flufftail territories, Mt Currie, January 1992 .	267
<b>Fig. 6.36</b>	Monthly totals of Redchested Flufftail territories at Mt Currie, January 1989 to January 1992 . . . . .	268
<b>Fig. 6.37</b>	Monthly totals of Redchested Flufftail territories at Mt Currie by survey block, January 1989 to January 1992 . . .	269
<b>Fig. 7.1</b>	Natal distribution map for the Striped Flufftail (monthly data by quarter-degree square): (A) unpublished data; (B) atlas scheme data . . . . .	294
<b>Fig. 7.2</b>	Distribution map of the Striped Flufftail in South Africa, by quarter-degree square . . . . .	295
<b>Fig. 7.3</b>	Distribution map of 59 Striped Flufftail territories at Mt Currie . . . . .	310
<b>Fig. 7.4</b>	Characteristics of Striped Flufftail territories at Mt Currie: (A) dominant vegetation types; (B) other non-woody vegetation; (C) woody vegetation; (D) drainage line .	311
<b>Fig. 7.5</b>	Characteristics of Striped Flufftail territories at Mt Currie: (A) altitude; (B) aspect . . . . .	312
<b>Fig. 7.6</b>	Characteristics of Striped Flufftail territories at Mt Currie: (A) slope; (B) cover of rocks; (C) vegetation cover; (D) vegetation height . . . . .	313
<b>Fig. 7.7</b>	Mean cover at the Mt Currie Block 2 (A) and Block 3 (B) grassland sampling sites, October 1990 to July 1992 . . . .	318
<b>Fig. 7.8</b>	Mean cover at Mt Currie grassland sampling sites, July 1991 to July 1992 (A) and October 1990 to July 1991 (B), for different burning regimes . . . . .	319

<b>Fig. 7.9</b>	Mean vegetation height at the Mt Currie Block 2 (A) and Block 3 (B) grassland sampling sites, October 1990 to July 1992 . . . . .	320
<b>Fig. 7.10</b>	Mean vegetation height at Mt Currie grassland sampling sites, July 1991 to July 1992 (A) and October 1990 to July 1991 (B), for different burning regimes . . . . .	322
<b>Fig. 7.11</b>	Plot of mean vegetation cover against mean vegetation height at the Mt Currie Block 2 grassland sampling site, October 1990 to July 1992, showing periods of theoretically suitable vegetation structure . . . . .	324
<b>Fig. 7.12</b>	Plot of mean vegetation cover against mean vegetation height at the Mt Currie Block 3 grassland sampling site, October 1990 to July 1992, showing periods of theoretically suitable vegetation structure . . . . .	325
<b>Fig. 7.13</b>	Mean invertebrate density at the Mt Currie Block 2 (A) and Block 3 (B) grassland sampling sites, October 1990 to July 1992 . . . . .	327
<b>Fig. 7.14</b>	Mean invertebrate density at Mt Currie grassland sampling sites, October 1990 to July 1991 (A) and July 1991 to July 1992 (B), for different burning regimes . . . . .	328
<b>Fig. 7.15</b>	Mean invertebrate food density at Mt Currie grassland sampling sites, October 1990 to July 1991 (A) and July 1991 to July 1992 (B) for different burning regimes . . . . .	329
<b>Fig. 7.16</b>	Variation in month of return of Striped Flufftails to Mt Currie breeding territories by block (A) and burning regime (B) . . . . .	334
<b>Fig. 7.17</b>	January–December monthly density of seven arthropod groups at Mt Currie grassland sampling sites . . . . .	337
<b>Fig. 8.1</b>	Southern Africa distribution map for the Whitewinged Flufftail, by quarter-degree square . . . . .	359
<b>Fig. 8.2</b>	A-D: sonograms of Whitewinged Flufftail OOP calls . . . . .	376
<b>Fig. 8.3</b>	Sonograms of Crowned Crane multiple OOP calls . . . . .	380
<b>Fig. 8.4</b>	A-B: sonograms of Whitewinged Flufftail excited duet . . . . .	381
<b>Fig. 8.5</b>	Sonogram of Whitewinged Flufftail excited duet, showing inversion of one bird's notes . . . . .	382
<b>Fig. 8.6</b>	Sonogram of Whitewinged Flufftail duets (J.M. Mendelsohn) .	384
<b>Fig. 8.7</b>	Sonograms of: (A-C) claimed Whitewinged Flufftail calls from Rwanda; (D) similar calls of Crowned Crane . . . . .	385
<b>Fig. 8.8</b>	Sonograms of: (A & C) claimed Whitewinged Flufftail calls from Rwanda; (B & D) similar calls of Crowned Crane . . . . .	387
<b>Fig. 8.9</b>	Simple regression analyses of Whitewinged Flufftail flight behaviour . . . . .	391
<b>Fig. 9.1</b>	Natal distribution map for the Buffspotted Flufftail (monthly data by quarter-degree square): (A) data from this study; (B) atlas scheme data . . . . .	411

<b>Fig. 9.2</b>	Monthly distribution of Buffspotted Flufftail specimens: (A) coastal and inland; (B) resident and moving . . . . .	420
<b>Fig. 9.3</b>	Monthly distribution of Buffspotted Flufftail specimens designated resident and moving: (A) coastal; (B) inland . .	422
<b>Fig. 9.4</b>	Monthly distribution of adult and immature Buffspotted Flufftail specimens designated moving . . . . .	423
<b>Fig. 9.5</b>	Monthly variation in the duration of Buffspotted Flufftail daily activity at Scotston . . . . .	425
<b>Fig. 9.6</b>	Scotston: comparison between sunrise and sunset times and the start and end of Buffspotted Flufftail daily activity .	426
<b>Fig. 9.7</b>	A-B: frequency distribution of Buffspotted Flufftail comfort activities by two-hourly period of the day . . . .	430
<b>Fig. 9.8</b>	Ratio of the proportions of invertebrate groups in Buffspotted Flufftail gizzards to those in leaf- litter samples . . . . .	451
<b>Fig. 9.9</b>	Buffspotted Flufftail: percentages of potential food items (by group) in leaf-litter samples from three areas . . . .	453
<b>Fig. 9.10</b>	Ratio of the proportions of invertebrate groups in Buffspotted Flufftail gizzards to those in leaf-litter samples from coastal and inland sites . . . . .	454
<b>Fig. 9.11</b>	Percentages of invertebrate food items (by size class) in Buffspotted Flufftail gizzards and leaf-litter samples: (A) including, and (B) excluding, ants and termites . . . .	455
<b>Fig. 9.12</b>	Variation in consumption of mealworms by Buffspotted Flufftails by period of the day . . . . .	457
<b>Fig. 9.13</b>	Occurrence and breeding activity of Buffspotted Flufftails during two breeding seasons at Scotston . . . .	466
<b>Fig. 9.14</b>	Postnatal growth of the Buffspotted Flufftail (mass against age), with a fitted growth curve . . . . .	483
<b>Fig. 9.15</b>	Individual postnatal growth curves (mass) of Buffspotted Flufftails . . . . .	484
<b>Fig. 9.16</b>	Increase in bill length of young Buffspotted Flufftails with age, with a fitted growth curve . . . . .	485
<b>Fig. 9.17</b>	Individual growth curves (bill length) of Buffspotted Flufftails . . . . .	486
<b>Fig. 9.18</b>	Increase in wing length of young Buffspotted Flufftails with age, with a fitted growth curve . . . . .	487
<b>Fig. 9.19</b>	Individual growth curves (wing length) of Buffspotted Flufftails . . . . .	488
<b>Fig. 9.20</b>	Increase in tail length of young Buffspotted Flufftails with age, with a fitted growth curve . . . . .	489
<b>Fig. 9.21</b>	Individual growth curves (tail length) of Buffspotted Flufftails . . . . .	490
<b>Fig. 9.22</b>	Increase in tarsus length of young Buffspotted Flufftails with age, with a fitted growth curve . . . . .	491

<b>Fig. 9.23</b>	Individual growth curves (tarsus length) of Buffspotted Flufftails . . . . .	492
<b>Fig. 10.1</b>	Vegetation cover for 50 cm above ground level in coastal forest at Danville, July 1991 to June 1992 . . . . .	511
<b>Fig. 10.2</b>	Vegetation cover for 50 cm above ground level in deciduous thickets at Bisley Valley, July 1991 to June 1992 . . . . .	513
<b>Fig. 10.3</b>	Vegetation cover for 50 cm above ground level in mistbelt forest at Ferncliffe, July 1991 to June 1992 . . . . .	515
<b>Fig. 10.4</b>	Vegetation cover for 50 cm above ground level in exotic hedgerows at Scotston, July 1991 to June 1992 . . . . .	516
<b>Fig. 10.5</b>	Vegetation cover for 50 cm above ground level in <i>Chaenomeles</i> and <i>Kerria</i> hedgerows, Scotston, July 1991 to June 1992 . . . . .	518
<b>Fig. 10.6</b>	Comparison of overall mean vegetation cover for 50 cm above ground level at four Buffspotted Flufftail study sites . . .	519
<b>Fig. 10.7</b>	Numbers of invertebrates in leaf-litter samples at four Buffspotted Flufftail study sites, July 1991 to June 1992: (A) Danville; (B) Bisley; (C) Ferncliffe; (D) Scotston . .	521
<b>Fig. 10.8</b>	Number of invertebrate food items (by class) in January and July leaf-litter samples at: (A) Danville; (B) Ferncliffe .	522
<b>Fig. 10.9</b>	Number of invertebrate food items (by class) in January and July leaf-litter samples at: (A) Bisley; (B) Scotston . . .	524

## LIST OF TABLES

<b>Table 2.1</b>	Long-term means of precipitation for some study sites . . . . .	35
<b>Table 2.2</b>	Long-term means of maximum and minimum temperatures for some study sites . . . . .	36
<b>Table 2.3</b>	Sources of meteorological data for study sites . . . . .	38
<b>Table 2.4</b>	Dominant vegetation types at Wakkerstroom . . . . .	42
<b>Table 2.5</b>	Sizes and features of Mt Currie Nature Reserve blocks . . . . .	81
<b>Table 2.6</b>	Nights of frost at Mt Currie . . . . .	85
<b>Table 2.7</b>	Timing of burns at the Mt Currie Nature Reserve . . . . .	90
<b>Table 4.1</b>	Redchested Flufftail vocalizations . . . . .	145
<b>Table 4.2</b>	Mealworm consumption by captive Redchested Flufftails . . . . .	154
<b>Table 4.3</b>	Functions of Redchested Flufftail vocalizations . . . . .	157
<b>Table 4.4</b>	Redchested Flufftail breeding records obtained during the study, for wild and captive birds . . . . .	164
<b>Table 4.5</b>	Redchested Flufftail: earliest and latest dates of males' advertising calls . . . . .	166
<b>Table 4.6</b>	Redchested Flufftail: last dates on which calling immatures were recorded in parental territories . . . . .	171
<b>Table 5.1</b>	Flooding Types of Redchested Flufftail territories . . . . .	185
<b>Table 5.2</b>	Summer and winter sizes of permanent Redchested Flufftail territories by Flooding Type . . . . .	189
<b>Table 6.1</b>	Vegetation type, defoliation method and soil saturation of the Redchested Flufftail territories in which vegetation regrowth was measured . . . . .	219
<b>Table 6.2</b>	Return dates of Redchested Flufftails to different vegetation types following spring burns . . . . .	220
<b>Table 6.3</b>	Definitions of vegetation types and substrate-saturation factors recorded in Redchested Flufftail territories . . . . .	234
<b>Table 6.4</b>	Mean return dates of Redchested Flufftails to different vegetation types and soil saturations, as predicted by regression models and analyses of variance . . . . .	235
<b>Table 6.5</b>	Unique combinations of vegetation type and saturation factor recorded for Redchested Flufftail territories, with estimated mean return times after burning . . . . .	241
<b>Table 6.6</b>	Areas of potentially suitable habitat for Redchested Flufftails at Allerton, 1988-1991 . . . . .	244
<b>Table 6.7</b>	Sizes of Redchested Flufftail territories at Allerton, 1988-1991, with notes on significant events occurring during the study period . . . . .	246
<b>Table 6.8</b>	Gartmore: Redchested Flufftail habitat availability and usage, and mean territory sizes, December 1988-July 1992 .	251
<b>Table 6.9</b>	Gartmore: sizes of Redchested Flufftail summer and winter territories, December 1988-July 1992 . . . . .	252

<b>Table 6.10</b>	Allerton: invertebrate density in burned and mown sedge beds, October 1989 . . . . .	272
<b>Table 7.1</b>	Areas of the major habitat types at Mt Currie Reserve . .	287
<b>Table 7.2</b>	Records of the Striped Flufftail in Natal and Transkei, January 1969–December 1992 . . . . .	290
<b>Table 7.3</b>	Records of the Striped Flufftail in Natal and Transkei before 1969 . . . . .	291
<b>Table 7.4</b>	Records of the Striped Flufftail in Transvaal and Cape Provinces, January 1969–December 1992 . . . . .	292
<b>Table 7.5</b>	Records of the Striped Flufftail in Transvaal and Cape Provinces before 1969 . . . . .	293
<b>Table 7.6</b>	Arrival and departure dates of Striped Flufftails at Mt Currie Nature Reserve, 1989–1992 . . . . .	299
<b>Table 7.7</b>	Striped Flufftail vocalizations . . . . .	301
<b>Table 7.8</b>	Published breeding information for the Striped Flufftail, with results of confirmatory investigations . . . . .	307
<b>Table 7.9</b>	Striped Flufftail: area of suitable habitat, and numbers of breeding territories, at Mt Currie, 1988–1992 . . . . .	315
<b>Table 7.10</b>	Striped Flufftail: total numbers of breeding territories in burned and unburned vegetation, Mt Currie, 1988–1992 .	315
<b>Table 7.11</b>	Striped Flufftail: numbers of breeding territories, and months of occupation, by block at Mt Currie, 1988–1992 . .	332
<b>Table 7.12</b>	Radiation flux densities and mean surface temperatures at four sites at different altitudes on Mt Currie . . . . .	349
<b>Table 8.1</b>	Details of all known specimens of the Whitewing Flufftail held in collections throughout the world . . . . .	353
<b>Table 8.2</b>	Details of all known sight and sound records of the Whitewing Flufftail . . . . .	354
<b>Table 8.3</b>	Monthly totals of Whitewing Flufftails recorded throughout the bird's known range . . . . .	358
<b>Table 8.4</b>	Vegetation and substrate characteristics associated with this study's visual records of the Whitewing Flufftail .	361
<b>Table 8.5</b>	Vegetation and substrate characteristics associated with this study's sound records of the Whitewing Flufftail .	362
<b>Table 9.1</b>	First and last dates of Buffspotted Flufftail advertising calls heard in Natal during the study . . . . .	418
<b>Table 9.2</b>	Buffspotted Flufftail vocalizations . . . . .	433
<b>Table 9.3</b>	Functions of Buffspotted Flufftail vocalizations . . . . .	440
<b>Table 9.4</b>	Summary of an analysis of Buffspotted Flufftail gizzard contents . . . . .	447
<b>Table 9.5</b>	Detailed description of invertebrates found in 52 Buffspotted Flufftail gizzards . . . . .	449
<b>Table 9.6</b>	The influence of time of day and weather on the breeding-season calling of the Buffspotted Flufftail in Natal . . . .	462

<b>Table 9.7</b>	The influence of precipitation type on the breeding-season calling of the Buffspotted Flufftail in Natal . . . . .	463
<b>Table 9.8</b>	Buffspotted Flufftail: variation in calling frequency during the Natal breeding season . . . . .	463
<b>Table 9.9</b>	Buffspotted Flufftail breeding records obtained in Natal during the study . . . . .	465
<b>Table 9.10</b>	The location, situation and dimensions of seven Buffspotted Flufftail nests from the Underberg district . . . . .	471
<b>Table 9.11</b>	Materials used in the construction of seven Buffspotted Flufftail nests from the Underberg district . . . . .	472
<b>Table 9.12</b>	Occurrences of unknown young Buffspotted Flufftails in the Scotston garden during two breeding seasons . . . . .	499
<b>Table 11.1</b>	Comparison of the habitat, status, behaviour, breeding and mortality of four flufftail species . . . . .	538

## LIST OF PLATES

<b>Frontispiece</b>	A: adult male Buffspotted Flufftail. B: adult male and immature male Redchested Flufftail . . . . . . . . . i
<b>Plate 1</b>	A: an "island" of wetland habitat containing a permanent Redchested Flufftail territory. B: a controlled cool burn at the Gartmore Farm wetland . . . 126
<b>Plate 2</b>	A: male Striped Flufftail attacking its reflection. B: adult female Buffspotted Flufftail . . . . . . . . . 305
<b>Plate 3</b>	A: Striped Flufftail grassland habitat. B: a farm garden holding two Buffspotted Flufftail territories . . 309
<b>Plate 4</b>	A: eight-day-old Buffspotted Flufftail chick. B: 22-day-old immature Buffspotted Flufftail . . . . . 478

## CHAPTER 1

### INTRODUCTION

#### 1.1 The family Rallidae and the genus *Sarothrura*

The family Rallidae (order Gruiformes, suborder Grues) includes 133 living species and is of worldwide distribution: rails are absent only from polar regions and deserts. They are small to medium-sized terrestrial birds, usually with dull or cryptic plumage but sometimes with brightly coloured bare parts, and the sexes are usually similar. The wings are rounded, the tail is short and the bill ranges from long and slender in genera such as *Rallus* to short and stout in the gallinules. The body is short and laterally compressed, enabling the birds to move easily through dense low vegetation without causing any disturbance. The neck is short to moderately long and has 14-15 cervical vertebrae. The legs are short to rather long, usually slender, and the toes are often long. In many species (including some flufftails) the feathers are rather loose and soft. In some species the nostrils are perforate and rails have a good sense of smell (Ripley 1977). The young are precocial and nidifugous and in most species the natal down is black.

Rails are generally shy and difficult to see. Most species inhabit dense vegetation and are unwilling to fly, normally running into dense cover when alarmed. All species can swim and dive and may take refuge under water if threatened, while many also climb well. Rails are very vocal and many have a wide repertoire of calls. Many species flick the tail while walking or swimming. Rails are typically associated with marshes, both salt and fresh, but are also found in grassland, forest and dense bush, and on open water. Most species are non-specialized and omnivorous, being able to adapt to new habitats and food sources (Keith 1986). Although their normal flight appears weak and fluttering, many species are capable of sustained long-distance flight, either on regular migration or in more random dispersal, and any species may make use of atypical habitat when moving. Rails are successful colonizers of remote oceanic islands, where they have often become flightless, and predators introduced by man have caused the recent extinction of some flightless island taxa.

The flufftails or pygmy rails (subfamily Rallinae, genus *Sarothrura*) are confined to Africa (seven species) and Madagascar (two species). They are distinctive and somewhat atypical small rallids, being strongly sexually dimorphic, a rare character in the family. The males have much rufous in the plumage, especially on the head and neck, while the dark body is patterned with pale spots or streaks. The females are dark with pale markings. The wings are short and rounded, the tail is short, in some species fluffy (hence the generic name), and often rufous or barred, and the bill is short and

slender. The eggs are white and the downy chicks are black. Flufftails are very vocal and have distinctive voices, including loud and far-carrying moaning or hooting advertising calls.

Males are very similar in plumage to the forest-dwelling, chestnut-plumaged rails of the genus *Rallicula* of New Guinea, which shows less strong sexual dimorphism. Olson (1973) believes that the two genera are closely related, the forest-dwelling Whitespotted Flufftail *S. pulchra* being the closest link. If this is so, the occupation of wetland and grassland habitats by other flufftail species may be a secondary adaptation (Keith 1986). The Whitewing Flufftail *S. ayresi*, by virtue of its white secondaries, may be a link with the genus *Coturnicops* of Asia and America (Keith 1986). Although Sibley & Ahlquist (1985) proposed the elevation of the genus *Sarothrura* to a new superfamily, the Sarothruroidea, on the basis of DNA-DNA hybridization data, the genus is still retained in the Rallidae pending further investigation (Sibley & Monroe 1990). Throughout this study I follow the taxonomy of Keith (1986).

Flufftails are entirely terrestrial, inhabiting dense vegetation in forest, grassland and wetland, and feeding chiefly on insects and other small arthropods, although some species also take seeds (Keith 1986). They are very poorly known, are considered difficult to study, and at least four species are rare or threatened (Brooke 1984; Collar & Stuart 1985; Keith *et al.* 1970; Keith 1986). Most species are thought to be sedentary, or to have only local movements in response to seasonal habitat changes, but the Streakybreasted Flufftail *S. boehmi* is an intra-African migrant (Baker *et al.* 1984; Keith 1986) and the Whitewing Flufftail may be a long-distance migrant (Section 1.2.4). Current knowledge of the breeding habits of five African species (from forest, wetland and grassland habitats) indicates that all five are strictly monogamous, forming strong pair bonds which are either permanent or maintained throughout the breeding season (Keith 1986; Taylor & Taylor 1986; Wintle 1988). The birds are solitary nesters and are strongly territorial, at least when breeding. They nest on the ground or in grass tussocks, building cup-shaped or domed nests. Breeding is thought to be seasonal, occurring during the rains (Keith 1986). Because the species occupy such widely differing habitat types, the genus is a good one in which to compare mating systems and reproductive strategies in different environments.

## 1.2 A literature survey of the study species

### 1.2.1 *Sarothrura elegans* (A. Smith). Buffspotted Flufftail.

#### 1.2.1.1 Distribution and status

The Buffspotted Flufftail has a wide distribution, occurring in forest and thick bush throughout the forested regions of West, central and eastern Africa, northeast to Ethiopia and south to the Cape; it is absent from low-rainfall areas in southwestern Africa (Keith 1986). It has a wide altitudinal tolerance, from coastal regions (e.g. Clancey 1971; Pakenham 1979) and up to 3 200 m a.s.l. in Ethiopia and 2 500-2 600 m in Kenya and Zimbabwe (Ash 1978; Irwin 1981; Lewis & Pomeroy 1989). It is uncommon to frequent or locally common, though very rarely seen, and is thought to be resident throughout its range (Keith 1986). It is undoubtedly under-recorded and, although its known geographical range is less extensive than that of the Redchested Flufftail *S. rufa* (Section 1.2.2.1), it has a more continuous distribution than that species (see distribution maps in Keith 1986) and probably occurs more widely than is known. It is widely sympatric with the Whitespotted Flufftail, which occurs chiefly in lowland rain forest, usually near water, but it extends well beyond the range of the Whitespotted Flufftail in southern and eastern Africa (Keith 1986; Snow 1978).

The race *S. e. reichenovi* occurs in West Africa, being recorded from two localities in Liberia (Rand 1951; Colston & Curry-Lindahl 1986) and one in Ivory Coast (Thiollay 1985). It possibly occurs in Ghana (Grimes 1987) and there is one record from Nigeria (Elgood 1982). It occurs throughout suitable habitat in Cameroon, Gabon and Zaïre, being locally common in Gabon (Brossel & Erard 1986; Keith *et al.* 1970; Louette 1981); it is uncommon but widespread in southern and western Uganda (Britton 1980) and occurs in northern Angola (Keith *et al.* 1970); it is also known from Bioko (Fernando Po) (Basilio 1963). The nominate race occurs from northeastern to southern Africa. It is widely distributed, and possibly locally common, in southern Ethiopia (Ash 1978), has occurred once in northern Somalia (probably a vagrant: see Section 1.2.1.6) (Ash & Miskell 1983) and is known from two localities in southern Sudan (Nikolaus 1987). It is uncommon throughout the western half of Kenya (Lewis & Pomeroy 1989), occurs on Pemba Island but has not been proved to occur on Zanzibar (Pakenham 1979), is known from two mountain blocks in eastern Tanzania (Britton 1980) and is widely but sparsely recorded in Zambia and Malawi (Benson & Benson 1977; Benson *et al.* 1971). It is widely but sparsely known from southern Mozambique (Clancey 1971),

including the Vumba (Brooke 1966) adjacent to the eastern highlands of Zimbabwe in which it is widespread, and there are several records from other regions of Zimbabwe (Irwin 1981).

In South Africa it occurs principally in the high-rainfall eastern regions, from sea level to over 1 800 m, precise altitudes not being given in regional works. In the Transvaal it is locally common in the forest regions of the escarpment with a few records elsewhere (Tarboton *et al.* 1987). In Natal it is widespread but is not recorded from the grassland regions of the northwest (Cyrus & Robson 1980), and there is only one record from the Transkei, where it must occur more widely (Quickelberge 1989). It is mostly of coastal distribution in the eastern Cape, with some inland records (Skead 1967) and in the southwestern Cape it is uncommon but has increased in some areas in recent years (Hockey *et al.* 1989).

#### 1.2.1.2      Habitat

The Buffspotted Flufftail is known to tolerate a wide range of habitats associated with forest or thick bush (Keith 1986). Throughout its range it occurs both in the interior and at the edges of indigenous forest, including coastal and other lowland forests (Cyrus & Robson 1980; Keith 1986), *Cryptosepalum* (Mavunda) forest, *Baikiaea* forest (Mutemwa woodland) and riparian forest (Benson *et al.* 1970; Irwin 1981), *Piptadenia* and *Macaranga* forest (Keith *et al.* 1970), *Ficus* forest (Ash 1978; Erard 1974) and, at the highest altitudes, juniper, *Podocarpus* and bamboo forest (Benson 1947; Jackson & Sclater 1938; Roux & Benson 1969). It particularly favours forest clearings, secondary growth and scrub (Chapin 1939, 1948; Keith *et al.* 1970; Serle 1965; Zimmermann 1972) and also occurs widely outside forest in dense evergreen or deciduous thickets (Benson & Benson 1977; Britton 1980; Irwin 1981; Rand 1951) including *Bauhinia* thickets (Benson *et al.* 1971), and bushy hillsides and ravines (Ash 1978; Pakenham 1979). In West Africa it is reported from dense plantations such as banana groves (Chapin 1948) and arrowroot *Maranta arundinacea* plantations (Brossel & Erard 1986), while it is widely reported to favour old cultivation and other neglected areas (Bates 1927; Chapin 1939; Pakenham 1945; Sclater & Moreau 1933; Wood 1935), even having occurred in the centre of an African village in such habitat (Basilio 1963). In South Africa it is known to frequent suburban and farm gardens (Bray 1961; Cyrus & Robson 1980; Skead 1967). Dense low vegetation and/or plentiful ground cover are essential requirements (Astley Maberly 1935a; Keith 1986; Pakenham 1979) and on Pemba Island it avoids rocky ground (Pakenham 1943).

Unlike the sympatric Whitespotted Flufftail it is not regarded as being typically associated with water (Chapin 1939; Keith 1986) but in Gabon it is found on the floors of muddy valleys choked with low vegetation and palm trees (Brossel & Erard 1986), in Sudan it is reported from wet or

swampy areas of dense bush and grass in forested localities (Cave & Macdonald 1955; Macdonald & Cave 1948), and in South Africa it occurs near streams in deciduous thickets (Astley Maberly 1935a, 1935b; Cottrell 1949; Vernon 1972). Although Buffspotted Flufftails occasionally enter grassland when congeners are absent (Keith 1986) it is very doubtful if they are ever typically associated with grass, as might be inferred from van Someren (1939) (see Section 1.2.2.2), while an early reference (Smith 1839; also mentioned by Stark & Sclater 1906) to the bird's occurrence at the margins of stagnant water densely fringed with reeds or rushes is probably a misidentification (Keith *et al.* 1970) and a comment by Skead (1967) that it may be overlooked in marshes appears to have no factual basis. Details of its occurrences in atypical habitats, possibly when on migration, are given in Section 1.2.1.6.

### **1.2.1.3 Behaviour, food and predation**

Although visual observation of Buffspotted Flufftails is extremely difficult (Brossel & Erard 1986; Keith 1986) and few people have ever observed the birds in the field, more is known about their behaviour (including breeding) than about that of any other *Sarothrura* species. This is undoubtedly because of the Buffspotted Flufftail's wide distribution, its relative accessibility in dryland habitats (as opposed to wetlands), its occurrence in close proximity to human habitation and the interest generated by its remarkable song (Section 1.2.1.4). Important observations have been made by Astley Maberly (1935a, 1935b), Chapin (1948), Manson (1986) and Pakenham (1943); the information obtained by the early observers (who did not have access to modern taperecording and playback equipment) has never been improved upon and bears witness to the persistence and determination of these men, who were obviously fascinated by this difficult and intriguing species.

Most important behavioural observations have been made on calling and breeding birds, and are described in Sections 1.2.1.4 and 1.2.1.5. Apart from the predominance of advertising calling at night, there is no evidence that the birds are nocturnal. They forage by day in leaf-litter on the floor of forest and thicket, often in very dim light (Zimmermann 1972), moving with little hurried steps and ceaselessly searching for small invertebrate prey (Astley Maberly 1935b). They dislike coming into the open for more than a few moments at a time, and even then they take advantage of every piece of vegetation, however small, to hide behind (Astley Maberly 1935b). When alarmed they dart mouse-like into the undergrowth and they are almost impossible to flush: they fly only in an emergency and the flight is clumsy, fluttering, and seldom high or far (Astley Maberly 1935a, 1935b). They are most active in wet weather and from about 16:00 onwards (Astley Maberly 1935b). They often call from the interior of bushes and when approached while calling they will fly between

bushes and move with agility along branches and twigs (Pakenham 1943). Although normally shy and skulking they may occasionally be confiding (Maclean 1993) and may occasionally be caught by hand on the ground when they refuse to fly (Bates 1927; Chapin 1948; Irwin 1955).

Astley Maberly (1935b) saw a family searching for insects and spiders, while Cottrell (1949) watched a male eating seeds or insects from moss and other low growth. Gizzard contents are reported as insects (including termites and a small cockroach), small snails, seeds, shredded vegetable matter, quartz grains and grit (Chapin 1939, Keith *et al.* 1970; Pakenham 1943; Sclater & Moreau 1933; Serle 1954). A captive bird ate termites (Chapin 1948). There is no reference to predation anywhere in the literature on this species.

#### **1.2.1.4      Voice**

The remarkable song of this little bird has given rise to many local superstitions, some of which are entertainingly described by Chapin (1948). The song has been described as the wail of a banshee and has been variously attributed to a large land snail, a skink, a chameleon, a tortoise, the puff adder *Bitis arietans*, "crowning crested cobras", tree snakes, a climbing mammal and a nocturnal bird of prey (Ash 1978; Bates 1927; Benson 1953; Chapin 1948; Keith *et al.* 1970; Pakenham 1943; Wood 1935). The song is well described by Chapin (1939, 1948), Astley Maberly (1935a, 1935b) and Pakenham (1943), the last two of whom sat for long hours near singing males but failed to see them actually in the act of singing. It is normally a long, mournful, mellow, low-frequency note, usually written as *wooooooo* or *hooooooo* and has been likened to a miniature foghorn (Astley Maberly 1935a). It has the clarity and resonance of a tuning fork and is often ventriloquial; it usually begins softly and increases in intensity, becoming remarkably loud, stops after 2-4 s and is repeated every 5-10 s (Keith *et al.* 1970; Maclean 1993; Pakenham 1943). It is a much longer note than any known from other members of the genus, and is of quite a different quality (Keith *et al.* 1970). At times the song is given quietly (Pakenham 1943) and the normal song note sometimes rises in frequency towards the end to give a double note: *wooooooo-eeeeeee* (Astley Maberly 1935a, 1935b; Searle 1984).

Although the bird sometimes sings from the ground (Bray 1961; Pakenham 1943), it usually sings while well concealed among leaves in a bush or low tree, 1-2 m (once 8 m) above the ground (Gillard 1976; Pakenham 1943; Rand 1951). Most singing occurs in the evening (from about one hour before sunset) and at night, but song may also be heard in the early morning and even intermittently during the day, especially in overcast, wet or misty weather (Astley Maberly 1935a; Benson 1962; Benson *et al.* 1971; Keith *et al.* 1970; Pakenham 1943, 1979). Pakenham (1943) found that males

would choose a singing position where they could catch the slanting rays of the setting sun. Singing may continue, either intermittently or continuously, for several hours, even throughout the night, and may be audible up to 1 km away on calm nights (Astley Maberly 1935a; Gillard 1976; Pakenham 1943; Rand 1951). In most parts of the bird's range singing is seasonal, coinciding with known breeding periods, but in Gabon and Liberia the song may be heard throughout the year (Brossel & Erard 1986; Rand 1951).

The only person to have seen the bird singing is H. Beatty who (*in* Rand 1951) by torchlight watched a male nestled amongst a cluster of leaves on a branch 1 m up; "after a moment of relaxation the bird's body began to swell; then followed a sudden and perceptible shudder and the whistled note began". Both Chapin (1948) and Pakenham (1943) mention that local people said that the bird puffs out its throat when it calls, and both authors comment on aspects of the birds' anatomy which might contribute to the production of so loud and resonant a sound. Pakenham found that the whole inside surface of the skin of the neck had a coating of sticky, gelatinous matter, while Chapin found that this skin was loose and watery, and that the oesophagus could be inflated with a blow-pipe until the neck measured 5 cm in diameter, this presumably accounting for the swollen throat described by observers.

With regard to other vocalizations, Astley Maberly (1935b) remarks that the species has an astonishing repertoire of calls. He describes how birds moving around on the ground uttered repeated successions of crooning notes, rendered *du-du-dooo-dooo-dooo*, punctuated by subdued clucks, and how a pair maintained a running conversation of "juggling" notes, rendered *too-tookorook-tookorook-rook-ook-ook-ook-oooooooooooo*, this call also frequently preceding the full song note. He also heard (1935a) the song die away into soft *jug-jug-jug* notes, which were thought by Keith *et al.* (1970) to be annoyance calls (as are known from other *Sarothrura* species) probably because of the proximity of the observer. Pakenham (1943) heard a quiet short hum, merging into a wasp-like whine, a low growl, sometimes repeated and sometimes preceding a cat-like mew which rose in tone and volume, and (probably from this species) "an eerie tender wail as of feminine grief or pain". He also heard other vocalizations similar to those of the Redchested Flufftail, but a less varied repertoire: soft, chicken-like clucks, a husky or gritty whine and a *krrr krrr krrr* call.

Other adult calls, and some chick calls, have been described by several observers. Small downy chicks observed by Serle (1954) made "hissing rat-like squeaks" while the adults called to each other with low-pitched soft *ooo* notes. A female made crooning notes to chicks (Astley Maberly 1935b). Irwin (1955) describes a male making a subdued, deep *woo* call at close range, while Gillard (1976) heard an adult making similar soft hoots, with grunts, soft hisses and *ooo-phee* notes. Ash (1978) described contact calls as *moo* and *mair*, the latter note possibly from the female. Captive birds make low growls, and low hoarse *coo* and *coop* notes (Chapin 1939, 1948). Manson (1986) noted that

an incubating pair were silent at the nest until just before the eggs hatched, when both birds began to make soft rapid *whoo* or *whoo-whoo* notes, the female replying with croaks *wark* to the male's *whoo* while the male gave a sharp *kek* to the female's *whoo*. Gurgles, *zeep* calls and low-pitched *coodily-cooo* calls were also heard, and the young chicks made *peeps* and subdued chuckles.

#### 1.2.1.5 Breeding and moult

This study has confirmed several misidentifications of clutches or nests of this species. Three South African clutches attributed to the Striped Flufftail *S. affinis* are in fact of the Buffspotted Flufftail (Table 7.8); two of them are described by Chubb (1914), who suspected that they might be referable to the Buffspotted Flufftail. A nest found by Porter (1970), identified as that of a Buffspotted Flufftail, was in fact of a Striped Flufftail (Table 7.8), while one described by Pooley (1962) as being that of a Redchested Flufftail was clearly that of a Buffspotted Flufftail (Section 1.2.2.5).

The Buffspotted Flufftail is monogamous and is territorial when breeding (Keith 1986). There is no information on breeding dispersion, courtship, mating or nest building. The nest is always placed on the ground and is usually well hidden in ground vegetation or under the leaves of a herb or shrub. For example, Cottrell (1949) describes a nest hidden under a dense tangle of creepers, Bray (1961) found one in canna lilies, Chubb (1914) describes one in a tuft of grass, and Manson (1986) describes one nest hidden in the short forest grass *Oplismenus hirtellus* and two concealed by the leaves of the iris *Dietes prolongata*. Nests may be placed close to a fallen log or at the foot of a small tree, presumably for extra concealment (Chapin 1948; Lorber 1982; Manson 1984). The nest is made of dead leaves and/or dry grass, and is lined with similar materials or with rootlets (Bray 1961; Chubb 1914; Cottrell 1949; Lorber 1982; Manson 1984, 1986; Paterson 1945). Most nests are domed, with an entrance hole or short entrance tunnel at one end, but open, shallow cup-shaped nests have been recorded in situations where roofing cover was provided by growing "stag-horn moss" (Lorber 1982) or low shrubs (Manson 1984); an open nest seen by Chapin (1939) was thought to have had the roof removed by the finder (Chapin 1948). Some open and domed nests are built in a shallow depression in the ground. The external and internal (in parentheses) dimensions of one nest were: height 15 (9) cm; length 21 (15,5) cm; width 23 (17) cm; entrance 10 cm wide and 7 cm high; entrance tunnel 7,5 cm long; average thickness of walls 3-5,5 cm (Manson 1986). Nests have been found less than 2 m from a well used forest track (Lorber 1982), on ground sheltered by the eaves of a building (Bray 1961) and in the centre of an African village (Basilio 1963).

The eggs number 3-5 and are large for a flufftail, oval, white and glossy but sometimes stained (Keith 1986). One egg is laid per day and incubation takes 15-16 days, beginning when the

clutch is complete; both sexes incubate but have no regular times of doing so (Manson 1986). After hatching, the family remains in and around the nest for one day before leaving the area (Manson 1986). Three observers report that the parents are bold in the defence of the nest and chicks against human intruders. A male near a nest fluffed up his feathers and advanced menacingly to 1 m away with growls and hisses, and then ran up and down with growls (Cottrell 1949). Both parents will attack people's legs if chicks are approached (Oatley & Pinnell 1968). When disturbed, an incubating female rushed or flew out of the nest, spitting sharply like a cat and ran agitatedly around with wings drooping almost to the ground (Manson 1986).

Downy chicks are black, with black bare parts and no pale markings on the bill (Keith 1986; Manson 1986). Parents accompanied by young chicks have been seen foraging (Keith 1986), but no information is available on chick development and fledging, or on relationships within the family group, and there is no indication that the species is multibrooded. Immature plumage is described as being uniform sepia-brown, paler on the belly (Keith 1986).

In Natal breeding occurs in the rainy season, from September to March (Cyrus & Robson 1980), all Zimbabwe records are for the rainy period (Lorber 1982; Manson 1984; 1986) and on Pemba the species probably also breeds during the rains (Pakenham 1979). Records from other areas are too few (Keith 1986; Keith *et al.* 1970) to allow conclusions to be drawn about the seasonality of breeding.

The only information on moult comes from Mann (1985), who trapped a bird in primary moult at Kakamega, Kenya, in November-December, and Pakenham (1943) who collected two males moulting body feathers, one also moulting the central primaries (suggesting sequential primary moult) on Pemba in August.

#### **1.2.1.6      Movements**

Both Snow (1978) and Keith (1986) consider that there is no evidence for regular migration in this species. Keith points out that the habitat is not seasonal and that the bird is recorded throughout the year in South Africa, as it is in Gabon (Brosset & Erard 1986). Despite this, the literature contains several records of Buffspotted Flufftails being found far from suitable habitat or in situations strongly indicative of long-distance movement or migration, as follows.

- a) In southern Nigeria a female was caught in the evening of 2 April 1935 in a house surrounded by 100 m of cleared land (Bannerman 1935); this is the only record from Nigeria (Elgood 1982).

- b) The only record from Somalia is of a specimen collected at the foot of the Wagar Mts at c. 200 m a.s.l. around hot springs in desolate country (Archer & Godman 1937; Keith 1973).
- c) From Sudan, a male was collected outside a house in savanna at Torit on 27 January, apparently in atypical habitat (Cave & Macdonald 1955; Keith *et al.* 1970).
- d) A female collected at Kitgum, Uganda, on 31 Oct 1923, was in atypical habitat of long grass and was very fat, both facts being suggestive of migration (Keith *et al.* 1970).
- e) There are three records from semidesert country at Lake Turkana in northern Kenya. An adult male at Koobi Fora was seen hiding in the thatched roof of a small hut from 24 to 26 April 1971 and other birds had been seen a week before, running around in sparse "ouch! grass" on the lakeshore (Keith 1973). A bird, probably this species, was found under a refrigerator at Ferguson's Gulf Fishing Lodge in April 1975 and an adult male was found clinging to a windowsill at the Lodge in April 1985 (Lewis & Pomeroy 1989).
- f) In Zambia a female was killed at about 22:00 on 26 December 1956 at a lighted window of a house near Mbala at 1 500 m a.s.l., on high ground overlooking the southern end of Lake Tanganyika some 19 km to the north. The weather was overcast with rain and an Angola Pitta *Pitta angolensis* and three African Crakes *Crex egregia* (both Afrotropical migrants) also flew against the windows at the same time (Benson 1957).
- g) In Zimbabwe, single birds were found dead in Harare city centre on 17 December and Centenary Park, Bulawayo, on 16 December (Irwin 1981).

When reviewing those of the above records occurring before their respective publications, Benson *et al.* (1971), Keith (1973), Snow (1978) and Keith (1986) all attribute them to local movements or vagrancy, an opinion which is not shared by Moreau (1966) and Lewis & Pomeroy (1989), who suggest that long-distance migration may well occur. The Kenyan and Zambian records, at least, are strongly indicative of long-distance migration and cannot be dismissed merely as examples of local vagrancy. However the occurrence of a bird in a farm garden in South Africa, regarded as indicative of vagrancy (Skead 1967), can be explained by the bird's known habitat preferences.

## 1.2.2 *Sarothrura rufa* (Vieillot). Redchested Flufftail.

### 1.2.2.1 Distribution and status

The Redchested Flufftail is a relatively common resident of wetlands in sub-Saharan Africa, with isolated populations in Ethiopia and in West Africa east to Gabon, and a more continuous range from Cameroon east to Kenya and south to the Cape. Its known geographical range is the most extensive of any *Sarothrura* species (but see comments on the Buffspotted Flufftail, Section 1.2.1.1) but it is apparently largely absent from the extensive forested regions of Zaïre, and in eastern Africa it is mainly confined to the higher-altitude regions (occurring up to 2 700 m a.s.l. in Kenya), descending to lower levels in eastern South Africa (Keith 1986). Like the Buffspotted Flufftail it is mostly absent from the low-rainfall areas of southwestern Africa. It is often overlooked by observers unfamiliar with its calls, and its range may be more extensive than is known (Keith 1986).

In Ethiopia small numbers (race *S. r. elizabethae*) have been found in the Shoa, Kaffa and Wollega districts (Ash 1978; Erard 1974; Guichard 1948) and it has been recorded alongside the Whitewing Flufftail only at Gafersa, Shoa (Chapter 8, Section 8.5.4). The race *S. r. bonapartei* is thought to occur in Ivory Coast (Thiollay 1985) and probably in Ghana (Grimes 1987), and is known from single localities in Sierra Leone and Togo (Erard & Vielliard 1977; Keith 1986) and from two sites in Nigeria (Elgood 1982; Keith *et al.* 1970). The bird's distribution becomes more continuous from Cameroon and Gabon, extending through the Central African Republic (Bangui) where the race *S. r. elizabethae* reappears and ranges across northern and eastern Zaïre to Burundi and central Uganda (Brosset & Erard 1986; Keith 1986; Louette 1981; Roux & Benson 1970). Although only rarely reported from Uganda (Britton 1980), it is locally common in western and central Kenya (Lewis & Pomeroy 1989) but a record based on sound from the coast near Mombasa is incorrect (pers. obs.). In central Kenya, *elizabethae* is replaced by the nominate race which also occurs on Zanzibar and Pemba Islands, in northeastern and western Tanzania (Britton 1980; Keith 1986; Pakenham 1979), extends through southern Zaïre into Angola, most of Zambia and Malawi, most of the higher ground in Zimbabwe and adjacent highlands of Mozambique, and occurs sparsely in southern Mozambique (Benson & Benson 1977; Benson *et al.* 1971; Clancey 1971; Keith 1986; Irwin 1981). In Botswana it is known from the Okavango area and in Namibia only from Omambonde (Keith 1986).

In South Africa the nominate race is widely but thinly recorded throughout the Transvaal and Natal (Cyrus & Robson 1980; Tarboton *et al.* 1987); there are few records from the Transkei (Quickeberg 1989) and in eastern and southern Cape Province it is mainly coastal in occurrence

(Keith 1986), being widely distributed but infrequently recorded although it may be commoner than is known (Courtenay-Latimer 1964; Skead 1967). In the southwestern Cape it is locally common (Hockey *et al.* 1989). Its altitudinal range in South Africa is not given by any author, but in Natal it appears to occur from sea level to about 1 500 m (Cyrus & Robson 1980).

### 1.2.2.2 Habitat

The wide range of vegetation types mentioned in published habitat descriptions suggests that the Redchested Flufftail is catholic in its choice of habitat, occurring in a wide variety of essentially marshy areas. It inhabits permanent or semi-permanent swamps and marshes, occurring in reedbeds, sedges (including papyrus), rushes, tall dense tussocky grass and other tall rank vegetation and it is found in moist vleis, beside rivers and around pools and dams, always in thick vegetation (Irwin 1981; Keith 1986). Characteristic plant genera in its preferred marshy habitats in the Transvaal, South Africa, are *Carex*, *Juncus*, *Scirpus*, *Typha* and *Phragmites* (Tarboton *et al.* 1987) and it was collected in dense low *Paspalum tricolocladum* grass at a marsh edge in Tanzania (Sclater & Moreau 1932). In Zimbabwe it prefers the shallower parts of marshes and avoids densely matted vegetation (Hopkinson & Masterson 1984). In some areas it moves out of reedbeds during the rains to occupy the taller, denser parts of adjacent seasonally inundated grassland (P.B. Taylor *in* Keith 1986).

It is generally assumed that preferred habitats are wet at least seasonally, but in Cameroon Serle (1954) found it in dry rank grass in a forest clearing, and it is found in similar habitat in forested areas of northeast Gabon (C. Erard pers. comm.), where it is also very common in planted grasslands near human habitations, especially in *Paspalum* grass around huts (Brossel & Erard 1986). References to its frequenting "forests and forest streams" (V.G.L. van Someren *in* Jackson & Sclater 1938; van Someren 1939) are undoubtedly misleading as in forested areas it is replaced by the Whitespotted Flufftail along streams and the Buffspotted Flufftail away from streams (Keith *et al.* 1970; Ripley & Heinrich 1966; Taylor & Taylor 1986). Furthermore, van Someren (1939) also refers to East African specimens of the Buffspotted Flufftail collected in "swamp grass; river margin in grass; grass-land...", which are very atypical habitats for this species and are more akin to habitats of the Redchested Flufftail. Van Someren's descriptions of flufftail habitats may be neither accurate nor representative of those of the species concerned.

Detailed information on the Redchested Flufftail's ecological segregation from its congeners in wetlands is available only with respect to the Streakybreasted Flufftail, which normally occupies shorter, less dense, temporarily flooded grasslands, often in drier situations. In wetlands occupied by both species Redchested Flufftails occur in the taller, lusher mixed vegetation of the central regions

while Streakybreasted Flufftails inhabit shorter grassland at the edges (Benson *et al.* 1971; Keith 1986; Irwin 1981). In Gabon, where both species occur together in dry grassland, they occupy identical habitat (see above), although the Streakybreasted Flufftail is especially associated with areas having clumps of tall grasses scattered in a continuous cover of shorter vegetation (Brossel & Erard 1986). In a wetland where both Redchested and Whitewing Flufftails were found, the two species occurred in different areas but no corresponding differences in habitats were noted (Mendelsohn *et al.* 1983): for a full discussion of the habitat requirements of the Whitewing Flufftail, see Chapter 8. The uncommon Longtoed Flufftail *S. lugens* is known to occur alongside the Redchested Flufftail in Zambian dambos (Keith *et al.* 1970) and the limited information on its habitat (Chapin 1939; Keith 1986) suggests that it may prefer vegetation more dominated by grasses. In Gabon it prefers post-cultivation plant successions characterized by the presence of taller shade plants but also occurs at the edges of cleared areas, where it occurs alongside both Redchested and Streakybreasted Flufftails (Brossel & Erard 1986). Benson *et al.* (1971) suggest that it is a relict species in unsuccessful competition with the commoner Redchested Flufftail.

#### 1.2.2.3 Behaviour, food and predation

Despite its relative abundance the Redchested Flufftail is very poorly known and is often overlooked. The birds are very difficult to see and only Pakenham (1943) has made detailed observations of wild birds under natural conditions, although Steyn & Myburgh (1986) attracted a breeding pair to food and (from a hide) were able to observe adults with chicks. Although captive birds are also very secretive and difficult to observe, Wintle (1988) obtained much information on their behaviour.

Like other flufftails they are difficult to flush, fly a very short distance before dropping into dense cover, and are difficult to flush again (Clancey 1964; Maclean 1993; Mendelsohn *et al.* 1983). They are most active early and late in the day, during which periods they feed (Keith 1986; Pakenham 1943; Steyn & Myburgh 1986). White (1945) states that they are largely nocturnal but his evidence is not convincing, being explained by some known crepuscular activity. Both adults and chicks run extremely quickly on the ground and they are fond of climbing; they perch and creep around in small bushes and tangled vegetation, especially at dusk (Pakenham 1943; Wintle 1988). They sunbathe in the early mornings and members of a pair allopreen (Steyn & Myburgh 1986). The tail is often carried erect except when feeding and the birds swim well but prefer to feed when walking in shallow water (Stark & Sclater 1906; Wintle 1988).

Gizzard contents are given as snails, small ants (including workers of the genus *Myrmicaria*), termites, minute diptera, aquatic hemiptera, weevils, a beetle larva (Carabidae), unidentified insects, small seeds (including grass seeds) and grit (Benson 1948, 1959; Keith *et al.* 1970). Captive birds eat earthworms, insects, termites, mealworm *Tenebrio* larvae, chopped ox heart, seeds such as millet and munga (a type of sorghum) and cooked beaten egg with milk, and they feed small chicks on insects; they eat much more seed than do captive Streakybreasted Flufftails (Wintle 1988).

There are no recorded instances of natural predation, but Lockhart & Lamont (1984) twice attracted a Black Sparrowhawk *Accipiter melanoleucus* while playing back taped calls of the Redchested Flufftail. Although this raptor possibly catches most of its prey in the open, most of its avian prey averages 80-300 g and the smallest birds taken under natural conditions are forest greenbuls *Andropadus* spp. (Brown 1982). It is therefore unlikely that flufftails would be a regular item of its diet, especially as under normal conditions Redchested Flufftails would probably be difficult for it to locate and catch in dense marsh vegetation. However A. Brosset flew falconry-trained Black Sparrowhawks over grassland in Gabon and caught both Redchested and Streakybreasted Flufftails (Brosset & Erard 1986; C. Erard pers. comm.).

#### 1.2.2.4      Voice

The common calls are well documented and are summarized by Keith (1986), from which work the following descriptions are taken unless otherwise specified. The song is a series of clear hoots, shorter and higher-pitched than those of any African *Sarothrura* except the Whitespotted Flufftail, each 0,6-0,8 s long with an interval of 0,4-0,7 s between notes. Singing usually lasts less than 1 min. The note does not change frequency but increases in intensity, giving the impression of a rise in pitch at the end: *wooh*. Infrequently a second bird answers antiphonally with a higher-pitched *wah*. Sometimes the song is preceded by low grunts, which may be incorporated into the song: *g'wooh*, and sometimes a loud grunt (possibly from a second bird) follows each hoot: *wooh-boo*. A male giving the last call was collected by Pakenham (1943) and it is assumed that it is the male which normally sings (Benson 1956; Keith *et al.* 1970).

The commonest call is a series of loud notes rising in frequency and best rendered *dúeh-dúeh-dúeh-dúeh...* (Pakenham 1943), sometimes with a grunt incorporated, which may be uttered for up to 15 s. Differences in speed and intensity are attributed to different degrees of excitement in the calling bird (Keith *et al.* 1970). Both sexes give this call (Wintle 1988) and Pakenham (1943) records a higher-frequency version which he attributes to a sexual difference, while both he and Steyn & Myburgh (1986) record females giving a quiet version of the call to chicks.

Other calls include a deep grunting *boo* or *wuk*, sometimes answered by a second bird at a higher frequency; growls and wheezes; a high-pitched hum (a warning note); a plaintive chirp; and from chicks a monosyllabic cheep and a plaintive *wee-ick* (a begging call) (Pakenham 1943; Steyn & Myburgh 1986; Wintle 1988).

Benson (1956) states that the song is normally uttered only during and immediately after the breeding season. Pakenham (1943) records that the birds are most vocal in the very early morning and between sunset and nightfall, while drought has a silencing effect and threatened or actual rain a stimulating effect, and calling decreases after nesting has begun. Benson (1956) noted both daytime and nighttime calling. In Gabon, Brosset & Erard (1986) found that the species sings all year but they recorded breeding only in November-March. The calling throughout the year recorded in Zimbabwe (Hopkinson & Masterson 1984) presumably refers to the *dueh* call. Gillard (1976) maintains that all flufftail species are usually silent outside the breeding season, and also that the calls of the Redchested Flufftail are not audible over any distance, but these statements are entirely without factual foundation.

#### 1.2.2.5 Breeding and moult

Both wild and captive birds are monogamous, form strong (apparently permanent) pair bonds and are territorial during the breeding season (Brosset & Erard 1986; Keith 1986; Pakenham 1943; Wintle 1988). Breeding pairs in continuous habitat on Pemba were spaced at a distance of 50-100 m or less, and isolated pairs were sometimes found in very small areas (Pakenham 1943). Courtship and mating are undescribed. The nest (Broekhuysen *et al.* 1964; Brosset & Erard 1986; Hopkinson & Masterson 1984; Keith *et al.* 1970; Wintle 1988) is a cup of grass or dead plants, well hidden inside (or at the base of) a clump of grass or weeds, with or without a slight dome and often situated 20-30 cm above the substrate. Nests are built in grass at the edges of marshy areas, often where the ground is damp or shallowly flooded, and have been recorded in *Oryza* and *Pennisetum* grasses. A record of an enclosed nest on the ground, built entirely of leaves (Pooley 1962), undoubtedly refers to the Buffspotted Flufftail, especially as it was "on the forest floor".

The eggs are white, number 2-5 and are laid at intervals of 1-2 days (Keith 1986; Wintle 1988). The available records (Keith *et al.* 1970; Keith 1986) indicate that the bird breeds during the rains (November-May) in southern Africa but the breeding season is indeterminate in equatorial regions. Records from Cape Province, South Africa, are for November-January but Steyn & Myburgh (1986) recorded breeding in August-January in the southwestern Cape, while in Zimbabwe captive birds breed as early as August (Wintle 1988). In view of the possibility of confusion between breeding

records of Redchested and Streakybreasted Flufftails (Keith *et al.* 1970), some records of clutch size and breeding month may be incorrect and I can find no properly documented evidence that the Redchested Flufftail normally lays clutches of more than 2-3 eggs, either in the wild or in captivity.

Incubation is by both sexes and takes 14-16 days, the male sitting during the day and the female from the late afternoon through the night (Broekhuysen *et al.* 1964; Keith 1986; Wintle 1988). Chicks remain in the nest for 2-3 days and then follow the parents; they can feed themselves after four days but are fed until independent (Wintle 1988). Adults brood a small chick by holding it under a wing, and may even carry it for short distances like this (Steyn & Myburgh 1986). A female tried to lead an observer away from chicks by running away in full view and stopping every few feet (Pakenham 1943). The male constructs roosting nests in which the family spends the night (Wintle 1988).

Downy chicks are sooty black with a pronounced fluffy tail, black legs and a white bill with a black spot between the nostrils; at one week old the bill becomes pink with a black tip. The bill's pale colour is important in feeding, being highly visible to the parents in the dim light of the dense cover which the birds inhabit (Wintle 1988). Body feathers begin to appear at six days and at 23 days the chick is fully feathered except for the remiges and rectrices, which grow from this age; the black first plumage is complete at 42 days, when the chicks can fly (Wintle 1988). At this age the bill is almost black and the young immediately begin a postjuvenile moult to a dull version of the adult plumage, first-year females being much darker than adults and males having white spots rather than streaks (Liversidge 1968; Wintle 1988).

The species may be multibrooded and in captivity chicks are fed by young from the season's previous broods, which are tolerated by the parents throughout the breeding season (Wintle 1988). A wild pair which bred four times drove off young from the first two broods, only the third brood juveniles being allowed to help feed the final brood, but this aggressive behaviour may have been aberrant (Steyn & Myburgh 1986). From details given of this pair, the interval between the four clutches ranged from nine to only about 4½ weeks, the shortest period meaning that the third brood was just over two weeks old when the fourth clutch was started.

Redchested Flufftails moult the remiges sequentially and, although they sometimes lose as many as five feathers at once from each wing, they are never flightless during the moult (Wintle 1988).

### 1.2.2.6 Movements

Individual birds on Pemba Island spend weeks or months in the same few square metres of territory (Pakenham 1943) and Keith *et al.* (1970) regard the species as entirely sedentary within the regions where data are numerous enough to permit conclusions to be drawn, including southern Africa, where "there is as much seasonal contrast as anywhere within the range of the species". Although the species breeds during the rains in central and southern Africa there are numerous specimens taken throughout the dry season, indicating permanent residence. These authors mention the only two records indicative of movements in this species: Astley Maberly's (1961) capture of an exhausted adult male at his house in northeast Transvaal at 21:30 on 7 August 1958 and a bird found dead at the base of a cliff near Rustenburg in western Transvaal on 31 August, but regard these as representing individual strays, possibly blown out of their habitat after a storm.

### 1.2.3 *Sarothrura affinis* (Smith). Striped Flufftail.

#### 1.2.3.1 Distribution and status

The Striped Flufftail is an uncommon species found in widely separated areas of montane grassland from southern Sudan to the Cape, the race *antonii* occurring south to Zimbabwe and the nominate race being confined to South Africa (Keith 1986). Under existing climatic conditions this bird's distribution is essentially discontinuous and relict (Keith *et al.* 1970). In southern Sudan it is rare on the Imatong Mts, where it has not been recorded for over 50 years (Cave & Macdonald 1955; Nikolaus 1987). It is recorded only rarely in the highlands of western and central Kenya and the Kenya-Tanzania border (Britton 1980; Lewis & Pomeroy 1989), whereas Stoneham (1928) considered it quite common at Kitale, western Kenya, in the 1920s. In Tanzania it is reliably known only from the Matengo Highlands in the south (Britton 1980; Lewis & Pomeroy 1989; Sassi & Zimmer 1941). Benson & Benson (1977) and Benson *et al.* (1970) record its occurrence in the highlands of northern and southern Malawi, and extreme northeastern Zambia (Nyika Plateau), but give no indication of its status, although Benson & Holliday (1964) found it common in suitable habitat on the Zambian Nyika. In Zimbabwe it is known from only two localities in the eastern highlands but is likely to be more general in suitable habitat (Irwin 1981).

The nominate race is regarded as uncommon to rare in South Africa (e.g. Brooke 1984; Maclean 1993; Stark & Sclater 1906), although C.H.B. Grant, quoted by Sclater (1912), regarded it as "probably quite common" in Transvaal localities. (Grant's sight records (*op. cit.*) of this species

from coastal localities in Zululand and Mozambique were rejected by Keith *et al.* (1970) as possible misidentifications.) Its former distribution included eastern and northern Transvaal and Tarboton *et al.* (1987) give recent records from three eastern Transvaal localities, while Allan (1988) heard "many" calling birds at two other eastern Transvaal localities. In Natal it was recorded from only three places in the 1970s (Cyrus & Robson 1980), while a vague reference by Lawson (1971) to a "recent sight record from Westville" (Durban), although just possibly valid on the basis of previous distribution (see Section 7.4.1.1 and Table 7.3 for a 19th-century Pinetown record), is unacceptable without supporting details. It is uncommon to rare in Transkei, whence there are no recent records (Davies 1911; Quickeberge 1989). The only Lesotho record (Table 7.5) was rejected as unsatisfactory by Winterbottom (1964) but, in the light of our present knowledge of distribution, this record is perfectly credible. The scattered localities from the Cape mapped by Brooke (1984) are almost all pre-1970 but in recent years it has been found in several localities in the southwestern Cape, where it may prove to be more widespread and numerous than has been supposed (Graham & Ryan 1984; Hockey *et al.* 1989; Kakebeeke 1993; Martin 1985; Ryan 1987). The occurrences plotted by Brooke (1984) at 27°20'S, 31°20'E (southeastern Transvaal), 27°50'S, 24°25'E (northern Cape) and 28°40'S, 30°20'E (central Natal) are erroneous (R.K. Brooke *in litt.*). The bird's altitudinal range extends up to 3 700 m a.s.l. in Kenya and is between 1 615 and 2 300 m in Zambia, Malawi and Zimbabwe (Keith *et al.* 1970), while in South Africa it is mainly inland and submontane in distribution except in the southern Cape, where it descends to sea level (Brooke 1984).

### 1.2.3.2      Habitat

Over most of its range the Striped Flufftail typically inhabits dry upland grassland (Keith 1986), a habitat not occupied by any other flufftail species or indeed by any other rallid except the Corncrake *Crex crex*. The grass cover is dense and often short (Allan 1988; Nikolaus 1987; Tarboton *et al.* 1987) and may be mixed with bracken or *Protea* (Benson & Holliday 1964; Masterson & Child 1959). In some upland areas it is found in long grass (Davies 1907; Jackson & Sclater 1938; Skead 1967) and it also occurs in other vegetation types such as bracken-briar (Benson *et al.* 1970; Benson & Benson 1977) and "low brushwood" (Stark & Sclater 1906). In South Africa it is often found in grassland near forest edges (Keith 1986), and even occurs in croplands such as millet and lucerne (records are reviewed by Keith *et al.* 1970). In the extreme southwestern Cape it occurs in *Psoralea-Osmotopsis* fynbos and is found on south-facing slopes, in dense vegetation associated with small streams (Graham & Ryan 1984; Hockey *et al.* 1989; Ryan 1988).

Some confusion surrounds literature descriptions of Striped Flufftail's occurrence in wet habitats. It was collected in "open moorland bogs" on Mt. Kenya and the Aberdare Mts, Kenya, by Meinertzhagen (1937) but, as Meinertzhagen is known to have falsified data on stolen specimens, one should question the authenticity of data on specimens which he collected (or claimed to have collected) himself (Knox 1993). Sassi & Zimmer (1941) stated that in the Matengo Highlands, southern Tanzania, it was found mainly in damp places near water in the dry season but occurred away from water in the rains. But Stoneham (1928) records that, in an exceptionally wet breeding season in western Kenya, many fewer birds were present in the normal long grass habitat than were found in a drier year. Published accounts of its preference for marshy areas in South Africa are regarded as unconvincing by Keith *et al.* (1970), possibly being based on confusion with other species, and it is most likely that it enters wetter areas only in the dry season, when its normal dry habitat may be burned (Brooke 1984; Keith 1986; Keith *et al.* 1970). A reference to a preference for marshy patches in the southwestern Cape fynbos (Martin 1988) suggests that in such habitat the birds may enter small moist patches which are unsuitable for the wetland-dependent Redchested Flufftail.

#### **1.2.3.3 Behaviour, food and predation**

Almost nothing is known about the behaviour of the Striped Flufftail. It is very shy and skulking and, if flushed, flies a very short distance with feeble flight and rapid wingbeats before dropping into dense cover; it is very difficult to flush a second time (Cave & Macdonald 1955; Masterson & Child 1959; Meinertzhagen 1937; Sclater 1912). It is sometimes so unwilling to fly that it may be trodden on or picked up by hand (Keith *et al.* 1970; Kittenberger 1958). Stomach contents are recorded as small insects (including small beetles), seeds and some vegetable matter, also possibly termites and snails (Keith 1986). The only recorded instances of predation are of single males taken by a Lanner *Falco biarmicus* and a domestic cat (Davies 1911).

#### **1.2.3.4 Voice**

Only two calls are recorded: the song is a series of 1-second-long hoots, distinguishable on pitch and length from the hoots of other flufftail species (Keith 1986), and there is also a rattling, tinny note which is believed to come from the female (Benson & Holliday 1964). The song is given both day and night (Keith 1986).

### 1.2.3.5 Breeding

Keith *et al.* (1970) and Keith (1986) give details of the few definite and presumed clutches of this species and summarize further evidence from examination of gonads. The only two South African breeding records, both of eggs from Natal, are, however, not fully authenticated (Brooke 1984), and a record from eastern Transvaal of a male flushed near an empty nest (Allan 1986) is not conclusive. The mean clutch size is 4,3 eggs (Keith 1986) and all records are referable to the rainy season except a pre-rains record of two females in breeding condition collected on Mt Kenya in February 1936 (Meinertzhagen 1937); however, as discussed in Section 1.2.3.2, the accuracy of details on Meinertzhagen's specimens is questionable. The nest, a bowl of rootlets built into a grass tuft, is described by Masterson & Child (1959). No information is available on breeding behaviour.

### 1.2.3.6 Movements

It is generally assumed that Striped Flufftails show no regular seasonal movements or long-distance migration but that local movements to damper situations may occur seasonally in areas where the breeding grassland habitat becomes too dry or is burned (Keith *et al.* 1970; Keith 1986). Irwin (1981) records a nocturnal casualty at Inyanga in the Eastern Highlands of Zimbabwe, possibly indicative of such local movement.

## 1.2.4 *Sarothrura ayresi* (Gurney). Whitewing Flufftail.

### 1.2.4.1 Systematics and nomenclature

Although the first specimen was collected at King William's Town, Cape Province, in August 1876 (Table 8.1), the Whitewing Flufftail was first described as *Coturnicops ayresi* (Ayres 1877; Gurney 1877) from two birds obtained at Potchefstroom, Transvaal, in October and November 1876 (Table 8.1). A specimen taken in May 1905 at Charada, southwestern Ethiopia (Table 8.1) was described as a new species, *Ortygops macmillani* (Bannerman 1911), but subsequent comparisons with South African material showed it to be identical with *Sarothrura ayresi* (Grant & Mackworth-Praed 1941) and there are no significant morphological differences between the South African and Ethiopian populations (Benson & Irwin 1971; Keith 1986; Keith *et al.* 1970). The specific name has recently been given as *ayresii* by some authors (Hopkinson & Masterson 1984; Keith 1986), apparently in error as the original spelling (Ayres 1877) is *ayresi*.

#### 1.2.4.2 Distribution and status

The Whitewing Flufftail is certainly the rarest and most enigmatic of African rallids (Collar & Stuart 1985; Keith 1986), occurring in two widely separated populations, one in Ethiopia and the other in South Africa. All specimen and sight records are summarized in Tables 8.1 and 8.2. In Ethiopia it is known from several localities in the highlands around Addis Ababa and there is also one specimen from Charada, at a lower altitude to the southwest (Table 8.1). Apart from the 1905 Charada bird all Ethiopian specimens were obtained in the period 1939-1957 (Collar & Stuart 1985) and, despite intensive searching in the central highlands (Ash 1978; Erard 1974) there has been only one subsequent record, in August 1984 (Table 8.2). Even in 1947 Guichard (1948) found the species only in small numbers in the central highlands, and threats to the wetland habitats of that area from expanding agriculture, overgrazing and damming (Ash 1978; Massoli-Novelli 1986) give cause for great concern about the bird's prospects for survival in Ethiopia.

In South Africa the Whitewing Flufftail has been recorded only sporadically since its discovery in 1876, when three specimens were obtained from two localities (Table 8.1). Further single specimens were obtained in 1894 and 1901, whereafter there was a complete hiatus until the next specimen was obtained in the Transvaal in 1975 (Keith *et al.* 1970; Wolff & Milstein 1976). In their monograph on the genus Keith *et al.* (1970) found all sight records unacceptable but, in view of the distinctive appearance of this species in flight, sight records from reliable observers are now generally accepted (Collar & Stuart 1985; Hopkinson & Masterson 1977; Keith 1986); these include three records from the Cape Province and one from the Transvaal in 1955-56 (Table 8.2) and an old reference to the bird's occurrence in "the vleis about Durban", Natal (Stark & Sclater 1906). In October 1982 a small population was discovered at Franklin, Natal; one was collected and the birds were present intermittently until March 1983 (Mendelsohn *et al.* 1983; Table 8.2). Interest having been stimulated by this discovery, further searches revealed the bird's presence near Belfast, Transvaal, in late 1982 (Table 8.2). Most subsequent records are hitherto unpublished and fall in the period 1990-1992; they are reviewed in detail in Chapter 8, Section 8.4.1.

This species has never been found in large numbers in South Africa. Ayres (1877) found it very scarce and only 1-3 birds were recorded at any locality until 1982, when Mendelsohn *et al.* (1983) recorded a total of 35 birds flushed at Franklin Vlei in 1982-83; both they and other authors (Collar & Stuart 1985; Keith 1986) take this as an estimate of the total number present. However this estimate is based on the assumptions that individuals never flush more than once and that counts per visit may be totalled for the entire October-January occurrence period to give a population estimate (Mendelsohn *et al.* 1983). Such assumptions are obviously untenable and it is not possible to estimate

accurately a 1982-83 population at Franklin on the basis of the information published, as details of counts are inadequate. The best available estimates (Tables 8.2, 8.3) are the monthly totals given by the authors but these figures almost certainly include multiple counts of the same individuals. In view of the continual reduction of wetland habitats by damming, draining and grazing, the Whitewinged Flufftail is considered to have a precarious future in South Africa (Keith 1986; Mendelsohn *et al.* 1983).

In addition to the occurrences in South Africa and Ethiopia there are a few sight records from localities between these two centres of distribution. Near Harare, Zimbabwe, birds were seen in January-March 1977 and 1979, and one was seen in northwestern Zambia in November 1962 (Table 8.2). In the light of my knowledge of Zambian ornithology I prefer to regard as unsatisfactory a further sight record from Kitwe in February 1981 (Collar & Stuart 1985). In view of the presence of competent observers who have made extensive observations in suitable areas of these two countries since the early 1970s, it is probable that the Whitewinged Flufftail is a very rare and erratic visitor to such central African wetlands. The lack of records from Kenya, also a well known area ornithologically, suggests that the bird's regular occurrence there is very unlikely.

Although the lack of subspeciation between the Ethiopian and South African populations suggests that migration between the two areas might occur, the paucity of records from central and East Africa, and the August-September overlap of occurrences in South Africa and Ethiopia (Table 8.3), militate against this possibility (Collar & Stuart 1985). It is now generally assumed that the two populations are relict and largely unconnected, perhaps having been forced apart by competition from a congener such as the Streakybreasted Flufftail (Benson *et al.* 1970; Benson & Irwin 1971; Brooke 1984; Collar & Stuart 1985; Keith *et al.* 1970; Ripley 1977; Wolff & Milstein 1976) and that the Whitewinged Flufftail is a nomadic opportunist whose distribution never stabilizes but which undergoes periodic eruption and dispersal, sometimes over long distances if populations are high (Collar & Stuart 1985; Hopkinson & Masterson 1977). In this way gene-exchange could occur between the northern and southern populations.

In Ethiopia the Whitewinged Flufftail has been recorded at altitudes of 2 200-2 500 m a.s.l., with the exception of the Charada record at 1 130 m. The bird's altitudinal range in South Africa is wide, extending from 150 to 1 870 m a.s.l., but most recent records have been from the higher-altitude areas of Natal and the Transvaal, above 1 300 m a.s.l.

#### 1.2.4.3      Habitat

It is difficult to establish the habitat preferences of the Whitewing Flufftail by reference to published observations, as these differ considerably from one another. In the breeding areas of the Ethiopian highlands Guichard (1948) found the birds at Gafersa in a one-acre marsh with rushes and orchids growing in ankle-deep water and at Sululta in close grass clumps, partly submerged during the rains but dry later. At Sululta in 1984 one was flushed from flooded grass near a small river and landed in taller vegetation and reeds (R. Massoli-Novelli *in litt.*). In Zambia, Brooke (1964) found it at a "pan-like marsh" flying above marsh grass, while in Zimbabwe Hopkinson & Masterson (1977, 1984) saw the birds (a) in rank grass 1 m high alongside taller *Cyperus* in a soggy area, (b) in knee-high grass alongside a ditch in short grassland (the bird flew to dry fallow land), (c) on muddy wet ground in knee-high *Leersia* and *Hemarthria* grasses with taller *Cyperus digitatus*, and (d) in a small area (40 m x 70 m) of *Cynodon dactylon* grass in 5-15 cm of water with taller sedge and grass, bordering a clump of *Typha*.

South African records have come from (a) knee-high *Carex* on soft mud (Tarboton *et al.* 1987), (b) a strip of dense *Phragmites australis* on a stream in wet but not marshy ground (Wolff & Milstein 1976) and (c) at Franklin (Mendelsohn *et al.* 1983) usually wet but not flooded ground, in vegetation varying in height from tall *Phragmites* or *Typha* to sedges and water grass only 50 cm tall; the birds were apparently absent in November 1982 when the vlei was more flooded. At Franklin, Mendelsohn *et al.* (1983) obtained the impression that Whitewinged and Redchested Flufftails occurred "in pockets with little mixing of the two".

These records suggest a wide tolerance of vegetation types and heights with, in South Africa, a preference for moist but not flooded ground. Shallowly flooded habitats are, however, recorded from the other countries. Some of these habitat differences may possibly be explained by different habitat tolerances during and outside the breeding season, as exemplified by the varying vegetation types occupied by Redchested Flufftails at different times of the year (see Chapters 4-6). As there is no satisfactory evidence that the Whitewinged Flufftail breeds in any of the habitats described in published accounts from southern Africa (see Section 1.2.4.5), it is not clear whether these accounts refer essentially to breeding or non-breeding habitats.

#### 1.2.4.4      Behaviour, food and predation

As little is known about the behaviour of Whitewinged Flufftails as about that of Striped Flufftails (Section 1.2.3.3). In the breeding areas of Ethiopia the birds flew weakly and could be

caught by hand (Guichard 1948). Such behaviour may be simply the result of a reluctance to fly during the breeding season, the birds being extremely difficult to flush in July and August in Ethiopia (Moltoni & Gnechi Ruscone 1944), for elsewhere this species may show an unflufftail-like strong direct flight, remaining airborne for up to 200 m (Collar & Stuart 1985; Hopkinson & Masterson 1977; Mendelsohn *et al.* 1983). Millar, quoted by Stark & Sclater (1906), notes that the birds seen around Durban, Natal, were difficult to flush, made short flights and were seldom put up a second time. The birds are said to scramble to the reed tops before taking flight (Mendelsohn *et al.* 1983). Food is recorded only from the contents of two stomachs: water insects (Ayres 1877) and grain-seeds and vegetable mush (J.M. Mendelsohn *in* Collar & Stuart 1985). There are no recorded instances of predation.

#### **1.2.4.5      Voice**

On the basis of observations and sound recordings made at Franklin vlei in 1982-83, the call is given as a very deep *oooh oooh*, possibly a duet, by J.C. Sinclair in Keith (1986), and by Maclean (1993) and Mendelsohn *et al.* (1983). However J.C. Sinclair (pers. comm.) is not convinced that these recordings are of Whitewing Flufftails: the recordings were made in mist, the birds were not seen calling and they did not respond to playback of the calls. Other observers (G. Gibbon & T. Harris pers. comm.) have noted the great similarity between these recorded calls and the *oop* calls of the Crowned Crane *Balearica regulorum*, which was present in the same habitat at Franklin when the recordings were made. J.M. Mendelsohn (commentary on the tape held at the Fitzpatrick Bird Communications Library, Transvaal Museum) notes that there was no response to two hours of playback of these calls but gives as evidence that the sound came from Whitewing Flufftail, that a bird flew from "the precise spot" where the call had been heard. J.C. Sinclair (pers. comm.) also states that, when calls of several flufftail species were played from a hide at an observation track cut in the reeds, a male Whitewing Flufftail came out and looked at the hide, but not in response to the taped playback of the *oooh* calls. Thus the authenticity of the call is open to considerable doubt.

#### **1.2.4.6      Breeding**

The nest and eggs have not been described. In Ethiopia breeding was confirmed by the capture of a female with developing eggs on 18 July 1948 (Gajdacs & Keve 1968) and of a young bird, unable to fly, on 22 September 1948 (Guichard 1950). I have examined the latter, which is in the British Museum (Natural History) (Collection No. 1949.2.3) and, on the basis of flufftail chick

development patterns elucidated during this study, I estimate its age to be 15-20 days. Given an incubation period of approximately 15 days (this study) this bird was hatched from an egg laid in the second half of August.

There are no acceptable indications of breeding in South Africa. A record of an empty nest (not described) "associated with" Whitewing Flufftails found in December 1982 (Brooke 1984) is not convincing, especially as the locality must also have held breeding Redchested Flufftails at that time. A very brief sighting at Franklin on 6 January 1983 of two Whitewing Flufftails, described as small, partly grown, with stunted wings and apparently unable to fly far (Mendelsohn *et al.* 1983) has been taken to indicate breeding at Franklin by those authors and also by Collar & Stuart (1985) and Keith (1986). This record is unacceptable for several reasons. First, observations of chick development in other wetland flufftail species (Wintle 1988; this study) indicate that just-flying young would probably be at least 4-5 weeks old and this would indicate laying in the second half of November 1982, during which month the species was considered absent from Franklin due to high water levels (Mendelsohn *et al.* 1983). Second, the brief view obtained was almost certainly not sufficient to allow an accurate estimate of size to be obtained. Although nothing definite is known about this species' development it is highly unlikely that any flufftail of appreciably smaller than adult size would be able to fly: the young of three species (Redchested, Streakybreasted and Buffspotted Flufftails) appear from 80% to fully grown before the remiges develop sufficiently to permit flight (Wintle 1988; this study). Young Buffspotted Flufftails first fly at 19 days of age, when they have attained 75% of the mean adult mass and the wings are 80% grown (Chapter 9, Section 9.4.10.4.2). Redchested Flufftails begin to develop remiges only at 3-4 weeks of age (Liversidge 1968; Wintle 1988), and are able to fly when fully grown at 42 days (Wintle 1988), so the fact that Mendelsohn *et al.* (1983) recorded "several partly grown Redchested Flufftails [in December 1982] which were identifiable by their partly grown wings, small size and weak flight" suggests that their estimates of size and wing development were inaccurate. Third, weakness of flight in Whitewing Flufftails cannot be taken as indicative of young birds, as adults sometimes also fly weakly (Section 1.2.4.3).

As a final comment on possible breeding at Franklin, one should consider the observations of Mendelsohn *et al.* (1983) concerning the bird which they collected on 27 October 1982. This bird is in the Durban Museum (Collection No. 33901) and was identified as an adult female which showed no breeding activity (Mendelsohn *et al.* 1983). The specimen is, in fact, a full juvenile (from plumage descriptions in Keith 1986, and my observations during this study): it shows no trace of postjuvenile moult to rufous colouring on the head, neck or breast, it has dark blackish brown body plumage with small whitish spots on the upperparts (but tawny spots on the mantle) and whitish flecks on the breast, and the chin, throat and centre of the belly are white. I would estimate its age to be at least 7 weeks,

i.e. it would have hatched from an egg laid at the latest in August 1982, at which time neither the habitat nor the weather in the Franklin area would have been suitable for breeding.

#### **1.2.4.7        Movements**

It has already been noted (Section 1.2.4.1) that the Whitewing Flufftail is not thought to undertake regular long-distance migrations between its South African and Ethiopian centres of distribution, but is considered to be nomadic, undergoing periodic eruptions. Birds arrive on the Ethiopian breeding grounds in June and July, these highland areas being dry and extensively grazed by cattle in April-May, and migration is thought to be local, from the western Ethiopian swamps which provided the May Charada specimen (Guichard 1948). In South Africa the only record outside the August-March period (the May Rustenburg sight record) was noted as being within easy reach of highveld pans (Wolff & Milstein 1976). Both Brooke (1984) and Keith (1986) suggest that local movements occur in South Africa, Keith citing the temporary absence of birds from Franklin in November 1982 (when water levels were high) as evidence of this. The August Suikerbosrand specimen was found dead on a track through a vlei below a power line 8 m overhead, into which it was presumed to have flown during darkness or poor light (Wolff & Milstein 1976); this is also possibly indicative of movements.

### **1.3        Aims of the study**

The primary aims of this study fall into two groups: those directly related to the conservation of rare flufftail species and their habitats, and those involving the elucidation of those aspects of the fundamental biology and ecology of flufftails which are essential prerequisites to a thorough understanding of the relationships between these birds and their environment.

#### **1.3.1        Overall conservation objectives**

Almost half of the rare or threatened bird species in South Africa inhabit grasslands, wetlands or waterbodies (Brooke 1984). This suggests that such habitats have been subjected to greater ecological stresses than has commonly been realized, and it is clear that the biomes most in need of ecological study and conservation in South Africa are grasslands, marshes and estuaries (Brooke 1984). A primary aim of this study was to investigate the effect of human activities on the grassland and wetland habitats which support both rare and common flufftail species, in terms of the effects on the birds of habitat modifications caused by burning, mowing, grazing and trampling by domestic

stock. After establishing the precise habitat requirements of the study species (see Section 1.3.2) I intended to investigate the extent of suitable habitats for the two rare species (at least in Natal), to assess the threats to such habitats, and to formulate proposals for the conservation and management of important areas. A further objective was to investigate the difficulties involved in keeping and breeding flufftails in captivity, and to assess the practicability of future captive-breeding programmes for the rare and endangered species.

### **1.3.2 General research objectives**

Very little is known of the behaviour, breeding and ecology of most rallids in Africa (Taylor 1987) and, as a result, threats to the survival of many species, including all the flufftails, cannot be evaluated. Detailed studies of the genus *Sarothrura* are urgently needed, both in forest and in wetland, to establish the basic facts about these birds' biology and ecology and to plan their conservation (Brooke 1984; Collar & Stuart 1985). This study addresses this problem and also falls within the important area of studies in ecosystem structure and functioning which are recommended research priorities for wetlands (Begg 1986).

Although flufftails are notoriously difficult to observe, suitable field-study techniques for this project were developed during my previous work on these and other rallids in Africa (references reviewed in Section 1.1 and Chapter 3, Section 3.1). My original intention was to investigate the biology and ecology only of the three South African flufftails which occur in grassland and wetland, concentrating on the Whitewing Flufftail which is one of the rarest and most poorly known birds in Africa (Section 1.2.4). However the unpredictability of this bird's occurrence, and the very great practical difficulties involved in its observation (Chapter 8, Section 8.3), meant that its detailed study was not possible within the limits of time and finance. After initial investigations I therefore decided to include studies of the biology and ecology of the more common and accessible Buffspotted Flufftail because, in the time available, these would yield much information relevant to an understanding of the general biology and behaviour of the genus, especially with regard to breeding and migratory movements.

The principal research aims of this study are as follows:

- (a) to establish the distribution, status and habitat requirements of all four species, and to establish the extent to which the birds can tolerate seasonal and man-induced habitat changes;
- (b) to investigate ecological relationships between all the species, particularly the two wetland species (Redchested and Whitewing Flufftails);

- (c) to investigate the occurrence and extent of seasonal movements in all species, and the environmental factors influencing such movements;
- (d) to study the general biology of the four species, including their food, foraging methods, behaviour, vocalizations, breeding, predation and mortality;
- (e) to study territorial and aggressive behaviour, and the seasonal variations in such behaviour, and to make comparative studies of the behaviour of other rallid species occupying the same habitats;
- (f) in the two common species (Redchested and Buffspotted Flufftails) to investigate heterosexual behaviour, factors influencing breeding timing and success, parent-chick relationships, age of independence and juvenile dispersal;
- (g) to make life-history comparisons between the study species, particularly in terms of the effects of different environments on mating systems, reproductive strategies and movement patterns.

As work on the two common species progressed, it became clear that certain aspects were of particular interest and deserving of more detailed study, and efforts were made to concentrate on these aspects. In the Redchested Flufftail they included the effects of habitat type on territory size, the ways in which these essentially sedentary and permanently territorial birds respond to seasonal changes in habitat availability, and the factors influencing the timing of their return to burned vegetation. In the Buffspotted Flufftail, differences in periods of occurrence and migratory status at different study sites were particularly interesting, as were the overall movement patterns of the species in Natal and the birds' successful adaptation to alien vegetation types and the proximity of human habitation.

## CHAPTER 2

### SURVEY AREAS AND STUDY SITES

#### 2.1 Introduction and survey areas

Because travelling was limited by the time and resources available, surveys of potentially suitable habitat for the study species in Natal were confined mainly to the area south of a line drawn between points at 28°30'S 29°00'E and 29°15'S 31°30'E (Fig. 2.1). This region, hereafter referred to as the "survey area", was chosen because it includes most of the land in Natal above 1 500 m (Fig. 2.2) and contains more than half of Natal's sourveld (Fig. 2.3), this combination of features rendering it potentially more suitable than the northern half of Natal for the rare Striped and Whitewing Flufftails whose known distribution in Natal is restricted to the survey area (Brooke 1984; Cyrus & Robson 1980; Keith *et al.* 1970; Chapter 7, Tables 7.2 and 7.3; Chapter 1, Sections 1.2.3.1 and 1.2.4.1). It also includes the majority of the quarter-degree squares from which the two commoner species, Redchested and Buffspotted Flufftails, were recorded by Cyrus & Robson (1980) and it was therefore deemed more suitable for detailed investigation of these species' habitat preferences.

The 11 long-term study sites in Natal were located in the survey area and are described in Section 2.2. Two sites had populations of Striped Flufftail, two Whitewing Flufftail, seven Redchested Flufftail and five Buffspotted Flufftail; studies of more than one species were made at some sites.

Apart from a small number of visits to Natal coastal habitats north of the survey area, all other surveys and studies were done at wetlands in three areas: near Wakkerstroom and Belfast in eastern Transvaal and in the Bromley-Marondera area of northern Zimbabwe. Further details of these areas are given in Section 2.2 and in the relevant sections on the habitats of Redchested and Whitewing Flufftails (Chapters 4 and 8).

#### 2.2 The study sites: location, topography, vegetation, climate and management

The 14 long-term study sites are listed in north-south order, irrespective of their vegetation types and the species studied at them.



**Fig. 2.1** Natal and KwaZulu showing quarter-degree squares, grid references and place names referred to in the text. Game parks and nature reserves are represented by open circles. The line from 28°30'S 29°00'E to 29°15'S 31°30'E marks the northern limit of the Natal survey area.

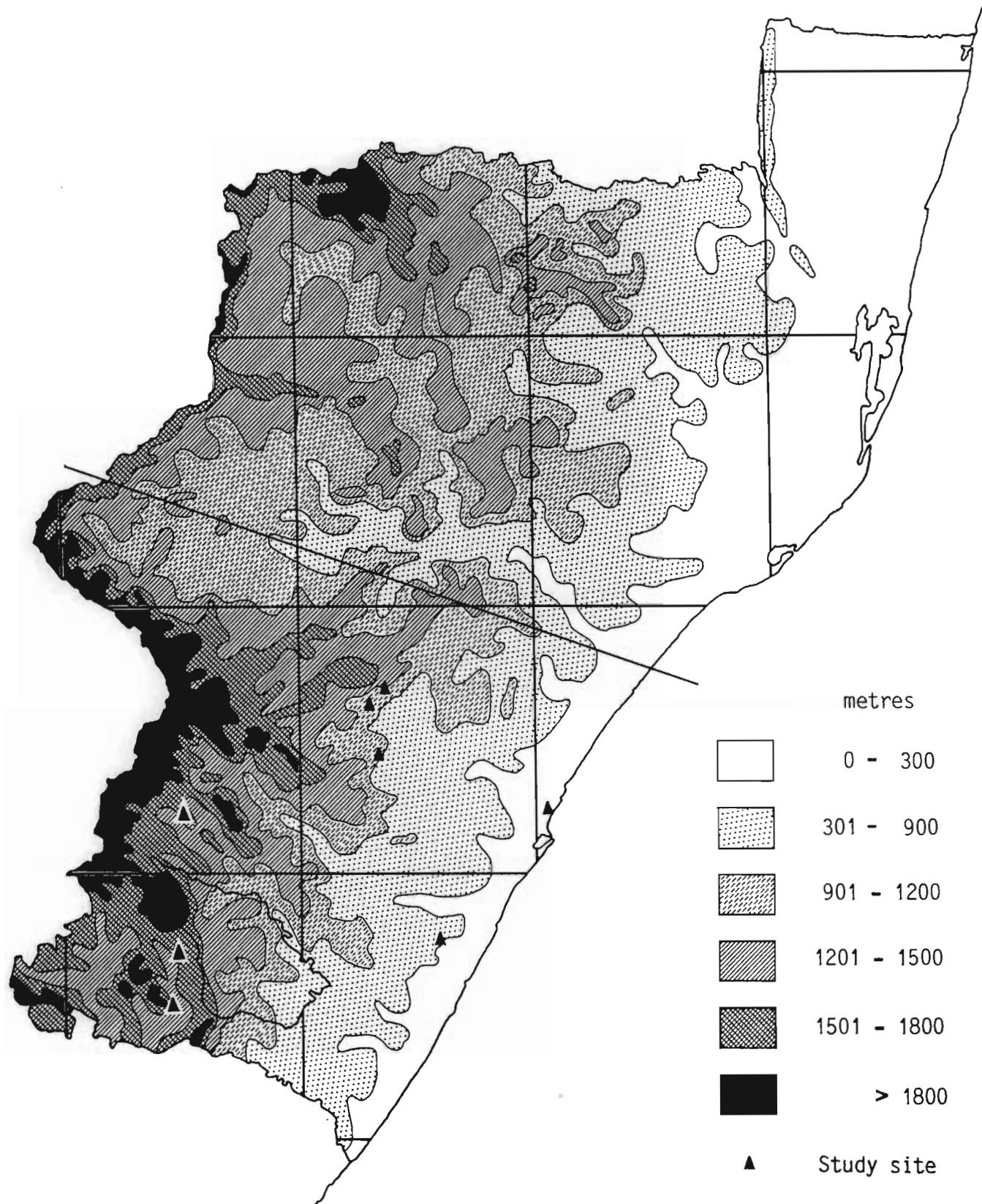


Fig. 2.2

Natal and KwaZulu: altitude. Source: Cyrus & Robson (1980).

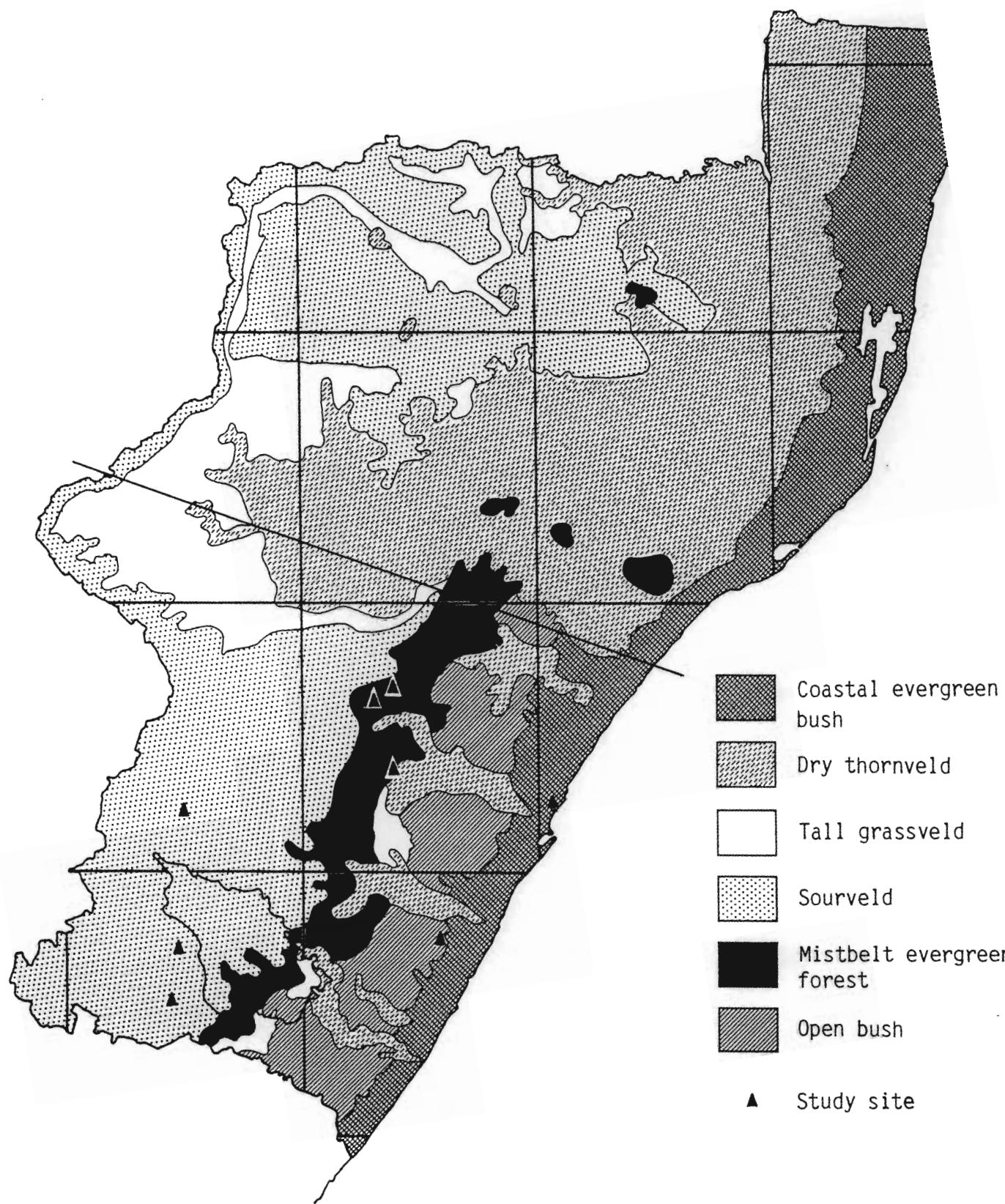


Fig. 2.3

Natal and KwaZulu: vegetation. Source: Cyrus & Robson (1980).

## 2.2.1           Bromley, Zimbabwe

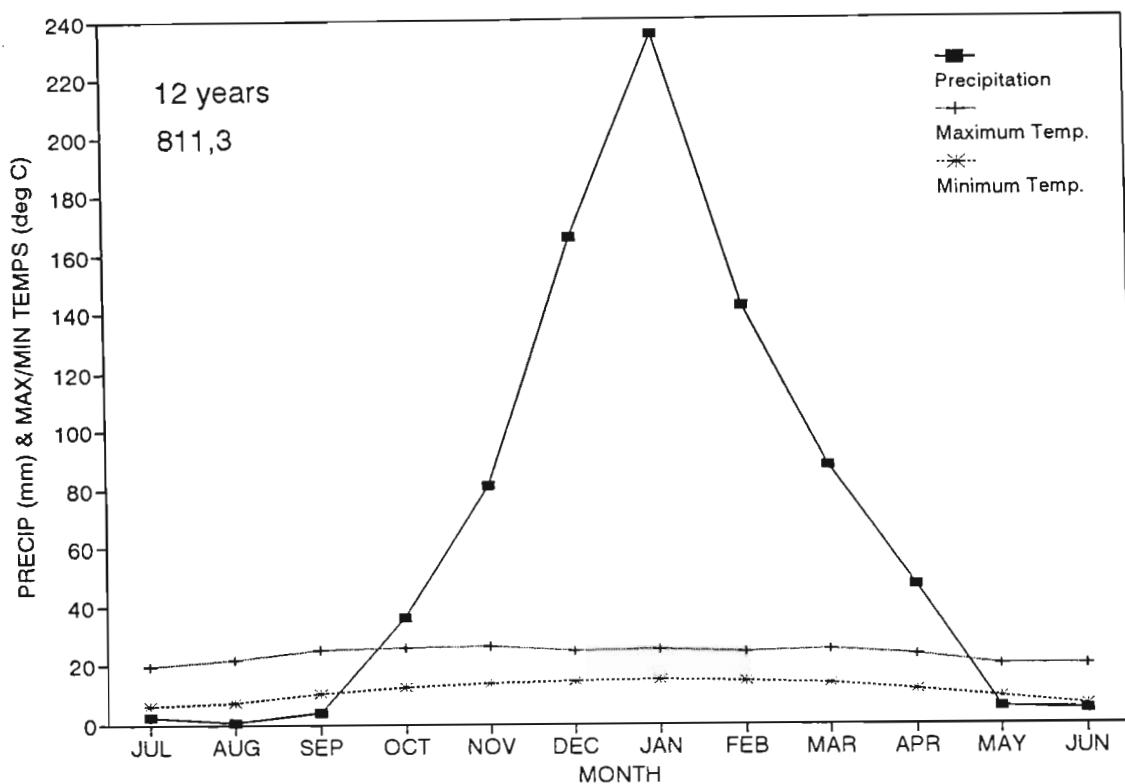
The study area lies on the central plateau of Zimbabwe at about 1 465 m a.s.l. Most ralid studies were made on captive birds in the aviaries established by C.C. Wintle on Chinyeka Farm, Bromley (18°45'S 31°30'E) (Wintle & Taylor 1993), but during visits in July 1990, November 1991 and April 1992, I also made observations on a population of Redchested Flufftails at a permanent stream running through light *Brachystegia* (Miombo) woodland on a nearby farm. This study site runs from the outflow of a holding dam along the drainage line for 500 m until the banks become too steep to permit the existence of muddy areas and associated wetland vegetation along the stream. For most of this distance the substrate is black hydromorphic soil on flat ground up to 40 m in width, through which the stream runs. A perennial spring feeds the stream and, although water flow is reduced in the dry season, much of the black soil remains saturated to flooded all year and supports a thriving wetland flora.

### 2.2.1.1       Climate and weather

Mean monthly maximum and minimum teperatures were obtained from Marondera Research Station (18°11'S 31°28'E, 1 631 m a.s.l.) for the 11 years from July 1980 to June 1991. Monthly rainfall data for July 1981 to June 1993 were obtained from Liemba Farm (18°45'S 31°28'E, 1 550 m a.s.l.). The climate of the area is subtropical, the hottest period of the year being September-November (Fig. 2.4 & Table 2.2) and most rain falling from October to April (Fig. 2.4 & Table 2.1); annual precipitation averages 811,3 mm at Liemba Farm. The period May-July is cool and dry, with occasional light frosts (Irwin 1981). In the most severe drought period (July 1991-June 1992) the total precipitation was only 462 mm, 57% of the annual mean total.

### 2.2.1.2       Vegetation

Along the course of the study stream dense beds of *Typha capensis* and *Phragmites australis* predominate, the latter in the most deeply flooded areas. Elsewhere, on permanently saturated to shallowly flooded ground, *Carex cognata* dominates over large areas, *Fuirena stricta*, *Pycreus unioloides*, *Schoenoplectus brachyceras* and the fern *Cyclosorus confluens* being locally common. In peripheral less saturated areas shorter sedges occur, species recorded being *Pycreus mundii* (dominant), *Cyperus esculentus*, *Fimbristylis dichotoma*, *Juncus* spp., *Kyllinga melanopsperma*, *Pycreus albomarginatus*, *P. flavescens*, *P. pelophilus* and *Schoenoplectus muriculatus*. In the drought



**Fig. 2.4** Bromley, Zimbabwe: mean monthly precipitation (mm) and maximum and minimum temperatures ( $^{\circ}\text{C}$ ), July-June. The number of years of precipitation records, and the mean annual precipitation, are shown.

TABLE 2.1

Long term means of monthly and total annual precipitation (mm) for some study sites. All periods run to December 1992 unless otherwise stated (see text for explanation). Sites are listed in north-south order.

<b>Study site</b>	<b>Jan</b>	<b>Feb</b>	<b>Mar</b>	<b>Apr</b>	<b>May</b>	<b>Jun</b>	<b>Jul</b>	<b>Aug</b>	<b>Sep</b>	<b>Oct</b>	<b>Nov</b>	<b>Dec</b>	<b>Total</b>	<b>Yrs</b>
Bromley	234,8	142,2	87,8	46,8	5,5	4,7	2,4	0,7	4,0	36,1	81,0	165,3	811,3	12 <sup>1</sup>
Dulstroom	110,1	85,8	69,2	68,5	16,4	9,8	8,0	10,6	25,6	107,7	137,7	148,9	797,8	12 <sup>2</sup>
Wakkerstroom	161,5	104,9	65,8	46,2	13,0	6,5	5,0	16,7	28,5	79,5	116,2	101,2	745,0	17 <sup>3</sup>
<hr/>														
Gartmore	179,9	166,5	130,6	61,1	21,8	11,7	13,7	33,8	75,7	92,8	128,0	166,2	1081,8	23
Ferncliffe	198,1	186,1	175,6	52,6	21,5	21,0	16,9	42,0	104,5	157,3	167,5	184,1	1327,2	11
Allerton	182,7	131,9	125,6	53,9	27,5	12,2	14,6	30,5	50,9	102,3	132,9	134,8	999,8	42
Bisley Valley	110,5	94,2	87,5	44,9	24,6	9,6	9,7	28,1	48,6	62,0	86,6	93,7	700,0	39
Danville	134,5	128,1	118,7	78,7	64,6	34,7	30,2	49,1	69,4	96,6	122,4	113,1	1040,1	59
Underberg	152,1	152,2	123,0	51,7	19,9	11,8	10,2	23,0	36,7	69,6	104,0	136,1	890,3	51
Vernon Crookes	99,6	111,2	118,8	52,9	60,1	17,8	26,2	51,2	93,6	102,2	122,8	119,8	976,2	25
Franklin	106,8	112,1	81,2	35,9	9,9	7,6	9,6	16,8	30,4	54,7	89,6	89,0	663,3	23 <sup>4</sup>
Mount Currie	126,7	123,9	99,3	46,9	22,7	14,9	12,0	20,1	38,9	67,1	97,4	108,0	777,9	60

<sup>1</sup> = July 1981 - June 1993; <sup>2</sup> = 1960-1971; <sup>3</sup> = 1961-1982; <sup>4</sup> = 1968-1990.

TABLE 2.2

Long-term monthly means of maximum (Max<sub>t</sub>) and minimum (Min<sub>t</sub>) temperatures (°C) for some study sites. All periods run to December 1992 unless otherwise stated (see text for explanation). Sites are listed in north-south order. No figures are available for the Dullstroom, Wakkerstroom, Franklin, Gartmore and Allerton study sites.

Study site		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Yrs
Bromley	Max <sub>t</sub> :	24.9	24.3	24.9	23.5	19.8	19.9	19.7	21.8	25.1	25.7	26.2	24.6	11 <sup>1</sup>
	Min <sub>t</sub> :	14.9	14.7	13.7	11.7	9.0	6.5	6.1	7.2	10.3	12.3	13.8	14.7	
Ferncliffe	Max <sub>t</sub> :	25.4	25.1	24.6	22.6	19.8	16.5	17.0	19.1	21.0	21.8	23.2	25.0	11
	Min <sub>t</sub> :	16.3	16.3	15.5	13.5	10.8	8.3	8.2	9.6	11.0	12.3	13.3	14.6	
Bisley Valley	Max <sub>t</sub> :	26.0	26.2	26.0	24.3	22.5	20.5	20.9	22.0	23.3	23.6	23.6	25.6	34
	Min <sub>t</sub> :	16.5	16.8	15.9	13.7	11.0	9.0	8.8	10.0	11.6	12.6	14.2	15.6	
Danville	Max <sub>t</sub> :	27.2	27.3	26.8	25.5	24.0	22.5	22.1	22.3	22.9	23.7	24.8	26.5	27
	Min <sub>t</sub> :	20.3	20.3	19.3	16.8	13.9	11.2	10.9	12.2	14.5	16.0	17.5	19.3	
Underberg	Max <sub>t</sub> :	25.0	24.6	23.5	21.1	19.2	17.3	18.8	20.3	22.0	22.0	23.1	24.6	41
	Min <sub>t</sub> :	13.1	13.1	11.6	8.3	4.4	1.0	1.2	3.7	6.8	8.8	10.5	12.1	
Vernon Crookes	Max <sub>t</sub> :	27.2	27.3	27.1	26.1	24.5	23.0	22.9	23.0	23.2	23.7	24.8	26.4	25
	Min <sub>t</sub> :	19.3	19.3	18.3	15.4	11.7	8.6	8.5	10.1	12.9	14.6	16.1	18.0	
Mount Currie	Max <sub>t</sub> :	25.7	25.2	24.2	22.3	20.0	17.7	18.2	19.6	21.5	22.4	23.4	25.0	25
	Min <sub>t</sub> :	12.7	12.5	11.1	7.7	4.1	0.9	0.7	2.8	5.9	8.1	9.8	11.5	

<sup>1</sup> = July 1980 - June 1991.

years of 1991-92 about 50% of the wetland dried out and by April 1992 the most significant change in the vegetation was the decrease of *Carex cognata* and its replacement in newly dry areas by *Schoenoplectus* spp. and forbs such as *Polygonum* sp. and the tall willowherb *Epilobium hirsutum*.

### **2.2.1.3      Use and management**

The wetland is fenced off so that cattle are largely excluded, and burning is patchy and occasional, so the wetland vegetation suffers relatively little disturbance or modification.

## **2.2.2      Dullstroom, near Belfast, Transvaal**

The study site at Dullstroom ( $25^{\circ}30'S$   $30^{\circ}07'E$ ) is on farmland at 1 870 m a.s.l. and comprises a wetland about 17 ha in extent, part of the extensive Lakenvleispruit vlei system. The vlei has been extensively modified by human activity: two ditches have been dug along its entire length to increase drainage and cattle graze it regularly. Between February 1990 and October 1992 the study site was visited regularly to investigate the seasonal occurrence of Whitewing Flufftails in the vlei.

### **2.2.2.1      Climate and weather**

There are no detailed weather records for the site, the nearest meteorological station being about 16 km to the southwest, near Belfast (Table 2.3). Only historical precipitation figures are available and the long-term mean monthly values are given in Table 2.1. Most rain falls from October to April (Fig. 2.5) and the mean annual precipitation is 797,8 mm. The climate is probably similar to that at Wakkerstroom (Section 2.2.3.1), summers being mild and winters cold to very cold with frosts (sometimes severe) from May to October.

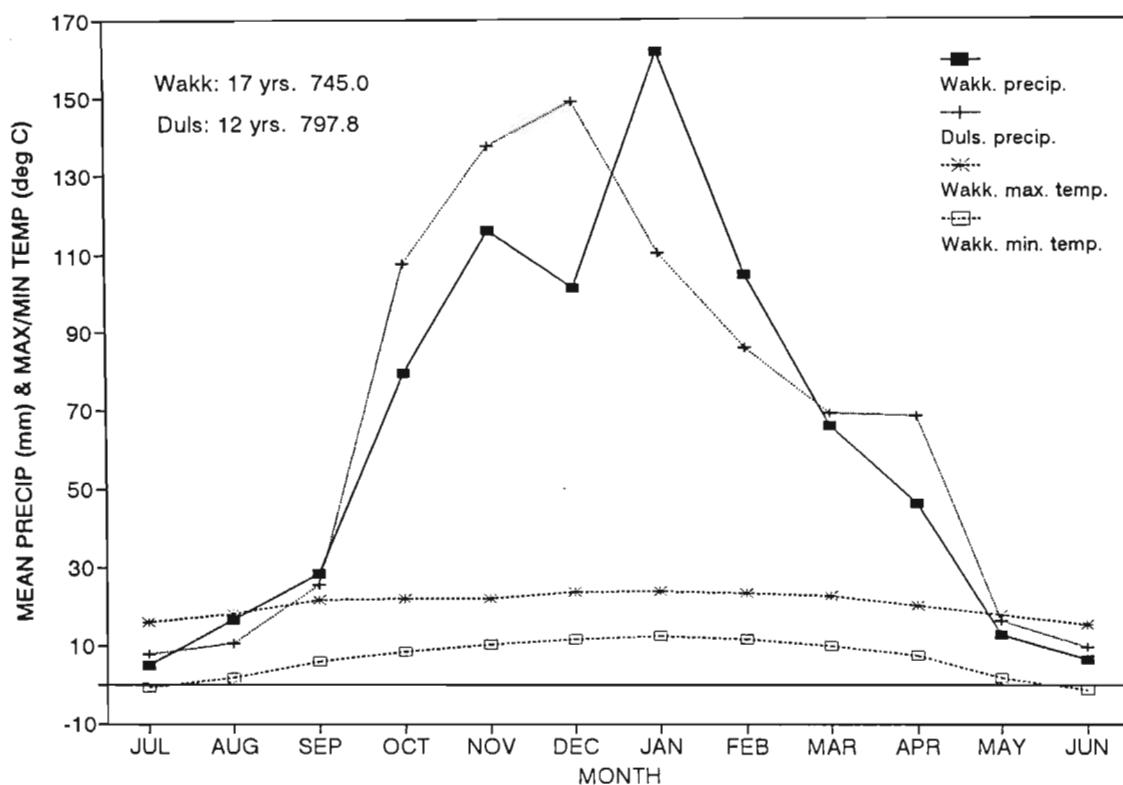
### **2.2.2.2      Vegetation**

The wetland is surrounded by grazing land of Veld Type 57, North-Eastern Sandy Highveld (Acocks 1988). As a result of the artificial drainage, the area of permanently saturated or flooded wetland has been reduced to the central portion of the vlei. In this area the dominant vegetation is *Phragmites australis*, which extends into the periodically saturated/flooded ground, where it forms a mosaic with *Typha capensis* and *Carex* sp. (almost certainly *C. acutiformis*, although no flowering

TABLE 2.3

Sources of meteorological data for study sites. Sites are listed in north-south order. Agric. Coll. = Agricultural College; C.C.W.R. = Computer Centre for Water Research (University of Natal); Met. = Meteorological; Res. = Research; R.S. = Research Station; W.W. = Waterworks. Data types: P = precipitation; T = temperature.

Study site	Meteorological data site	Co-ordinates	Alt (m)	Data type	Source
Bromley	Marondera R.S.	18°45'S 31°30'E	1 465		
		18°11'S 31°28'E	1 631	T	Harare Met. Office
	Liamba Farm	18°45'S 31°28'E	1 550	P	C.C. Wintle
Dullstroom	Belfast	25°30'S 30°07'E	1 870		
		25°39'S 30°00'E	1 889	P	C.C.W.R.
Wakkerstroom	Biki Baia	27°22'S 30°07'E	1 740		
		27°21'S 30°09'E	1 810	P,T	C.C.W.R.
<hr/>					
Gartmore	Loskop Farm	29°21'S 30°16'E	1 080		
		29°22'S 30°15'E	1 110	P	C. Mackenzie
Ferncliffe	D.V. Harris W.W.	29°33'S 30°21'E	1 010		
		29°33'S 30°20'E	990	P,T	D.V. Harris W.W.
Allerton	Allerton Farm	29°34'S 30°21'E	703		
		29°34'S 30°21'E	710	P	Allerton Res. Lab.
Bisley Valley	Ukulinga Res. Farm	29°40'S 30°24'E	710		
		29°40'S 30°24'E	775	P,T	Ukulinga Res. Farm
Danville	Mt Edgecombe R.S. Durban Botanic Gardens	29°46'S 31°03'E	15		
		29°42'S 31°02'E	104	T	Mt Edgecombe R.S.
		29°51'S 31°00'E	91	P	Municipality
Underberg	Banavie Farm	29°48'S 29°29'E	1 500		
		29°52'S 29°31'E	1 524	P,T	H. Briscoe
Vernon Crookes	Esperanza Sugar Estate	30°17'S 30°36'E	320		
		30°19'S 30°38'E	195	P,T	Mt Edgecombe R.S.
Franklin	Franklin (Police)	30°19'S 29°28'E	1 510		
		30°19'S 29°27'E	1 524	P	C.C.W.R.
Mt Currie	Kokstad Agric. R.S.	30°30'S 29°24'E	1 420		
		30°31'S 29°25'E	1 372	P,T	Cedara Agric. Coll.



**Fig. 2.5** Wakkerstroom and Dullstroom, Transvaal: mean monthly precipitation (mm) for both sites, and maximum and minimum temperatures (°C) for Wakkerstroom only, July-June. The number of years of precipitation records, and the mean annual precipitation, are shown.

or seeding examples have been collected). In some areas, particularly at the northeastern end of the vlei, the *Carex* forms a very dense uniform cover with no other species present (as it also does at Mt Currie and Franklin). In the less frequently saturated or flooded areas a sedge-marsh mosaic of species occurs, including the three species already mentioned, plus *Carex cognata* (sparse), *Cyperus denudatus* and *C. fastigiatus* (co-dominant), *Juncus oxycarpus*, *Pycreus nitidus* and *P. unioloides* (occasional) and *Schoenoplectus corymbosus* (common). Towards the edge of the vlei the vegetation grades to seasonally moist short sedges and hygrophilous grassland, a dominant species here being the sedge *Fuirena pubescens*.

#### **2.2.2.3      Use and management**

Apart from the ditching and regular grazing already mentioned, the vlei is also subjected to burns, usually of the entire wetland, which occur frequently though not every year. On two occasions since early 1991 I have seen considerable damage done to the wetland vegetation by birdwatchers who trample the sedge beds while searching for the rare Whitewing Flufftail. This has not only disturbed this species (see Chapter 8), but must also have affected the breeding of other wetland birds, particularly the Redchested Flufftail, and it is clear that such disturbance is greatly detrimental and should be controlled (Chapter 8).

#### **2.2.3      Wakkerstroom Vlei, Transvaal**

Wakkerstroom Vlei ( $27^{\circ}22'S$   $30^{\circ}07'E$ ) lies immediately adjacent to the village of Wakkerstroom in the southern Transvaal, the main body of the vlei being within the Transvaal but its outlet being just inside the Natal border (Begg 1989). The vlei is 9 km long, 950 ha in extent and its central area lies at about 1 740 m a.s.l. It is crossed by the Volksrust-Wakkerstroom Road near its centre. Its hydrology is reviewed by Begg (1989) and a detailed account of its vegetation, current and past use, and significance is given by Kotze (1992b). It is regarded as a priority wetland, occupying a key position in the Tugela River catchment: it is considered to have high water-purification and stream-flow-regulation values, and the variety of downstream users dependent on assured yields of good quality water make it a wetland of regional significance (Begg 1989; Kotze 1992b).

Between February 1992 and January 1993 I visited Wakkerstroom three times to investigate the seasonal occurrence of Whitewinged Flufftails in the vlei.

### **2.2.3.1 Climate and weather**

The vlei lies within Bioclimatic Subregion 4g and experiences mild summers and cool to very cold winters with severe frost and some snowfalls, as well as a high lightning frequency (Begg 1989; Kotze 1992b; Phillips 1973). Weather records from Wakkerstroom (Table 2.1 & Fig. 2.5) give a mean annual precipitation of 745 mm, most rain falling from October to April.

### **2.2.3.2 Vegetation**

Six principal vegetation types were identified in the vlei by Kotze (1992b), the wettest areas being dominated by *Phragmites australis* or *Carex acutiformis*, or a mixture of both. Kotze (1992b) found the most widespread vegetation type to be "sedge/bulrush marsh", on permanently flooded to periodically saturated ground, dominant species being *Typha capensis* and the sedges *Cyperus fastigiatus*, *Eleocharis* spp. and *Schoenoplectus corymbosus*; this grades into sedge meadow (with *Andropogon appendiculatus*, *Eleocharis* spp., *Pycreus macranthus* and *Kyllinga erecta*) and then into hygrophilous grassland as the ground becomes less permanently saturated. My own observations indicate that, in the area immediately south of the Wakkerstroom-Volksrust Road, *Carex acutiformis* marsh and sedge/bulrush marsh intergrade over a wide area, *Carex* often being dominant in the wetter parts of the latter vegetation type, while the hygrophilous grass *Leersia hexandra* is an equally common to dominant constituent species of this region. A large *Polygonum* species is widespread here and scattered patches of sparse *Phragmites* also occur. A line transect of 1 440 m was walked south from the road through the *Carex*/sedge/bulrush marsh on 14 February 1992, keeping about 30 m from the belt of tall *Phragmites* along the vlei centre, and the relative abundance of the principal plant species is shown in Table 2.4. It is clear that *Carex* and *Leersia* are much more widely dominant (both individually and as co-dominants) than any other species, the other large sedges and the bulrush being frequent but rarely fully dominant.

### **2.2.3.3 Use and management**

Almost the entire vlei is owned by Wakkerstroom Municipality and most of the main body of the wetland is commonage, while some parts are leased to farmers. From July 1991 the Wakkerstroom Natural Heritage Association leased 650 ha of the vlei and intend to apply certain restrictions (by mutual agreement) with users of this land in order to improve the wetland's value for birds (Kotze 1992b). Much of the vlei is bordered by grazing land and all the wetland vegetation

TABLE 2.4

Relative abundance of dominant and co-dominant vegetation types on a transect through sedge marsh at Wakkerstroom vlei, 14 February 1992. All substrates were permanently to semi-permanently saturated/flooded. + = co-dominant; *Ca* = *Carex acutiformis*; *Lh* = *Leersia hexandra*; *Sc* = *Schoenoplectus corymbosus*; *Tc* = *Typha capensis*; *Cf* = *Cyperus fastigiatus*.

Vegetation type:	<i>Ca</i>	<i>Lh</i>	<i>Cf</i>	<i>Sc</i>	<i>Tc</i>	<i>Ca+</i> <i>Lh</i>	<i>Ca+</i> <i>Tc</i>	<i>Lh+</i> <i>Sc</i>	<i>Lh+</i> <i>Cf</i>	<i>3 of</i> <i>Ca/Lh/Sc/Cf</i>	Total
Extent of dominance along transect (m):	204	221	23	0	23	473	92	70	80	214	1 400 m
Extent of dominance along transect (%):	14,6	15,8	1,6	0	1,6	33,8	6,6	5,0	5,7	15,3	100%
% of transect along which individual species were dominant or co-dominant:	69,8	70,7	14,4	18,7	8,2						

types are grazed by cattle, while the hygrophilous grassland and (in very dry years) the marsh are extensively cut for hay, and the vlei is burned almost every year (Kotze 1992b).

#### **2.2.4 Karkloof Forest, near Howick, Natal**

The Karkloof Forest lies north of Howick between 29°17'S 30°09'E and 29°14'S 30°28'E and covers an estimated area of 6 000 ha, comprising a number of forest patches mainly restricted to the steep south- and east-facing slopes of the Karkloof Range and varying in altitude from 800 to 1 700 m a.s.l. (Wirminghaus 1990). The study site is at 1 260 m a.s.l. on the farm "The Forest" (29°19'S 30°21'E), in the southeast of the Karkloof Forest on the lower south-facing slopes of Mboma Mountain. Intensive behavioural studies of Buffspotted Flufftail were made at this site from October 1988 to November 1990, when the area was abandoned in favour of the more productive sites for this species at Underberg and Durban.

##### **2.2.4.1 Climate and weather**

No detailed precipitation and temperature measurements are available for the site but the climate is mild, with summer temperatures up to about 32°C, an occasional light frost in the period June-September and hot dry berg winds in August (P. Burdon pers. comm.). The Karkloof Forest receives a mean annual rainfall of about 1 600 mm (Wirminghaus 1990) and, lying within Bioclimatic Subregion 3a (Mist Belt Forest and Thicket), the area experiences no severe climatic conditions (Phillips 1973).

##### **2.2.4.2 Vegetation**

The study site comprises somewhat modified forest on sloping ground with small streams, surrounded by wattle, pine and gum plantations. A detailed checklist of the Karkloof Forest's vegetation is given by Wirminghaus (1990) and the study site contains no species unusual to the area. Common trees include *Calodendrum capense*, *Celtis africana*, *Clausena anisata*, *Combretum kraussii*, *Halleria lucida*, *Maytenus mossambicensis*, *Podocarpus latifolius*, *Rhus chirindensis*, *Xymalos monospora* and *Zanthoxylum davyi*, while *Dracaena hookeriana* and *Piper capense* are frequent in the understorey and the alien *Solanum mauritianum* is common at forest edges. The tree-fern *Cyathea dregei* also occurs. Much of the ground under forest trees at the study site has been planted with

*Clivia miniata*, which provides extensive cover. Stands of introduced bamboos (not identified) also occur.

#### 2.2.4.3 Management

Apart from the planting of *Clivia* for ornamental purposes, the forest at the study site is left undisturbed. Periodically, alien woody plants are cleared from forest margins, and attempts are being made to eliminate the alien bamboos.

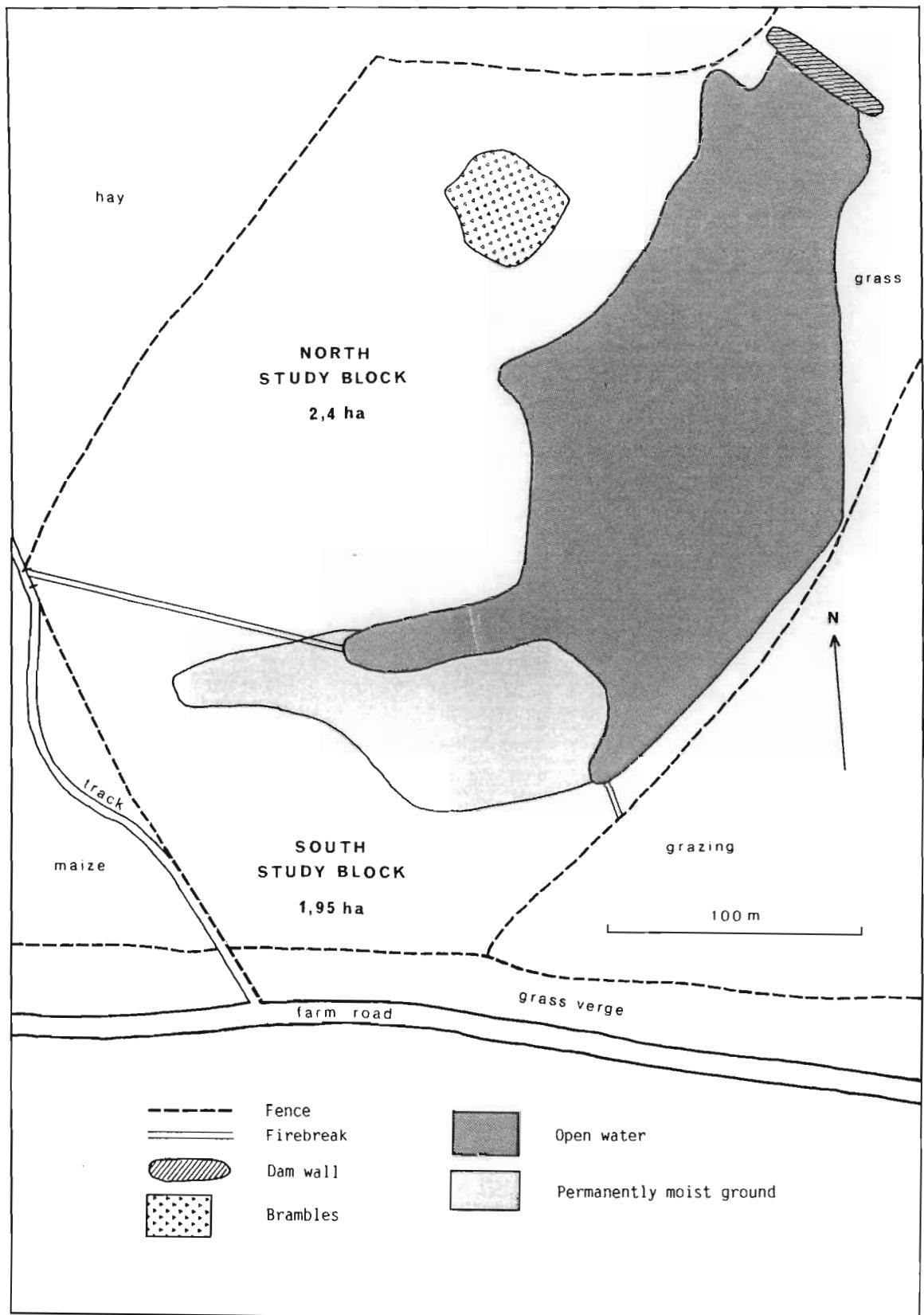
#### 2.2.5 Gartmore Farm, Karkloof Valley, Howick, Natal

This study site is located at 29°21'S 30°16'E on Gartmore Farm, about 18 km north-northeast of Howick. It comprises a patch of wetland and seasonally flooded grassland 4,35 ha in extent, adjacent to a shallow dam (Fig. 2.6). The site is on the floor of the Karkloof Valley at 1 080 m a.s.l. and is surrounded by grazing land, hay fields and maize cultivation. The extent and duration of seasonal flooding depend upon rainfall and evaporation, the dam not being used for irrigation, and during the study period at least 10% of the study site remained saturated throughout the winter, principally the ground adjacent to the southwestern end of the dam (Fig. 2.6). During the summer the entire study site was often moist or shallowly flooded.

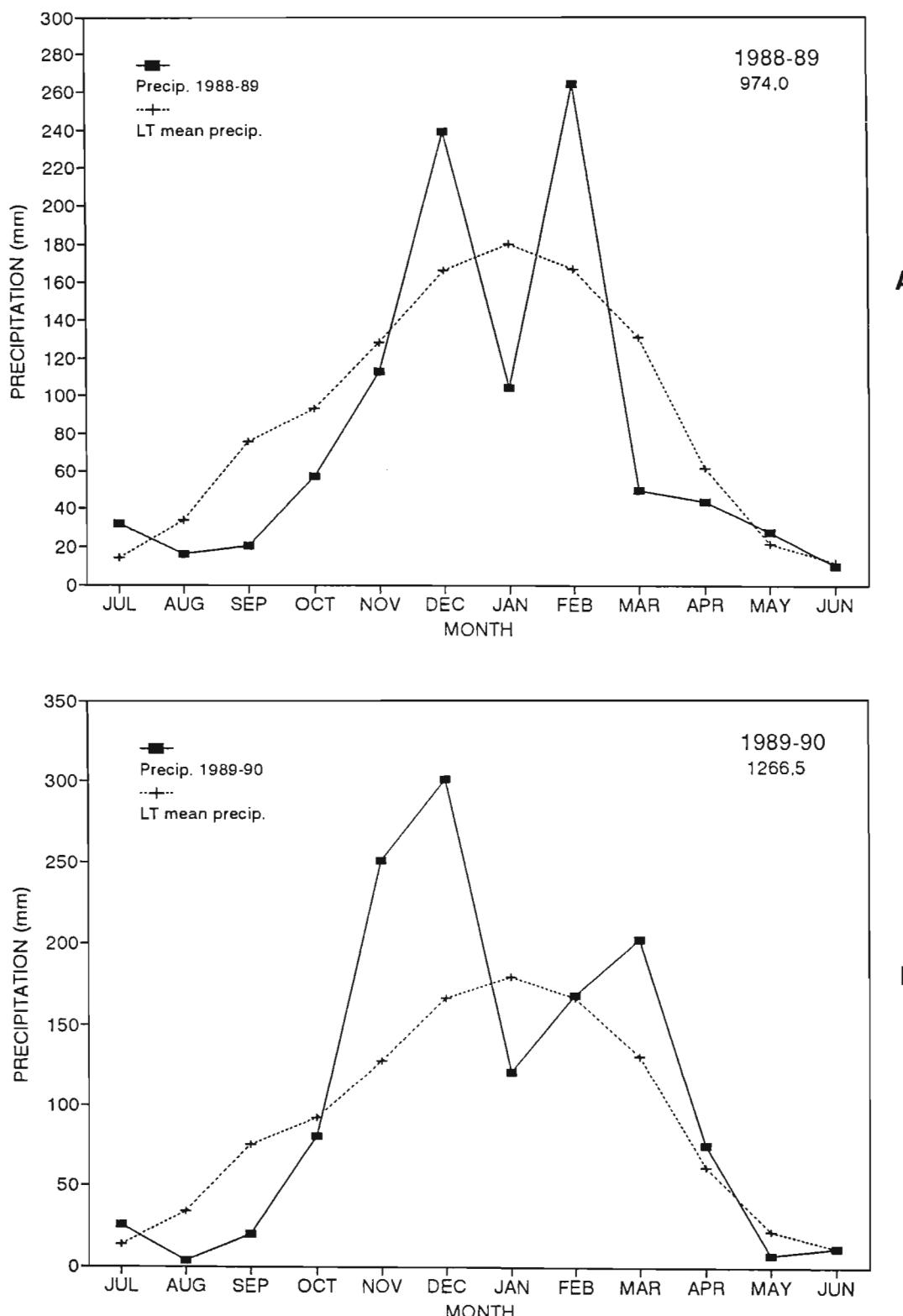
The dam was built for aesthetic reasons and the adjacent wetland is left largely undisturbed. The site was a study area for Redchested Flufftail from September 1988 to December 1992 and was used to assess the effects of burning on a wetland flufftail population.

##### 2.2.5.1 Climate and weather

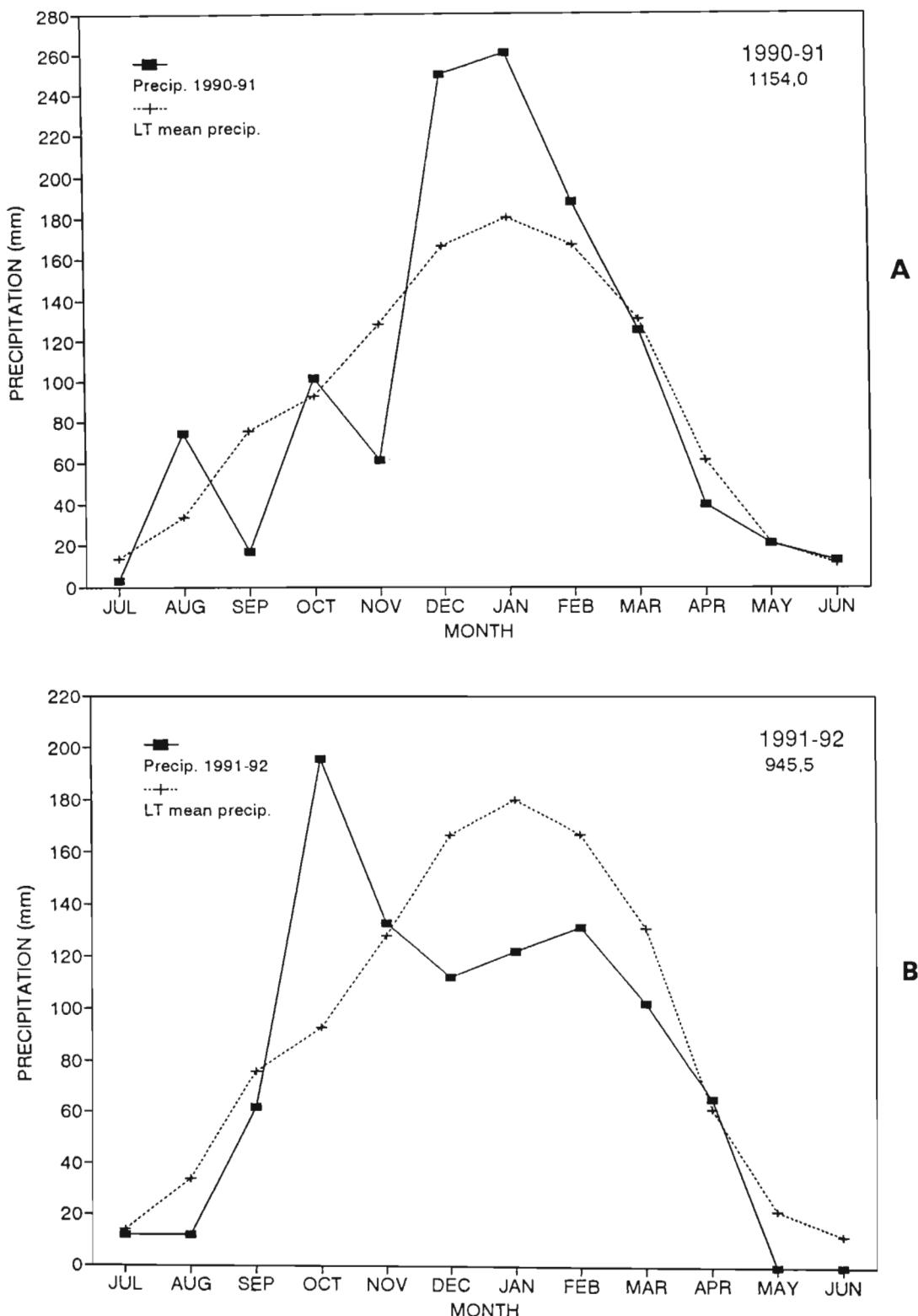
Daily precipitation records were obtained from the adjacent Loskop Farm (Table 2.3) and the monthly precipitation from July 1988 to June 1992, with the long-term mean, is shown in Figs 2.7 and 2.8. Annual precipitation averages 1081,8 mm and most rain falls from September/October to March. The summers are warm and the winters cold, with frost regular from May to July and occasional in August. No detailed temperature records are kept at Gartmore, and those from the nearest available station, De Jong Ranch (10 km due south), are not comparable because the station is on a warmer sea-facing slope. By virtue of its position in a hollow, Gartmore is colder in the winter even than adjacent farms and regularly experiences minimum temperatures of -3°C to -4°C (occasionally as low as -9°C during the study period); temperature ranges of up to 30°C in one day



**Fig. 2.6** The Gartmore Farm study site, near Howick, Natal.



**Fig. 2.7** Gartmore: monthly precipitation (with annual total) compared with long-term (LT) mean monthly precipitation (measured over 23 years). (A) July 1988-June 1989. (B) July 1989-June 1990.



**Fig. 2.8** Gartmore: monthly precipitation (with annual total) compared with long-term (LT) mean monthly precipitation. (A) July 1990- June 1991. (B) July 1991-June 1992.

may be recorded in winter (C. MacGillivray pers. comm.). Maximum summer temperatures in the mid-30s are not uncommon. The occurrence of hot dry berg winds in August-September give maxima up to 34°C in those months (W. N. MacGillivray pers. comm.). This combination of factors gives one of the largest temperature ranges recorded at the study areas (Fig. 2.9) and the farm certainly has a more severe climate than is given by Phillips (1973) for Bioclimatic Group 3 (Subregion a) in which it is located.

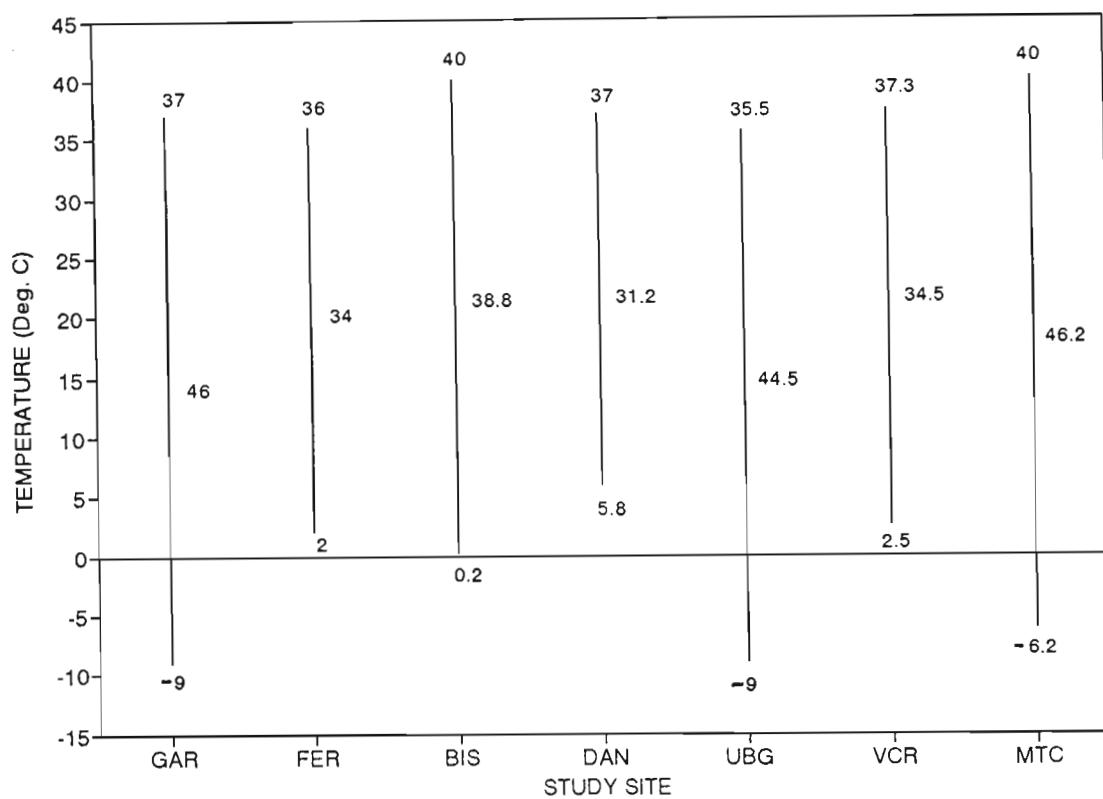
During the four July-June periods up to June 1992, annual precipitation was within  $\pm 17\%$  of the mean (Figs 2.7 and 2.8) but during the last six months of 1992 only 295,5 mm of rain fell, 58% of the long-term mean for that period.

#### **2.2.5.2 Vegetation**

The vegetation varies from permanently flooded sedge beds at the dam margin to seasonally moist grassland at the perimeter fences. Neither *Typha capensis* nor *Phragmites australis* occurs. The dominant sedge in the wettest areas is *Cyperus denudatus*, which grows in large clumps at the dam margin and extends into the seasonally flooded sedge meadow areas, where it is locally co-dominant with *Eleocharis acutangula*, *E. limosa*, *Juncus effusus*, *J. exsertus*, *Schoenoplectus paludicola* and the grass *Leersia hexandra*. The grasses *Echinochloa stagnina*, *Hemarthria altissima* and *Sacciolepis chevalieri* also occur here. In open wet areas between tussocks the smaller sedge *Isolepis fluitans* is common, often with *Aponogeton junceus* and the forb *Lentella asiatica*. On less flooded ground *Carex austro-africana*, *Eleocharis dregeana*, *Rhynchospora brownii* and *Schoenoplectus brachyceras* are common, while the dominant grass is *Agrostis barbuligera*, which grows in clumps. The sedges *Ascolepis capensis* and *Pycreus macranthus* occur on drier ground, while *Cyperus denudatus* extends through the more peripheral seasonally wet areas which are largely occupied by hygrophilous grasses, *Agrostis barbigulera* and *Eragrostis planiculmis* being the dominant species. The naturalised South American grass *Paspalum urvillei* is co-dominant with *Andropogon appendiculatus* in the driest areas along the perimeter fences. A clump of alien brambles *Rubus* sp. covers about 0,1 ha at the northern end of the study site (Fig. 2.6), and smaller patches of the same vegetation occur in other fairly dry spots near the perimeter, especially with *Hyparrhenia*.

#### **2.2.5.3 Use and management**

The site is very rarely grazed by cattle, while the few Reedbuck *Redunca arundinum* on this part of the farm also have little effect on the vegetation. Before the study commenced the site had not



**Fig. 2.9** Temperature ranges ( $^{\circ}\text{C}$ ) at some long-term study sites in Natal during the study period: Gartmore Farm, Howick (GAR); Ferncliffe Forest, Pietermaritzburg (FER); Bisley Valley, Pietermaritzburg (BIS); Danville Park, Durban (DAN); Scotston Farm, Underberg (UBG); Vernon Crookes Reserve, Umzinto (VCR); Mount Currie Reserve, Kokstad (MTC).

been burned for four years and, from 1989 onwards, with the help of the Natal Parks Board a system of spring burns was established, the wetland being divided into a northern and a southern block by a firebreak (Fig. 2.6) and each block being burned biennially in September. Thus in September 1989 and 1991 the southern block was burned and in 1990 the northern block. In view of the drought in late 1992, and the consequent scarcity of temporary habitats for displaced Redchested Flufftails, no burn took place that year. In an attempt to control the spread of the alien brambles, patches of the study site are occasionally mown, thus in October 1989 1,47 ha at the extreme northern end of the site were cut.

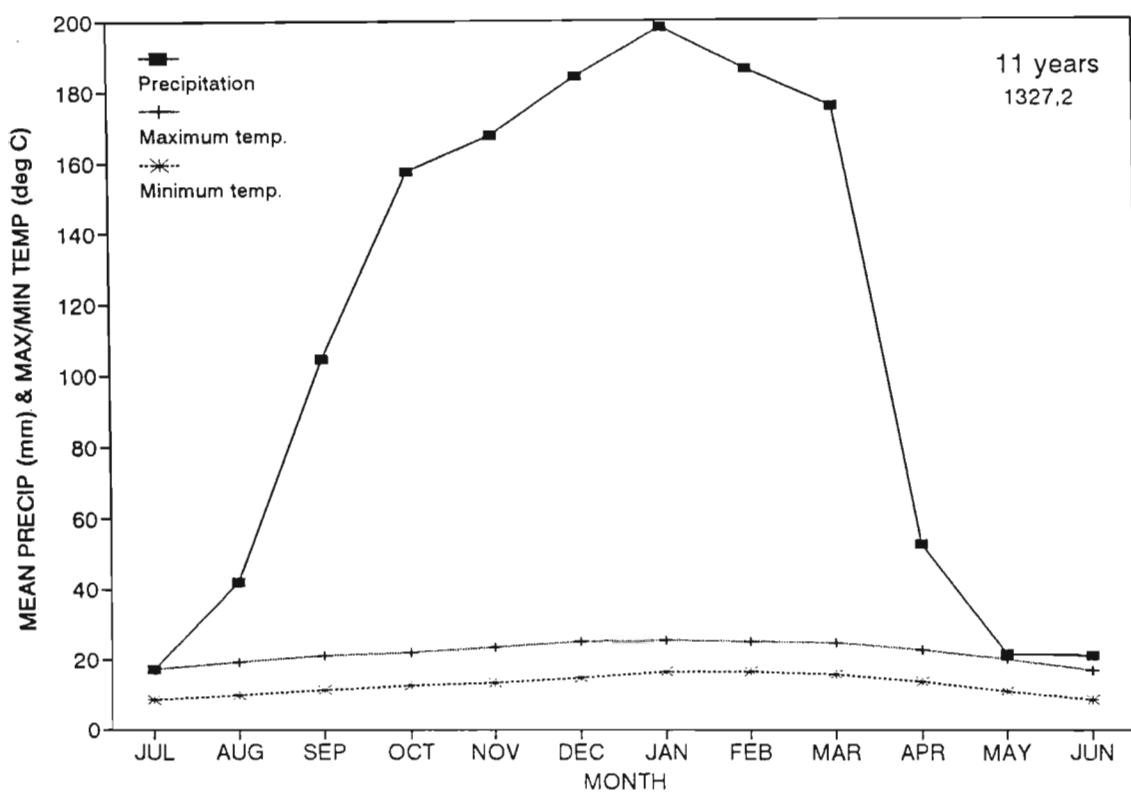
## **2.2.6 Ferncliffe Forest, Pietermaritzburg, Natal**

Ferncliffe Forest was zoned as a Conservation Area under the Town Planning Act in 1985. The Conservation Area covers about 250 ha on the upper slopes of the escarpment immediately north of Pietermaritzburg, extending east from the D. V. Harris Waterworks along the south-facing slopes overlooking the city and then continuing north almost to Otto's Bluff (R. Bartholomew pers. comm.). The largest unbroken tract of indigenous forest ( $29^{\circ}33'S$   $30^{\circ}21'E$ ) covers about 78 ha of the south-facing slopes, from 960 m a.s.l. to the city boundary on the escarpment crest at 1 100 m. It is surrounded by wattle and gum plantations, which have replaced almost all the indigenous vegetation on the high ground to the north and northwest of the city. From about 1860 to the early 1900s quarrying took place in this forest but after about 1920 the area was allowed to recover and the forest became re-established (R. Bartholomew pers. comm.).

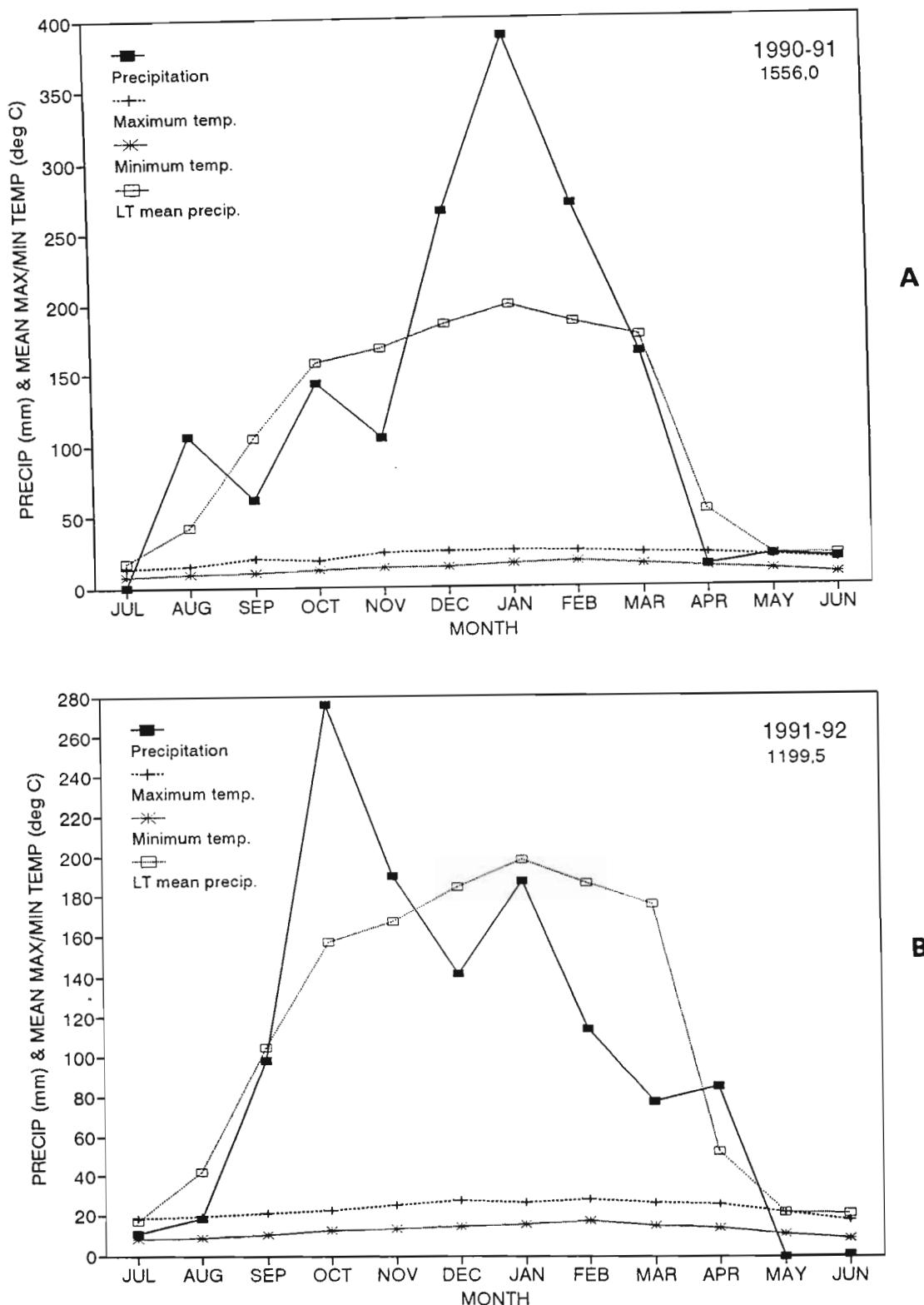
From September 1990 to June 1992 studies were made of the behaviour and seasonality of Buffspotted Flufftails in this forest. Seasonal changes in vegetation structure and invertebrate abundance were also recorded, monthly vegetation sampling being continued until August 1993.

### **2.2.6.1 Climate and weather**

Daily precipitation and temperature data were obtained from the D. V. Harris Waterworks at the western end of Ferncliffe Forest. The long-term mean monthly precipitation and maximum and minimum temperatures are shown in Fig. 2.10. In addition to mist the forest receives a mean annual rainfall of 1 327,2 mm, most of which falls between September and March. The area lies within Bioclimatic Subregion 2b (Phillips 1973), where summers are normally warm and winters mild, but the forest itself is a relatively cool environment and Ferncliffe has the lowest June-July mean maximum temperatures of any of the study areas, whether forest or open ground (Table 2.2), although the site's mean minimum winter temperatures are slightly higher than those at Bisley Valley, another



**Fig. 2.10** Ferncliffe Forest, Pietermaritzburg, Natal: mean monthly precipitation (mm) and maximum and minimum temperatures (°C), July-June. The number of years of weather records, and the mean annual precipitation, are shown.



**Fig. 2.11** Ferncliffe: monthly precipitation (with annual total) compared with long-term (LT) mean monthly precipitation, and monthly mean maximum and minimum temperatures. (A) July 1990-June 1991. (B) July 1991-June 1992.

Buffspotted Flufftail study area (see Section 2.2.8). The lowest minimum temperature recorded during the study period was 2°C (Fig. 2.9). From July 1990 to June 1991 (Fig. 2.11A) rainfall was 17% more than the mean and from July 1991 to June 1992 (Fig. 2.11B) it was 10% less. In the 1992 calendar year it was 70,8% of the mean, a much less drastic decrease in rainfall than was experienced at most other study sites during 1992.

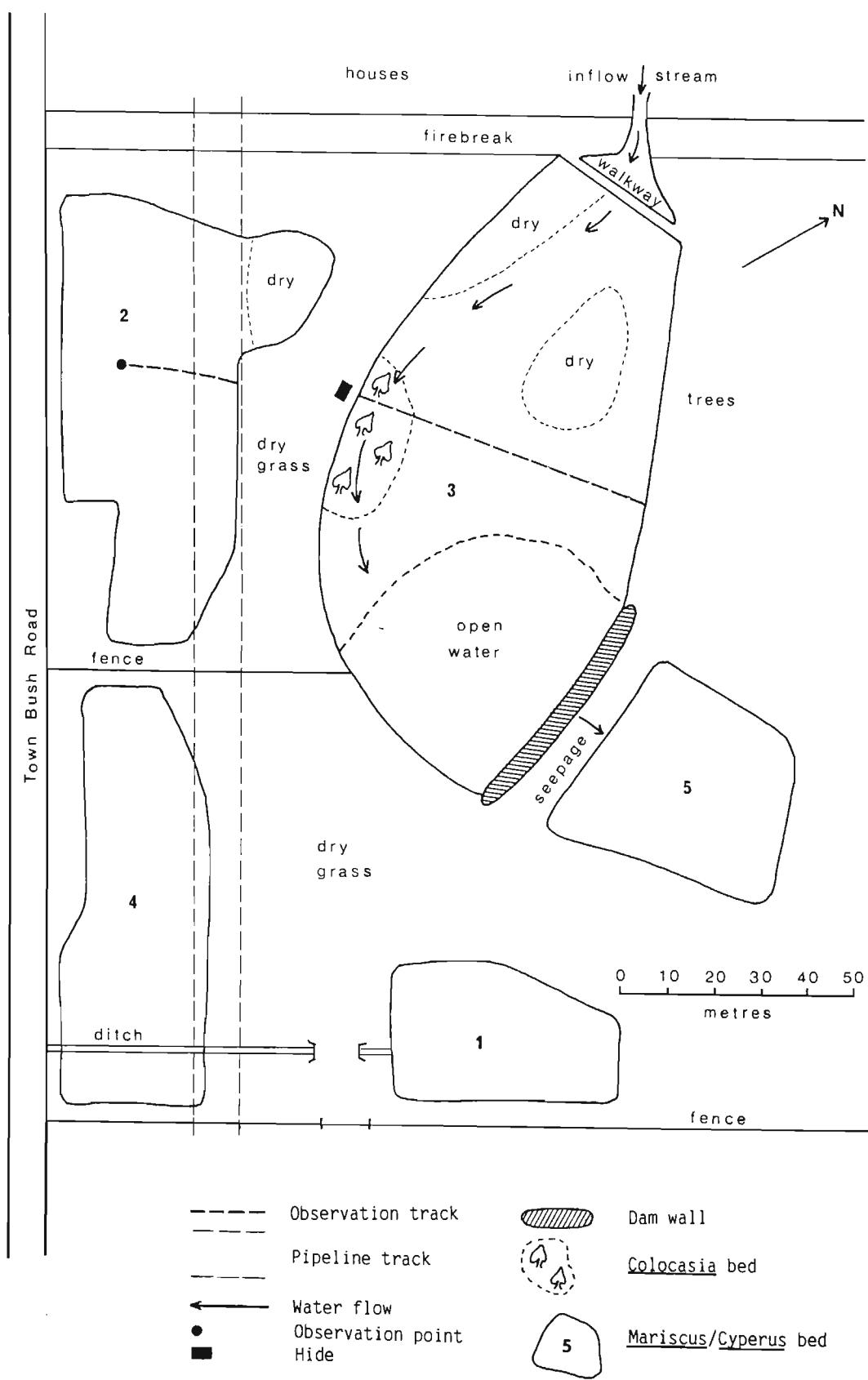
#### **2.2.6.2 Vegetation**

Ferncliffe is a long-established mid-altitude mistbelt forest, predominantly secondary in structure and with a significant proportion of alien invader plants, particularly Inkberry *Cestrum laevigatum* and Bugweed *Solanum mauritianum*. Characteristic indigenous tree species include *Celtis africana*, *Clausena anisata*, *Halleria lucida*, *Podocarpus latifolius*, *Rhus chirindensis*, *Rothmannia globosa*, *Trimeria grandifolia*, *Xymalos monospora* and *Zanthoxylum davyi*. *Dracaena hookeriana* and *Piper capense* are common understorey plants. Much of the forest grows on very steep slopes with rock outcrops and large boulders (a legacy of landslips and old quarrying operations), a topography not conducive to the development of a dense ground-herb layer, but in the less rocky areas and at forest edges ground cover is well developed, important constituent species being ferns (not identified), the forbs *Desmodium repandum*, *Hypoestes triflora* and *Impatiens hochstetteri* var. *hochstetteri*, and the grasses *Oplismenus hirtellus*, *Panicum aequinerve* and *Setaria megaphylla*.

#### **2.2.7 Allerton, Pietermaritzburg, Natal**

The Allerton study site (29°35'S 30°21'E) is on farmland at the Allerton Veterinary Research Station, Pietermaritzburg. The site is 703 m a.s.l. and covers 3,78 ha, including a small dam (Fig. 2.12). It is adjacent to Town Bush Road, being bordered on other sides by housing, grazing land and exotic tree clumps, and contains five discrete permanent reedbeds, including that at the dam itself. The area is protected and access is restricted. An underground water pipeline and adjacent oil pipeline run through the property parallel to Town Bush Road (Fig. 2.12).

The reedbeds are usually moist to flooded throughout the year, that at the dam (No. 3) being maintained by the inflowing permanent stream which spreads out to inundate the reedbed close to the southwest shore so that flowing water is visible in the area immediately in front of the hide. Reedbed No. 5 (Fig. 2.12) is maintained by seepage from the dam wall and is sometimes almost dry in winter, while Reedbed No. 1 is fed by runoff from higher ground via an open channel and is moist even in winter. Reedbed No. 2 is flooded throughout the year, possibly from a spring and also perhaps from



**Fig. 2.12** The Allerton study site, Pietermaritzburg, Natal.

slight water-pipeline leakage, and water seeps from it down the slope to Reedbed No. 4, which is usually drier than any reedbed except No 5.

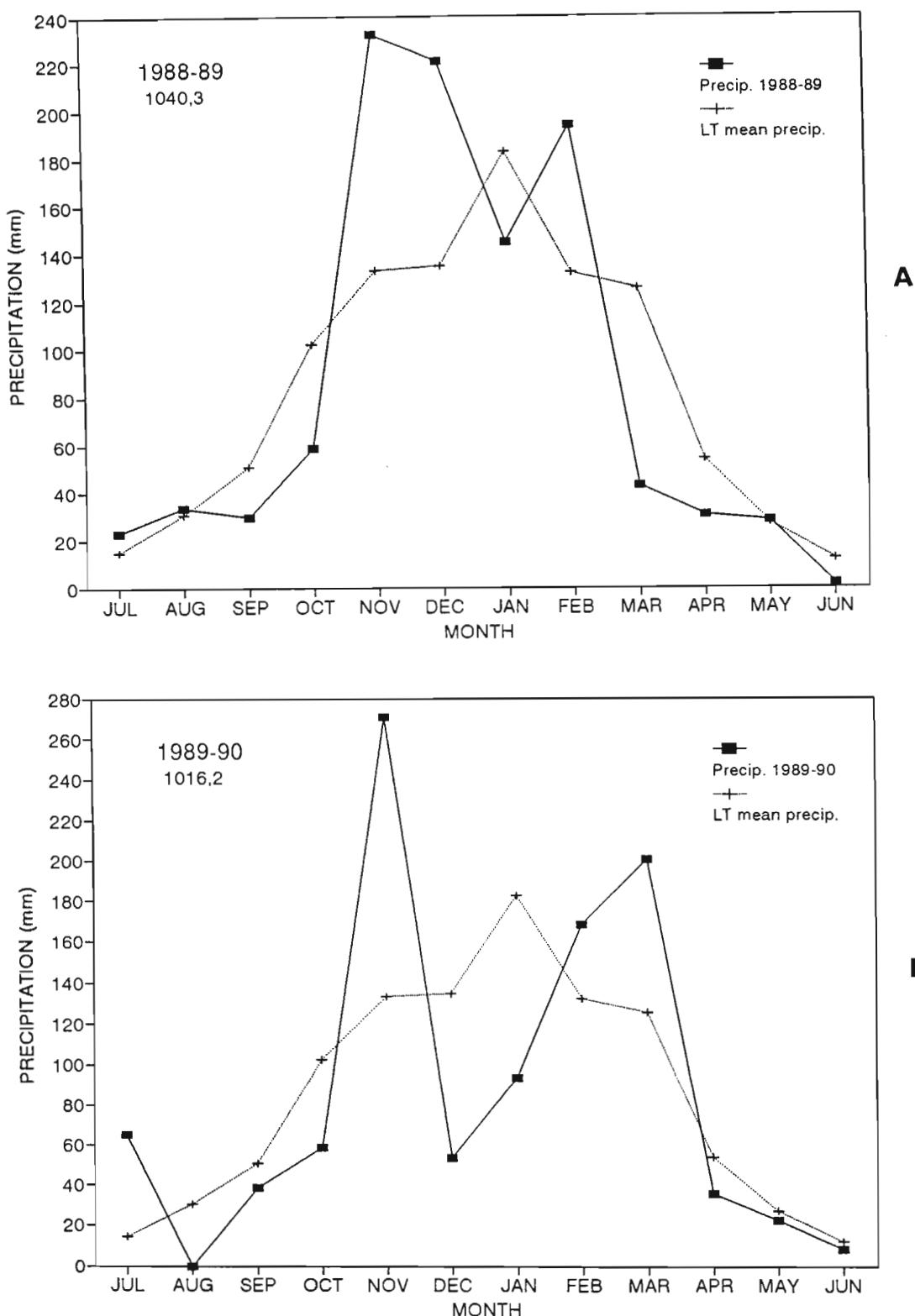
The area was a study site for Redchested Flufftail from September 1988 to July 1992, being used for studies of behaviour and the effects of seasonal burning on reedbed vegetation and the rallids inhabiting it. In 1989 the Natal Midland Bird Club erected a permanent hide at the dam edge, for my use during the project.

#### **2.2.7.1 Climate and weather**

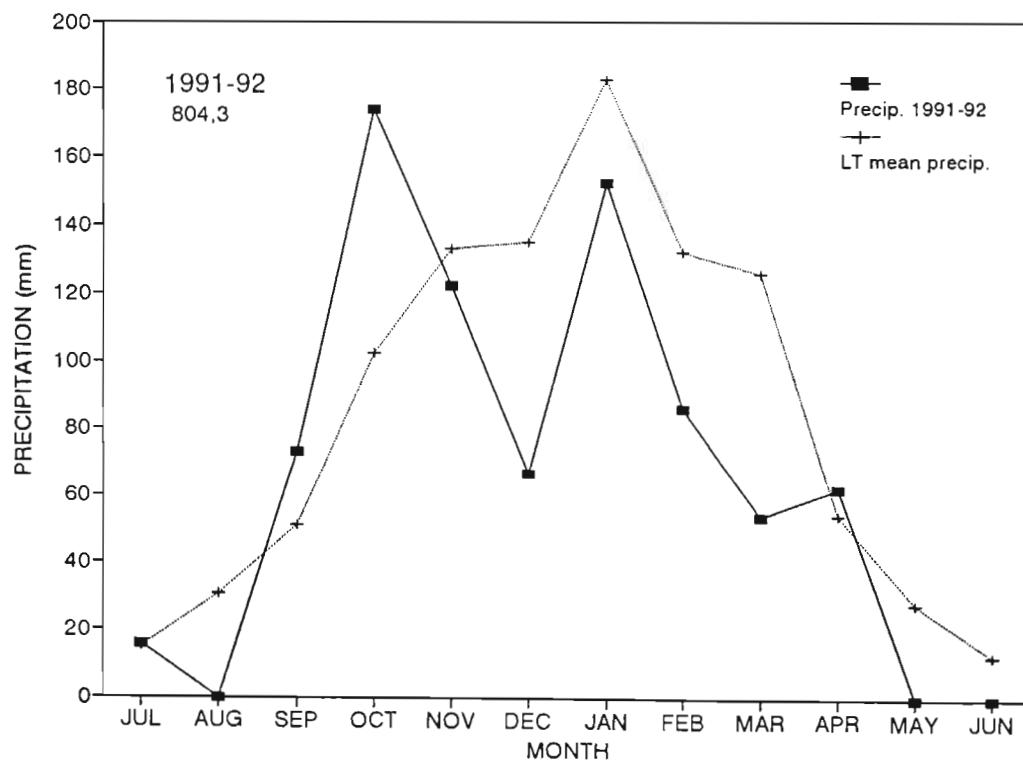
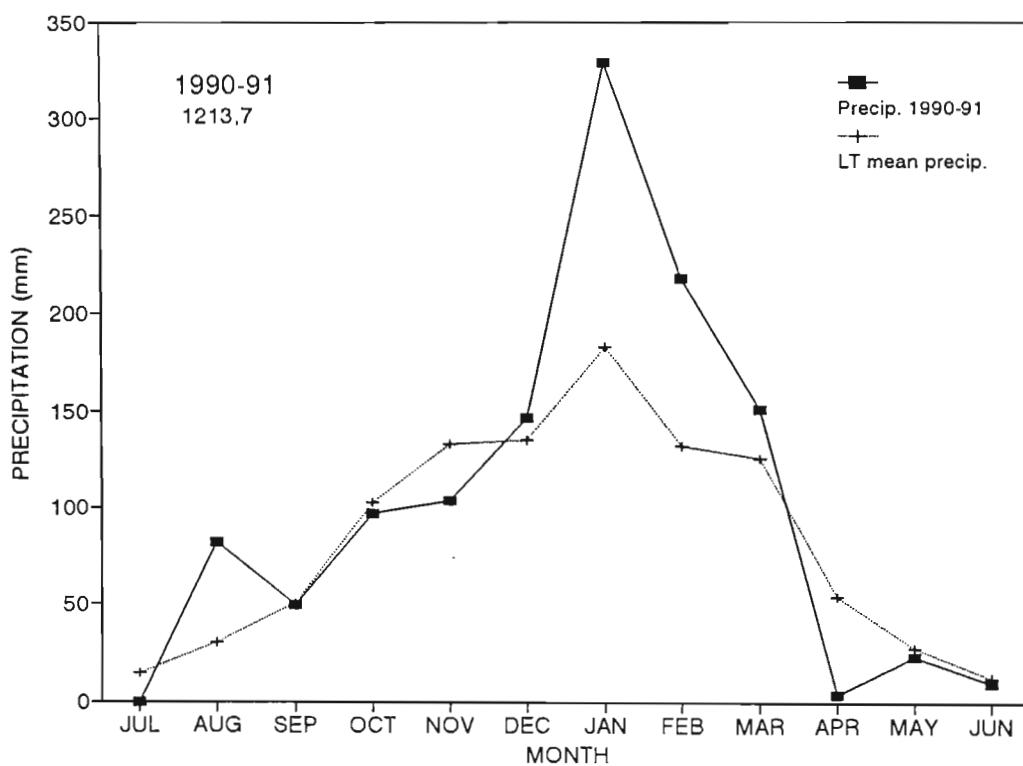
Data on daily precipitation were obtained from Allerton Farm, of which the study site is a part. No temperature records are kept, so only the total monthly and long-term mean precipitation figures are shown in Figs 2.13 and 2.14. The site is only 3 km from Ferncliffe but receives only 75% of the rainfall recorded at the forest, mean annual precipitation being 999,8 mm and most rain falling in the October-March period (Table 2.1). As expected, the exposed nature of the site and its position in a valley give rise to greater extremes of temperature than at Ferncliffe, with summer maxima of 36-40°C and 1-2 degrees of frost not uncommon from June to August (S.J.E. Bosch pers. comm.). During the first two July-June periods of the study the total precipitation was less than 5% above the long-term mean, in 1990-91 it was 21% above and in 1991-92 20% below (Figs 2.13 and 2.14). The effects of the drought were felt in 1992, the total precipitation for the calendar year being 631,8 mm, only 63% of the mean.

#### **2.2.7.2 Vegetation**

The largest reedbed is that at the dam and its vegetation is predominantly a mixture of three large sedge species, *Cyperus dives*, *C. latifolius* and *Mariscus solidus*, the first species being dominant in saturated to shallowly flooded areas and the others dominating in the drier areas. In the more deeply flooded parts, particularly adjacent to the open water and along the course of the flowing water near the southwest shore, *Typha capensis* is common to dominant. In front of the hide, where the flowing water is deepest and the substrate is very deep soft mud, the vegetation is dominated by tall "elephant's ear" *Colocasia antiquorum* var. *esculenta* (Fig. 2.12), which dies back after winter frosts to expose the water surface. The other four reedbeds, all moist to shallowly flooded, are dominated by *Cyperus latifolius*, with the other two large sedges and *Typha capensis* also occurring at varying densities. The western end of Reedbed No. 3 (Fig. 2.12) has a considerable *Typha* component and in the drier parts the fern *Cyclosorus interruptus* is common. At reedbed edges, in damp grass, the



**Fig. 2.13** Allerton: monthly precipitation (with annual total) compared with long-term (LT) mean monthly precipitation (measured over 42 years). (A) July 1988-June 1989. (B) July 1989-June 1990.



**Fig. 2.14** Allerton: monthly precipitation (with annual total) compared with long-term (LT) mean monthly precipitation. (A) July 1990-June 1991. (B) July 1991-June 1992.

smaller sedges *Cyperus esculentis*, *Mariscus sumatrensis* and *Pycreus intactus* occur. The five reedbeds are separated by areas of dry grass and in some places are fringed by clumps of alien tree species. The occasional small alien *Sesbania* sp. tree occurs in the reedbeds.

#### **2.2.7.3      Use and management**

The study site is not grazed and, apart from occasional cutting of the grass, no management is practised by the Veterinary Department. The Umgeni Water Board sometimes mows a strip of grass and reedbed vegetation 5-10 m wide along the course of the water pipeline; during the study this took place in March 1989 and July 1992. In late 1988, because of the lack of recent burning, Reedbeds 1, 3, 4 and 5 showed relatively little new growth through a dense mass of dead vegetation and it was decided to burn certain areas during the study to assess the effect on the vegetation and the birds. Accordingly, the western half of the Dam Reedbed (No. 3) was burned by the Municipality on 13 September 1989, using the cut trapping ride (Fig. 2.12) as a firebreak. On 21 August 1990 Reedbeds 1 and 5 were burned, and also part of the Dam Reedbed (in error), while on 4 September 1991 the eastern half of the Dam Reedbed was burned, the fire spreading inadvertently to the northwestern section.

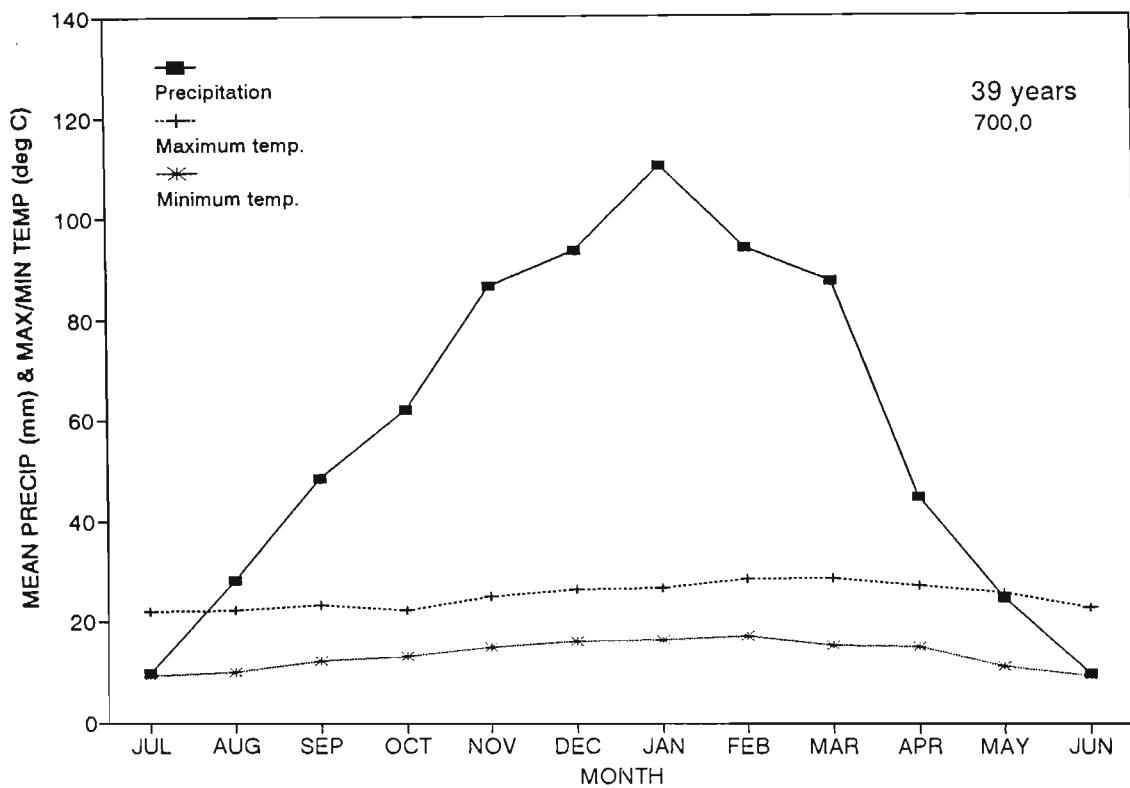
#### **2.2.8      Bisley Valley, Pietermaritzburg, Natal**

Bisley Valley ( $29^{\circ}40'S$   $30^{\circ}24'E$ ) is an area of *Acacia*-dominated woodland and thickets in a north-facing valley situated at the southern end of Pietermaritzburg adjacent to a residential area. It has been a Municipal Nature Reserve since 1985, having previously been used for grazing domestic stock and before that having been a rifle range. The study site is 710 m a.s.l. and covers about 2 ha of dense thickets near one of the reserve's three seasonal streams.

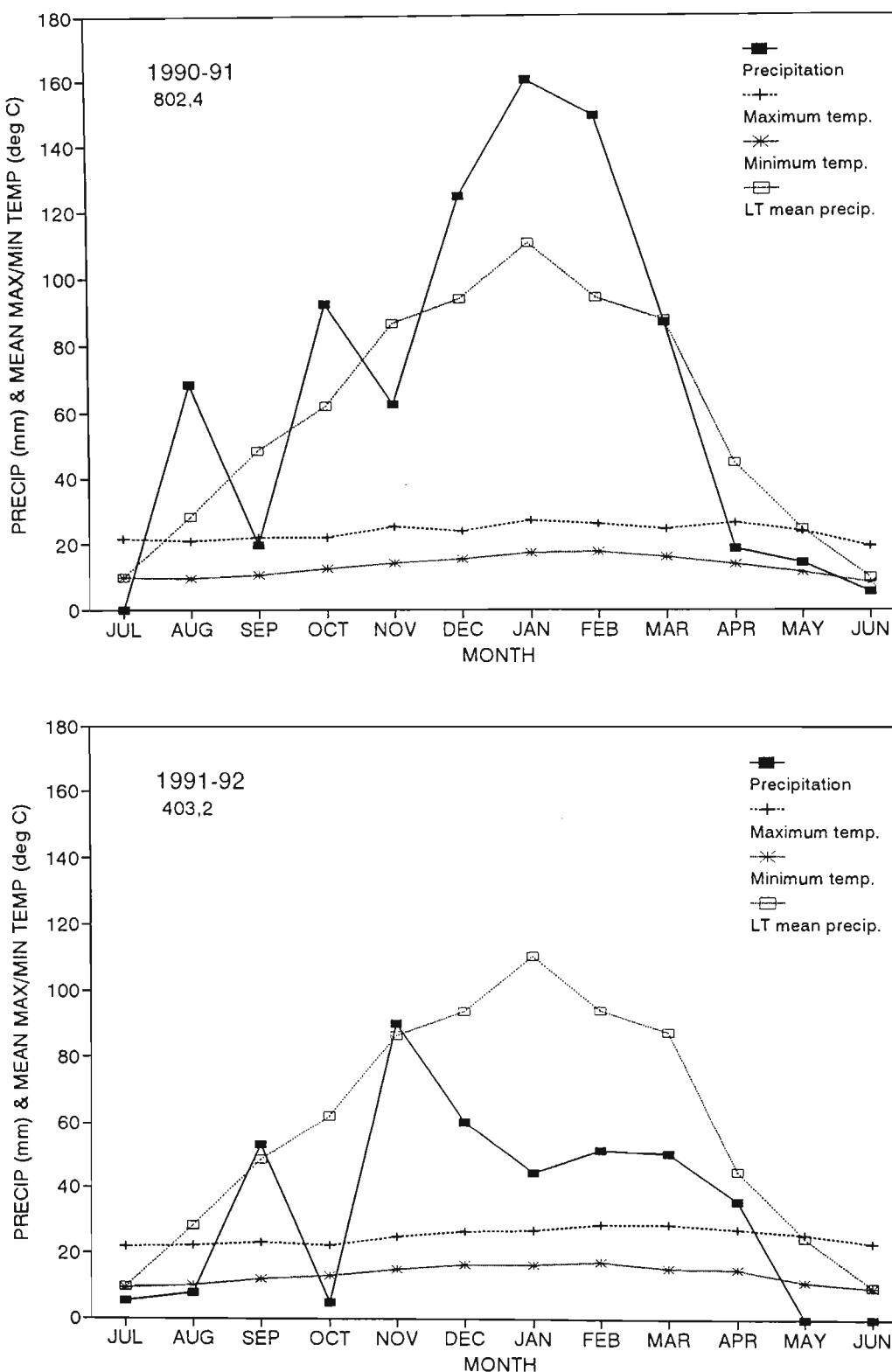
From May 1991 to June 1992 a study was made of the occurrence and behaviour of Buffspotted Flufftails at the study site, and seasonal changes in vegetation structure and invertebrate abundance were investigated.

#### **2.2.8.1      Climate and weather**

Data were obtained from the University of Natal's Ukulinga Agricultural Research Station adjacent to Bisley Valley and at a slightly higher elevation (Table 2.3). The long-term mean annual precipitation is 700 mm, most rain falling from September to March (Table 2.1 & Fig. 2.15). The



**Fig. 2.15** Bisley Valley, Pietermaritzburg, Natal: mean monthly precipitation (mm) and maximum and minimum temperatures (°C), July-June. The number of years of precipitation records, and the mean annual precipitation, are shown.



**Fig. 2.16** Bisley: monthly precipitation (with annual total) compared with long-term (LT) mean monthly precipitation, and monthly mean maximum and minimum temperatures. (A) July 1990-June 1991. (B) July 1991-June 1992.

summers are warm and the winters cool, the mean minimum and maximum temperatures in the coolest months (June-July) being higher than those at any other study site in the Natal interior (Table 2.2) and the temperature range over the study period being almost 40°C (Fig. 2.9). Figure 2.16 shows that precipitation was rather erratic in the early summer of both 1991 and 1992 and, while the total rainfall from July 1990 to June 1991 was 14,5% higher than the mean, that for the corresponding 1991-92 period was only 57,6% of the mean. Rainfall in 1992 was very low, only 260 mm of rain (37% of the mean) falling in the calendar year.

#### **2.2.8.2 Vegetation**

The vegetation of the reserve is described in some detail by Adie (1991). The vegetation type is defined as Valley Bushveld (Veld Type 23) by Acocks (1988) and the study site falls within the habitat type designated Dense Riverine Thicket by Adie (1991). This is the most densely vegetated of the reserve's habitats and its dominant tree species are *Acacia karroo* and *A. nilotica*, with scattered *Grewia occidentalis* and *Ziziphus mucronata*. The indigenous creeper *Trichomeria sagittata* is ubiquitous at the study site, hanging from canopy to ground level and providing much dense cover. Of the alien woody plants, the tree *Melia azedarach* and shrub *Caesalpinia decapetala* occur at the study site (the latter dominates the vegetation nearer to the stream (Adie 1991)), while the understorey contains much *Lantana camara* and some *Solanum mauritianum*. As well as the low cover provided by *Trichomeria* and *Lantana* growth, a significant amount of ground cover in some places is given by the forb *Protasparagus virgatus*; this cover is important in that it persists in winter, when the *Trichomeria* becomes leafless and the *Lantana* partially so.

#### **2.2.8.3 Management**

The savanna areas are burned annually in June and an attempt is being made to eradicate alien trees and other plants (Adie 1991); neither of these management procedures affected the study site during this project.

#### **2.2.9 Danville Park Reserve, Durban North, Natal**

Danville Park Reserve ( $29^{\circ}46'S$   $31^{\circ}03'E$ ) is situated 600 m from the Indian Ocean, in a residential area immediately inland of Virginia Airport at Durban North. It lies at an altitude of 15 m a.s.l. and is surrounded by houses except at its southern end where it extends along two sides of

Municipal playing fields which were originally part of the forest (Fig. 2.17). The reserve covers 6,2 ha, of which 5,45 ha are forest and 0,75 ha a shallow dam. The site has been forested for at least 60 years and was fenced off as a Municipal Nature Reserve in 1983 (G. Nichols pers. comm.). The dam was created in stages between 1983 and 1987 (P. H. Stewart-Dunkley pers. comm.), and is unusual in that its floor is built on three levels, each ledge thus produced having a different depth of water and encouraging a different type of vegetation. Most of the deepest level is open water (0,23 ha) and the other two levels have emergent reeds and other dense vegetation which cover 0,52 ha (69%) of the dam's surface. The dam is fed by a spring and has a continuous outflow at the southern end (Fig. 2.17).

From May 1989 to June 1992 intensive studies were made on the Redchested Flufftails and Black Crakes *Amaurornis flavirostris* at the dam and the Buffspotted Flufftails in the forest. In late 1989 a permanent hide was built in the middle of the dam reedbed (Fig. 2.17).

#### **2.2.9.1 Climate and weather**

No meteorological data exist for the reserve so records were obtained from the nearest possible coastal sites, both at slightly higher elevations than Danville (Table 2.3). Rainfall data were taken from the Durban Botanical Gardens 9,5 km to the SSW and temperature data from the South African Sugar Association's Mount Edgecombe Research Station 8 km to the north-northwest. The long-term mean annual precipitation is 1040,1 mm and most rain falls in September-April but in no month does the mean total fall below 30 mm (Table 2.3 & Fig. 2.18). The climate is typical of the Natal coast: winters are mild, with mean minimum temperatures not falling below 10,9 °C (Table 2.2), and summers hot and humid. The overall temperature range during the study period was the least of any study site (Fig. 2.9). During the four years of the study, rainfall was rather erratic (Figs 2.19 and 2.20) but for the three years from July 1988 to June 1991 the total precipitation was within ±6,5% of the mean. However, from July 1991 to June 1992 the total of 706,7 mm was only 68% of the mean and in the calendar year of 1992 only 494,6 mm of rain fell (47,5% of the mean): in 1992 the effect of the drought was visible in dieback of forest vegetation, although the dam's vegetation was hardly affected.

#### **2.2.9.2 Vegetation**

The vegetation is primarily of coastal dune-forest type, with some different species because of the greater degree of shelter (G. Nichols pers. comm.), and the forest is secondary in character

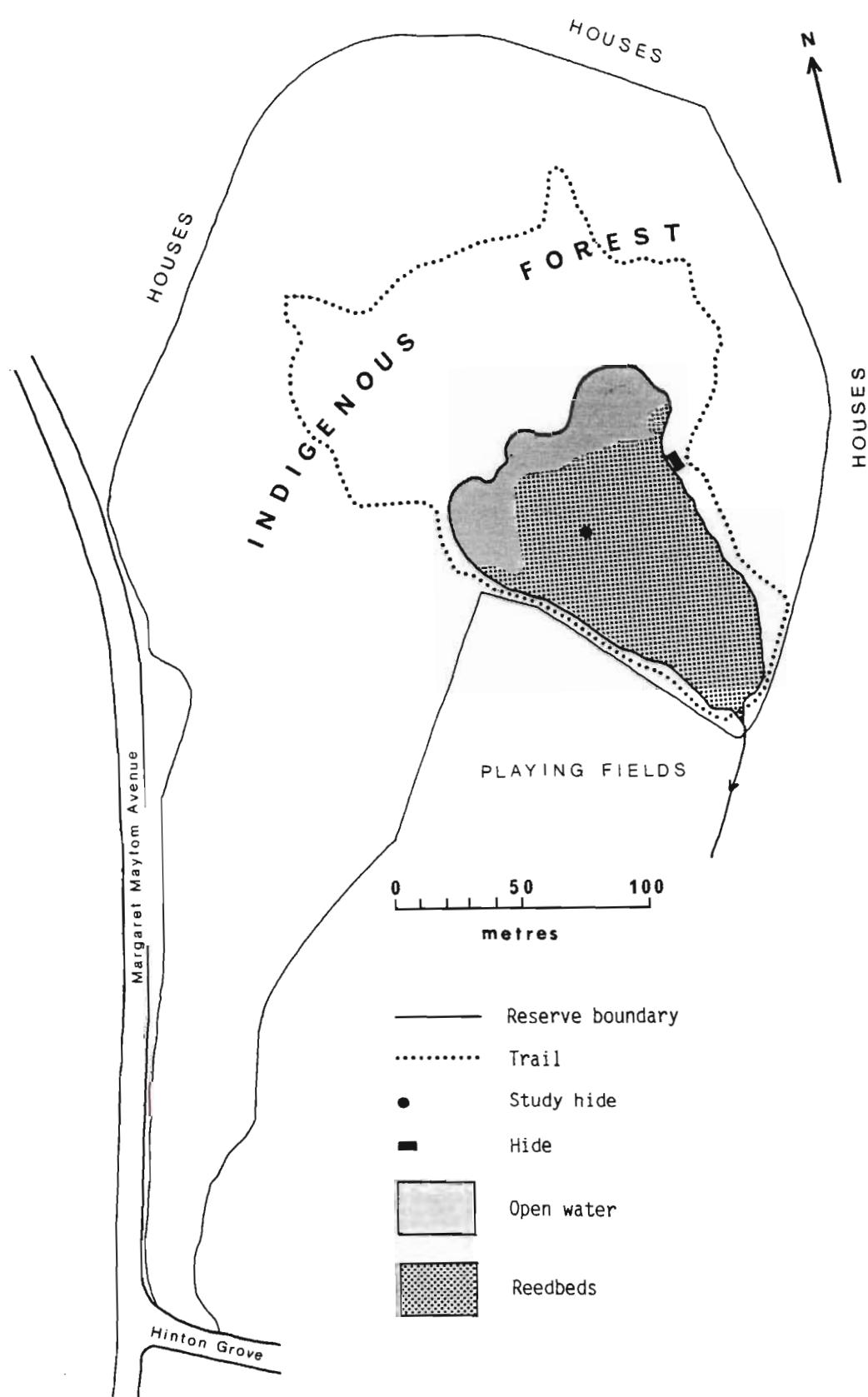
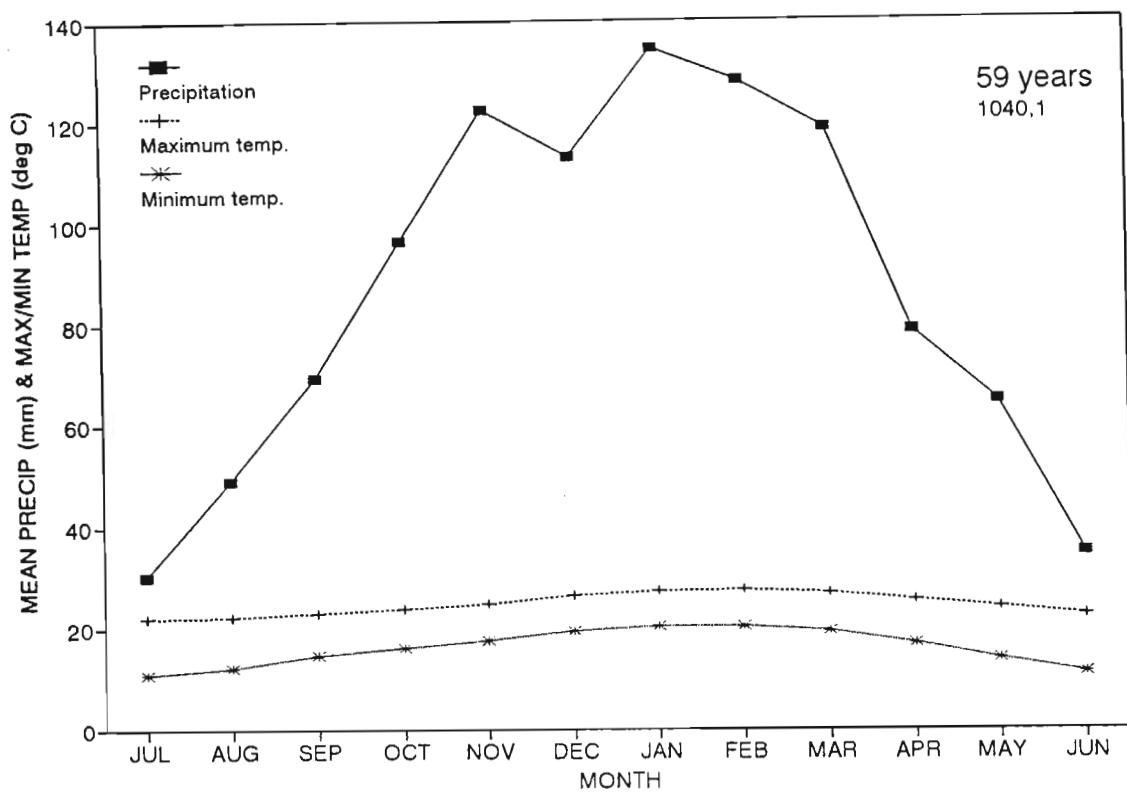
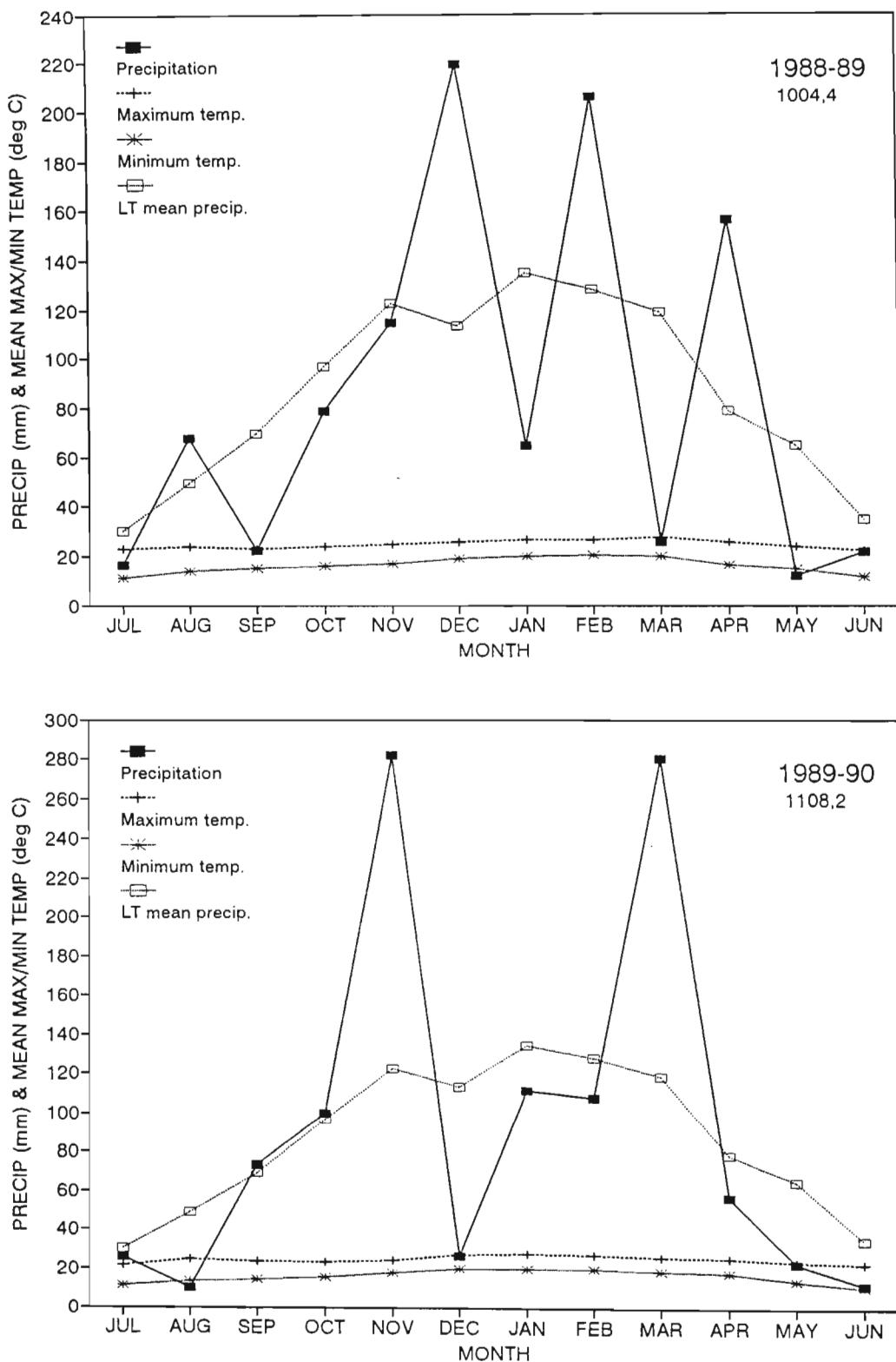


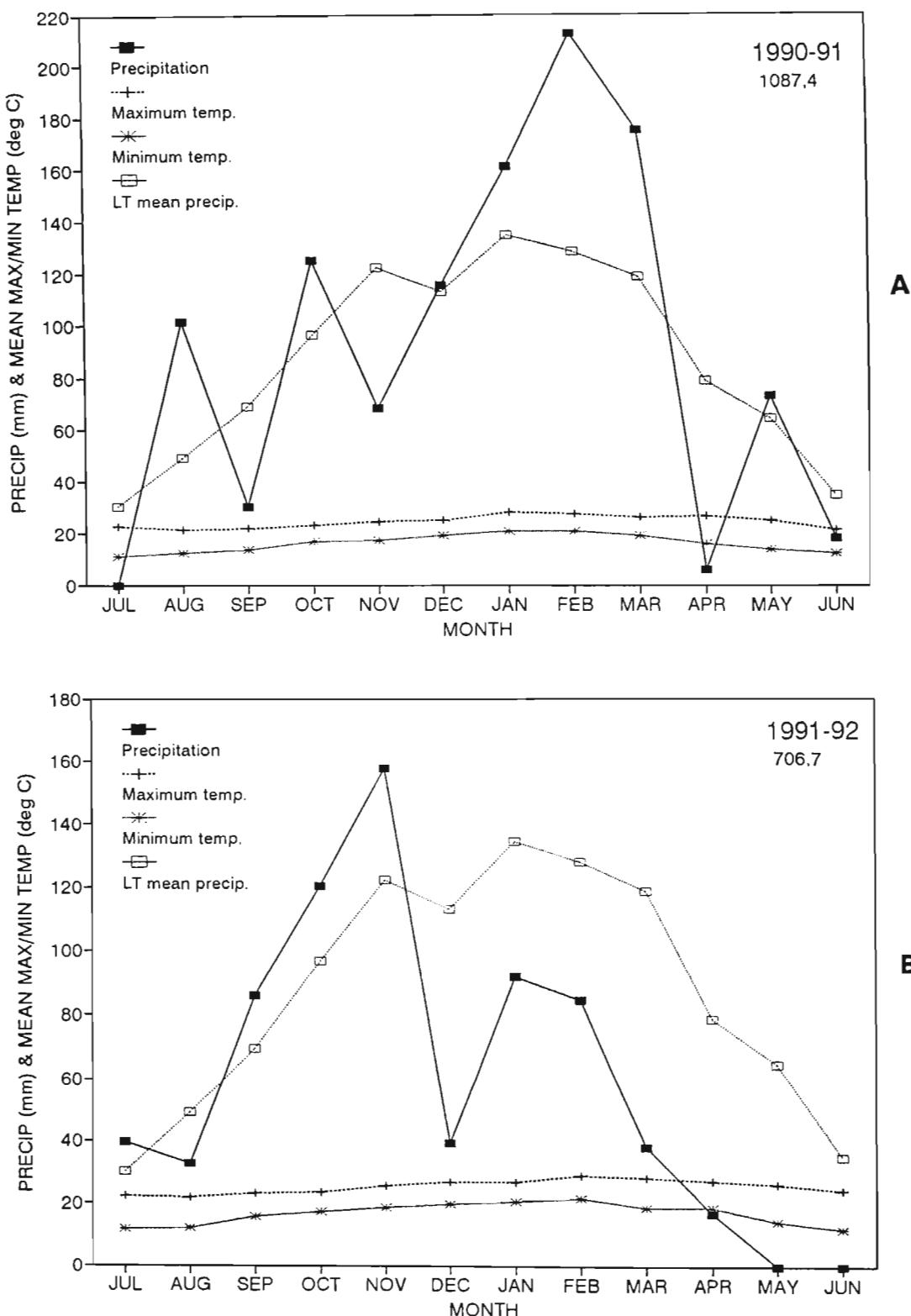
Fig. 2.17 The Danville Park study site, Durban, Natal.



**Fig. 2.18** Danville: mean monthly precipitation (mm) and maximum and minimum temperatures ( $^{\circ}\text{C}$ ), July-June. The number of years of precipitation records, and the mean annual precipitation, are shown.



**Fig. 2.19** Danville: monthly precipitation (with annual total) compared with long-term (LT) mean monthly precipitation, and monthly mean maximum and minimum temperatures. (A) July 1988-June 1989. (B) July 1989-June 1990.



**Fig. 2.20** Danville: monthly precipitation (with annual total) compared with long-term (LT) mean monthly precipitation, and monthly mean maximum and minimum temperatures. (A) July 1990-June 1991. (B) July 1991-June 1992.

because of past disturbance and the encroachment of alien species (now largely eradicated). The dominant tree is *Chaetacme aristata*; other common species include *Albizia adianthifolia*, *Apodytes dimidiata*, *Brachylaena discolor*, *Croton sylvaticus*, *Ficus natalensis*, *Psychotria capensis* and *Psydrax obovata* (G. Nichols pers. comm.). The Pigeonwood *Trema orientalis* occurs at the forest margins. In many parts of the forest a dense understorey of *Isoglossa woodii* is present, plants sometimes being 2-2,5 m in height at the edges of forest tracks. The dominant grass of the forest floor is *Oplismenus hirtellus* and in open areas the ground is covered with a dense growth of the creeping forbs *Asystasia gangetica* and *Commelina africana*.

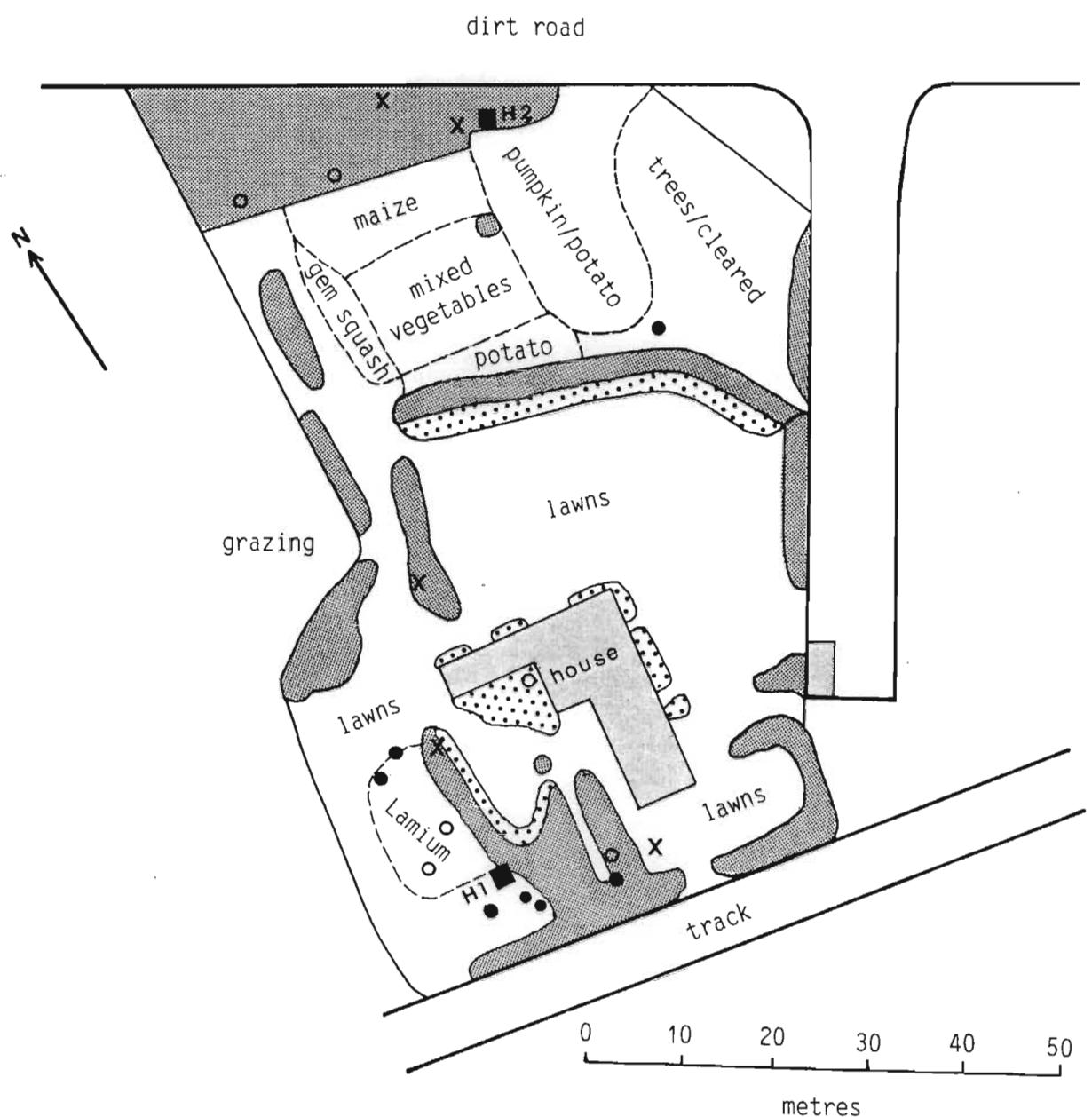
The dam reedbed is a mosaic of patches of *Typha capensis*, *Phragmites australis* and *P. mauritianus*. The *Phragmites* often reaches a height of 2,5-3 m where growing most profusely on the middle of the three ledges, and 4-5 m at the edges (*P. mauritianus*), while the *Typha* is predominant on the shallowest ledge. These plants grow in water up to 50 cm deep on a sandy substrate with overlying deep soft black mud and are interspersed with clumps of the shrub *Ludwigia octovalvis* and large patches of creeping *Commelina benghalensis* and *Ipomoea* sp. (possibly *I. ficifolia*). The fern *Cyclosorus interruptus* is a common constituent of the vegetation at the edges of muddy tracks and open-water patches.

#### **2.2.9.3 Management**

Apart from the regular clearing of plants which encroach on the forest trail and the track bordering the dam, no significant management is practised. The dam reedbed is left completely undisturbed.

#### **2.2.10 Scotston Farm, Underberg, Natal**

The Underberg study site is the garden of the Scotston farmhouse (29°48'S 29°29'E) at 1 500 m a.s.l. on an east-facing slope above the Mzimkulu River 2,5 km southwest of Underberg. The farmhouse and garden occupy 0,88 ha, of which 0,845 ha is garden, comprising lawns, flowerbeds, hedgerows, shrubs, large trees, and a vegetable plot (Fig. 2.21). From November 1990 to June 1992 this garden was the site of intensive studies of the breeding biology and behaviour of Buffspotted Flufftails, two permanent hides being established in late 1990, while occasional observations of Redchested Flufftails and other rallids were made on the farm.



- |                 |                           |
|-----------------|---------------------------|
| Garden boundary |                           |
| ● ●             | Large tree (oak or plane) |
| ○               | Nest                      |
| X               | Calling site              |
| ■               | Hide (H1 and H2)          |
|                 | Building                  |
|                 | Flower beds               |
|                 | Hedges and bushes         |

**Fig. 2.21** The Scotston Farm garden study site, Underberg, Natal.

### **2.2.10.1 Climate and weather**

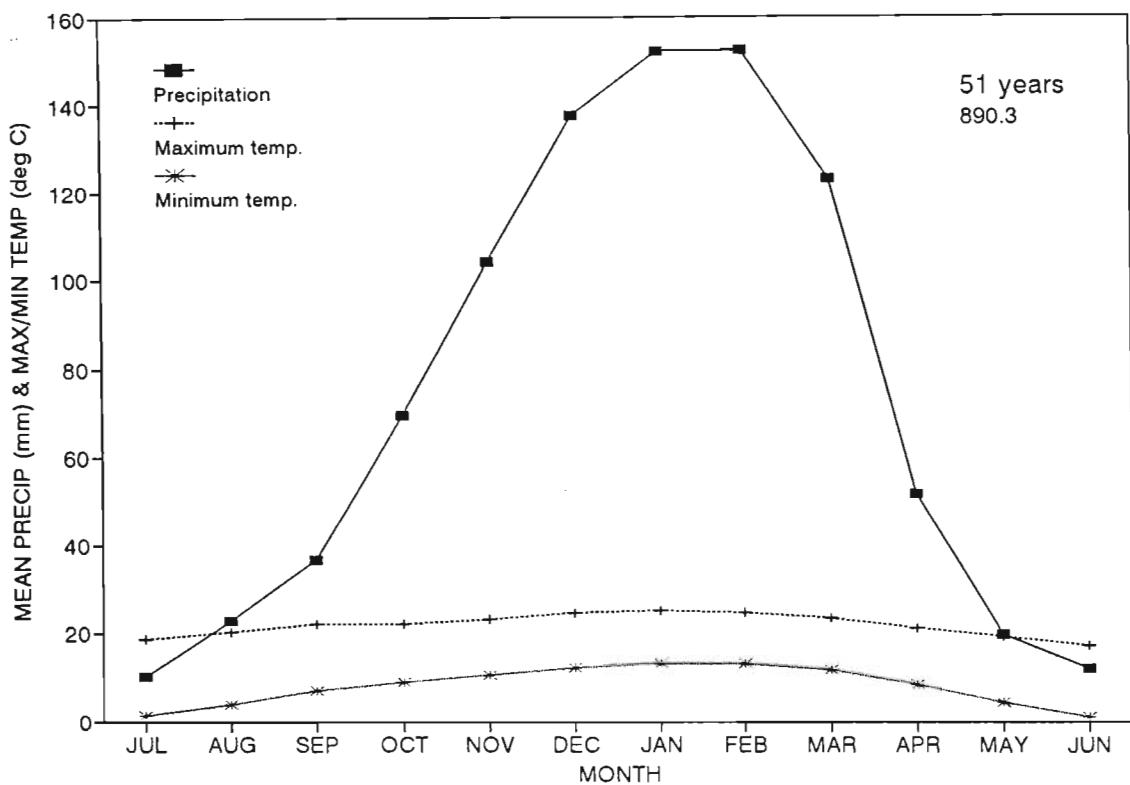
Meteorological data were obtained from the farm Banavie, which is 7,5 km south-southeast of Scotston and has a similar altitude and aspect. The long-term mean annual precipitation is 890,3 mm, most rain falling from October to March (Table 2.1 & Fig. 2.22). The area is within Bioclimatic Group 4 (Phillips 1973) and experiences all the climatic extremes given for that Group, including occasional hot dry berg winds. The summers are warm and the winters cold, with frosts possible at any time from late April to mid-September. Snowfalls are very occasional in June, August and September, but occur mostly at higher altitudes, while in summer lightning is very frequent and each summer one or two hailstorms usually occur on the farm (P. Clowes pers. comm.). A wide range of temperatures was recorded during the study period (Fig. 2.9). Rainfall from July 1990 to June 1991 followed a normal pattern (Fig. 2.23A) and was 96% of the mean, while that of the 1991-92 period (Fig. 2.23B) was more erratic and was 89% of the mean. Unusually dry conditions prevailed for the latter half of 1992, total precipitation for the calendar year being only 578,1 mm (65% of the mean).

### **2.2.10.2 Vegetation**

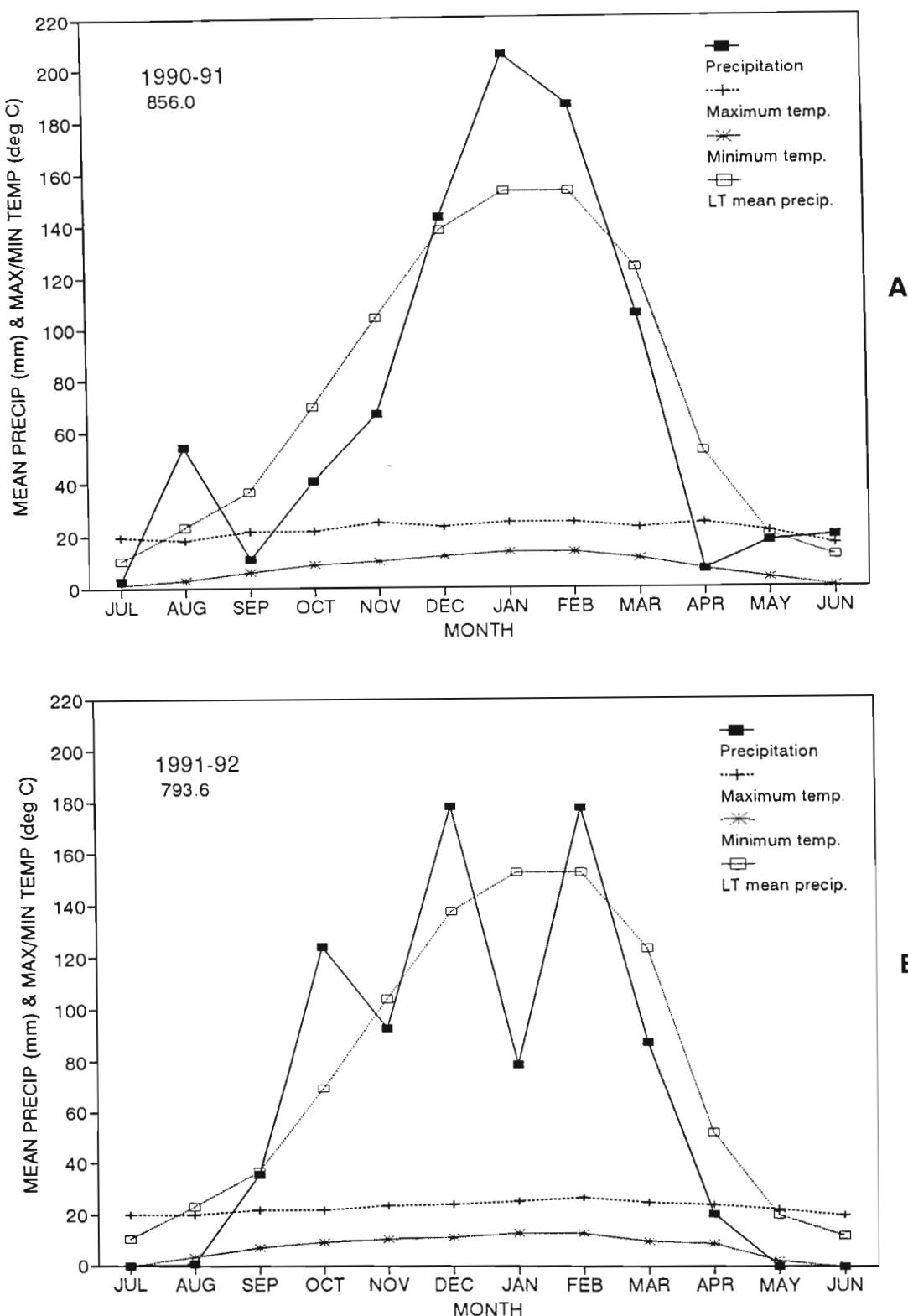
The general layout of the garden is shown in Fig. 2.21. There are virtually no indigenous plants in the garden and much of the dense vegetation cover is seasonal, the trees and shrubs being largely deciduous and the vegetable plot bare in winter. In summer the hedges of *Kerria japonica* and Japanese Quince *Chaenomeles lagenaria* give dense cover, while extensive patches of ground are covered by creepers (*Lamium* and periwinkle *Vinca*) and in the vegetable garden dense low cover is provided by beds of maize, potatoes, gem squash, etc. Clumps of pampas grass *Cortaderia selloana* and some azalea *Rhododendron* bushes provide permanent dense cover. No insecticides or herbicides are used in the garden.

### **2.2.11 Vernon Crookes Nature Reserve, Umzinto, Natal**

Vernon Crookes Nature Reserve (30°17'S 30°36'E) is on the Natal South Coast approximately 60 km southwest of Durban and 15 km inland. It covers 2 189 ha and lies between 200 and 546 m a.s.l. It was proclaimed a reserve in 1973 and is under the control of the Natal Parks Board. Before this the land was subjected to a variety of uses, including cattle ranching and some localized cultivation. Much of the reserve consists of steep-sided valleys and drainage lines, which arise from an undulating plateau in the northern section. The area is primarily a mosaic of grassland



**Fig. 2.22** Scotston: mean monthly precipitation (mm) and maximum and minimum temperatures (°C), July-June. The number of years of precipitation records, and the mean annual precipitation, are shown.



**Fig. 2.23** Scotston: monthly precipitation (with annual total) compared with long-term (LT) mean monthly precipitation, and monthly mean maximum and minimum temperatures. (A) July 1990-June 1991. (B) July 1991-June 1992.

and forest, with scattered small patches of bushes and trees in the grassland. There are no large wetlands and only three small dams.

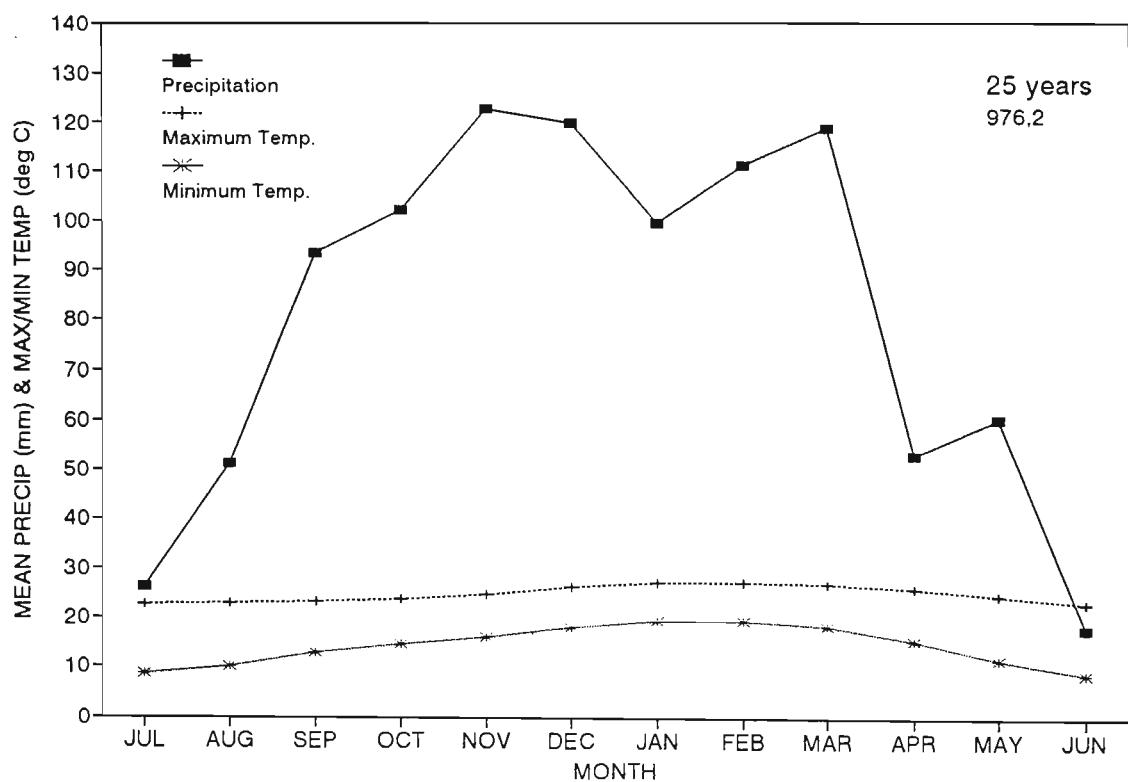
The reserve was a study site for Striped Flufftail from early 1989 to late 1992. Visits were brief and were made only to assess seasonal changes in status and behaviour of the flufftail population, so no detailed study was made of the vegetation.

#### **2.2.11.1 Climate and weather**

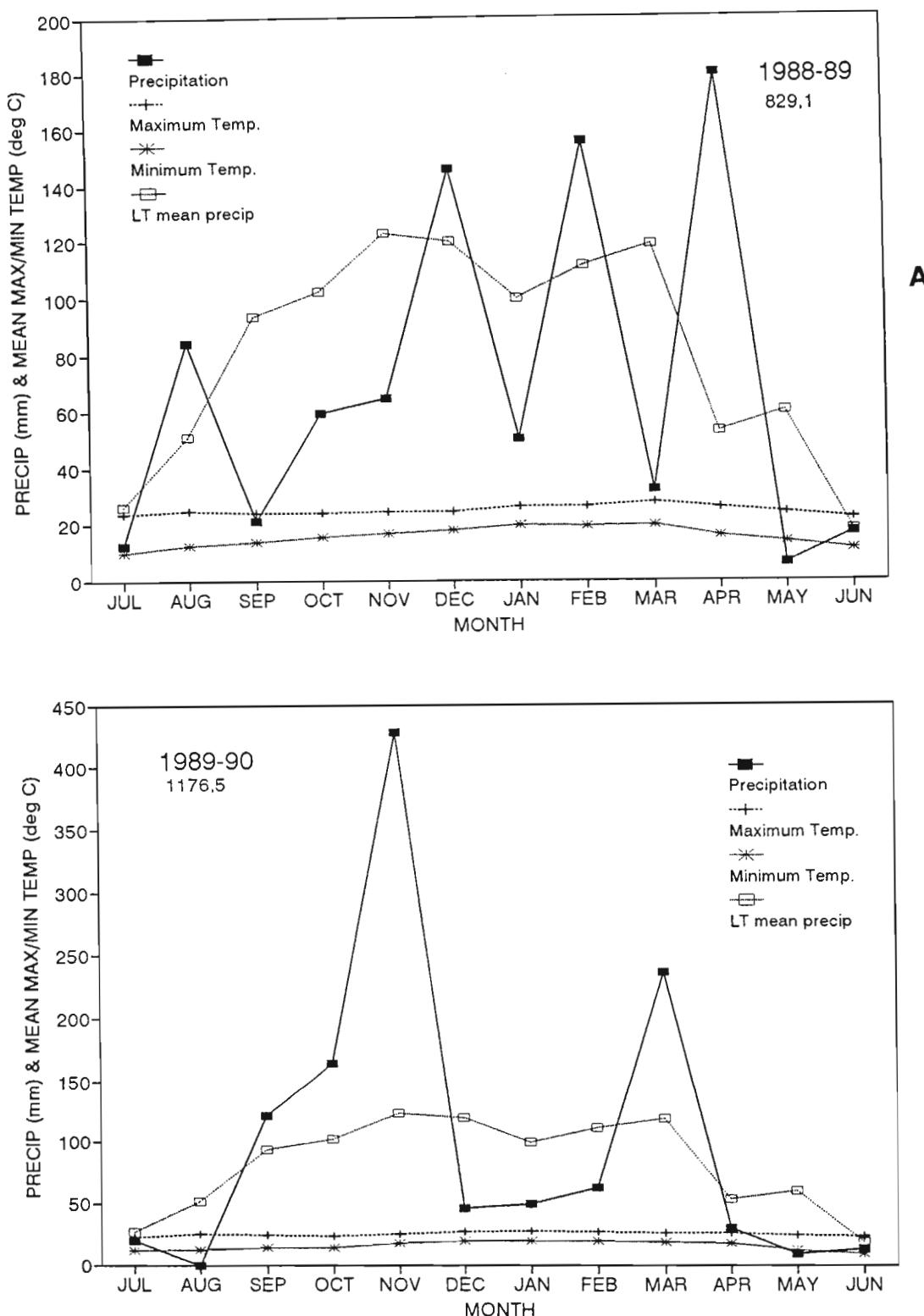
Accurate and consistent records of temperatures and precipitation over a long period were not available for the reserve itself, so climatic data were obtained from the Esperanza Sugar Estate which lies about 4 km to the southeast at a slightly lower altitude (Table 2.3). The climate is warm to hot and humid, being described as sub-tropical by Sandwith & Brown (1981) and humid-subhumid with warm summers and mild winters (Bioclimatic Subregion 2b) by Phillips (1973). The temperature range is relatively small and frosts do not occur, the lowest mean minimum temperatures (8,5°C) being recorded in June-July (Fig. 2.24 & Table 2.2). Annual precipitation averages 976,2 mm, most rain falling in the period September-March (Fig. 2.24). Over the four July-June periods of the study, precipitation was rather erratic (Figs 2.25 and 2.26) but was within  $\pm 20\%$  of the mean in all but 1991-92 period, when the total of 571 mm was only 58,5% of the mean. Fig. 2.26B shows that the effects of the prevailing drought were apparent from December 1991 onwards, and the total precipitation for the 1992 calendar year was only 326,2 mm, 33,4% of the mean.

#### **2.2.11.2 Vegetation**

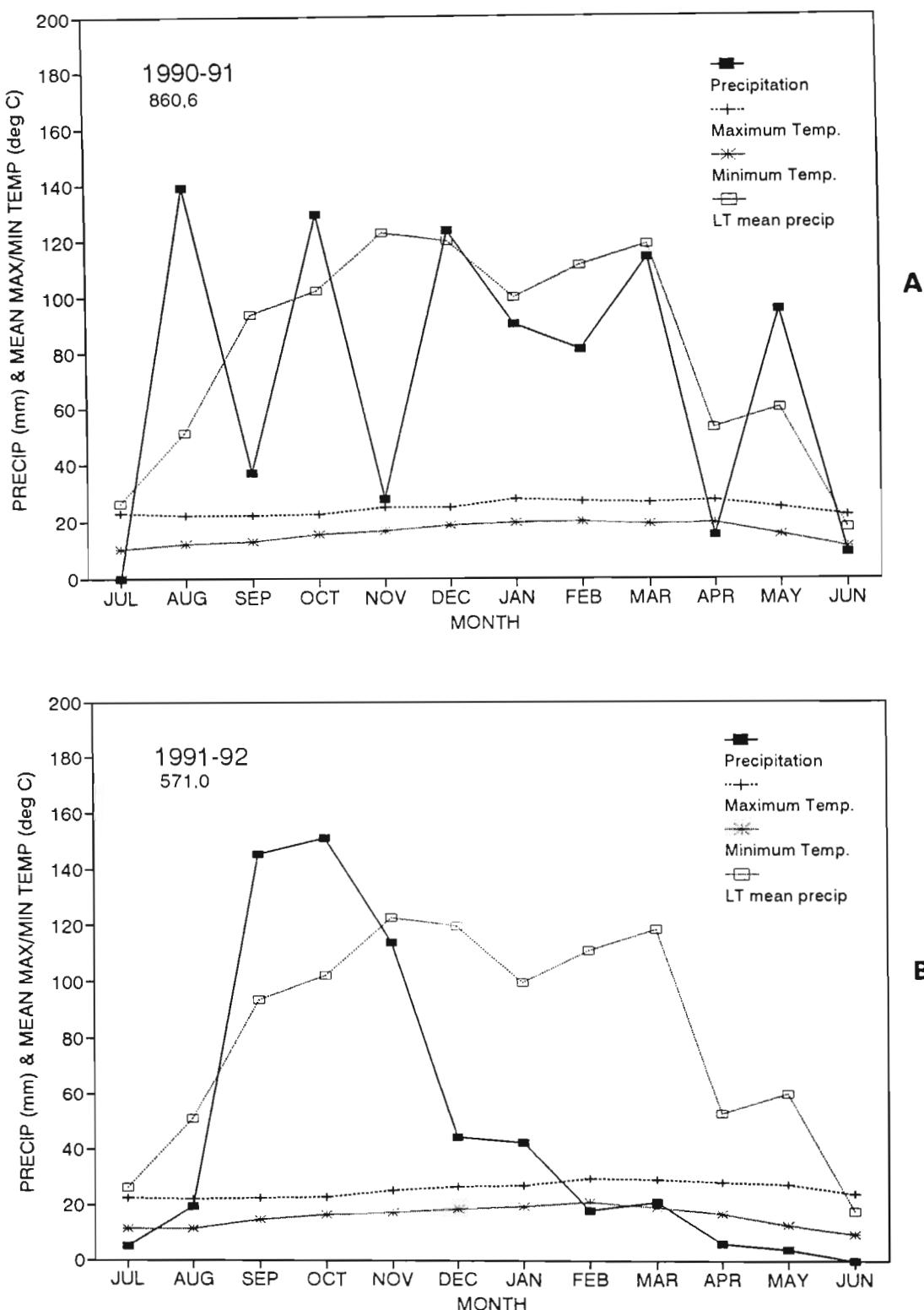
The reserve's vegetation is described in some detail by Sandwith & Brown (1981). One of the effects of previous cultivation has been the introduction and spread of several alien woody plants. The forest is typical Coast-belt Forest of Veld Type 1a (Acocks 1988) and the grassland is sourveld, dominated by tall *Themeda triandra* on the steeper slopes where it has been relatively unmodified. In some areas where domestic stock were grazed, especially on the flatter plateau area, *Aristida junciformis* dominates, while dense patches of *Cymbopogon excavatus* occur on some ridge-tops. Other grass species include *Digitaria* sp., *Hyparrhenia hirta*, *Panicum maximum* and *Paspalum dilatatum* (Sandwith & Brown 1981), while clumps of bracken *Pteridium aquilinum* also occur, particularly at forest edges.



**Fig. 2.24** Vernon Crookes Nature Reserve, Umzinto, Natal: mean monthly precipitation (mm) and maximum and minimum temperatures ( $^{\circ}\text{C}$ ), July-June. The number of years of weather records, and the mean annual precipitation, are shown.



**Fig. 2.25** Vernon Crookes: monthly precipitation (with annual total) compared with long-term (LT) mean monthly precipitation, and monthly mean maximum and minimum temperatures. (A) July 1988-June 1989. (B) July 1989-June 1990.



**Fig. 2.26** Vernon Crookes: monthly precipitation (with annual total) compared with long-term (LT) mean monthly precipitation, and monthly mean maximum and minimum temperatures. (A) July 1990-June 1991. (B) July 1991-June 1992.

### **2.2.11.3 Grazing and management**

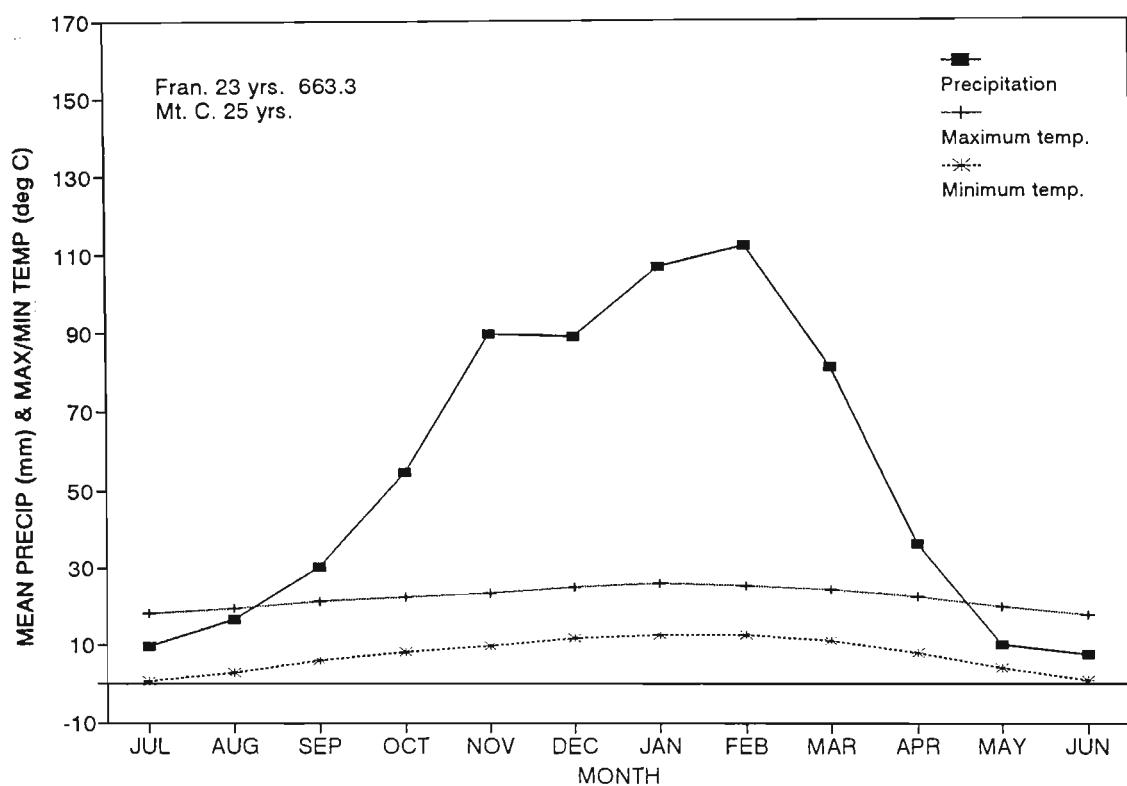
The reserve supports over 200 large herbivores, including about 100 Burchell's Zebra *Equus burchelli* 35 Blue Wildebeest *Connochaetes taurinus*, 20 Blesbok *Damaliscus dorcas phillipsi*, 20 Impala *Aepyceros melampus* and four Eland *Taurotragus oryx* (Natal Parks Board survey figures: I. Gordon pers. comm.). The usual Natal Parks Board biennial burning schedule by compartments is applied, burns taking place between June and September and being controlled so that minimal damage results to forest margins.

### **2.2.12 Franklin Vlei, East Griqualand, Natal**

Franklin Vlei ( $30^{\circ}19'S$   $29^{\circ}28'E$ ) lies on the East Griqualand plains, immediately east of the Swartberg-Kokstad Road. It lies in the upper reaches of the Mzintlava catchment and receives water from the Mzintlava and Mzintlanga Rivers. It is a large and important wetland, occupying 5 244 ha and extending for 32,2 km, and occupies a key position in its catchment, its flood-peak attenuation, sediment trapping and run-off interception probably being highly effective (Begg 1989). From a conservation point of view it rates as one of the most important wetlands in Natal (Begg 1989). Its middle reaches (the only area surveyed during this study) lie at about 1 510 m a.s.l. and include the wetland on the farm Vogelvlei, which was a long-term survey area and occasional study site for Whitewing Flufftail and other rallids from September 1988 to December 1992. During this period ornithological surveys were also carried out regularly in other parts of the middle reaches.

#### **2.2.12.1 Climate and weather**

There is little detailed information on climate but, like Mt Currie Reserve, Franklin Vlei is within Bioclimatic Subregion 4f (Phillips 1973) and experiences similar climatic conditions, i.e. warm summers and cold to very cold winters with regular frosts from May to August/September, sporadic hail and frequent lightning in summer, and frequent strong cold to hot dry winds throughout the year. Precipitation figures from Franklin Village give a long-term annual mean of 663,6 mm, the lowest of any study site, and show that most rain falls in the period October-March (Tables 2.1, 2.3 and Fig. 2.27).



**Fig 2.27** Franklin, East Griqualand, Natal: mean monthly precipitation (mm), and maximum and minimum temperatures ( $^{\circ}\text{C}$ ) from the nearest meteorological station (Mt. Currie, Kokstad), July-June. The number of years of precipitation and temperature records, and the mean annual precipitation, are shown.

### **2.2.12.2 Vegetation**

The vlei is surrounded by grazing land of Veld Type 56, Highland Sourveld to *Cymbopogon-Themedea* Veld Transition (Acocks 1988). My own studies of vegetation have been made principally across the vlei at the farm Vogelvlei and at several other areas of the middle reaches. The most deeply flooded areas are dominated by extensive beds of *Phragmites australis* and *Typha capensis*, while the permanently shallowly flooded to predominantly saturated ground is dominated by large sedges, principally *Carex acutiformis*, *Cyperus fastigiatus* and *Schoenoplectus corymbosus*, often with scattered stems of *Typha* and *Phragmites* intermixed. In seasonally wet peripheral areas and depressions, sedge meadow communities contain *Cyperus denudatus*, *Eleocharis dregeana*, *Fuirena pubescens*, *Juncus spp.*, *Kyllinga spp.*, *Pycrus macranthus* and *Schoenoplectus decipiens*, grading into hygrophilic grassland (not surveyed: see Begg (1989) for details of this vegetation type). In ditches and pools *Lagarosiphon major*, *Potamogeton trichoides* and *P. thunbergii* (submerged species), *Polygonum lapathifolium* (emergent) and *Ludwigia stolonifera* (in shallows or on mud) are common.

### **2.2.12.3 Use and management**

Cattle are regularly grazed in the marshes, while ridge-and-furrow cultivation is still practised in some areas and much of the vlei is burned every year. Much of the wetland is permanently waterlogged and large volumes of water are removed for irrigation, while the vlei has probably been altered to a moderate extent by ditching and canalization (Begg 1989). The wetland at Vogelvlei is less disturbed by grazing than are most areas, and is not burned every year.

### **2.2.13 Mt Currie Nature Reserve, Kokstad, East Griqualand, Natal**

Mt Currie Nature Reserve ( $30^{\circ}29'S$   $29^{\circ}25'E$ ) lies 3 km north of Kokstad, East Griqualand. Originally grazing land, the area was fenced off as the Phil Leary Nature Reserve in 1963 and was under the control of Kokstad Municipality until it was handed over to the Natal Parks Board on 1 April 1979. The reserve covers an area of 1 741 ha and lies between 1 400 and 2 225 m a.s.l., its northern boundary crossing the summit of Mt Currie (Fig. 2.28). Its vegetation is primarily fire-maintained tussock grassland, with some *Protea* savanna. Crystal Dam, which covers 21 ha at the southern end of the reserve, provides Kokstad's water supply, and the valley floor (1 440-1 480 m a.s.l.) between the dam and Crystal Spring holds most of the reserve's permanent wetland vegetation

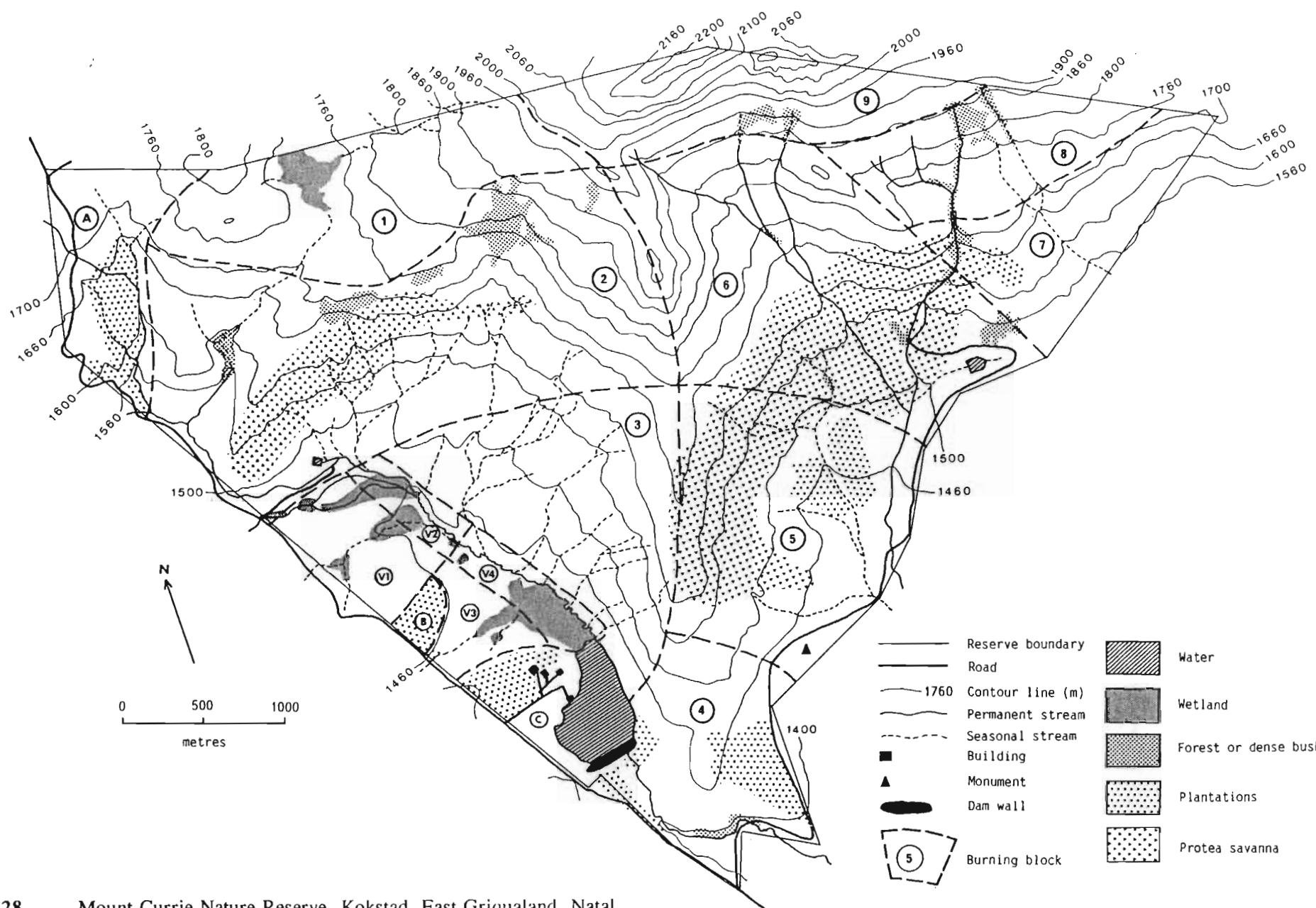


Fig. 2.28

Mount Currie Nature Reserve, Kokstad, East Griqualand, Natal.

patches, the only other significant wetland being at 1 750 m in the northwest corner. The permanent stream which feeds Crystal Dam runs approximately parallel to the road on the reserve's western boundary and also takes water from Crystal Spring. Many other streams, most of them seasonal, flow down the mountainside, the western slopes being particularly rich in springs and small streams. Permanent streams usually flow in deeply cut channels and most marshy areas adjacent to them (e.g. in Blocks V2 and V3) are created by tributaries and springs. The reserve is divided into blocks for fire management (Fig. 2.28; Table 2.5).

Mt Currie Reserve was an intensive study site for both Redchested and Striped Flufftails from December 1988 to July 1992. Its vegetation was therefore studied in some detail, seasonal changes in vegetation cover, invertebrate abundance and the populations of all bird species were noted, and the effects of burning were assessed. This reserve was the most intensively investigated of the project's study sites.

#### **2.2.13.1      Climate and weather**

Daily precipitation and temperature data were obtained from the Kokstad Agricultural Research Station which abuts the reserve to the southeast. Fig. 2.29 shows the mean monthly precipitation, maximum and minimum temperatures over the 60-year period to December 1992. The monthly precipitation and monthly mean maximum and minimum temperatures for the four years of the study are shown in Figs 2.30 and 2.31. Annual precipitation averages 777,9 mm and most rain falls in the period October-March (Table 2.1). The summers are warm and the winters cold, with below-zero temperatures possible at any time from April to October and most frequent in June and July (Table 2.6 gives the number of nights of frost per month for the years 1988-1992), while snowfalls may occur from June to as late as October. Snow does not usually lie for more than 24 hours, except on the highest ground. The area has the largest temperature range recorded at any study site during the study period (Fig. 2.9). In summer lightning is frequent, while hailstorms are occasional but may do considerable damage (usually very localized); the effects of a severe hailstorm are described in Chapter 7, Section 7.4.6, 7.4.7 and 7.4.11. Winds are often strong and cool, but hot dry berg winds also occur, such conditions being typical of Bioclimatic Group 4 (Phillips 1973), Subregion 4f of which includes the study sites at Mt Currie, Franklin and Penny Park.

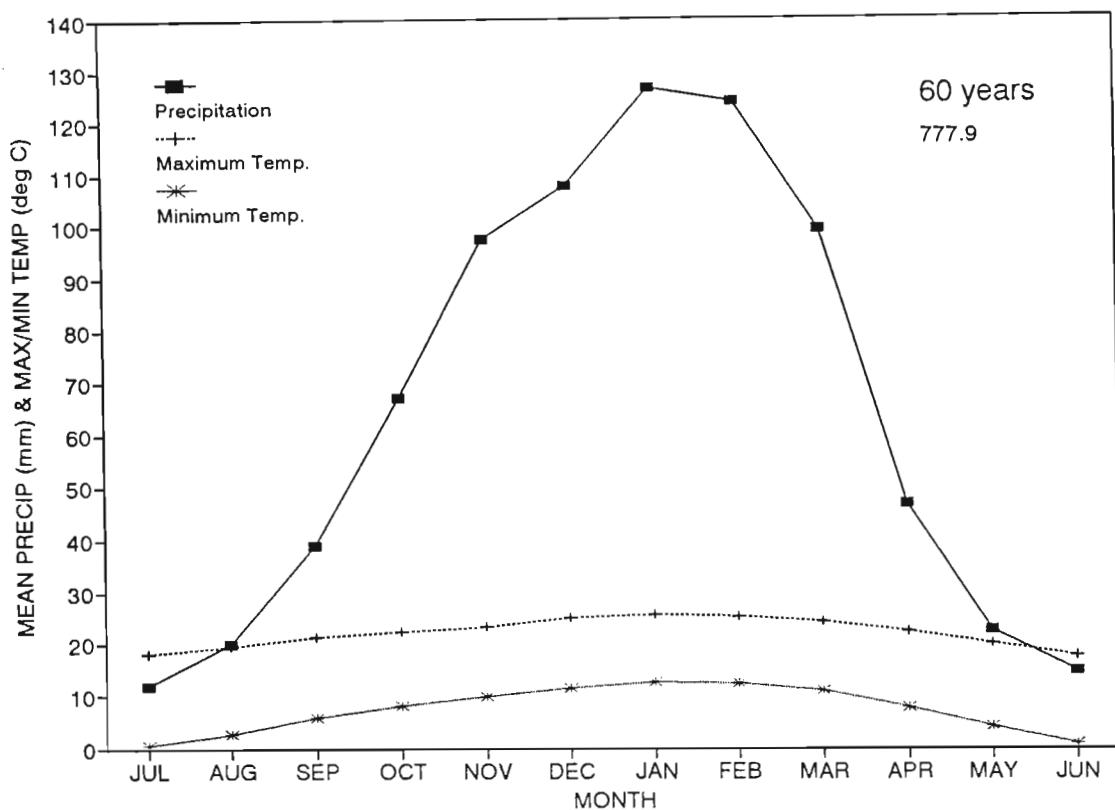
Total precipitation was 30% higher than the mean in the period July 1988-June 1989 (Fig. 2.30A) and within  $\pm 9\%$  of the mean in the other three years. The effects of the prevailing drought were not as apparent at Mt Currie as at other study sites, and the precipitation for the period July-December 1992 was 266,7 mm, 77,5% of the mean.

TABLE 2.5

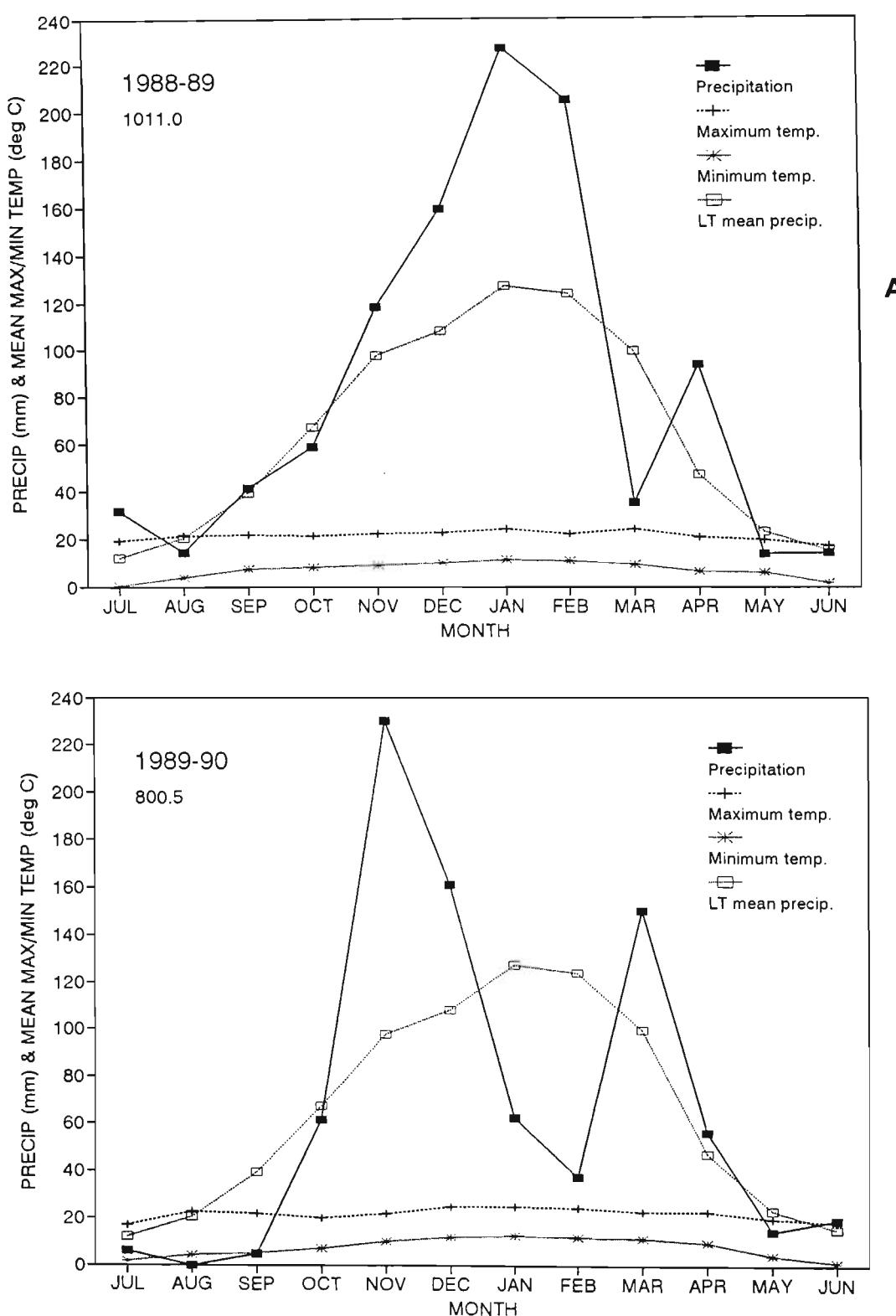
Sizes and major features of Mt Currie Nature Reserve blocks.

Block No.	Area (ha)	Major features
1	163	Grassland, with one permanent wetland of 10 ha.
2	375	Grassland, forest and scrub patches, <i>Protea</i> on south slopes above Crystal Spring at 1500-1700 m.
3	166	Grassland, from valley to rocks on ridge.
4	124	Grassland, exotic plantations (wattle and gum).
5	171	Grassland, <i>Protea</i> from 1500 to 1680 m (to ridge), wattle plantations.
6	252	Grassland, forest and scrub patches, small dam, <i>Protea</i> at 1520-1700 m.
7	90	Grassland, <i>Protea</i> , wattles, riverine forest, scrub.
8	102	Grassland, forest and scrub.
9	100	Mountain peak: rocky outcrops, cliffs, grassland.
A	44	Pine plantations and disturbed grassland.
B	5	Pine plantation.
C	40	Crystal Dam (21 ha), campsite & housing, pines.
V1	49	Grassland (cleared plantations), 2 drainage lines.
V2	15	Valley floor grassland and wetland.
V3	24	As V1, with one major drainage line.
V4	21	Dam intake reedbeds, wetland, grassland.

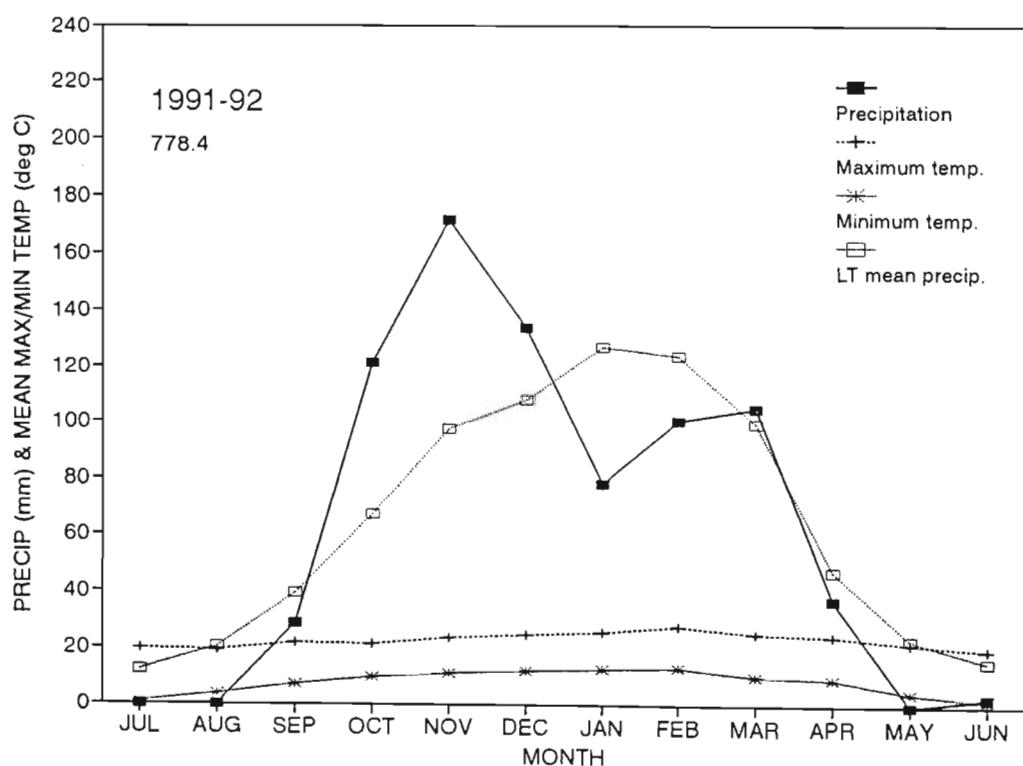
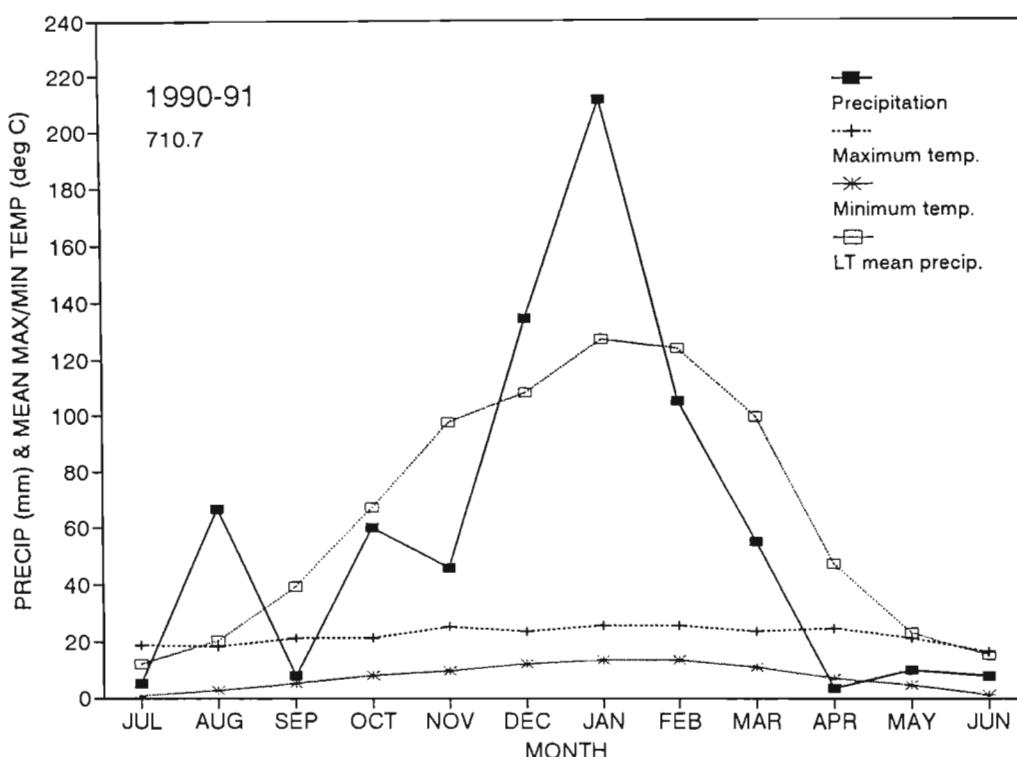
Total area: 1 741 ha



**Fig. 2.29** Mount Currie: mean monthly precipitation (mm) and maximum and minimum temperatures ( $^{\circ}\text{C}$ ), July-June. The number of years of precipitation records, and the mean annual precipitation, are shown.



**Fig. 2.30** Mount Currie: monthly precipitation (with annual total) compared with long-term (LT) mean monthly precipitation, and monthly mean maximum and minimum temperatures. (A) July 1988-June 1989. (B) July 1989-June 1990.



**Fig. 2.31** Mount Currie: monthly precipitation (with annual total) compared with long-term (LT) mean monthly precipitation, and monthly mean maximum and minimum temperatures. (A) July 1990-June 1991. (B) July 1991-June 1992.

TABLE 2.6

Number of nights when temperatures below 0°C were recorded at Mt. Currie (Kokstad Agricultural Research Station) in the years 1988-1992, with the mean number of nights of frost per month for the period.

Year	Month:	Number of nights of frost per month				
		Apr	May	June	July	Aug
1988		1	3	13	13	5
1989				8	12	2
1990			3	11	11	5
1991			5	10	13	4
1992			5	8	9	5
Mean		0,2	3,2	10,0	11,6	4,2
						0,8

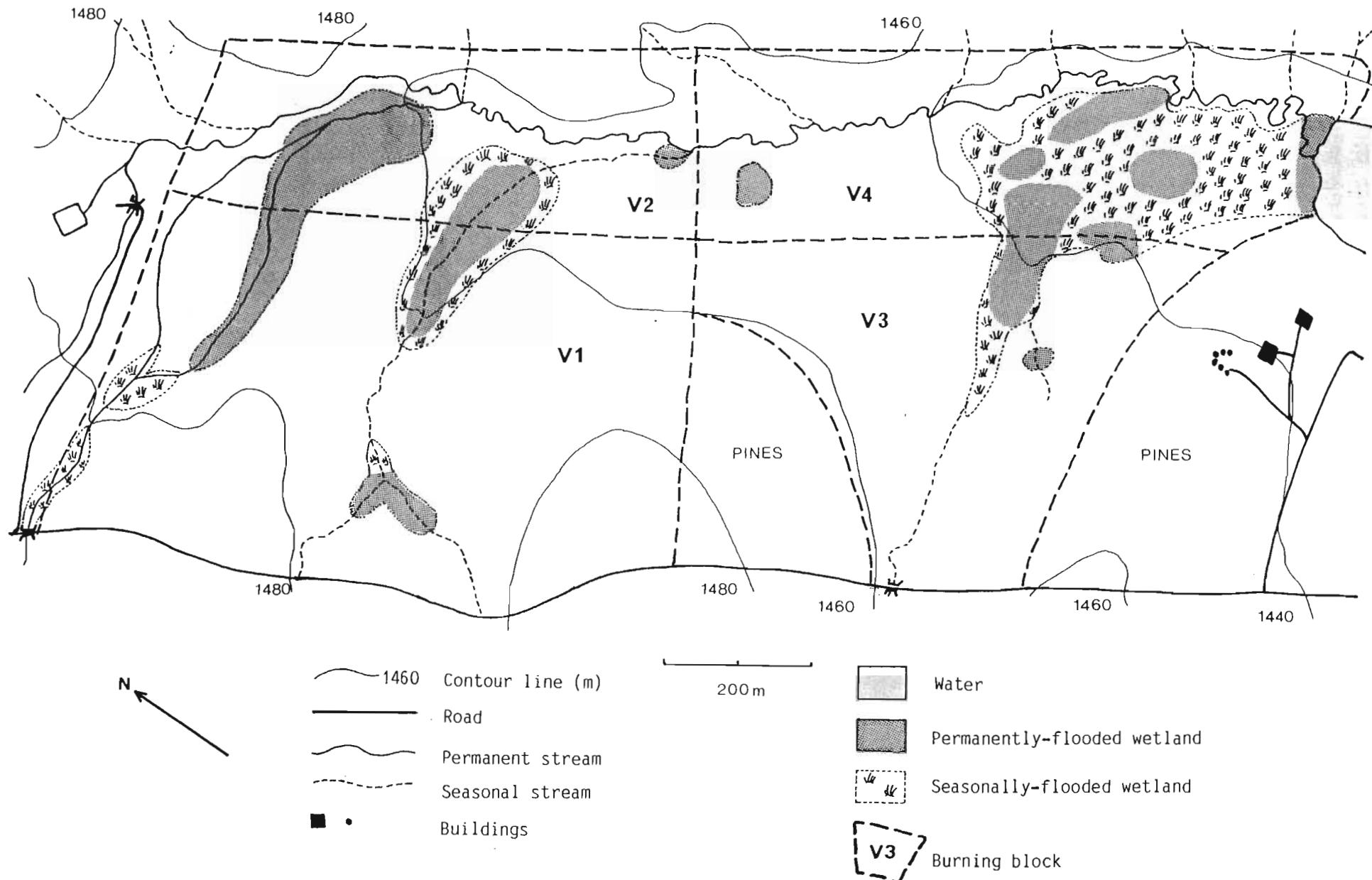
### 2.2.13.2 Vegetation

The vegetation of the area is predominantly grassland, broadly defined as Highland Sourveld (Veld Type 44a), which grades into a Highland Sourveld to *Cymbopogon-Themedea* Veld Transition (Veld Type 56) at lower altitudes outside the reserve to the south and east (Acocks 1988). Since 1963 the veld in the reserve has not been grazed by domestic stock and has been subjected to a biennial burning regime. The dominant grass over much of the reserve is *Themeda triandra*, while *Tristachya leucothrix* is also common, being dominant in a few areas in the north and east. Other common grasses include *Alloteropsis semialata*, *Diheteropogon filifolius* and *Trachypogon spicatus* (generally distributed), and *Harpochloa falx*, *Heteropogon contortus*, *Koeleria capensis*, *Microchloa caffra*, *Panicum natalense*, *Rendlia altera*, *Setaria nigrirostris* and *Sporobolus africanus* (localized). The grass *Eragrostis curvula* is dominant, and *E. plana* and *E. racemosa* are locally common, on previously poorly-managed or disturbed land, especially around the valley bottom area in the southwest (Blocks V1-V4, Fig. 2.28). In this area the thatch grass *Hyparrhenia hirta* is common to dominant over large areas, with *H. dregeana* also present.

On some mountain slopes of Blocks 2, 5, 6, 7 and 8, at altitudes of 1 450-1 700 m (Fig. 2.28), the veld is a savanna of *Protea caffra*, with *P. roupelliae* on the higher ground and ridges. Isolated patches of tall dense forbs occur, principally on ground cleared of wattle plantations and especially above the small dam at the border of Blocks 6, 7 and 8, while about 4 ha of bracken-briar (a mixture of *Pteridium aquilinum* and *Rubus pinnatus*) covers some low slopes here.

The few forest patches are small (Fig. 2.28), mostly on steep and often rocky ground above 1 600 m and associated with watercourses. Of the 24 tree species identified by D.N. Johnson (pers. comm.), common trees include *Clausena anisata*, *Dais cotinifolia*, *Halleria lucida*, *Heteromorpha arborescens*, *Kiggelaria africana*, *Maytenus undata*, *Olinia emarginata*, *Rhamnus prinoides*, *Rhus dentata* (forest margins) and *Scolopia mundii*. *Buddleja salviifolia* and *Leucosidea sericea* occur in the forest and also form dense patches on valley sides and around screes at all altitudes. Some exotic tree plantations (pine, wattle and gum) exist (Fig. 2.28) but are being systematically cleared; all the dry grassland in Blocks V1 and V3 was formerly under pines, two small stands of which still remain.

Some of the permanently wet areas of Blocks V1-V4 (Fig. 2.32) are dominated by beds of *Typha capensis* in mud and shallow water, *Phragmites australis* principally along streams and at the dam intake, and extensive areas of pure *Carex acutiformis* marsh at the northern end of Blocks V1 and V2. These species also occur throughout sedge marsh in the other permanently saturated to flooded areas, in a mosaic with other sedges and rushes including *Carex austroafricana*, *Cyperus denudatus*, *C. longus*, *Eleocharis dregeana*, *Isolepis costata* var. *macra*, *Juncus effusus*, *J. exsertus*,



**Fig. 2.32** The wetland at Mount Currie, a long-term study site for the Redchested Flufftail.

*J. oxycarpus*, *Mariscus congestus*, *Schoenoplectus corymbosus*, *S. muricinux* and *S. paludicola*. In the seasonally wet transition area between sedge marsh and dry grassland above the dam intake in Block V4, the wettest areas of sedge meadow contain the sedges *Bulbostylis schoenoides*, *Eleocharis dregeana*, *Fuirena pubescens*, *F. coerulescens*, *Pycreus macranthus* and *P. oakfortensis*, with a transition to *Carex glomerabilis*, *Schoenoxiphium caricooides* and the grasses *Agrostis lachnantha*, *Andropogon appendiculatus*, *Eragrostis planiculmis*, *Festuca caprina*, *Harpochloa falx*, *Koeleria capensis*, *Pennisetum thunbergii* and *Tristachya leucothrix* in hygrophilous grassland on somewhat drier ground. The higher altitude wetland patch in Block 1, which becomes almost dry in winter, contains (among others) the sedges *Ascolepis capensis*, *Bulbostylis schoenoides*, *Carex austroafricana*, *Eleocharis dregeana*, *Fuirena pubescens*, with *Juncus exsertus* and the grass *Poa binata* (which was not recorded in the other wetland).

The tall herb *Epilobium hirsutum* occurs in moist parts of Blocks V1 and V2, usually in small patches, but in the relatively dry summer of 1992-93 this species increased dramatically in areas of *Carex* marsh and adjacent sedge-mosaic marsh which are normally permanently wet but were then moist to dry. A similar increase was noted at the Bromley (Zimbabwe) study site in 1992 (see Section 2.2.1.2 above).

#### 2.2.13.3 Grazing and management

The grazing pressure in the reserve is minimal, large herbivores being restricted to a herd of about 30 Blesbok, a small number of Oribi *Ourebia ourebi*, a few Reedbuck in the southwest vlei, and Mountain Reedbuck *Redunca fulvorufula* and Grey Rhebok *Pelea capreolus* on the mountain slopes.

Before 1989 the reserve blocks were burned according to the Drakensberg schedule, which is in line with Forestry Department practice, i.e. biennial burns, varying the burn timing on the following cycle: May (autumn), June/July (winter) and August/September (spring), early burns being done in order to reduce damage to *Protea* woodland (P. Thomson pers. comm.). However as legislation permits burns of this grassland type in agricultural districts only in August-September, special permission is needed to burn early and this sometimes causes problems. As it is thought that there is no significant difference in the damage done to *Protea caffra* woodland by a burn at any time during the May-September period, as long as the burn is controlled, cool and patchy (P. Thomson pers. comm.), it is judged preferable to burn in spring, and this has been done at Mt Currie since 1989.

The established biennial schedule at Mt Currie involves burning Blocks 1, 2, 4 and 5 in year 1 and Blocks 3, 6, 7 and 8 in year 2. Blocks A-C are fire exclusion blocks while Block 9, the mountain peak, falls outside the Natal Parks Board's controlled burning area and is not normally burned. Prior to 1990 the entire valley floor between Crystal Dam and Crystal Spring was burned with Block 3. After the first full year of this study it was obvious that burning the entire wetland was likely to have a detrimental effect on the area's sedentary Redchested Flufftails, which thereby lost virtually all available habitat and were forced to emigrate. Accordingly, from 1990 the valley floor area was divided into four burning blocks (V1-V4), Blocks V2 and V3 being burned in year 1 and V1 and V4 in year 2.

Firebreaks are burned throughout the reserve in May and June. The timings of block burns during the study period are given in Table 2.7. During the relatively dry year of 1992 Blocks 6, 7, 8 and 9 were burned by runaway fires in July, while Block 5 was ignited by lightning (Table 2.7).

#### **2.2.14 Penny Park, near Kokstad, East Griqualand, Natal**

The Penny Park wetland lies on the Mzintlava River at 30°30'S 29°29'E and is 18,5 km south of the Mzintlava's outflow from Franklin Vlei and 8 km east of Mt Currie Reserve Staff Quarters (Mt Currie dominates its western horizon). It comprises about 120 ha of permanently and seasonally flooded ground with oxbows, along the flat valley floor east of the river, at 1 300-1 320 m a.s.l., and is 1,9 km in length and up to 0,9 km wide. Much of the area's seasonal flooding comes from the Manzimnyama River, which enters the wetland from the east. The wetland is surrounded by grazing land and maize cultivation.

The wetland was a study site for Whitewinged Flufftail and other rallids from February 1991 to March 1993. Surveys of the entire avifauna were also made monthly for comparison with those made at Mt Currie Reserve.

##### **2.2.14.1 Climate and weather**

No detailed information is available for the site, but its climate and weather are very similar to those of Mt Currie (see Section 2.2.13.1) except that winter frosts are more severe and long-lasting because of the site's position on the valley floor.

TABLE 2.7

The timing of burns at Mt Currie Reserve during the study period. ? = no date recorded; \* = accidental or runaway fire. Before 1990 Blocks V1-V4 were burned with Block 3 (see text). Blocks 7 and 8 are always burned together; Block 9 (mountain peak) is not included in the burning schedule.

Year	Block:	Dates on which Blocks (1-8 and V1-V4) were burned								
		1	2	3	4	5	6	7/8	V1/V4	V2/V3
1988		30 Aug	19 Jul	-	30 Aug	27 Jun	-	-	-	-
1989		-	-	7 Sep	-	-	11 Oct	? Oct	V1-V4: 7 & 18 Sep	
1990		2 Sep	2 Sep	-	4 Sep	4 Sep	-	-	-	5 Sep
1991		-	-	4 Sep	-	-	10 Sep	10 Sep	4 Sep	-
1992		-	-	2 Sep	29 Sep*	6 Jul*	6 Jul*	-	-	

#### 2.2.14.2 Vegetation

The permanently wet to saturated areas along the Manzimnyama River's meandering course and in the lowest depressions of the vlei are dominated by extensive beds of *Typha capensis*, while the tall sedges *Cyperus fastigiatus* and *Mariscus congestus* are locally dominant to co-dominant in smaller areas, especially on less deeply flooded ground, and clumps of *Cyperus denudatus*, *C. haematocephalus*, *Juncus effusus* and *Schoenoplectus decipiens* also occur. The sedge species persist into permanently saturated to seasonally flooded areas, where they occur with dense clumps of *Eleocharis limosa* and the hygrophilous grass *Leersia hexandra*. Seasonal flooding is extensive and often deep (up to 50 cm) in the peripheral hygrophilous grassland, which is dominated by large tracts of *Leersia hexandra*, clumps of *Paspalum dilatatum* also occurring in the less deeply flooded areas.

#### 2.2.14.3 Use and management

The vlei is heavily grazed by cattle which do considerable damage to the vegetation, both by eating new growth and by trampling and destroying vegetation cover. The entire vlei is burned every year, usually in September. There is some shooting of the flocks of ducks and geese which inhabit the vlei in the winter months. A proposal, made in 1991, to flood the entire wetland by constructing a storage dam for irrigation purposes has apparently been withdrawn.

## CHAPTER 3

### GENERAL METHODS

#### **3.1 The location and observation of flufftails**

Rallids which inhabit dense vegetation in marshes, grassland and forest are usually shy and secretive, flying rarely and being difficult to observe. The wetland and grassland flufftails are probably the most difficult of all rallids to observe in Africa because of their extreme unwillingness to fly and their virtual confinement to the interior of stands of very dense vegetation (Keith *et al.* 1970; pers. obs.); compared with flufftails, even the normally highly secretive *Aenigmatolimnas*, *Crex* and *Porzana* crake species may be flushed relatively easily and may occasionally be observed feeding and walking around in fairly open situations (Cramp & Simmons 1980; Taylor 1980, 1984, 1985a, 1987; pers. obs.). Fortunately, flufftails have very distinctive voices (Keith *et al.* 1970; Keith 1986), call frequently and, unlike some other rallids sharing their habitats, may be stimulated to make some sort of vocal response to taped playback of their calls at any time of year. Thus the only practical way of locating and identifying grassland and wetland flufftails is usually by auditory information, obtained either from unstimulated calling or from response to taped playback.

Initial location of the two forest flufftail species is usually also dependent on auditory information, but my previous field experience of these flufftails in the Afrotropics indicates that, once located, both species are relatively easy to observe because they are frequently active on areas of the forest floor where ground-level cover is sparse or patchy. Thus the shallow streams frequented by Whitespotted Flufftails in the forest interior are sometimes almost bare except for overhanging woody vegetation, while both Whitespotted and Buffspotted Flufftails often forage in leaf-litter on open patches of ground under trees, on stream banks or in the interior of thickets.

Observations of the wetland and grassland species in undisturbed habitats are usually confined to the very brief rare appearances made by the birds in open patches or at the edges of dense cover, and my previous field studies have shown that any prolonged and detailed study of their behaviour necessitates habitat modification by clearing observation rides and patches in the vegetation, the use of hides to conceal observer equipment, and the use of some method whereby the birds may be attracted to the area under observation - such as the provision of decoy models and/or an artificial food supply (for an example of the success of artificial feeding, see Steyn & Myburgh (1986)).

Little or no habitat modification is required to observe the two forest species as long as they can be attracted to areas sufficiently open to allow observation, this being achieved by the methods

just mentioned. In neither species is a hide absolutely necessary for concealment: most of my detailed behavioural studies of Whitespotted Flufftails in Kenya (Taylor & Taylor 1986) were made while sitting completely in the open, often within 1-2 m of the birds and their chicks, and I have achieved a similar degree of contact with Buffspotted Flufftails in South Africa. However the birds are sometimes alarmed by the frequent observer movements necessitated when manipulating photographic, video and sound-recording equipment, and under these circumstances concealment by a hide is advisable. Likewise it is obvious that the birds' normal behaviour may be modified by the presence of a visible observer, so it is advisable to make at least control observations of behaviour from a totally concealed position.

In contrast to the difficulty experienced in observing flufftails during their normal diurnal activities, the observation of nests is relatively easy. Incubating birds are very tolerant of the presence of an observer (either completely or partially concealed) close to the nest and the birds will tolerate some intervention at the nest, such as partial clearing of concealing vegetation cover and moving the incubating bird to examine the nest contents (Kakebeeke 1993; Manson 1986; video film of Striped Flufftail provided by B. Kakebeeke). In my study, however, I made no close observations of nests because the few which I located were relatively inaccessible in dense cover, and I considered that the value of nest observations was outweighed by the risks involved in vegetation clearance and other intervention. Not only might the birds have deserted, but the chance of predators locating the nests would have been greatly increased, as has been demonstrated for Striped Crake *Aenigmatolimnas marginalis* by Hopkinson & Masterson (1975) and has been observed for other African rallids (A. N. B. Masterson, G. Hopkinson and D. R. Aspinwall (pers. comms); pers. obs.).

In view of these problems it was necessary to develop surveying and mapping methods based largely upon auditory information, and to undertake some behavioural studies under partially manipulated conditions. Except in some situations where colour-ringed Redchested and Buffspotted Flufftails could be regularly observed over long periods (see Chapters 4 and 9), non-visual methods were normally used for locating flufftails, establishing the extent of their territories and monitoring their activities. Three non-visual methods were originally considered: radio tracking to determine home ranges and movements, call counts for censusing, and taped playback of calls for censusing and territorial mapping studies (see Sections 3.3-3.5).

### **3.2 Definitions of home range and territory**

The home range of an animal is the area in which it normally lives, except when dispersing or migrating (Brown & Orians 1970; Wittenberger 1981). It is defined without reference to any

particular type of behaviour or to the presence or absence of other animals, so that it does not imply a defended area or one from which conspecifics are excluded (Brown & Orians 1970). The calculated size of a home range increases with the number of observations, approaching an upper limit or asymptote at least during a given season (Wittenberger 1981).

The simplest definition of a territory is a behavioural one: that it constitutes any defended area (Noble 1939). This flexible definition does not imply exclusive possession of the defended area but Brown & Orians (1970) maintain that the concept of defence traditionally implies successful defence, and hence that exclusive possession is an essential characteristic of a territory. However, as animals may exclude intruders to different degrees, depending on how closely an intruder approaches the resident's core area, other biologists (reviewed by Wittenberger (1981)) have redefined territory in terms of site-specific dominance i.e. that the territory includes areas of overall dominance as well as those from which intruders are fully excluded. In contrast to these behavioural definitions, Pitelka (1959) and Schoener (1968) regard territoriality as an ecological concept, considering a territory to be any exclusively occupied area, its fundamental importance lying not in the behavioural mechanism (e.g. defence or mutual avoidance) by which it is associated with its occupants but in the degree to which it is used exclusively by those occupants.

For the purpose of my study I define a territory as a defended area which exhibits the following three characteristics, modified from those given by Brown & Orians (1970) and Wittenberger (1981): (1) it is normally a fixed area for at least the duration of the breeding season, outside which its size may be significantly affected by factors such as burning, desiccation or grazing, (2) it is essentially used exclusively by the territorial birds, conspecifics never penetrating the core area but occasional penetrations by adjacent territory holders being tolerated at common boundaries, and (3) within it the occupants advertise their presence by vocalizations and respond to taped playback. For mapping purposes the territory boundary is defined by the outermost points to which the territorial pair will follow and respond to the tape (see Section 3.4 (f)).

Home ranges were mapped (in most cases only for the breeding season) by noting all points at which identifiable territory holders were recorded visually, by spontaneous vocalization, or by vocal response to taped playback. The outermost points were then connected to form the smallest possible convex polygon (Wittenberger 1981). For records of birds flushed outside the normal territory area the bird was assumed to be a territory occupant if it flew into a known territory without subsequently being harassed by any other occupant.

### 3.3 Radio tracking for studies of territory size, behaviour and movements

Radio tracking is a very useful technique for the systematic collection of data on the behaviour of shy or elusive animals (Kenward 1987) and has been used in studies of rallid species to determine home ranges, movements and activity patterns (Bookhout & Stenzel 1987; Johnson & Dinsmore 1985; Massey & Zembal 1987; Stowe & Hudson 1991; Zembal *et al.* 1989). Superficially it appeared a very attractive technique for studies of flufftails, but on investigation several problems became apparent. I considered the feasibility of radio-tagging the three wetland and grassland flufftail species to achieve two principal objectives: the determination of home ranges and daily activity patterns throughout the year, and the investigation of local and long-distance movements. The following considerations were taken into account.

(a) Size of the transmitter package relative to the mass of the bird. Flufftails are small birds, Redchested Flufftails having a mean mass of 37,7 g (Chapter 4, Section 4.4.6) and Striped Flufftails weighing about 29 g (Keith 1986). There are no masses available for Whitewing Flufftail but my field observations confirm that it is one of the smallest species, measurements (Keith 1986) indicating that it is little larger than the Striped. Although the smallest birds seem to fly well carrying a transmitter package of 10-15% of their mass (Kenward 1987), there is no indication that small birds can perform all their normal activities unhindered if carrying a package of this size, and I considered it inadvisable to fit a large package to flufftail species which frequently need to move rapidly through very dense tangled vegetation. Kenward (1987) considers a 4-6% loading increase enough for animals above 50 g and the smallest rails to which transmitters have been attached appear to be Yellow Rails *Coturnicops noveboracensis*, which have a mass of 50-60 g (Ripley 1977), but the study in question (Bookhout & Stenzel 1987) gives no details of the size of the transmitter package used. Other studies (Johnson & Dinsmore 1985; Massey & Zembal 1987; Zembal *et al.* 1989) have been of larger species and have used packages of 4-5% of the body mass. Thus to avoid undue stress it seemed advisable to use transmitter packages of no more than 5% of the bird's mass, which limits package mass to about 1,5 g for the two smaller species and 1,9 g for Redchested.

(b) Package mass and performance. Using the smallest possible components the lightest package would be about 1,1 g, including a mercury battery of 300 mg which would transmit for 10-15 days, while a 1,3-g package containing a 500-mg battery would transmit for 3-5 weeks (Kenward 1987). Larger batteries give a total mass in excess of the limit. Bearing in mind that battery life may be reduced by environmental effects, one should estimate battery performance at the theoretical minimum. Detection ranges increase with transmitting antenna length and thickness; using a long whip antenna (possibly impractical for small flufftails in dense ground vegetation) is recommended but,

even with this, the feasible packages would give a maximum line-of-sight ground-level range of only 100-600 m (AVM 1987; Kenward 1987). Thus not only would the transmitting units not be adequate for monitoring long-distance movements, but tagged birds would need to be retrapped frequently in order to replace batteries.

(c) Adverse effects of capture and tagging. These may be acute, especially at critical times of the year. Breeding birds may desert clutches or abandon chicks, while the disturbance involved in tagging may be enough to stop a dispersing individual securing a territory (Kenward 1987). In a breeding study of two rallid species, Virginia Rail *Rallus limicola* and Sora *Porzana carolinensis*, Johnson & Dinsmore (1985) reported that, of 20 birds tagged, one Virginia Rail died when her transmitter antenna became tangled in vegetation and two brood-rearing Sora females quickly disappeared from the nest area. Thus breeding and dispersing flufftails might be seriously affected by tagging.

(d) It was considered advisable to trap at least two pairs (or five individuals) of each species to ensure a sufficient number of successfully tagged birds to make the study feasible. In view of the short battery life of the transmitter pack (see (b) above), these birds would have to be retrapped frequently for battery replacement. My flufftail trapping work (see also Section 3.8.2) suggested that, although sufficient Redchested Flufftails could be trapped initially, any attempt at frequent retrapping, particularly involving the trauma of reattaching packs, might cause individuals to become extremely wary and even to leave the area. Striped and Whitewinged Flufftails proved so difficult to catch that it would have been impractical to trap enough for initial tagging, and probably impossible to retrap them.

In view of the probable adverse effects of disturbance on territorial and breeding birds, and the impracticality of frequent retrapping, it was decided that radio telemetry was not a suitable technique for use in this study.

### **3.4 Censusing and territorial mapping using call counts and taped playback**

Counts of spontaneous auditory signs, or call counts, have been used in censusing birds for at least 60 years (Johnson *et al.* 1981). They do not involve the use of playback to elicit responses, but rely on counts of the number of spontaneously calling birds located. Playback has been used in avian sampling and census work since the mid-1950s (Campbell & Lack 1985: 467; Falls 1981; Johnson *et al.* 1981; Marion *et al.* 1981), and has proved an effective censusing and mapping tool both for readily-visible songbirds (Falls 1981; Johnson *et al.* 1981) and for species which present special problems because of their elusiveness, secretiveness or nocturnal habits (Marion *et al.* 1981).

Playback has been particularly effective in censusing and territorial mapping work on secretive wetland rallid species (Glahn 1974; Johnson & Dinsmore 1986a, b; Kaufmann 1987a, 1988; Marion *et al.* 1981; Zembal & Massey 1987).

I used both call counts and taped playback extensively in all habitats for all species during this study. Call counts were used only during the breeding season, predominantly in two situations: (a) during night surveys, to locate and estimate roughly the numbers of calling Striped Flufftails and Buffspotted Flufftails (and concomitantly the occasional calling Redchested Flufftail), before more detailed daytime exploration using taped playback, and (b) at dawn and dusk to locate and estimate numbers of calling Whitewinged Flufftails, which often responded poorly to taped playback (see Chapter 8). The approximate positions of the calling birds were plotted on large-scale maps for further investigation. When working in the study areas on other aspects of the research, such as vegetation sampling and observations of other bird species, all spontaneous calls of the study species were also noted and were subsequently added to territorial maps for reference.

Taped playback was the main census and mapping method used, being employed in overall population counts and in the mapping of individual territories. Various workers have pointed out the difficulties associated with the playback method, and have suggested ways in which to standardize its use (reviews in Campbell & Lack 1985: 467, Johnson *et al.* 1981, Marion *et al.* 1981). The census techniques described by these authors, and also those used for rallids by Glahn (1974), Johnson & Dinsmore (1986a) and Kaufmann (1988), are basically similar and all authors stress the necessity for standardization of playback times, periods, intervals and volumes at all sites, and for attention to be given to weather conditions which might affect the birds' responses.

My techniques were based on those recommended by the above authors. I attempted to standardize the playback method used for all species in all habitat types, but preliminary results, and my own previous field experience, demonstrated the need to modify the method for different species and at different times of the year.

All playback tapes used in this study contained calls recorded by me, mainly in South Africa, but a few in Kenya, Zambia and Zimbabwe. For each call used the date, time, habitat and circumstances of the recording were known so that, even if the function of the original call was unclear, the available data could be used in an attempt to interpret the call in relation to other birds' responses to it under experimental conditions. For each species a playback cassette tape was assembled containing the male's breeding-season advertising call and the major territorial and alarm calls of both sexes. The total length of this tape was between 3 and 10 min, depending on the species and the variety of calls available. (Further details of the calls included on tapes are given in the relevant species accounts in Chapters 4 and 7-9). A second tape containing a variety of the same calls

made by other individuals was used if response to the original tape waned at any time. For Redchested and Buffspotted Flufftails a further tape was made containing a series of breeding and other calls, often of low intensity and infrequent occurrence, which were played back during experiments and observations to determine the functions and seasonality of the calls.

All playback tapes were composed of calls of the highest available quality. When background noise affected the quality and clarity of call sequences required for playback, the frequency spectra of the flufftail calls were analyzed and the recordings were then sonically filtered to remove unwanted extraneous noises outside these frequency spectra. When necessary, call sequences were re-recorded to the full dynamic range of the original recording so that the playback sound pressure level (SPL) could be adjusted to the optimum level without the introduction of distortion or significant background hiss.

The following standard methods were applied to all playback-dependent censusing and territorial mapping work.

(a) All calls were played back on a Marantz C 205 portable cassette recorder, using only the built-in loudspeaker, this equipment generating a sufficient SPL for all situations. Flufftails approach an observer closely as long as they can remain in dense cover, and birds would often approach to within 1 m of the operator holding the machine, and would usually follow quickly when the operator moved to other points within or near the territory being mapped. An extension loudspeaker on a 20-m cable was used only for behavioural studies in which birds were attracted to fixed observation points away from the observer.

(b) Calls of "strange" individuals were always used for playback, except in experiments to determine the response of birds to their own calls or those of neighbours, mates or offspring, when specially prepared tapes were used.

(c) To optimize responses for territorial mapping, playback was usually made at SPLs judged to be equal to, or slightly higher than, those normally produced by the species concerned, the playback SPL being measured at a standard distance of 1 m from the loudspeaker. It was often impossible to determine accurately the correct SPL to use, as (a) accurate measurement of the SPLs of calls made by concealed birds was usually impossible since the exact distance from the observer could not be judged, and (b) the territorial-call SPLs of any individual often varied considerably, depending on the season, the stage of calling reached (territorial calls often began quietly, getting louder as the birds became more excited), the direction in which the bird was facing relative to the observer, and the density of intervening cover. Playback SPLs were determined by trial and error and were then standardized at optimum levels for each playback sequence. They usually varied between 60 and 85 db, most territorial and advertising calls being broadcast at 70-80 db; in general each

increase of 3 db produces a change in volume discernible to the human ear. For more general census work, especially in a large expanse of habitat, playback was made at the maximum SPL possible without distortion (up to 90 db) to elicit responses from as large an area as possible.

(d) The intervals between playback of calls and the sequence of calls played simulated as far as possible the birds' normal performance at that time of year.

(e) In census work an attempt was always made to cover all available habitat, playing the tape at points separated by distances of 30-60 m, depending on species, circumstances and site (see individual species accounts). It was usually possible to walk through the whole area to do this with minimum disturbance, but when complete penetration was not possible (e.g. in deeply flooded reedbeds, very deep mud, impenetrable thickets, or places where nesting birds would have been disturbed) the tape was played around the perimeter of the area. The playback tape was run for a maximum of three complete passes at each point, or until a bird responded from a distance less than that between two playback points, when the playback machine was immediately moved to the next point. All playback points and all vocal registrations (including call type and duration) were recorded on a large-scale map of the site, a new copy being used for each visit; any incidental visual records were also marked on this map. Section 3.5 describes the method of analysis of these data.

(f) In territorial mapping work, playback at any point was discontinued if the birds did not respond after three complete plays of the tape. The whole area of habitat was covered at one visit and separation of playback points was made according to the criteria described in section (e) above. I tried to locate both members of each territorial pair, plus any calling juveniles present. When the birds had been located they were attracted as close as possible and then playback positions were changed repeatedly in order to determine the total area over which the birds would approach the tape and to map the territorial boundary. Although adjacent pairs usually called only on their own side of a common territorial boundary, some birds occasionally penetrated adjacent territories in response to playback, the degree of penetration being least in the breeding season; this was taken into account when plotting common territorial boundaries. All playback points, and all vocal registrations and visual records of all individuals were plotted on a large-scale map, a new copy being used for each visit.

(g) In situations in which it was difficult to hear quiet or distant responses, the observer periodically moved away from the playback machine to a distance (20-30 m) at which all responses would be audible.

(h) In all playback work a dictaphone was used to record spoken commentary on response types and durations, any behavioural information obtained, incidental observations on habitat, and other relevant data. The dictaphone proved particularly useful for making unplanned recordings of

unfamiliar or rarely-heard vocal responses at close range; sonically filtered copies of good-quality dictaphone recordings could be used for playback.

(i) At long-term study sites a complete census was made at least once or twice per month throughout the study period. At times when migratory birds were arriving, or when territory holders might be departing after burning or other habitat destruction, censuses were made more frequently. For example, censuses of Striped Flufftails were made at 3-7 day intervals when nocturnal call counts indicated new arrivals, while Redchested Flufftails were censused immediately before, and at least once immediately after, a planned burn. In general 1-2 censuses per month were sufficient and no appreciable decline in response rate was noted in resident pairs at this census interval. An interval of 1-3 months was allowed before remapping territories at these sites, to avoid excessive disturbance or possible habituation to playback.

(j) Although all flufftails except Whitewing will respond to tape playback at any time of the day, in the warm summer months the best responses were obtained in the four hours after dawn and the three hours before dusk, and playback was normally confined to these periods. In the cold winter months, responses were at their best after the ambient temperature in the morning has risen sufficiently to encourage general foraging (this may be judged by the activity of other insectivorous birds in the vegetation) and before the temperature has dropped too much in the evening (i.e. up to the time when general bird activity ceases and small passerines go to roost). In hot summer weather response rates were very poor in the period between 10h00 and 15h00, when high temperature and humidity may also adversely affect the playback machine. Although some Redchested Flufftail pairs will respond with territorial calls to playback on still moonlit nights at the height of breeding activity, the other species did not respond at night and in general nocturnally-singing males of all species never responded to song playback (except sometimes to fall silent themselves). Responses were poor in wind, rain and mist, and playback in such weather conditions was avoided.

(k) In territorial mapping, unless another bird appeared, playback was continued to 20-30 m beyond where the bird last approached closely, before the operator moved to another territory. When birds lack close neighbours, they may follow playback far into unoccupied areas, giving extremely large estimates of territory size (Falls 1981). This was true especially for isolated Striped Flufftails at Mt Currie, and care had to be taken to recognize this occurrence when mapping: in most cases it was not possible to map the territories of such birds. Mapping the territory of any Redchested Flufftail pair isolated in a small patch of suitable habitat was relatively easy, as the territory usually covered all the suitable habitat available.

(l) Only one bird or pair was mapped at a time except for neighbouring pairs at common boundaries.

(m) When several birds approached the observer simultaneously during mapping, playback positions were changed rapidly in an attempt to separate the birds and to lead each back towards the centre of its own territory. I also learned to distinguish some resident individuals by ear, on the basis of consistent individual differences in the advertising and territorial calls, and in the low-frequency sounds preceding the latter. This was possible with a number of the Redchested Flufftails at long-term study sites such as Mt Currie, Allerton and Gartmore. Occasionally two observers were used to pinpoint calling birds accurately.

(n) During mapping, if a bird suddenly stopped responding, the observer would return to a spot where it had responded just beforehand and would determine whether the bird still responded there, i.e. whether or not it had become habituated to playback.

(o) Instead of making a grid of marked points for reference in mapping work (Falls 1981), natural features such as isolated trees, rock outcrops, clumps of a particular type of vegetation, tracks, channels, streams, etc. were plotted on maps and used as reference points. Occasional use was made of plastic tags or marker wands where insufficient natural features were available.

(p) As any colour-ringed resident Buffspotted or Redchested Flufftail was normally seen only in a small area from a fixed observation point well within the territory, information from such observations was usually only of value in census work, and was included on the census maps. Any observations of identifiable colour-ringed birds elsewhere were also recorded on the territorial maps.

### **3.5 Estimating populations from census data**

When interpreting census results two or more responses of a bird of the same age and sex from approximately the same position, unless heard simultaneously, were assumed to be from one individual. During any census not all the birds present at a locality may be stimulated to call, and the population estimate from a single census was invariably lower than that from a detailed territorial mapping survey. At long-term study sites, by combining over periods of 1-2 months all census data and the locations of spontaneous calls and sightings made during other visits, a more accurate population estimate could be obtained. Clusters of registrations from repeated visits, and simultaneous responses from adjacent pairs, were used to define territory locations, which were comparable to the detailed territorial maps. The existence of resident individuals which could be identified by voice or (for some Redchested and Buffspotted Flufftails) by colour rings considerably improved the effectiveness of this procedure. To achieve an acceptable separation of adjacent clusters, it was normally deemed essential that at least 30% of the registrations in a cluster were contemporary with those from each adjacent cluster.

As this method was applied to populations of non-colonial birds, both breeding and non-breeding, which were normally stationary, the results were suitable for evaluation according to the international standard mapping method for bird census work (Svensson 1970), and were considered to give an accurate estimate of the total population in each study area. The estimates thus obtained formed a useful comparison with those generated by territorial mapping work. If any census result indicated the sudden appearance of new individuals, or the departure of resident birds, a more detailed mapping survey was carried out in the area concerned at the earliest opportunity.

### **3.6 Vegetation sampling**

As explained in Chapter 1, flufftails inhabit only dense vegetation and it was hypothesized that, in grassland and wetland, the amount of cover and the height of the vegetation are important factors determining the suitability of sites for foraging, shelter, breeding and concealment from predators, while in forest the amount of cover provided by both ground vegetation and low-growing understorey woody plants would be the equivalent variables. Vegetation sampling was carried out in all three major habitats (grassland, wetland and forest) in an attempt to discover the factors affecting the suitability of the vegetation for occupation by flufftails and to relate the effects of changing vegetation structure to the presence and movements of the study species. The sampling methods used, and the duration of the sampling periods, varied with the habitat type and the variables under investigation. For sampling vegetation cover and height in grassland and wetland (as described in Sections 3.6.1.1-2, 3.6.2 and 3.6.3.2-3) minimum sample sizes were originally determined by calculating the standard deviation of data gathered during November trials at the sampling sites and determining the sample size required to give a 0,05 level of accuracy at the 0,95 confidence level (Lehner 1979). The minimum sample sizes thus calculated were 20 for grass cover samples, 40 for grass height samples, and 20-25 for wetland vegetation samples. If practical, larger sample sizes than the calculated minimum were selected (see the relevant sections below for details). It was subsequently found that the selected sample sizes usually gave acceptable accuracy except at the start of regrowth at some sites, when variations in height and cover could be much greater than later in the summer.

#### **3.6.1 Measurements of vegetation cover**

In grassland and wetland vegetation, cover is properly defined as the proportion of the ground occupied by perpendicular projection onto it of the aerial parts of the plant species under consideration; as the values for all species are summed the total cover may exceed 100% because of

spatial overlap of plants of different species (Greig-Smith 1983). In this study the total cover is defined as the overall percentage of ground obscured by vegetation when viewed from above; overlap is ignored so that the maximum possible cover is 100%. The definition and sampling of the relevant vegetation cover in forest is more difficult, and in this study I define this vegetation cover as the proportion of a unit area, in a vertical plane at a constant distance from the observer, which is obscured by the intervening vegetation at each of several heights above the ground, each observation being made from the same height as that of the unit area being observed (see Section 3.6.1.3). Ground cover in regenerating wetland vegetation (Section 3.6.1.2) is defined as the overall percentage of ground obscured by the aerial parts of all plants at a height of 5 cm above the substrate and is a rough measure of the amount of clear ground available to flufftails for foraging and moving around in different vegetation types.

### **3.6.1.1      Grassland**

In seasonal Striped Flufftail territories at Mt Currie Reserve the cover was estimated by determining the percentage (to the nearest 5%) of ground obscured by all vegetation (grass and forbs) in each of 20 1-m-square quadrats positioned randomly in each survey plot during each sampling period. The mean cover and standard deviation were calculated for each data set. Although giving only a rough measure, this method was quick and easy and was judged sufficiently accurate to indicate any differences in the overall vegetation cover between plots, burning regimes and months which might be expected to have a significant effect on the vegetation's suitability for occupation by Striped Flufftails. Comparative measurements were made in grassland in each of the three normal stages of the burning cycle, i.e. spring-burned less than one year before, spring-burned 1-2 years before, and firebreak-burned, i.e. burned every year in May-June. Each survey plot was sampled monthly for at least one year. The firebreak-burned grassland measurements were taken principally for comparison of spring growth rates with those at burned sites, as no Striped Flufftail territory was ever located completely within the narrow confines of a firebreak. Comparative measurements were made in permanent territories at Vernon Crookes Nature Reserve in July 1992.

### **3.6.1.2      Wetland**

The wetland vegetation in Redchested Flufftail territories at Allerton, Gartmore and Mt Currie was sampled only to determine the rates of vegetation regrowth, and the time required for effective cover to develop, after a burn. Sampling normally began in September-October, up to 2 months after

a burn and as soon as noticeable regrowth had started, was repeated at intervals of up to one month and ceased when the burned territories were reoccupied by Redchested Flufftails, a maximum of four months later. At each site measurements were made only in stands of the dominant plant species in the territory under investigation, and comparative measurements were made in portions of the territory which differed in their degree of soil saturation and/or the timing or method of defoliation. This enabled a comparison to be made of the growth rates of the dominant vegetation types under various combinations of these variables experienced in the territory during the experimental period. Table 6.1 (Chapter 6) shows the combinations of these variables at each sampling site.

At Allerton cover was measured by determining the total length of interception made by the growing leaves of the plants on line transects, the proportion of the total length intercepted giving a measure of the cover (Greig-Smith 1983). This method was found to be relatively quick and easy and, because the vegetation was very uniform in structure with very little mosaic pattern (only one or two plant species were usually present and plants grew at fairly regularly spaced intervals), it was possible to obtain sufficient accuracy with a number of short transects rather than few long lines (Greig-Smith 1983). A modification of the line-intercept method of measuring vegetation cover (Mueller-Dombois & Ellenberg 1974) was used, this method often being used for measurement of basal cover and providing a reliable estimate of this in tropical grassland savanna (Walker 1970). Instead of a wire or tape being stretched between two pegs at the soil surface, a 2-m steel rod marked at 1-cm intervals was positioned parallel to, and 20 cm above, the substrate, each end held by a laboratory retort clamp and stand. On each visit to each sampling site, 25 randomly-placed 2-m lines were measured in each vegetation type under study and the mean percentage cover was calculated for each vegetation type. In unburned plots at Allerton, where dense moribund vegetation always provided about 100% cover, new growth was measured along 2-m lines placed immediately above the dense matted vegetation, 35-50 cm above the substrate.

At Gartmore, where the occupied vegetation was principally a mixture of sedges and hygrophilous grasses, cover was measured by quadrat as described for grassland in Section 3.6.1.1. At Mt Currie, where stands of pure *Carex* and *Typha* were measured, an attempt was made to assess the relative openness of these vegetation types at ground level compared to their density at canopy level. To measure ground cover the line-transect method described in Section 3.6.1.2 was used, the 2-m measuring rod being positioned horizontally 5 cm above the substrate. Twentyfive transects were measured in each vegetation type on each visit and the means were calculated for each data set. Cover at canopy level was estimated either by quadrat or, where this was difficult, simply by general observations in the area concerned.

### 3.6.1.3 Forest

Measurements of cover were made in Buffspotted Flufftail territories at all four long-term study sites for this species, namely Ferncliffe Forest, Bisley Valley, Danville Park Reserve and Scotston Farm. There is no recognized method of sampling the vegetation cover which I considered to be an important factor affecting the suitability of any area for occupation by Buffspotted Flufftails, and which can be equated with the ground cover measured for the grassland and wetland species. Prolonged observations of both Buffspotted and Whitespotted Flufftails in forest have led me to conclude that the most important property of cover in the low forest stratum which they occupy is the extent to which it conceals these terrestrial birds and their activities from observation by potential predators at ground level and up to about 2 m above the ground, at which height the secondary growth which they inhabit often has a more or less closed canopy preventing their being observed from above. In simple terms, the farther one can see into a thicket from a low level, the less suitable it appears to be for the flufftails.

In secondary forest and thickets, vertical measurements of the proportion of ground covered by the aerial parts of plants are neither easy to make nor perhaps as relevant (see above) as measurements made horizontally or from a small angle down to the ground. I decided to measure vegetation cover using a modification of the density board method described by MacArthur & MacArthur (1961) for measuring foliage density at different heights. In this method a board marked in squares is moved horizontally away from the observer until 50% of its surface is obscured from view by foliage. The distance from the observer is measured and the foliage density calculated by formula (MacArthur & MacArthur 1961). The procedure is repeated at a series of heights above the ground. In the present study, not only was the calculation of foliage density unnecessary but the use of a second person to move the board was impractical in view of the number of sites to be covered and the duration of the experiment. The method was therefore modified to require only one operator and to measure the most important variable relevant to this study, i.e. the variation in the amount of cover provided by low-level vegetation at different times of the year.

Measurements were made only in known flufftail territories. A square white board 50 cm x 50 cm was subdivided into 100 squares of 5 cm x 5 cm (for accuracy of measurement) comprising five sections 10 cm high x 50 cm wide. The board was placed resting perpendicular to the ground, at a constant distance of 5 m from the observer, who estimated the amount of each section 10 cm high x 50 cm wide obscured from view by the intervening vegetation. Each section was viewed from approximately its own maximum height above the ground, e.g. the 0-10-cm section at 10 cm height, etc. The board was placed at four different locations in each study area, to give readings in different

types of cover e.g. inside dense thickets, in areas with short dense ground vegetation, and off forest tracks fringed by tall woody forbs. All readings were repeated, with the board in exactly the same positions, at monthly intervals for at least one year. For each study site the variation in percentage cover was plotted graphically (a) for the mean at each 10-cm level for all locations combined and (b) for the overall mean of all five levels at each location.

Measurements were not made at levels higher than 50 cm because of the difficulty in positioning the board vertically (and of making horizontal observations) at any greater height. I considered that observations directed downwards at a vertical board from a higher level would not give accurate estimates of percentage cover.

Using exactly the same locations for measurements over a long period requires that the locations remain completely undisturbed for the entire period. Any significant damage caused by trampling, browsing, tree fall, etc., changes the vegetation structure sufficiently to render further measurements pointless, while the measurements obtained before the damage occurred may cover too short a period to be useful. This type of damage occurred at one measuring site at Ferncliffe, and was caused by tree-felling and a flash flood. It is advisable, therefore, also to make measurements at one or more alternative sites throughout the study period (this was done at Ferncliffe), so that these may be used if the original sites are destroyed.

### 3.6.2 Measurements of vegetation height

Measurements of vegetation height were made in the same grassland and wetland territories of Striped and Redchested Flufftail in which vegetation cover was measured, and were concurrent with the sampling of cover in each territory (see Section 3.6.1). The mean heights obtained were used primarily to highlight significant differences in the timing and rate of spring and early-summer growth between different vegetation types, burning regimes and (for wetland territories) degrees of soil saturation. An attempt was then made to relate the timing of occupation of grassland by returning migratory Striped Flufftails, and the timing of reoccupation of burned territories by Redchested Flufftails, to the overall height of the vegetation and the percentage cover it provided.

In the Mt Currie grassland territories it was considered most relevant to measure the overall mean heights of vegetation patches and tussocks (in the shelter of which the Striped Flufftails would find concealment and nesting sites) rather than to measure the maximum heights of individual stems. To achieve this I decided to construct an instrument based on the disc pasture meter described by Bransby & Tainton (1977). The disc pasture meter consists of a 1.8-m metal rod and a 1.2-m metal sleeve which slides freely on the rod and has an aluminium disc 46 cm in diameter attached at its

lower end. The rod is held resting perpendicular to the ground and the sleeve is dropped so that the disc falls on to the sward. The settling height is read off from calibrations on the rod. This method is suitable for use on dense swards which are relatively resistant to compression by the disc, but on vegetation more sensitive to compression the disc should be placed gently on the sward surface and allowed to settle to a constant height (Bransby & Tainton 1977).

For the purpose of this study the disc was required to rest on the top of the sward, tussock or sedge bed concerned without significantly compressing the vegetation. Field trials with a standard disc meter showed that some grass clumps were compressed below their normal overall height, while wetland vegetation was greatly flattened, by the combined mass (1.5 kg) of the disc and sleeve. Accordingly a lighter apparatus was constructed, with an aluminium disc for grassland and a strong cardboard disc for wetland vegetation. Each disc was 46 cm in diameter and had a short sleeve to keep it positioned at 90° to the rod. The overall mass of the grassland disc was 500 g and the wetland disc 100 g. The central rod was 2 m in length, graduated in 1-cm divisions and had a small steel plate welded 10 cm from its tip to prevent it sinking in wet ground.

In grassland territories at Mt Currie the height of the vegetation was measured with this apparatus at 80 randomly-selected points in each territory on each visit, while in wetland vegetation at all three study sites 30-50 measurements were made of the dominant plant species in each territory under investigation.

### **3.6.3 Other measurements of wetland vegetation regrowth**

One of the aims of this study was to investigate alternative methods of assessing cover and regrowth in wetland vegetation, both to compare the rates of increase of cover obtained with different methods and to measure other vegetation characteristics which might affect flufftails and other birds living on or near the ground in reedbeds. Little time was available for this work so only a very few simple measurements were made at Mt Currie and Allerton, in burned vegetation of uniform structure, i.e. dominated by either *Typha capensis* or by one sedge species. As well as measuring cover at different levels in different vegetation types (see Section 3.6.1.2), two other variables were measured:

#### **3.6.3.1 Light within the reedbed**

The interior of a dense reedbed is a dim place, little of the incident light reaching the substrate. As the amount of light penetrating to low levels is affected both by the height and density

of the vegetation cover, measurement of the light levels near the substrate in different vegetation types might be a simple and useful method of comparing overall cover, as well as showing the level of light available to terrestrial birds for foraging and other activities within the reedbed. At Allerton and Mt Currie, in the vegetation types being sampled for height and cover, monthly measurements were made of the percentage of the incident light which penetrated the vegetation. A Gossen Lunarsix-3 light-meter was used, the instrument being chosen for its large overall range (350 000 lux) and its sensitivity to light at extremely low levels (down to 0,17 lux). At each sampling point the level of incident light was measured immediately above the reedbed and 20 readings were taken within the reedbed at a standard height of 20 cm above the substrate, ensuring that the incident light remained constant for all samples. The light-meter readings were converted to lux values (on a logarithmic scale), the mean percentage of the incident light reaching the measuring level was calculated for each data set, and the results were compared with those of the vegetation height and cover.

### **3.6.3.2 Number of leaves**

At Allerton an alternative measure of growth and cover was made by counting the relative numbers of growing leaves on the dominant species under investigation. The principal reason for making these measurements was to obtain a further comparison between growth in burned and unburned *Cyperus/Mariscus* sedge beds at the site. The unburned vegetation had relatively few living leaves which were very variable in height, growing through a more or less continuous 100% ground cover of moribund vegetation, and the other measurements of cover and height were not possible to an accuracy equivalent to that in burned or mown sedges. Leaves were counted along the same line transects used for measuring vegetation cover (Section 3.6.1.2). The number of leaves intercepting or overlapping the 2-m horizontally placed measuring rod was counted, and the count was repeated at 25 randomly selected points in each sample plot. In the unburned vegetation the rod was positioned horizontally immediately above the dense mat of moribund vegetation, at a height of 30-50 cm above the substrate. The means were calculated for each data set.

## **3.7 Invertebrate sampling**

In studies of habitat suitability and the possible factors influencing the seasonal occurrence of flufftails in all habitats, it was necessary to investigate the availability of potential food as well as the amount of cover. Flufftails are known to eat mainly small invertebrates and some vegetable matter and seeds (Keith 1986), and my observations of all the African species except Whitewing (for which

there is no information on feeding methods) suggest that they are entirely terrestrial in their foraging behaviour. In all habitats the birds always take food while walking on the ground, in shallow water or on floating vegetation; they feed from the substrate surface or in leaf-litter, mud or shallow water, or by stretching up to take food items from low vegetation. Thus some method had to be devised to sample the invertebrate population at these levels in the habitats under investigation. The methods used differed according to the substrate and vegetation types under consideration.

### 3.7.1 Grassland

The commonly used methods for sampling invertebrates in grassland, reviewed by Southwood (1978), include catching free-flying individuals above the vegetation (e.g. in malaise traps), sweep-netting invertebrates in the vegetation, and trapping terrestrial individuals (e.g. in pitfall traps). At the start of this research little was known about the Striped Flufftail's foraging methods but I assumed that the birds would feed entirely on the ground, sometimes in dense vegetation, and therefore that the first two sampling methods would be unsuitable for catching many of the low-level and terrestrial invertebrates which would be available to the birds. Likewise, terrestrial trapping methods would not sample the invertebrates above the ground in low vegetation. The major problem therefore was the sampling of small invertebrates in dense low growth and one method of overcoming this problem appeared to be by suction sampling, using a portable air suction machine such as the D-vac (Dietrick 1961; Southwood 1978); it was hoped that such a machine would also collect invertebrates from the surface of the substrate. The portable D-vac is powered by a petrol engine, needs only one operator, is carried in a backpack and has a hand-held collecting unit comprising a collecting cylinder and bag at the end of the flexible air duct.

Accordingly a portable D-vac machine was obtained from the South African Sugar Association at Mt Edgecombe Research Station, Durban, and after being overhauled it was tested in the field. It was found that the suction, although sufficient to pick up invertebrates resting on short vegetation and fairly clear ground, was insufficient for collecting samples from the dense tussocky vegetation inhabited by Striped Flufftails.

In view of these problems it was decided that the only practical method of sampling the full range of potential food items available in this type of grassland was by detailed visual investigation and direct counting. The method used was to locate visually, estimate the approximate length of, and identify to order or family (if possible), all the invertebrates in each of 40 randomly positioned 50-cm-square quadrats per survey plot per sampling visit. Comparative counts were made in grassland of each of the three normal stages of the burning cycle (see Section 3.6.1.1), and all counts were made

between 10h00 and 12h00 in fine weather with little or no wind. The flying arthropods (grasshoppers, Lepidoptera, flies, etc.) which left the quadrat as the vegetation was disturbed were also counted, although they were unlikely to be potential food items for the flufftails. Details of all invertebrates were recorded and up to 2 min were allowed to search each quadrat, so that the substrate and all dense low vegetation could be properly examined. I hoped that the pattern and duration of the search would identify all the invertebrates which a Striped Flufftail would be likely to encounter during its foraging, and thus the following limitations were placed on the search methods: (1) no examination was made of the interior of the bases of very dense tussocks which were judged inaccessible to a foraging flufftail, (2) dead leaves and grass were moved aside to the extent which a flufftail might be expected to disturb them (based on personal observations), (3) rocks and stones were left undisturbed and (4) only animals 1 mm or more in length were counted, my observations of several flufftail species indicating that prey smaller than this is rarely taken.

Using this method it was not possible to collect the invertebrates for biomass measurements, but the samples did give a good estimate of the variation in abundance and diversity of the invertebrate fauna in grassland at different stages in the burning cycle and at different times of the year.

### 3.7.2            Wetland

The wetland vegetation and substrates in Redchested Flufftail habitats are rich in invertebrates which, by virtue of their abundance and variety, and their presence in water, mud, and tall dense vegetation, are even more difficult to sample than those in grassland. Similar considerations to those given in Section 3.7.1 apply regarding the unsuitability of normal sampling methods for catching invertebrates at low levels in the vegetation, while the D-vac machine proved even less effective in dense wetland vegetation than in dense grass. In summer the height and density of the vegetation rendered impractical any standard sampling methods or detailed visual searches and prevented the application of any reliable and consistent method of sampling in shallow water and mud inside the reedbeds. Only in recently burned areas, and those with only a light cover of dead vegetation in winter, was it possible to sample invertebrates effectively.

Thus normally it was not possible to sample the invertebrates in Redchested Flufftail territories, although a few samples were made after burns at some sites. These samples, and generalized personal observations both of feeding rallids and invertebrate abundance in Redchested Flufftail territories, indicated that, in permanently moist to flooded areas, the potential invertebrate food never fell to a critically low level except possibly in the 3-4 weeks immediately after a close

burn, in which period the burned area was inaccessible to foraging flufftails because of the total lack of cover. At all other times the density of invertebrates was probably sufficient to support the flufftails (see Chapter 6, Sections 6.4.3 and 6.5.5 for further discussion). Furthermore, as Redchested Flufftails were found to subsist on seeds in some territories which became dry in winter, and as they also eat seeds throughout the year (Chapter 4), seasonal decreases in the invertebrate population may not necessarily reflect a critical reduction in available food, as alternative vegetable foods could be available. It was therefore considered that invertebrate food was probably not normally a factor limiting occurrence in wetland territories, and thus that wetland invertebrate sampling was not essential.

### 3.7.3 Forest

My previous observations of Buffspotted Flufftails in eastern, central and southern Africa indicated that this species forages principally in leaf-litter, and sometimes also on clear ground or in very short ground vegetation or by gleaning food items from low overhanging vegetation. To investigate seasonal changes in food availability at the four study sites for this species (Danville, Bisley Valley, Ferncliffe and Scotston) it was considered sufficient to sample the leaf-litter in the territories. Accordingly a standard method was adopted of taking a monthly sample at each site, when a volume of 5 l (uncompressed) of leaf-litter was collected at randomly-selected locations. Observations indicated that the flufftails searched within the litter only to a depth of 2-4 cm, so the sample was collected from the top 5 cm of the undisturbed litter (including the layer of small decayed vegetation fragments on the soil surface if this was within the maximum depth). As foraging birds investigate small pieces of rotten wood and bark, these items were included in the samples when encountered. The moisture content of the litter sample was noted on a simple scale of dry, damp or wet, and the date of the last significant rain at the site was also recorded. The monthly sampling was repeated over a period of one year at each site.

After collection each sample was processed immediately. The leaf-litter was scattered in small quantities on a circular white plastic tray 30 cm in diameter and all invertebrates over 1 mm in length (see the comment in Section 3.7.1 on the limitations of search methods) were located, counted and their lengths measured to the nearest millimetre. Identification to the level of order or family was attempted and a spirit collection was made of representative species for further identification and for comparison with fragments found in Buffspotted Flufftail gizzards (see Chapter 9).

### 3.8 Trapping flufftails

Depending on the species and the vegetation type concerned, flufftails range from being relatively easy to extremely difficult to trap, and during the study tests were made of all trapping methods which I deemed feasible based on my previous experience of trapping rallids in Africa. The most successful methods are detailed below under the relevant species headings and usually involved walk-in traps of two types. The simple drop-door trap design given by Schmitt (1973) proved effective but, as flufftails sometimes either fail to touch the trip-string which causes the door to fall, or manage to jump quickly out of the trap as the door closes, I found it most effective to sit 5-10 m from the trap and to pull away the door support at the correct moment by means of a hand-held cord.

I have also found that the Ottenby maze traps (Davis 1981), originally used for catching waders on open shorelines, are very effective for trapping small to medium-sized rallids and other birds in dense vegetation. They have the advantage that no triggering mechanism is required, the birds simply finding their way into the maze trap and then being unable to find the way out again. For general-purpose rallid trapping work, lines of maze and/or walk-in traps, connected by low mesh fences, were sometimes set through reedbeds along specially cleared rides.

Mist-nets are usually ineffective for catching flufftails on the ground, as the birds quickly become aware of the nets and very rarely become entangled by walking in and trying to push through them; the only reliable way to secure a flufftail in a net is to drive it in and then to secure it immediately, before it has a chance to run out. Mist-nets set immediately above the reedbed vegetation to catch flufftails in flight (i.e. when flushed) have a very limited potential use because of their visibility and the difficulty of ensuring that the flushed birds fly either in the right direction, or far enough, to encounter the nets. Furthermore, one spends much time extracting the many other birds (hirundines, warblers, queleas, *Euplectes* spp., etc.) which enter such nets and the amount of disturbance caused by these operations effectively clears the immediate area of all flufftails and other rallids.

#### 3.8.1 Buffspotted Flufftail

Although I have very occasionally caught this species in mist-nets set down to ground level, I have found that the best method is to entice the birds into drop-door traps, either by providing mealworms (*Tenebrio* larvae) as bait or by placing a model flufftail in the trap and playing back selected calls from a loudspeaker concealed nearby. During the breeding study at Scotston (Chapter 9) the study pairs and their chicks were regularly fed inside an open trap and could therefore be

caught whenever required; after release they were usually back in the trap feeding again within a very short time.

### 3.8.2 Redchested Flufftail

Both drop-door traps and maze traps are sometimes effective, either set in lines and preferably baited with mealworms, or used singly, baited or containing a decoy model flufftail to which the birds are attracted by taped playback. In general, the most reliable method is to use single baited traps at regular feeding and observation sites. At times Redchested Flufftails will enter traps readily, sometimes they will not enter them whatever the stimulation. Frequent trapping causes an unacceptably high level of disturbance in the territories, and permanently sited trap lines may not be a solution as the flufftails learn to avoid these locations completely. Low mist-nets, set from a height of 1.5 m down to ground level, are sometimes effective if the birds are driven in and secured immediately, but the birds will do everything possible to avoid being forced to enter the nets. They are adept at avoiding being driven, usually managing either to conceal themselves while the drive passes by or to run back between the beaters. An example of how adept this species is at avoiding capture is given by an attempt made at Bromley, Zimbabwe, to trap a pair for captive breeding. The territory was in a narrow reedbed along a drainage line and two trap lines were set in rides 30 m apart, each at 90° to the drainage line and completely spanning the wetland vegetation (here 12-15 m wide). For two trapping mornings, although the birds were heard both within the fenced-off section and on either side of it, they would enter neither low-set mist-nets nor traps, despite the provision of food and decoy models, and periodic tape stimulation. On the third morning the birds were attracted by tape into the central section, both mist-nets and traps were set along the rides and six men, evenly-spaced in a line across the wetland vegetation, then walked the whole length of the central section three times from one trap ride to the other, each man disturbing the surrounding vegetation with a stick as he moved. No birds emerged into either trapping ride, none took flight, and the men, who had walked close to each other, saw no flufftails on the ground. The drive was abandoned to avoid further disturbance and, as the vehicle containing the men drove away, the flufftails began calling from within the central area, where they must have remained safely concealed throughout the entire operation.

### **3.8.3            Striped Flufftail**

Observations indicated that it should be possible to catch Striped Flufftails in single maze traps or walk-in traps, either baited or with the help of decoys and tape playback, but setting lines of traps in extensive grassland habitat (such as that at Mt Currie) is probably pointless as the birds would easily be able to avoid the trapping lines. It proved so difficult to get close to Striped Flufftails (with or without a hide) that, on the relatively few occasions when the birds could be observed at close quarters, no attempt was made to trap them, as it was considered more important to make detailed observations of their behaviour.

### **3.8.4            Whitewing Flufftail**

No effective method of trapping this species was found, and no birds were caught, despite attempts with (a) mist-nets set at both ground level and above the reedbeds, and (b) lines of traps, both baited and unbaited. This species usually responds very poorly to tape playback and is extremely difficult to observe on the ground (see Chapter 8); it was never seen to be attracted to the vicinity of trap lines or nets.Flushed birds twice narrowly avoided flying into nets at dawn and dusk, and this may be the best method of capture, but a good coverage of nets is essential and it is probably only worth attempting this method when reasonably large numbers of birds are present to improve the chances of capture. The problems of disturbance at the nets, described in the introduction to this section, appear to apply particularly acutely to this species.

## **3.9        Recording biometric and other data from trapped flufftails**

Unless otherwise stated, measurements were made and moult details were recorded according to the criteria given by Svensson (1984). The following details were recorded:

- (a) mass, to the nearest 0,1 g;
- (b) wing length (maximum length of the flattened and straightened wing);
- (c) tail length (tip to base of central rectrices);
- (d) culmen (tip of bill to skull);
- (e) tarsus length (from the notch on the back of the intertarsal joint to the lower edge of the last complete scale before the toes diverge);
- (f) age and sex (for ageing criteria);

- (g) remex wear and/or moult, the latter scored according to the method given by Ginn & Melville (1983);
- (h) moult and wear of rectrices and body feather tracts;
- (i) colour of bare parts;
- (j) indicators of breeding - the presence and state of development of the incubation patch; swelling of the abdomen or the presence of an oviduct egg; cloacal enlargement;
- (k) date, time, exact location and method of capture;
- (l) full details of SAFRING ring number and colour rings.

All birds retrapped within the same trapping period were reweighed to record diurnal and overnight variations in mass. All colour-ringed birds were photographed in the hand at least once, and the juvenile Buffspotted Flufftails which were regularly trapped for the recording of growth rate and plumage development were photographed and video-filmed to show the significant changes in plumage.

### **3.10 Marking flufftails**

Each flufftail caught was ringed on the right tarsus with a SAFRING incoloy 4.3-mm ring (usually overlapped), and was also fitted with one or two coloured plastic rings on the left tarsus for individual identification in the field. The colours used had to be easily distinguishable and well visible in poor light, and combinations of red, yellow, green, blue, purple and white were found adequate, rings being either of a single colour or having two bands of contrasting colours. The male and female of a flufftail pair had one ring colour in common, and all chicks of a brood had one ring colour in common.

### **3.11 Collection of general data from other sources**

The entire literature on flufftails was searched for relevant information on distribution, status, habitat requirements and all other aspects of the birds' biology and ecology. The organisers of the Southern African Bird Atlas Project (Harrison 1987) provided complete Atlas data on flufftail distribution and breeding in South Africa. I made a personal examination of all flufftail specimens held by the following museums: Albany Museum, Durban Natural Science Museum, East London Museum, Transvaal Museum, South African Museum (South Africa); Bulawayo Museum (Zimbabwe); Nairobi Museum (Kenya); British Museum (Natural History), Tring (England). All flufftail eggs in the collections at Durban, Bulawayo, Nairobi and Tring were personally examined

and full information was obtained from those in the other collections. I also personally examined all flufftail eggs in three private collections in Zimbabwe. All relevant information on flufftail species was obtained from the Southern African Ornithological Society Nest Record Card Scheme and the South African Bird Ringing Unit (University of Cape Town), the Zimbabwe Nest Record Card Scheme (Bulawayo Museum) and the East African Natural History Society Nest Record Card Scheme (Nairobi Museum).

## CHAPTER 4

### THE DISTRIBUTION, STATUS, GENERAL BIOLOGY AND BEHAVIOUR OF THE REDCHESTED FLUFFTAIL

#### 4.1 Introduction

The Redchested Flufftail (Frontispiece (B)) is relatively common and widespread over much of sub-Saharan Africa, and more is known about its habits, behaviour and breeding than about those of any other flufftail species except the Buffspotted Flufftail *S. elegans* (Chapter 1, Section 1.2.1). However the extent of this knowledge is still very limited: the bird's range is probably more extensive than is known, its status is uncertain in many areas (including much of South Africa) and its habitat requirements have been defined only loosely (Chapter 1, Sections 1.2.2.1-1.2.2.5). Nothing is known about any movements which it might make in response to seasonal changes in its wetland habitats (Chapter 1, Section 1.2.2.6).

Current knowledge raises some interesting questions about the Redchested Flufftail's biology and ecology, which are worthy of detailed study. For example, the bird's calling patterns suggest that the pair bond is permanent and that a pair may defend its multipurpose territory (Type A, as defined by Nice 1941) throughout the year. Nonbreeding territories are not commonly reported in secretive rallid species and most Palaearctic and Afrotropical rallids are territorial only during the breeding season. However, individual nonbreeding feeding territories are established by the sedentary Water Rail *Rallus aquaticus* (Cramp & Simmons 1980), by Palaearctic migrant Corncrakes *Crex crex* and Spotted Crakes *Porzana porzana* in Africa (Taylor 1984, 1987), and by the African Crake *C. egregia* in its Afrotropical nonbreeding areas (Taylor 1985a), while permanent territories are maintained (when resources permit) by the largely aquatic Moorhen *Gallinula chloropus* and Eurasian Coot *Fulica atra* (Cramp & Simmons 1980). The Whitespotted Flufftail *S. pulchra* is permanently territorial in stable streamside forest habitats (Taylor & Taylor 1986), as was the Striped Flufftail *S. affinis* when permanently resident in one Natal breeding area (Chapter 7). However no sedentary rallid of dense wetland habitats is known to maintain a territory throughout the year and the available evidence suggests that the two sedentary rallid species occurring commonly alongside the Redchested Flufftail, the Black Crake *Amaurornis flavirostris* and the African Rail *R. caerulescens*, are territorial only during the breeding season (Schmitt 1975, 1976). It is not clear whether the Redchested Flufftail is properly territorial throughout the year, or what advantage there may be in maintaining a permanent

territory in dense wetland habitat which is subject to considerable seasonal changes in flooding and availability of cover.

In view of its wide distribution, its abundance and its wide tolerance of wetland habitats (Chapter 1) the Redchested Flufftail is obviously a successful species, especially when compared with other wetland flufftails such as the Whitewing Flufftail *S. ayresi* and the Longtoed Flufftail *S. lugens*, both of which are relatively rare and restricted in distribution although they apparently occupy similar wetland habitats to those of the Redchested Flufftail (Keith 1986; Keith *et al.* 1970; Chapter 1). Why is the Redchested Flufftail so much more successful and widespread? Furthermore, the apparent ability of Redchested Flufftails to colonize very small patches of isolated wetland habitat which are not occupied by other African rallids suggests that they are tolerant of a wide variety of conditions (including marked seasonal changes in substrate saturation and vegetation growth) and that they have good powers of dispersal; both of these are subjects worthy of detailed investigation.

Although the conservation of the Redchested Flufftail and its habitat is not as urgent a problem as that of the rarer wetland Whitewinged Flufftail (Chapter 8) and grassland Striped Flufftail (Chapter 7), the constant and ever-increasing threat to wetland habitats both in Natal and elsewhere in South Africa (see references reviewed in Chapter 1, Section 1.2.4 and Chapter 8, Section 8.5.1) means that there is no cause for complacency about the long-term survival prospects of this, or any other, wetland flufftail. It was therefore thought important to investigate the effects on the species of events such as burning, mowing, grazing, and the damming and drainage of wetland areas. It is also important to investigate the bird's ability to survive in artificially created wetland areas and in small isolated wetland patches in areas now under agriculture.

Studies of the responses of Redchested Flufftails to seasonal habitat changes are described in Chapters 5 and 6. Chapter 4 deals with the investigations of those aspects of the fundamental biology and ecology of the species which are essential prerequisites to an understanding of the relationships between the bird and its environment. In the general investigations, the following topics were selected for study:

- (a) the bird's distribution and status in Natal;
- (b) its habitat requirements in southern Africa;
- (c) seasonal variations in habitat type and extent;
- (d) daily activity patterns;
- (e) relationships with sympatric wetland rallid species;
- (f) territorial behaviour and the permanence of territories;
- (g) food and feeding methods;
- (h) vocalizations and calling patterns, including seasonal variations;

- (i) breeding season and breeding behaviour;
- (j) the relationships within the family group, including the role of immatures in territorial defence;
- (k) postbreeding dispersal, predation and mortality.

Not all of these topics could be investigated in detail but sufficient results were obtained to give an insight into the biology and behaviour of this species, and these results were especially illuminating when compared with those obtained for the forest-dwelling Buffspotted Flufftail and Whitespotted Flufftail (Chapters 9 and 10; Taylor & Taylor 1986). They also provided an insight into some important characteristics of the genus as a whole, and facilitated the interpretation of some of the less comprehensive results (especially of behaviour) obtained for the two rare species studied.

#### **4.2 Survey areas, study sites and study aviaries**

Chapter 2 gives details of the southern Natal survey area and the long-term study sites. Populations of Redchested Flufftails were studied at four sites in Natal: Gartmore, Howick (Section 2.2.5); Allerton, Pietermaritzburg (Section 2.2.7); Danville Park, Durban (Section 2.2.9); and Mt Currie Reserve, Kokstad (Section 2.2.13). Less regular observations were also made at all the other wetland study sites, at many wetlands throughout the survey area, and at wetlands in the eastern Transvaal during work on the Whitewing Flufftail (Chapter 8).

At Bromley, Zimbabwe (Chapter 2, Section 2.2.1), where observations were made of both wild and captive birds, Redchested Flufftails have been bred successfully in aviaries with other bird species, including other rallids, since 1978 (Wintle 1988; Wintle & Taylor 1993). At the beginning of this study only two female Redchested Flufftails remained, one in each of two aviaries which also contained ducks and small passerines, and these females were observed during a visit in July 1990. The birds were siblings, hatched in captivity in February 1989. They were subsequently released and a wild-caught adult male and female (not an established pair) were introduced into one aviary on 7 November 1991; this pair settled down well and bred annually thereafter. Their aviary was built against the house and a large window of the lounge opened into the enclosure; this facilitated observation and enabled the birds to become habituated to human activity so that they were less wary than usual (but they were still extremely retiring in their habits). The aviary was 24 m<sup>2</sup> in area, 2.5 m high, and contained a pool of about 8 m<sup>2</sup> surface area. The pool's water level was allowed to fluctuate so that feeding substrates of mud and plant roots were exposed and covered every few days. The vegetation comprised indigenous sedges and grasses around the pool and in clumps elsewhere, plus bamboos, trees and bushes, and there was plenty of dense cover for shelter and nesting. An open, partially short-grassed area at one end of the enclosure provided clear space for observation, and food

was placed there. The aviary also contained a breeding pair of Pygmy Geese *Nettapus auritus* and several small waxbills, canaries and doves.

#### **4.3 Methods**

##### **4.3.1 Surveys, censusing and territorial mapping**

Surveys were based on auditory information and were made at as many wetlands as possible in the southern-Natal survey area (Chapter 2, Section 2.1) throughout the project. Their purpose was to investigate the distribution and status of the bird in the area, as well as to contribute data to studies of habitat, behaviour and calling. To show the distribution of the species by month, survey results were plotted on summary maps using the Natal quarter-degree-square grid and symbol conventions of Cyrus & Robson (1980). Each quarter-degree square represents one sixteenth of a one-degree square ( $15' \times 15'$ ) and contains a circular symbol divided into 12 segments, each representing a month of the year, clockwise from January to December as shown by the inset on each map. Occasional surveys were also made in other areas, such as the Transvaal and Zimbabwe, during work on other species and while travelling to study sites in these regions. The primary purpose of these remote surveys was to collect data on habitat preferences and seasonal calling behaviour; they could not be extended to contribute to a detailed knowledge of the bird's overall distribution and status in these regions.

Regular census and territorial mapping work was done at the study sites listed in Section 4.2. The methods, largely involving taped playback, are described in Chapter 3, Section 3.4. Repeated observations of colour-ringed birds at Allerton and Danville contributed to the mapping work. After preliminary investigations, no work was done on the home ranges of Redchested Flufftails, principally because it was difficult to separate home range and territory: the birds behaved very territorially throughout the whole area which they inhabited, while apparently penetrating adjacent territories only infrequently (Section 4.4.5).

##### **4.3.2 Territorial behaviour**

The territorial behaviour of wild birds was observed throughout the project period, and detailed studies were made on captive birds at Bromley in July 1990, November 1991, and April 1992. Some further observations of the newly-established pair of captive birds were made by C.C. Wintle from November 1991 onwards. As most behaviour was very difficult to observe in the field,

studies of territorial behaviour included investigations of the birds' vocal responses to taped playback, while the nature of agonistic behaviour, and of the seasonal variations in its form and intensity, were principally made with the help of models and mirrors to which the birds were attracted by taped playback from a concealed loudspeaker. The nature and intensity of their reactions to these stimuli were recorded verbally and on video film for later detailed analysis (not a part of this thesis): about 11 hours of video film were made of many aspects of the behaviour of this species, both in the wild and in captivity. Models were life-sized, usually with glass eyes (birds showed greater and more sustained interest in models with lifelike eyes), and were painted in accurate representation of the plumage of adult and young Redchested Flufftails and other flufftail species. In some experiments, painted plywood flufftail shapes on sticks were used in isolated experiments to compare the birds' reactions to different plumage patterns and colours. Models made from flufftail skins were also used whenever possible, but only one Redchested Flufftail specimen, a juvenile male with uniformly black plumage, was available for use during the study.

Taped playback was also used on captive birds, when it stimulated vocal responses comparable to those obtained from wild birds. However models and mirrors were not used in aviaries, preliminary studies having shown that such visual stimulation sometimes provoked low-key responses from territorial birds, their behaviour possibly being affected by the lack of means of escape from potential aggressors in the aviary.

The use of models is a long-established technique in behavioural studies of birds (Campbell & Lack 1985; Smith 1971) and in the rallid family a classic study on the breeding and aggressive behaviour of the Corncrake (Mason 1940, 1941, 1944, 1945, 1947, 1950, 1951) was based on experiments with models. Mirror-image stimulation has become an increasingly preferred method for studying aggressive displays in birds, being a very effective and consistent way to provoke prolonged bouts of threat display (e.g. Gallup 1968, Gallup & Capper 1970, Serpell 1982 and references reviewed therein). Mirror experiments, performed at widely-spaced intervals (fortnightly or longer) to avoid habituation, were very useful in comparative studies of the intensity of the birds' display and aggressive behaviour throughout the year, and were used in the overall assessment of seasonal variations in territorial behaviour.

Observations were also made of the birds' reactions to the Black Crakes and African Rails which existed alongside them at some study sites, and to models of these species. Seasonal variations in the territorial and agonistic behaviour of these two larger rallid species were also made throughout the study period, for comparison with the behaviour of the flufftails.

#### **4.3.3 General behaviour**

Throughout the study general behavioural observations of both wild and captive birds were made at every available opportunity, from hides (at Allerton, Danville and Underberg), with the observer concealed by temporary screens, or with the observer not concealed in any way. Male Redchested Flufftails sometimes took little notice of a visible observer, but rarely remained in the open for more than 30 s; females and young were much more retiring. Most detailed observations were made when the observer was concealed, thus eliminating the risk that a visible observer might affect the bird's normal behaviour. Narrow observation tracks were cut, and periodically cleared, in dense reedbed vegetation at hides and at other observation sites, and these tracks were also used when trapping the birds. To facilitate observation, flufftails were often attracted to the vicinity of the observer by taped playback, which was discontinued when the bird appeared, and at the three permanent hides the birds were regularly provided with food in the form of mealworms (*Tenebrio molitor* larvae), which often encouraged them to forage and rest on or near the observation tracks as well as to take the food provided. The mealworms also attracted resident Black Crakes and African Rails, and comparative studies were made of these species at the same time.

#### **4.3.4 Feeding and energy requirements**

Although it was not possible to undertake controlled feeding experiments to establish daily energy intake, some observations were made on both wild and captive birds which were provided with an unlimited supply of live mealworms (in a smooth-sided container from which they could not escape) during the observation periods. At the Zimbabwe aviary in April 1992 an excess of mealworms was provided over a eight-day period and the live weight of mealworms consumed by the four captive birds was recorded each day, at hourly intervals on four days and at longer intervals on the other days. As all birds were seen to spend approximately similar times at the feeding station, the total weight of mealworms consumed was divided by four to give the mean consumption per bird. Because of the difficulties of observing these birds in dense cover it is normally not possible accurately to monitor variations in foraging activity during the day, either in the wild or in captivity, but the figures for hourly consumption gave an acceptable indication of the feeding activity of the birds throughout the day. At Danville Lake, Durban, in April 1991 a newly-arrived immature male fed continually at mealworms for two days and the total consumption was recorded. The energy value of mealworms was calculated by bomb calorimetry (Horowitz 1970). The daily energy requirement of the Redchested Flufftail was calculated from generalized formulae in the literature, the field

metabolic rate (FMR) for the species being obtained (Nagy 1987; Velásquez *et al.* 1991) from the equation

$$\text{FMR} = 10,9M^{0.64}$$

where  $M$  is the mean wet mass of the species in grams. This FMR value was corrected for assimilation efficiency by dividing it by 0,75, the factor applicable to birds which eat invertebrates (Cooper 1978; Hockey 1984), to give an estimate of daily energy intake (DEI) which was then compared to the energy value of the mealworms consumed.

#### 4.3.5      Vocalizations

Throughout the study detailed notes were kept of all vocalizations made by all birds encountered in the wild, and of captive birds during periods of intensive study. During survey and territorial mapping work the nature, intensity, frequency and duration of all birds' responses were noted, and the typical calls of regularly encountered pairs were monitored to ascertain (a) the nature of seasonal variations in call types and calling patterns, and (b) whether any individuals could be recognized on the basis of distinctive types or patterns of notes not shared with nearby birds. The recognition of some birds by their unique vocalizations assisted in the study of site fidelity and the permanence of territories. The vocalizations most valuable in individual recognition proved to be (a) distinctive forms of the common territorial and advertising calls, such as broken hoots and modified *DUEHs*, (b) individual peculiarities in the nature, frequency and intensity of subsidiary vocalizations such as grunts, gulps and growls which accompanied these calls, and (c) the nature of the vocalizations preceding and following sequences of territorial or advertising calls.

Calls were tape-recorded whenever possible, using a Marantz CP230 stereo cassette recorder and an Audio Technica AT815a unidirectional microphone. This equipment gave recordings of high quality, from which sonograms could be made easily. In circumstances where there was no opportunity to use this equipment, some calls were recorded at close range on the Sanyo TRC 5680 microcassette recorder which I always carried for verbal note-taking; if made under calm atmospheric conditions these recordings often produced acceptable sonographic traces.

#### 4.3.6 Breeding

It was extremely difficult to study courtship and mating behaviour in wild birds, but some observations were made and were compared with those obtained from the study of captive birds. No active attempt was made to locate nests in the wild because I considered that the necessary frequent systematic searches would have disturbed the birds and the vegetation to an unacceptable extent, and would have greatly increased the chances of nest predation, as was demonstrated for the Striped Crake (Hopkinson & Masterson 1975), African Crake and other secretive wetland rallids (Taylor 1985a; pers. obs.). The most practical method of obtaining dated breeding records was to age the chicks and juveniles observed during fieldwork and to calculate laying dates from this information. It was possible to age these young birds accurately using criteria established from observations of captive birds both before (Wintle 1988) and during this study.

Behavioural studies of family groups were also difficult in the wild, and the limited information obtained was compared with observations of birds in captivity. Further insights into the breeding and social activity of wild birds were obtained from studies of calling patterns and the reactions of both sexes to models, mirrors, and taped playback.

### 4.4 Results

#### 4.4.1 Distribution and status

Figure 4.1A shows the monthly distribution of occurrences recorded in Natal during the study while Fig. 4.1B summarizes all other Natal distributional data, combining records from Cyrus & Robson (1980) and the Southern African Bird Atlas Project (SABAP) data bank. In Natal I have found this species to be widespread and, although never abundant (because of its territorial and sedentary existence), to be present throughout the year in virtually every patch of suitable wetland habitat which I have located in the survey area. I have frequently found it in habitat patches which are too small not only for other rallids but also for most other wetland-dependent birds except Levaillant's Cisticola *Cisticola tinniens* and some *Euplectes* species (see Chapter 5 for details of territory sizes in different habitat types). It even occupies completely isolated small habitat patches, such as those in undisturbed wet depressions within cultivated fields (Plate 1A), and in November 1986 one was flushed at a small pan on the airfield at East London, Cape Province (C.J. Vernon *in litt.*). It occupies suitable undisturbed wetland vegetation along drainage lines through cultivated fields and forestry plantations, in some cases when the width of the wetland may be as little as 8-10 m in places.

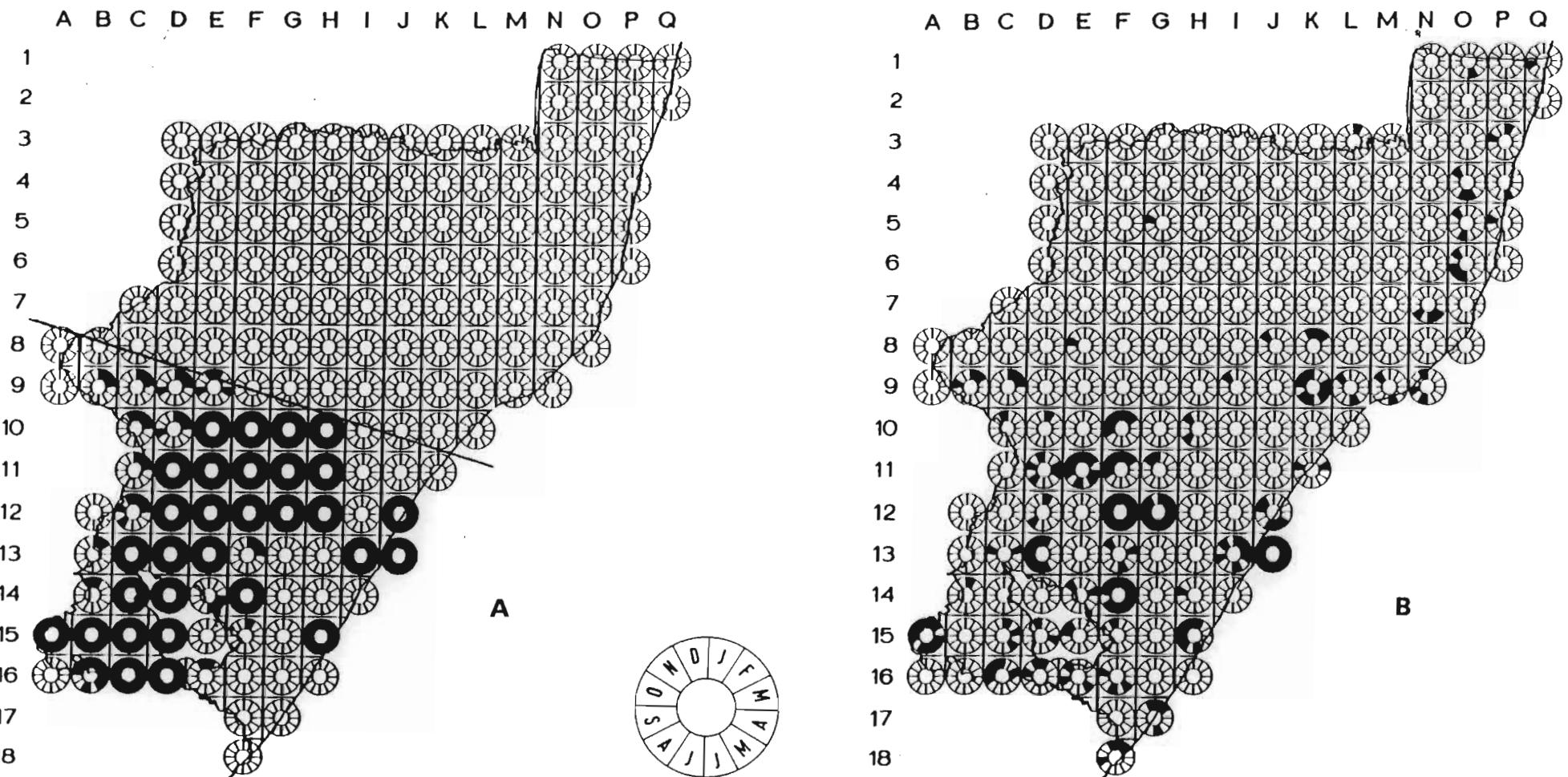


fig. 4.1

Monthly distributional data for the Redchested Flufftail in Natal, by quarter-degree square. A: data from the southern Natal survey area collected from August 1988 to December 1992; all observations by myself except for square F14, which are from J. Morford and myself. B: combined data from Cyrus & Robson (1980) and the Southern African Bird Atlas Project. Data presentation follows the mapping system used by Cyrus & Robson (1980), described in Section 4.3.1. Inset: Monthly information, (January to December) recorded clockwise within each quarter-degree-square symbol.



A



B

**Plate 1**

A: an "island" of wetland habitat in a grass field at Scotston Farm, Underberg, comprising *Phragmites*, *Cyperus* and hygrophilous grasses, March 1991. About 1 700 m<sup>2</sup> were permanently moist, increasing to 2 750 m<sup>2</sup> during the summer. The site was permanently occupied by one pair of Redchested Flufftails.

B: the result of a controlled cool burn at the Gartmore Farm wetland study site, September 1990, showing unburned patches which may provide shelter for Redchested Flufftails during the fire.

The highest altitudes at which I have recorded this species in South Africa are at 2 120 m a.s.l. at Veloren Vlei in the eastern Transvaal ( $25^{\circ}17'S$   $30^{\circ}09'E$ ) in late November (see Section 4.4.2), and in Natal at 2 030 m at High Moor ( $29^{\circ}19'S$   $29^{\circ}37'E$ ), at 1 740 m at Mgeni Vlei ( $29^{\circ}29'S$   $29^{\circ}48'E$ ) and 1 750 m at Mt Currie Reserve. In the southern-Natal survey area Redchested Flufftails are ubiquitous in suitable dense freshwater wetland vegetation from sea level to these altitudes, and the upper altitudinal limits in Natal and the Transvaal are undoubtedly a result of the scarcity of suitable vegetation cover above 2 000 m a.s.l. (see Section 4.4.2). The bird's wide climatic tolerance is shown by the range of climatic and weather conditions recorded at the Natal study sites (Chapter 2, Section 2.2; Tables 2.1 & 2.2; Fig. 2.9). It is permanently resident in areas where subzero winter minimum temperatures and ground frosts are common, and at Mt Currie in July birds were seen walking on ice in reedbeds in the early mornings. In these reedbeds most ice had normally thawed by midday and by about 09:00 on fine days many small flying insects were visible near the ground in sun-warmed vegetation. During my observations at Natal high-altitude study sites, snow did not lie on occupied wetland vegetation for longer than a day and probably had little effect on the birds.

There is no reason to suppose that the species is normally anything other than sedentary throughout its range, both in South Africa and elsewhere. This study produced no evidence of regular movements, apart from the dispersal of young (see Section 4.4.11 and Chapter 5, Section 5.5.6), but a fairly complex pattern of local movements and wandering does exist in response to seasonal habitat changes (see Chapter 5).

The only other new information on distribution and status comes from Namibia, where R. Simmons (*in litt.*) heard a single bird at 948 m a.s.l. in the Nkasa Island area of the Linyanti swamps in the Eastern Caprivi. A local resident claimed to be familiar with the species on the eastern floodplain, where it apparently calls (with DUEHs) most frequently in September-October; however as the entire area dries out when the Zambezi is low, the species may be erratic in occurrence there (R. Simmons *in litt.*).

#### **4.4.2           Habitat**

Redchested Flufftails occur in a very wide range of freshwater wetland vegetation types, being able to live and breed in almost any area which provides dense cover and is not so uniformly deeply flooded as to have no mud, firm ground or short vegetation on which the birds can walk and forage. Occupied vegetation varies from seasonally inundated grassland, which dries out almost completely in the winter, to permanently flooded beds of sedges, *Typha* or *Phragmites*, the last two of which may grow up to 3 m high. Examples of the vegetation types occupied are given in the detailed wetland-

habitat descriptions (Chapter 2) of those sites where this species was studied. At Bromley, Zimbabwe (Section 2.2.1), the birds occurred along the study stream in all vegetation except the deeply flooded *Phragmites* beds. At Dullstroom (Section 2.2.2) they were present throughout the wetland except in the shortest (< 60 cm tall), driest peripheral areas of sedges and hygrophilous grassland. They were also present throughout the Wakkerstroom wetland (Section 2.2.3), except in (a) the deeply flooded central regions dominated by *Phragmites* and *Typha*, (b) the "short marsh" vegetation type (Chapter 8, Section 8.4.2.5) defined by Kotze (1992b) and (c) the permanently flooded sparse beds of *Carex acutiformis* (from which they were also absent in wetlands around Dullstroom and throughout the Natal survey area). They occupied virtually all the wetland vegetation at Gartmore (Section 2.2.5) and Allerton (Section 2.2.7), including moist areas dominated by the fern *Cyclosorus interruptus* and flooded areas of elephant's ear *Colocasia antiquorum* at Allerton. However, *Colocasia* was not favoured during the winter when cover was reduced as frosts killed its leaves. The most deeply flooded *Phragmites* at the Danville Park reedbed (Section 2.2.9) was not occupied, while at Franklin Vlei (Section 2.2.12) deeply flooded vegetation was also avoided, as was peripheral short vegetation which was burned annually or grazed regularly. At Mt Currie (Section 2.1.13) all shallowly flooded to seasonally moist wetland areas were occupied, the birds even extending into peripheral dry areas of tall *Hyparrhenia* both in summer and winter. Deeply flooded areas along streams and at the dam were not frequented. The Penny Park wetland (Section 2.2.14) was too deeply flooded for Redchested Flufftails during the summer except in mixed sedge beds on shallowly flooded ground away from the main river channel, but during the winter birds sometimes moved temporarily into *Leersia*, *Typha* and *Cyperus* beds when summer floods had receded to leave these areas moist to shallowly flooded.

Observations in other areas of Natal, Transvaal and Zimbabwe, as well as my previous experience in central and East Africa, confirm the general preference of the birds for moist to shallowly flooded ground and their usual avoidance of deeply flooded areas and of vegetation which is very short or sparse. In summer, when breeding territories may be extended into hygrophilous grassland at wetland margins (Chapter 5), some birds even penetrate completely dry hayfields adjoining their wetland habitat. For example, during mowing operations in tall *Eragrostis* hayfields near Cedarville adults, sometimes accompanied by young chicks, have been found foraging up to 25 m from moist areas (I. Sparg pers. comm.). Furthermore, in January 1984 a male was seen in a lucerne field at Sterkstroom in the Eastern Cape (C.J. Vernon *in litt.*). At several sites it was noted that the temporary deep flooding of breeding territories after exceptionally heavy rain forced the birds to move into adjacent dry grassland or abandoned cultivation until the floods subsided, sometimes several days later.

Temporary nonbreeding territories (seasonal movements are discussed in detail in Chapter 5, Section 5.4.7) were found in small areas of marginally suitable or atypical habitat which were not occupied during the breeding season because of their small size, their unsuitable vegetation types, or their deep summer flooding. Examples of such areas from Mt Currie (see Chapter 5, Section 5.4.7) are (a) a narrow strip (up to 4 m wide) of flooded *Typha* plus up to 2-3 m of adjacent dry *Themeda* grassland at the dam margin, (b) a small patch of flooded *Typha* and *Phragmites* near the dam spillway, usually deeply flooded in summer, and (c) small areas of tussocky, dense, dry *Hyparrhenia*-dominated grassland on sloping ground near streams; examples from Penny Park are given earlier in this Section.

Habitat at very high altitudes in South Africa appears to be very restricted in extent. For example, in the Veloren Vlei system (see Section 4.4.1) at altitudes above 2 000 m the wetlands, although extensive, were largely unsuitable for occupation by Redchested Flufftails, having mainly short vegetation (predominantly hygrophilous grasses, forbs and short sedges less than 50-60 cm tall) with patches of *Carex* sedges which were usually too flooded, sparse or restricted in area for occupation. Only two calling birds were located in a marshy depression with taller sedges and *Typha* reedbeds which provided suitable cover. It is unlikely that large expanses of suitable habitat exist anywhere in South Africa at this or higher altitudes.

More precise details of the birds' requirements in terms of vegetation structure and substrate saturation are given in Chapters 5 and 6. Table 5.1 summarizes the saturation types and associated vegetation types defined for investigations of habitat type and territory size (see Chapter 5, Section 5.3.1 for definitions). The only other flufftail which normally occurs alongside the Redchested Flufftail in Natal is the Whitewing Flufftail and Chapter 8 contains a detailed comparison of the habitat preferences of these two species and of their spatial overlap during the Redchested Flufftail's breeding season; it also contains a discussion of both species' association with *Carex*-dominated vegetation types and the relative suitability of such habitat.

Redchested Flufftails readily colonize new wetland patches, including those created artificially. When new dams are constructed the flufftails occupy seepage areas below the dam walls as soon as sufficiently extensive dense patches of wetland vegetation have become established. Such patches are often dominated by *Typha*, *Juncus* and the taller sedges such as *Cyperus* and *Schoenoplectus*, often include peripheral moist grassland, and frequently remain permanently moist from seepage; they thus represent excellent habitat for the flufftails if undisturbed by large grazing animals. The birds also occupy suitable wetland vegetation which may develop as a result of increased shallow flooding of ground at dam intakes and along feeder streams. In an experiment at Cedarville, moist patches around a newly built dam were seeded with *Typha capensis*, domestic stock was excluded from them, and

in less than two years the vegetation in these areas had become dense and was permanently occupied by Redchested Flufftails (K. Nel pers. comm.). They avoid wetland areas in which poplar trees have been planted, even if the substrate remains saturated, probably because of reduced cover levels in the ground vegetation and also reduced food supply.

Seasonally flooded vegetation which is dry throughout the winter appears to be permanently attractive only if its constituent plant species are primarily wetland ones (including hygrophilous grassland, as at Gartmore) rather than dry-grassland species which may be irregularly flooded. Thus at Mt Currie some territories which were occupied only during the summer included a preponderance of grassland which was only irregularly flooded and contained grasses such as *Eragrostis*, *Paspalum* and *Pennisetum*. However two other summer territories were located in flooded dam-intake reedbeds which were not usually extensive enough to provide an area sufficiently large to support the species (one example is given in Chapter 5, Section 5.4.2).

#### **4.4.3 Seasonal variations in permanent habitat type and extent**

Observations of territorial birds in Natal show that territory size does not vary with altitude but does vary markedly with vegetation types and the degree of flooding (which itself influences vegetation type and structure). Thus the largest territories occur in habitats predominantly of hygrophilous grassland and the smallest in permanently flooded beds of reeds and sedges (see Chapter 5, Section 5.4.2). In addition, seasonal variations in territory size are often considerable (Chapter 5, Section 5.4.3 and Chapter 6, Section 6.4.2). In winter and early spring suitable habitat in the permanent territories is often reduced as a result of burning, grazing, vegetation dieback, and the drying out of seasonally moist areas, but is also increased (in certain habitat types) by the availability of moist or shallowly flooded dense vegetation which is too deeply flooded for occupation during the breeding season. In summer birds often extend their territories into seasonally flooded sedge meadow and hygrophilous grassland adjacent to their nonbreeding areas, this behaviour having been observed not only in South Africa and Zimbabwe during this study but also in Zambia in the 1970s (P.B. Taylor *in* Keith 1986).

This species is remarkably tolerant of quite considerable damage to nonbreeding habitat: not only can it accommodate reductions of up to 70% in its territorial area by burning (Chapter 5) but it can tolerate considerable disturbance by grazing cattle. At the Bromley study site, a pair survived throughout the 1991 nonbreeding season (during the prolonged drought period) in a marshy area which was trampled and grazed by cattle so that available cover was limited to small patches (0,25-2 m in diameter) of undamaged (i.e. unpalatable) vegetation, such as *Carex* and *Schoenoplectus*

sedges, up to 5 m apart and separated by trampled and grazed short-grassed or muddy areas. However, in several other areas it was noted that winter grazing of reedbed vegetation by domestic stock damaged and fragmented the habitat to such an extent that areas became unsuitable for occupation. Spring and early-summer grazing in burned reedbeds often effectively prevented the vegetation growing enough to allow reoccupation as early as normal, if at all.

#### **4.4.4 General behaviour**

##### **4.4.4.1 Activity patterns and characteristic behaviour**

Redchested Flufftails are normally entirely diurnal and crepuscular in their activities. They usually appear at daybreak and go to roost at dusk, and are most active in the three-hour periods immediately after daybreak and before sunset, during which periods the feeding rate is highest (Section 4.4.6). The only nocturnal activities encountered during the study involved calling. During the breeding season males made advertising hoots periodically throughout the night, especially from November to February. Such birds did not move around and usually showed no reaction to taped playback of advertising or territorial calls, continuing to call from the same spot and only occasionally falling silent. However on clear, bright, moonlit nights both members of a pair would sometimes give territorial *DUEHs* and gulps in response to playback of territorial calls or to the close approach of an observer, and would move around a little, possibly because they could see quite well in the moonlight. The timing of young birds' attempted departure from aviaries coincided with an increase in the territorial calling of the adults, some calls being heard at night, and roosting aviary birds gave occasional *DUEH* calls in response to disturbance at all times of the year.

Aviary birds rested for long periods during the day, the male and female often together in an old nest. Most birds appear to roost off the ground, probably often in breeding or roosting nests, and both adults and immatures were frequently seen climbing around in bushes and tall wetland vegetation in the period just before sunset. An unusual situation was noted by C.C. Wintle (*in litt.*) where a single flufftail in an aviary with Singing Quails *Dactylortyx thoracicus* roosted on the ground with the quail, forming part of the circle of birds which slept, heads facing outwards, in grass about 20 cm tall.

Although essentially terrestrial in their habits, Redchested Flufftails climb freely in grass, sedges, reeds and bushes, especially to obtain better views of the cause of any disturbance, such as a human observer. During taped playback birds on the ground will approach literally to the observer's feet and still be invisible in the dense vegetation, and they move around at very close range without

causing any visible or audible disturbance; in comparison, all non-rallid birds and small mammals are relatively noisy and easily detected. As a general rule, if one sees or hears any movement (even rustling of dead leaves) in suitable habitat at wetland, grassland or forest sites, it will not be caused by a flufftail. However, when confident, Redchested Flufftails may make a considerable noise in the vegetation, as described in the following sections, and when startled into a rapid escape run they may also cause a little noise or movement in the vegetation.

Redchested Flufftails, especially females and young, are often unwilling to emerge into the open in the presence of an exposed observer; they may just look out briefly from cover or rush, with raised tail, across an open patch to obtain a view. When confident they normally hold the tail horizontally, but when they are nervous or uncertain (e.g. in the presence of an unconcealed observer) the tail is raised - when it looks rather like that of a domestic chicken - and sometimes flicked; in aggressive displays the tail is sometimes flattened and fanned out (Section 4.4.5.2). They are extremely difficult to flush in dense cover, preferring to escape by running, often through tunnels in the vegetation which may be made by the birds themselves (I have no evidence for this) or by small mammals. However they may sometimes be flushed after calling them up, by waiting until they have climbed up into nearby vegetation for a better view (their position may be judged by pinpointing the source of their calls), and then moving quickly towards them, when they may fly rather than scramble back down to the ground. They are more difficult to flush than the Streakybreasted Flufftail *S. boehmi*, probably because of the relative height and density of the cover which they inhabit.

When out of cover they are almost always seen in shaded places, and they seem unwilling to remain in the open in full sunlight. They normally sunbathe only for short periods (Section 4.4.4.3) and, when handled for ringing and measuring, they become distressed very quickly if exposed to full sunlight. Their vision in poor light is obviously acute, light usually being dim within their preferred dense ground cover, especially when they emerge at daybreak before other diurnal non-rallid birds are active in this habitat.

#### **4.4.4.2        The pair bond**

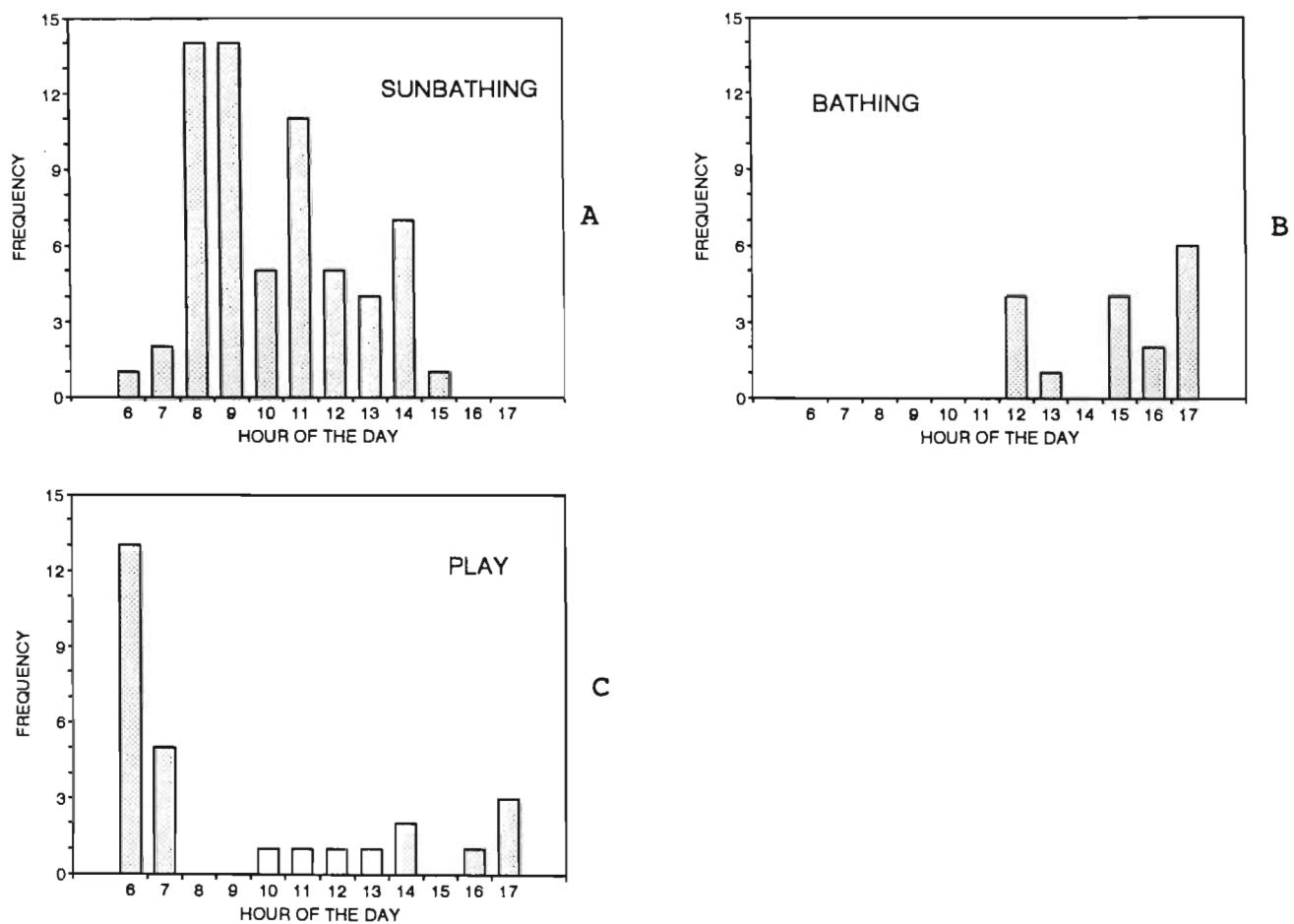
In captive birds the pair bond was permanent and the male and female were almost always close together, whether feeding, resting, engaging in territorial activity or caring for chicks. All evidence from wild birds, including that from birds recognized by colour rings and vocalizations (see Section 4.4.5), indicated a similar situation. In captivity contact notes were frequently uttered, at least by the female (Section 4.4.8), and in all situations allopreening between pair members was regular, although not frequently observed (being seen no more than once per day). Occasional allopreening

was also observed in pairs of Whitespotted Flufftails, which are also permanently territorial (Taylor & Taylor 1986), but never in Buffspotted Flufftails, for which no definite evidence was found for a permanent pair bond in nonmigratory adults (Chapter 9, Section 9.4.4.2). On rare occasions the male Redchested Flufftail of a pair was also seen to feed the female, even outside the breeding season.

#### 4.4.4.3      Comfort activities

Redchested Flufftails sunbathe frequently, usually on the ground in patches of sunlight between dense clumps of vegetation. Sunbathing was observed only infrequently in the wild, probably because the observation areas had few visible sunlit patches. Captive birds of all ages sunbathed daily and during observations in April 1992 notes were made of all sunbathing, which was largely social, two, three or all four of the birds usually sunbathing together. The birds usually either crouched or lay flat on the ground, with the tail spread and the wings open: drooped, raised, partially or fully spread, or with the wingtips crossed across the back. During the observation period (6-19 April) sunbathing took place between 06:58 local time (one hour after sunrise) and 15:26 (2½ hours before dusk). The distribution of the 64 recorded sunbathing bouts is summarized in Fig. 4.2A, and shows that most sunbathing activity took place between 08:00 and 10:00, with secondary peaks at 11:00-12:00 and 14:00-15:00. The distribution of this activity was to some extent dictated by the availability of sunlit patches in the aviary. After the sun first touched the topmost leaves of the tallest bamboo clump at 06:55 single birds occasionally flew up to this sunlit patch and basked there in the early warmth, this occurring until about 08:00. The first patches of sun appeared on the ground at 08:20 and this marked the start of the most intensive sunbathing activity, which ended when the last patch disappeared at about 14:30. Small sunlit patches then appeared in the topmost leaves of some aviary trees until 15:35 and birds occasionally flew up to them for short periods. Apart from the initial "warming up" basking between 06:55 and 08:00, when birds remained in the sun for between 4 min 40 s and 10 min, most sunbathing periods were short, of mean duration 1 min 40 s ( $n = 28$ ; S.D. = 53 s). The birds frequently preened vigorously while sunbathing.

Bathing was also probably a daily activity but was more difficult to observe in the aviary because it was often performed under the cover of overhanging vegetation. Both adults and young bathed regularly, and of 17 recorded occurrences (Fig. 4.2B), all took place after midday, with peaks in the hottest part of the day (12:00-14:00) and in the last 2½ hours of daily activity. The duration of bathes ranged from 47 s to 6 min 17 s, but accurate timing was often impossible because the birds were very wary and were often not seen for the full period. After bathing they invariably preened and



**Fig. 4.2** A-C: frequency distribution of various Redcheasted Flufftail activities by hour of the day (local time).

shook themselves vigorously for several minutes, in a sunlit patch if this was available. Two or more birds sometimes bathed and preened together.

In the aviary preening occurred on many occasions throughout the day, especially in the early morning, but its occurrences were not recorded in detail. On most days the birds preened in the last available patches of afternoon sun on the ground, and all birds preened vigorously and thoroughly after bathing. Allopreening occurred regularly between adults and immatures.

#### **4.4.4.4 Flight**

Redchested Flufftails normally fly very little, usually to escape from potential predators and aggressive conspecific individuals. However the captive birds observed in April 1992 regularly made short flights, mostly in the periods of greatest activity, up into tall vegetation. These flights were made during play activities (Section 4.4.4.5), as a means of reaching high sunbathing perches early or late in the day (Section 4.4.4.3), and to attain elevated observation posts (Section 4.4.4.5). The birds are quite adept at perching on narrow stems for periods of several minutes.

#### **4.4.4.5 Play and inquisitiveness**

Play is recorded in a wide variety of birds, usually involves young individuals, and is more difficult to distinguish from other activities in birds than in mammals; some reported cases appear to be a result of threshold lowering, which is usually regarded as distinct from play. Three types of play have been described in birds: locomotory, object and social play, the last being the least frequently recorded type (M. Bekoff *in* Campbell & Lack 1985; Ficken 1977).

During observations of the captive Redchested Flufftail family in April 1992, behaviour which could be regarded as play was recorded daily. It met the criteria used in defining play by the above authors, and it could not be explained as a vacuum activity, redirection or response to suboptimal stimuli (Ficken 1977). Most of the observed activities apparently fell into the category of social play (see Discussion) and involved at least two, frequently three and sometimes all four of the birds, in any combination of individuals. The incidence of this activity throughout the day is summarized in Fig. 4.2C, which shows that most of the sequences took place early in the morning, in the period when other activities, especially feeding (Fig. 4.6), were at a high level. Continuous play periods varied from 30 s to 39 min, and periodic play sometimes continued for as long as one hour.

Play activities usually combined display, aggressive, escape and apparently exercise behaviour. A sequence would often begin with one bird standing on tiptoe and performing vigorous

wing-flapping, or making several short, rapid dashes in various random directions. The bird might then suddenly crouch and dash at another bird, or another might run at it while it was still performing the initial solitary activity. One bird would suddenly dash from cover at another which was quietly feeding, or two well separated birds foraging in the open would suddenly become involved in an attack or chase sequence for no apparent reason. Initial actions frequently seemed to be invitations for other individuals to participate in the play.

When thus approached, a bird would sometimes dash off and a vigorous chase would ensue, the birds often running with wings flapping or raised above the back and always with raised tails. Chases ended when the fleeing bird escaped into dense cover, or the pursuer gave up the chase, or the pursued bird stopped and made wing flaps or just faced its pursuer, when the birds would usually crouch, bow to each other and then resume normal activities. (The male Buffspotted Flufftail sometimes gives a similar bow before attacking a model; see Chapter 9). If pecked by the attacker, the other bird would assume a submissive crouch with lowered head and (sometimes) drooped wings, when aggressive actions would cease immediately. Occasionally the chase became so frantic that the birds ran in circles round a clump of grass at a dizzying speed, one such chase ending with the pursued bird flying rapidly up into overhanging branches, watched intently by the other. Chases involved all combinations of individuals, but most frequently an adult and a juvenile; the female was often chased by a juvenile but the adult male was rarely chased. Sometimes a third bird, or even all four, would join in a chase.

Another common form of play was for two to four birds to dash towards each other, suddenly stop when almost touching, crouch, stare at each other and then make a small bow, often with the wings raised over the back, before resuming normal activities. Such encounters might include some low-intensity pecking of the head and neck, wing-flapping, preening or allopreening.

During periods of intense activity, especially in the early morning, single birds would sometimes fly up into bamboo clumps or bushes and climb noisily around for some time before flying down again; this behaviour might be repeated soon afterwards. The birds also chased other aviary occupants such as lizards, small passerines and small doves, this behaviour being intensified if the chased birds had obvious areas of red in the plumage, such as Bluebilled Firefinches *Lagonosticta rubricata* and Common Waxbills *Estrilda astrild*.

Fragments of these activities were also observed in the field, usually individuals flapping or crouching on observation tracks, chases across tracks, and birds running to meet in the open with wing flaps or bowing. They were not understood until the aviary play was seen, and it is clear that such behaviour is not confined to captive birds. Chases of other species were also seen in the field,

and male Red Bishops *Euplectes orix* in breeding plumage sometimes provoke very aggressive reactions.

Redchested Flufftails are very inquisitive and they often investigate the human observer, sometimes climbing up into vegetation to get a better view. While watching the aviary family I occasionally missed one or two individuals and, on looking down, I would see them standing in the open under the observation window, watching me. On two occasions one bird (the male and an immature) flew up, landed precariously on a thin branch immediately in front of the open observation window and watched me for over a minute: I could have touched them from where I was sitting.

#### **4.4.5 Territoriality and aggressive behaviour**

##### **4.4.5.1 Territoriality**

Experiments with models and taped playback, long term field observations of birds, and work on calling patterns, all indicate that Redchested Flufftails are monogamous, form a permanent pair bond and are strongly territorial throughout the year, both members of a pair taking an active part in territorial defence. Adult males attack or threaten a model male throughout the year but the attacks are less pronounced from March to June (Fig. 4.3), during which period territorial calling is reduced and vocalizations vary in type and intensity (Section 4.4.8; Figs 4.8 and 4.9A). Males also show interest or attack responses to a female model outside the breeding season (Fig. 4.3) and they attack or threaten their image in a mirror throughout the year. Females (Figs 4.9B and 4.3) are very active in territorial defence, calling throughout the year; they were seen to react aggressively to a female model from July to January and to have a weaker reaction to the model from March to June (no February observations were made).

Both sexes make many territorial calls throughout the year (Figs 4.8 and 4.9). Either sex may initiate a calling bout, either spontaneously or in response to taped playback, but the female usually did not call as soon, as frequently or as continuously as the male and sometimes failed to call at all. Females in aviaries, however, often called at least as frequently as males (C.C. Wintle pers. comm.). Females make fewest territorial calls during the breeding months, when the level of the male's territorial calling also declines (Figs 4.8B and 4.9B): see Section 4.4.8 for further details.

Monthly recordings of the calls of selected resident pairs revealed not only that the intensity of reaction to playback varies during the year (e.g. birds respond for shorter periods during the winter months, and often take longer to respond to taped playback), but also that the structure and type of territorial calls show seasonal variations (see Section 4.4.8). The volume of information collected on

**REDCHESTED FLUFFTAIL, MALE**

Stimulus	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Model M												
Model F												
Mirror												

The table illustrates the seasonal reactions of adult Redcheasted Flufftail males to different stimuli. The months are represented by columns from July to June. Shaded columns indicate months where egg-laying was recorded. Dashed arrows between columns represent specific behavioral sequences:

- Model M: A strong attack followed by a display/attack.
- Model F: Interest/mild attack followed by courtship/mate, which is followed by interest/mild attack again.
- Mirror: A display/attack sequence.

**REDCHESTED FLUFFTAIL, FEMALE**

Attacks model F, July to January; displays or calls to model F, March to June.  
 Shows interest in model M throughout the year. Reactions to mirrors were not observed.

FIGURE 4.3. Reactions of adult Redcheasted Flufftails to model male (M) and female (F) Redcheasted Flufftails, and reactions of adult males to their reflections in a mirror. Shading indicates months in which egg-laying was recorded during the study. Abbreviation: m.att = mild attack.

seasonal variations in calling patterns and intensity of reactions is too great to allow detailed analysis to be made for this thesis.

From February and March the territorial calls of resident immatures are frequently heard in the parents' territories (Fig. 4.10) and these calls may continue until the beginning of the next breeding season (August or September) when the last young finally leave the parental territories. Aviary observations of behavioural responses to taped playback indicate that young males often react as strongly as adult males during the winter, while immature males in the wild were occasionally seen to attack models and display aggressively to them. This parallels the situation in the Whitespotted Flufftail, where immature males also took an active part in territorial defence (Taylor & Taylor 1986).

The birds' behaviour in the nonbreeding season makes a strong contrast with that of the two other wetland rallids which share their habitats in Natal. Black Crakes (Fig. 4.4) attack a model only during the peak breeding period and ignore or avoid it between March and August; their reactions to mirror reflections are stronger but they still avoid the mirror from June to September. Their calling decreases markedly during the nonbreeding period, when their reaction to taped playback is also much reduced. When breeding, they may violently attack a male model Redchested Flufftail, but from April to September they usually avoid the model: this is in sharp contrast to the Redchested Flufftails, which avoid the Black Crakes when the latter are strongly territorial but either ignore them (including models) or even attack them (live crakes) during the winter months, when we have even observed female flufftails attacking Black Crakes. These observations confirm that Black Crakes are territorial only during the breeding season.

Relatively little work was done on the African Rail, but results (Fig. 4.5) show that calling decreases markedly outside the breeding season and reactions to taped playback are poor for 2-3 months after the breeding season, when a rattle call is normally given instead of the usual loud trill. These rails began strong territorial calls very early in the season (from July) at some sites, but in all areas appeared to relinquish territories for several months during the winter. Their reactions to models were incompletely studied but they called strongly, made threat displays and sometimes attacked an African Rail model from late September to December, while at feeding stations they avoided male Redchested Flufftail models in August and October, and made mild attacks on them in May and August. The flufftails always either ignored or avoided African Rail models.

Observations indicated that one pair of Redchested Flufftails may occupy a territory for several years. An adult male colour-ringed at Allerton on 14 October 1988 was regularly observed in the same territory for two years 11 months, until regular observations were discontinued in September 1991. Another adult male, colour-ringed at Danville on 6 July 1989, maintained a territory there until 7 November 1990 (16 months later), when both male and female disappeared, probably

**BLACK CRAKE, ADULTS**

Stimulus	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun					
Model BC	ignore/avoid	ignore/intrst.	interest/attack (variable)				<----- ignore/avoid ----->										
Mirror	<----- avoid ----->			<---- interest/attack (variable) ---->				mild attack/ignore			avoid						
Playback	<--- poor --->		<- moderate ->		<----- strong (variable)----->				moder.	<--- poor --->							
No. calls	very few	moder.	<----- many (variable) ----->				moder.		<- very few -->								
Model RCF	<--- ignore/avoid --->			<----- interest/attack ----->				<--- ignore/avoid --->									

**BLACK CRAKE, JUVENILES**

Make mild attacks on mirror reflection and flufftail model throughout winter (June to September). Other reactions similar to adults.

**FIGURE 4.4.** Reactions of adult and juvenile (less than one-year-old) Black Crakes to model Black Crakes (BC) to a model male Redcheasted Flufftail (RCF), taped playback of Black Creak calls, and their own reflection in a mirror. The frequency of spontaneous duetting (No. calls) is also given. Shading indicates months in which egg-laying was recorded during the study. Abbreviations: intrst. = interest; moder. = moderate.

**AFRICAN RAIL, ADULTS**

Stimulus	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Playback	moderate to strong			<----- strong ----->				moderate to strong		<---- poor ---->		
No. calls	moderate			<----- many ----->					<-- few (variable) -->			

**AFRICAN RAIL, JUVENILES**

Call frequently, March to June, with feeble version of the adults' territorial call (see text). During this period adults give predominantly the rattle call (see text).

FIGURE 4.5. Reactions of adult and juvenile (less than one-year-old) African Rails to taped playback, and the frequency of spontaneous calling (No. calls). Shading indicates months in which egg-laying was recorded during the study.

as a result of the appearance of a Water Mongoose *Atilax paludinosus*, which may have killed or driven away the birds. The site was unoccupied until 19 April 1991, when a pair of immature birds arrived and set up a territory. The mongoose was trapped and relocated in May 1991 and the territory was continually occupied by the flufftails until observations ceased in April 1992. Although these birds were not ringed, studies of calls indicated that the male, at least, was the same individual throughout this 11-month period. In contrast, an immature male sharing the territory with the original male and colour-ringed on the same day (6 July 1989) was last seen on 24 August 1989 (when the first advertising calls were heard in this territory), after which it was presumably ejected by the adult pair (see Section 4.4.11).

Regular observations at other sites provided more evidence of long term residence by individual males on the basis of recognizable individual vocalizations. Three such males at Gartmore were heard in their original territories for four years (from December 1988 to December 1992), despite their having been forced by burning temporarily to vacate the territories, two in 1989 and 1991 and the third in 1990. At Mt Currie two males, easily recognized by distinctive calls and response patterns, were heard on every monthly visit for three years and four months (from January 1989 to May 1992), when regular observations were discontinued. Only one of these birds had been forced temporarily to vacate its territory after one spring burn, and both survived the January 1991 hailstorm. Five other males at Mt Currie were fairly confidently identified within their original territorial areas for between 10 and 23 months, although the territories of two adjacent birds underwent some displacement during a 22-month period.

Females were much more difficult to trap, observe and recognize by calls, and relatively little information was obtained on their fidelity, either to their mates or their territories. A female colour-ringed at Allerton on 2 December 1988 was last seen in the same territory on 8 April 1990, one year and four months later, still with the male which had been colour-ringed in October 1988. Two females at Mt Currie were deemed recognizable on calls, but were not heard in every month of the study; one was heard frequently throughout the three years and four months during which her mate was continually present (see above), the other was heard irregularly in one territory for two successive breeding seasons (1989-90 and 1990-91; there was no intervening burn) but her mate was not readily recognizable on call. Observations of captive birds showed that the pair bond was maintained throughout the year, while in both captive and wild birds each member of a resident pair did not tolerate strange adults of its own sex in the territory during the breeding season, and a permanent, monogamous relationship appears to be normal.

Although I have no definite evidence, it is probable that some unpaired males may maintain territories, at least for short periods. There were several cases, covering all seasons, of permanent

territories in which the calling male was regularly heard but no female was located for 2-6 weeks. Such males had possibly lost their mates and had then attracted new females. However, because of the relative difficulty of observing and (sometimes) of calling up females, it was never certain that the original female was not present throughout the period when no female was heard.

As mentioned in Section 4.3.1, it was not possible to differentiate home range from territory in this species. The birds apparently behaved very territorially throughout the whole area which they inhabited, usually penetrating adjacent territories only infrequently, principally when attracted by prolonged taped playback near the territorial boundary.

As well as being kept in other aviaries of approximately the area ( $24\text{ m}^2$ ) of the one used during this study, Redchested Flufftails have also been housed in aviaries of  $100\text{-}125\text{ m}^2$ . No more than one pair has ever bred successfully in any aviary: the dominant male and female harass other birds, which may be killed if they are not removed, and the dominant female is particularly aggressive to other females (Section 4.4.5.2).

#### **4.4.5.2 Aggressive behaviour**

On numerous occasions throughout the year the reactions of territorial male Redchested Flufftails to models and mirrors were observed and filmed from hides. The birds were first attracted by taped playback of territorial and advertising calls, which was continued during the birds' displays and attacks. When presented with a mirror or a model male, the bird approached as close as possible in cover, often with head and neck stretched forward and in line with the body and tail, before emerging near the stimulus object. Three types of threat display were observed, the first (1) being given only in response to mirror-image stimulation in the evening, as the light was fading rapidly. The male approached the mirror on straight legs, standing quite tall with neck retracted, body, head and tail in a horizontal line, the tail somewhat flattened and fanned out and all the plumage raised. It stood close to the mirror, its body swelling markedly (presumably as the plumage was further raised), called with quiet *DUEHs*, and sometimes repeatedly moved its body slowly up and down. It then often walked slowly and stiffly around in front of the mirror before moving off into cover, from which it called with *DUEHs* and gulps before emerging to repeat the display.

The most common display (2) was more aggressive and was often followed by an attack on the model or the mirror. The male approached with a slow creeping walk on somewhat flexed legs, the body, neck and head plumage raised and the tail slightly elevated and spread. The neck was often retracted but sometimes stretched out, and the head was usually slightly raised and was sometimes moved backwards and forwards. The tail was flicked only if the bird was not fully confident, e.g. in

the presence of an unconcealed observer. The approach was accompanied by low-pitched gulping calls (Table 4.1, Calls M30, M31, M43 and M48), which continued as the male sometimes walked slowly round the model before attacking it, usually from the side. The bird rushed at the model and fluttered up and down around it, pecking at its head and neck and sometimes striking with the feet. The attack was usually short, lasting no more than 5 s, but in more prolonged attacks the male sometimes pecked the model from all sides and even stood on its back and tried to pull feathers out of it. Attacks on the mirror were brief and similar to those on the model, involving fluttering jumps, pecks at the head, kicks and occasional buffeting with the wings. The sequence was often repeated several times, the bird sometimes running briefly into cover between attacks. In contrast to the Striped Flufftail (Chapter 7, Section 7.4.3), the male Redchested Flufftail did not display its tail prominently during threat or attack sequences.

The third display (3) occurred between attacks on the mirror. The male remained close to the mirror and crouched, with its body higher at the front so that its tail touched the ground and its head and neck were raised. In this position it made quiet *DUK* calls (Table 4.1, Call M28).

In common with the other two species studied (Chapter 7, Section 7.4.3 and Chapter 9, Section 9.4.5.3), after making a few attacks the male Redchested Flufftails often examined the edges and back of the mirror, looking for the adversary. They even jumped on to the top and looked down on both sides of the mirror, sometimes pecking between their feet at the reflection.

The male's aggressive reactions to a model female involved a similar threat display (No. 2) and attack sequence to those given against a model male, except that the attack was not usually so violent and never involved standing on the model and pecking it. During the breeding season, males often attempted to mate with model females (Section 4.4.10.1; Fig. 4.3). The reactions of territorial female Redchested Flufftails to models were less frequently observed, and I was not successful in inducing females to react to mirrors. Females were aggressive to model females for much of the year (Fig. 4.3), in the breeding season often making attacks as violent as the strongest seen from males to models. Their threat display to models, similar to display No. 2 of the male, was given throughout the year to model females and sometimes also to model males. In captivity, females were more aggressive than males and unpaired females were sometimes killed by paired females (Wintle 1988; C.C. Wintle *in litt.*).

Vocal stimuli appear to be important for the release of attack behaviour and models were seldom attacked unless taped playback preceded and accompanied the presentation. However visual signals are equally important, mirror images sometimes being attacked without any playback having occurred, while the presentation of a male model with a somewhat different colour or pattern from

TABLE 4.1

Redchested Flufftail vocalizations described during the study. All calls are repeated as a sequence unless otherwise specified. F/Y, M/Y, M/F = equivalent calls of female, male or young: see relevant sections of table for details. Contexts: A = advertising; C = courtship; G = aggression; M = mating; T = territorial; X = warning/alarm; Z = contact; ? = context uncertain. Secondary or possible contexts are placed in parentheses.

## ADULT MALE

No.	Description & phonetic rendering	Context	F/Y
M1	Rising hoot: <i>WOOAH</i>	A	
M2	Hoot or broken hoot (two pitches): <i>WOOO</i> or <i>WOOO-EE</i>	A	F1
M3	Short mellow hoot: <i>WOOP</i>	A	
M4	Gulping hoot: <i>GOOP</i> or <i>GOOP-OO</i>	A(T)	
M5	Quiet hoot-gulp: <i>WOOO-GUG</i> or <i>WOOOEE-GUG</i>	T(A)	
M6	Quiet wavering <i>OOOOOOO</i> , descending in pitch	A	F2
M7	Feeble wavering <i>OOO-AA-GUG</i>	A(G)	
M8	Prolonged wavering <i>OOOOOOO</i> , varying in pitch	A	
M9	Low-pitched quiet <i>BOOP</i> notes, often before hoots	A	
M10	<i>DUEH</i> or <i>DOO-A</i> , with or without gulp or grunt	T	F3
M11	Hoarse raucous <i>KOOO-EE</i>	T(G)	F4
M12	Hoarse wavering <i>GDUI</i>	T	
M13	Rapid, high-pitched, ringing <i>KLOOI</i>	T	
M14	Squeaky <i>dueh</i> derivative: <i>SQUOO-EH</i> , with or without gulp	T	F6
M15	Squeaky <i>SQUEE-A</i>	T	
M16	Rapid <i>DEE-DEE</i> with gulps (sometimes follows call M16)	T	
M17	Very rapid slurred <i>dueh</i> : <i>DAAI-DAAI</i>	T	
M18	Wheezy rapid <i>DU-DU</i>	T	
M19	Moaning <i>DOOOO</i> , varying in pitch and intensity	T	
M20	Low-pitched clear <i>DOOO-DOOO</i> , often preceding <i>duehs</i>	T	
M21	Slow metallic <i>DUNG-DOO</i>	T	
M22	Wavering, inverted, very angry <i>dueh</i> : <i>DEEEU</i>	T	
M23	Rising hoot/ <i>dueh</i> , first part explosive: <i>KAH-WURT</i>	T	
M24	Loud clear <i>KEVIC</i> or <i>KVIC</i> , sometimes followed by M10	T	F7
M25	Very quiet <i>KEK-KEK</i> , often with gulps or quiet <i>duehs</i>	T	
M26	Very annoyed loud <i>GUG-DOO</i> , usually after <i>dueh</i> sequence	T	
M27	Long <i>DUUUUU</i> , rising in pitch, preceding <i>duehs</i>	T	
M28	Annoyed <i>DUK</i> , sometimes before other territorial calls	T(G)	
M29	Grunts: <i>GRG</i> , often accompanying hoots or <i>duehs</i>	T	F13
M30	Gulps: <i>GUG-A-DUG</i> or <i>GU-DUG</i> , with or without other calls	T(G)	F14

/continued

TABLE 4.1 (continued)

## ADULT MALE (continued)

No.	Description & phonetic rendering	Context	F/Y
M31	Rapid short gulps, often preceding duehs: G-G-G-G	T(G)	F15
M32	Rapid KEEKEE-KEEKEE	T	
M33	Slow loud KER, sometimes less harsh: KEP	G	F16
M34	Strident KEK or KIP, sometimes with gulps: GUG-GUG-KEK	G(T)	
M35	Spitting KECK-KECK or NEH-NEH	G	F17
M36	Very rapid and excited KE-KE-KE	G	
M37	Rapid chattering CHIK-CHIK	G	
M38	Sneezing CHEEE when attacking immature	G	
M39	Rattling KRRRRRRRRR note, followed by duehs or gulps	G	
M40	Hissing SHHHHH	G?	F18
M41	Angry KSSK when fighting	G	F19
M42	Angry KZEEP attack call	G	F20
M43	Rapid low GUG-DOO when attacking model (see also M26)	G	
M44	Growls GZRMM-GZRMM, sometimes with gulps GUG	G	
M45	Very loud growls, descending in pitch: GRRRRRRR	G	
M46	Very faint growls when handled: GRRR-GRR	G(X)	F22
M47	Rattling DRRR-DRRR, may be followed by G-G-G (see M31)	G(T)	
M48	Rapid galloping GDK-GDK, sometimes followed by G-G-G	G	
M49	Low hard GRRRK to model female	G	
M50	Rapid KER-KER, when retreating (e.g. chased off nest)	X(G)	F26
M51	Rapid high-pitched KI-KI, indicative of great stress	X	F27
M52	Very fast high-pitched DWER-DWER	X	
M53	Single explosive KREK	X?	
M54	Loud KWEK, sometimes becoming KER (M50)	X	F28
M55	Quiet sharp CHEK, following model snake	X	
M56	Very quiet little grunt when handled: GRK	X	F31
M57	Hoarse low-pitched BOO	C	
M58	Mellow OOP when displaying to female	C	
M59	Quiet GEEP-GEEP	C	
M60	Quiet GRUK to model female	C	
M61	Quiet Turtur-dove-like HOO-HOO or HOO-HOO-HOO	Z	
M62	Deep, low-pitched, soft OOO	Z	
M63	Small hoarse GRUK to chicks	Z	F37
M64	Bubbling noise to female	Z	F38
M65	Rattle TRRRRR when flying up into bush or tree	Z	F39

/continued

TABLE 4.1 (continued)

## ADULT FEMALE

No.	Description & phonetic rendering	Context	M/Y
F1	Hoot or broken hoot: WOOO or WOOO-EE	A	M2
F2	Quiet wavering OOOOOOO, descending in pitch	A	M6
F3	DUEH or hoarse TOO-WA, accent usually on second syllable	T	M10
F4	Hoarse, raucous KOOO-EE	T(G)	M11
F5	Very harsh DUEH, accent on first syllable	T(G)	M10
F6	Squeak-gulp: SQUEE-GUG	T	M14
F7	Loud, high-pitched, clear to strident KEVIC or KEVEEK	T	M24
F8	Quail-like WHIT or KWI	T	
F9	Wheezy KHER-KHER following KEVIC sequence	T	
F10	TEE-DI-DI TEE-DI-DI TI-TI-TI-TI-TI sequence	T?	
F11	Buzzing ZE or softer DE sequence, before feeble duehs	T	
F12	Rapid DU-DU after KEVICS	T	
F13	Grunts: GRG, often accompanying other calls	T	M29
F14	Gulps GUG-A-DUG or GU-DUG, with or without other calls	T	M30
F15	Rapid short gulps, often preceding duehs: G-G-G-G	T	M31
F16	Slow loud KER or KEP	G	M33
F17	Spitting NEH	G	M35
F18	Hissing SHHHHH during fight with Black Crake	G	M40
F19	Angry KSSK during fights	G	M41
F20	Angry KZEEP attack call	G	M42
F21	Aggressive ZEEK, ZERK, CHERK or CHEK when handled	G	
F22	Very faint growls, especially when handled: GRRR-GRRR	G(X)	M46
F23	Wailing moan: DOOOOWH, when very aggressive	G	
F24	Rapid PITTA-PATTA-PITTA-PATTA-KD-KD-KD-KD, then call F15	G	
F25	Run-together, very rapid DOOE-DOOE	G(T)	
F26	Rapid KERK-KERK or KEEK-KEEK, in great agitation or fear	X(G)	M50
F27	Rapid high-pitched KI-KI, indicative of great stress	X	M51
F28	Loud high-pitched KWIK	X	M54
F29	Loud KIK	X	
F30	Rapid KIRRI or KEREE notes followed by KI-KI sequence	X	
F31	Very quiet little grunt when handled: GRK	X	M56
F32	Tiny soft DI-DI or KI-KI calls	C	
F33	Quiet short OOP	C	

/continued

TABLE 4.1 (continued)

## ADULT FEMALE (continued)

No.	Description & phonetic rendering	Context	M/Y
F34	Tiny high-pitched <i>KIK</i>	M	
F35	Tiny squeaks, following <i>KIK</i> (F34)	M	
F36	Quiet <i>KREE</i> or <i>ZEEP</i>	M	
F37	Small hoarse <i>GRUK</i> to chicks	Z	M63
F38	Bubbling noise to male	Z	M64
F39	Rattle <i>TRRRRR</i> when flying up into bush or tree	Z	M65
F40	Short rapid <i>CHAK-CHAK</i> when flying up into bush or tree	Z	
F41	Single quiet <i>TACK</i>	Z	
F42	Short quiet <i>TK-TK</i> to juveniles	Z	I13
F43	Quiet short <i>VIC</i> to juveniles	Z	I9
F44	Feeble <i>IK-IK</i> notes when birds first appear in morning	Z	
F45	Quiet <i>KWEK</i> , rising in pitch, to male	Z	
F46	Quiet <i>TRK-A-TRK</i> or <i>TRK-TRK</i> to male	Z	
F47	Very quiet <i>CHRRR</i> or <i>CRRRK</i> to male	Z	
F48	Very quiet, rapid, little <i>GUK-GUK</i> or <i>GRK-GRK</i> to male	Z	
F49	Low-pitched <i>KEEP</i> to male and juveniles	Z	

/continued

TABLE 4.1 (continued)

## ADULT, SEX UNKNOWN

No.	Description & phonetic rendering	Context
A1	Plover-like, sharp, descending <i>KEEOO</i> from tree perch	A?
A2	Mellow rapid <i>OOA-OOA</i> , to tape playback	T
A3	Harsh <i>TCHAA</i> in play-fight chase	G
A4	Nasal <i>NYAA</i> with scuffle for preening position in sun	G
A5	Sharp <i>ZIK-ZIK</i> to human intruder	X
A6	Breathy <i>OOH</i>	C/M
A7	High-pitched <i>NYEE</i>	C/M?
A8	Scratchy prolonged <i>TZEEEE</i>	C/M
A9	Quiet <i>WEEP</i>	C/M?
A10	Quiet <i>BUP</i>	C/M
A11	Soft short <i>UH-UH</i> or <i>UK-UK</i>	C/M
A12	Quiet <i>KEK</i>	Z
A13	Quiet <i>CHEP</i>	Z

/continued

TABLE 4.1 (continued)

## IMMATURE

No.	Description & phonetic rendering	Context	M/F
I1	Faint <i>DUEH</i>	T	M10
I2	Rapid high-pitched <i>KLOOI-KLOOI</i>	T	
I3	Loud clear <i>KEVIC</i> (second syllable accented)	T	M24
I4	Harsh loud <i>KREEK</i> , occasionally <i>KVEEK</i>	T	
I5	Plaintive high-pitched <i>KEE-KEE</i>	X?	
I6	Rapid sharp <i>TCHK-TCHK</i> when in bush watching intruder	X?	
I7	Harsh <i>ZERK</i> or <i>ZEK</i> when chased by adult male	X	F26
I8	Faint grunts when handled: <i>GRK</i>	X	M56
I9	High-pitched feeble <i>VIC</i>	Z	F43
I10	Quiet <i>CHK</i> to sibling when bathing	Z	
I11	Dry rattle: <i>TRRRRR</i> , when flying up into bush or tree	Z	M65
I12	Sharp quiet <i>KIP</i>	Z (X)	
I13	Quiet ticking: <i>TK-TK</i> , at roost with adult female	Z	F42

## DOWNY CHICK

No.	Description & phonetic rendering	Context	M/F
C1	Plaintive cheeping: <i>PEE-PEE</i>	X (Z)	
C2	Faint ticking: <i>TK-TK</i>	Z	F42
C3	Quiet <i>IP</i> or <i>IK</i>	Z	F44
C4	Quiet dull <i>UP</i> or <i>DUP</i>	Z	

the normal (such as spots on the body instead of streaks, or barring on the tail, or a black head) would elicit great interest from the male bird, but no threat or attack behaviour.

#### 4.4.6 Feeding methods, food and energy requirements

The foraging behaviour of both wild and captive birds was observed at length, and the birds were found to be generalist feeders on a wide variety of invertebrate prey, as are the other species studied during this project and also the Whitespotted Flufftail (Taylor & Taylor 1986). They were seen to eat many types of insect, including small ants, flies, aquatic and terrestrial Hemiptera and Coleoptera, and Lepidoptera, as well as earthworms, small spiders, small gastropods and fallen grass seeds. Captive and wild birds ate not only mealworm larvae but also pupae and adults, which other flufftail species did not; they also ate millet seed frequently. Low plants were searched for prey, usually lepidopterous larvae, small moths, flies, and adult Coleoptera and Hemiptera. The birds foraged on dry to moist substrates, and in mud and shallow water, sometimes immersing the head in water to seize submerged prey. They were adept at catching pond skaters (Gerridae) such as *Eurymetra natalensis* in shallow water and, like Baillon's Crakes *P. pusilla*, they probed into the ends of rotten branches and stumps to search for beetle larvae and other invertebrates. They dug with the bill among plant roots, where they found small cockroaches and other insects, and they frequently fed among the roots of emergent plants as these became exposed or flooded by fluctuating water levels. They searched for earthworms which were forced to the surface as water levels rose, and they dug with the bill in moss and soft earth to extract large earthworms. When searching the ground they also used the bill to push aside lumps of moss, leaves and dead plant material. During early-morning feeding in the Bromley aviary they ate insects which had been attracted to night lights. Occasional bouts of rapid vertical pecking into shallow water were apparently aimed at small crustaceans, mosquito larvae, chironomid larvae and small water beetles. When feeding very actively, the birds often vibrated their tails rapidly from side to side, an action which was repeated during other periods of intense activity or excitement, such as courtship and mating (Section 4.4.10.1).

Both Redchested Flufftails and other rallids (principally Black Crakes and African Rails) were frequently attracted to feed at freshly cut or cleared observation tracks in reedbed vegetation (Section 4.3.3), especially if the substrate had been disturbed and muddied by trampling or by uprooting plants. Similarly, Redchested Flufftails in central Kenya fed at fresh hippopotamus trails through their habitat. Obviously invertebrate food was easily obtained in such disturbed areas, and similar reactions have been observed in other species, including the Little Crake *P. parva* at fresh vehicle tracks in flooded grassland (Taylor 1980), the Spotted Crake at new ditches (Taylor 1987) and Baillon's Crake

at exposed mud (pers. obs.). Reedbed warblers such as the Cape Reed Warbler *Acrocephalus gracilirostris* and the African Sedge Warbler *Bradypterus baboecala* were also attracted to feed on insects at the edges, and on the surfaces, of newly-cleared tracks.

It was obvious that soft seeds are a frequent item in the diet of the Redchested Flufftail. Grass seeds were taken and captive birds regularly ate millet seed, even when an unlimited supply of live food was available. However seed was not seen to be fed to chicks. In the wild, seeds were taken most frequently during the winter and may form a significant part of the diet in territories which largely dry out during this season, such as some of those at the Gartmore study site. Four birds caught during a September burn at this site all had their crops distended with small seeds.

Because of the bird's habit of defaecating into shallow water and liquid mud (Section 4.4.7) it was difficult to collect faecal samples. Those collected contained mainly arthropod fragments which were so minute that very few were recognizable, but included pieces of the elytra of small water beetles (Gyrinidae). The gizzards of two immature specimens were examined: one from Pietermaritzburg on 30 March contained fragments of several small ants (*Tetramorium* sp.), one large beetle, one crustacean (Amphipoda), three grass seeds, four small hard seeds and two quartz grains, while one from Ixopo on 15 April contained the remains of four beetles (Gyrinidae and Staphylinidae), two quartz grains and 97 seeds, 15 of grass plus many unidentified hard seeds, some of which may have been ingested to assist with grinding the food.

Further evidence of the frequency with which grass seeds are taken is provided by details attached to specimens in the Bulawayo Museum and the British Museum (Natural History). Of 15 specimens for which the stomach contents are given, 12 (80%) contained grass seeds, the birds being collected in Cameroon, Malawi and Zambia in months spanning both dry and wet seasons. The next most commonly listed food item was "Nyerere" ants, which were present in the gizzards of four birds collected by C.W. Benson in Zambia and Malawi. In the languages of Malawi this appears to be a general term for small ants: in Chinyanja it refers to small black ants, while in Nyanja "nyelele" signifies small house ants (D.R. Aspinwall *in litt.* to M.P.S. Irwin). Thus the ants were probably *Tetramorium* sp. workers, which are also commonly eaten by Buffspotted Flufftails (Chapter 9). Workers of another genus, *Myrmicaria*, were found in a Redchested Flufftail gizzard from Malawi (Benson 1948).

Calculations of daily energy intake (DEI) were made using a mean body mass of 37,67 g ( $n = 27$ ; both sexes, adults and immatures) calculated from live masses obtained during this study plus those obtained from literature sources, museum collections and the South African Bird Ringing Unit. The calculations gave a Field Metabolic Rate (FMR) of 111,13 kJ/day and a DEI of 148,2 kJ/day. The energy value of the mealworms was 26,46 kJ/g (dry weight); this value agrees well with

that of 26,66 kJ/g obtained by Ward (1987), also using the bomb calorimeter. On the basis of these calculations, the DEI of a fully grown Redchested Flufftail is equivalent to 13,95 g (fresh weight) of mealworms. The mean total intake of the four aviary birds was 23,09 g/day (Table 4.2), 5,77 g per bird, and this intake provided 41,4% of the theoretical DEI, or 39,4% using the mean mass (40,6 g) of the four birds, which were weighed once during the experiment. Although the DEI estimate can be regarded only as a rough approximation of the bird's energy requirements, these figures show that the captive birds did not rely only on mealworms for their nourishment, a fact which is supported by my observations of the frequency with which they ate both naturally occurring invertebrate food (such as insects and earthworms) and artificially provided food (seeds and cooked egg). The diet of these captive birds was certainly adequate, as shown by their frequent and successful breeding attempts (Section 4.4.10.2).

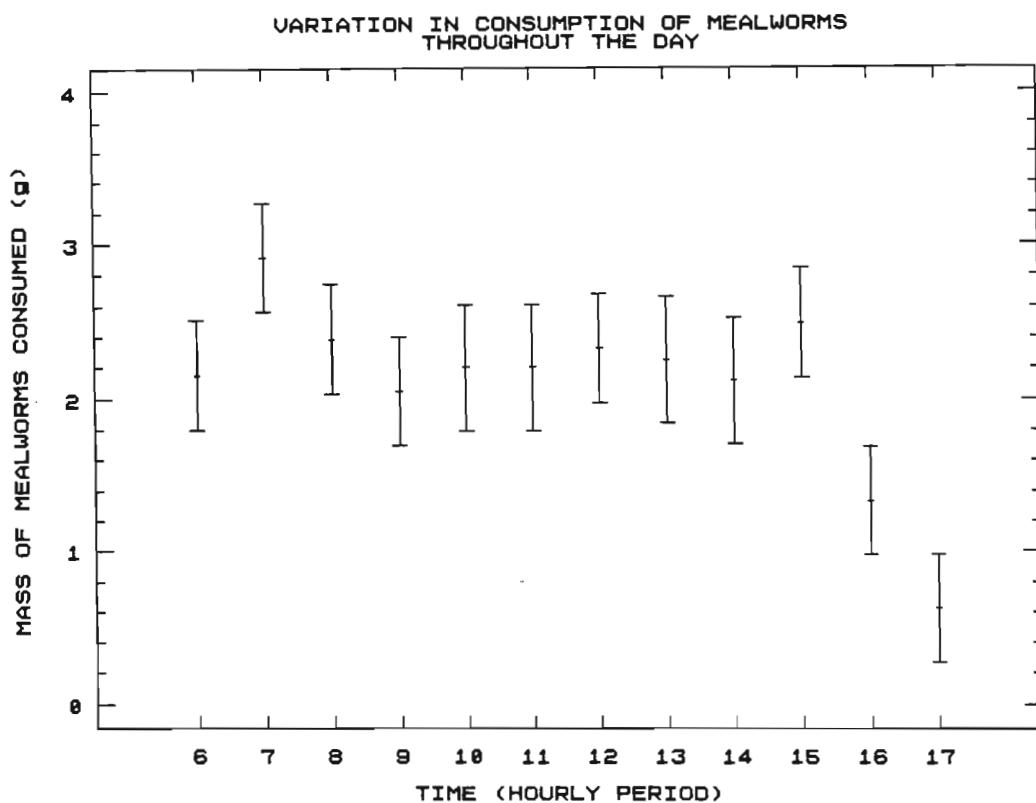
The two days of observation of the immature male at Danville Lake provided consumption figures of mealworms for the entire daylight period. Each recording period covered a different part of the day, the results being combined to give figures covering the period 06:00 to 18:00. The total intake of mealworms was 13,31 g, which is equivalent to 141,4 kJ of energy or 95% of the calculated DEI. The bird visited the mealworm dish more frequently than did the captive birds and when not feeding it appeared to spend most of its time resting under neighbouring vegetation. My impression was that it was eating virtually nothing else during the observation periods, so its total intake was possibly a good approximation of its daily requirement, and is very close to the calculated requirement.

In the aviary the birds began feeding almost as soon as they emerged at daybreak, fed most intensively between 07:00 and 08:30, and continued to feed at a reduced level throughout the day with another peak of activity from 15:00 to 16:00 and then a marked drop in feeding before they roosted at dusk. This agrees with observations made of wild birds, which had peaks of foraging activity at similar times and foraged regularly on observation tracks throughout the day except in bad weather (i.e. extremes of temperature or heavy precipitation). Table 4.2 and Figure 4.6 show the hourly variations in the food intake of the captive birds and a one-way analysis of variance on the hourly consumption rates showed that variances were equal ( $P > 0,05$ ) and that the data fell into four homogeneous and significantly different groups ( $P < 0,001$ ): the peak feeding hours (07:00-08:00 and 15:00-16:00), two periods of low feeding rates at the end of the day, and all other hours of the day (Fig. 4.7).

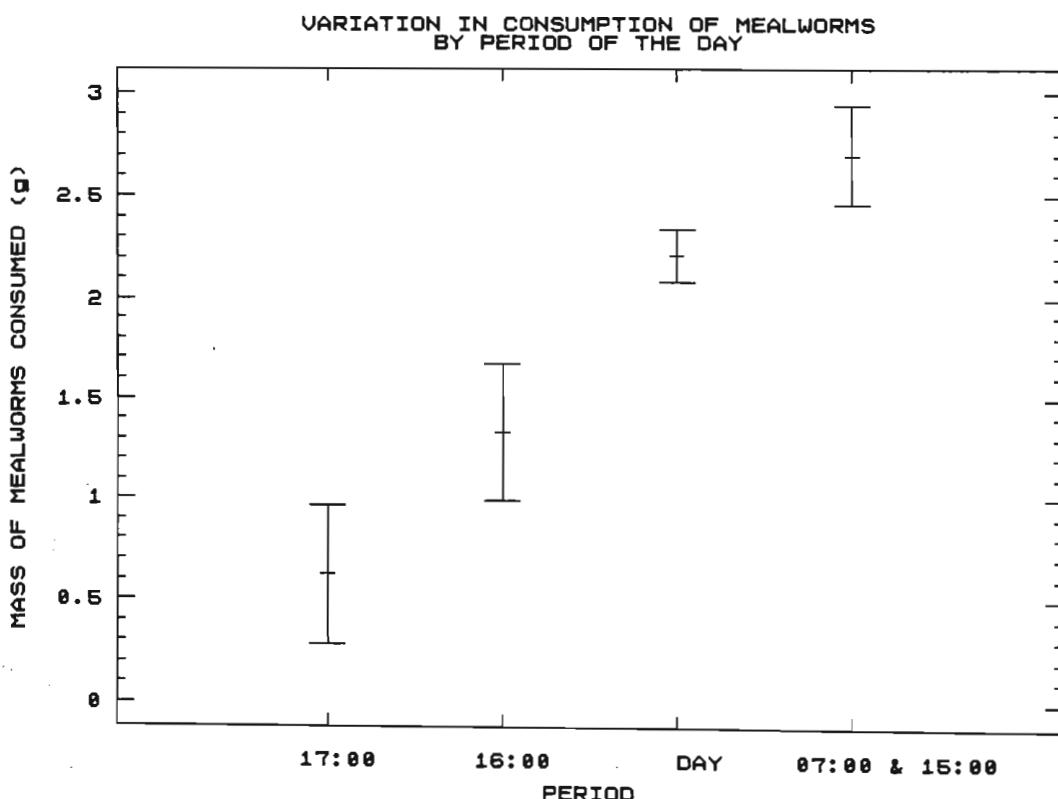
TABLE 4.2

Consumption of mealworms (*Tenebrio molitor* larvae) by captive Redchested Flufftails in the study aviary at Bromley, Zimbabwe, 10-18 April 1992. Figures represent the total fresh mass (in grams) of the mealworms consumed by all four birds for the given time periods. Measurements were made hourly whenever possible, otherwise at longer intervals, as shown. An excess of mealworms was always available to the birds. On 14 April recording ceased at 13:00, on 15 April no measurements were made and on 18 April birds trapped between 10:00 and 11:00, so no feeding took place during this hour.

Time period	Mass of mealworms consumed (g)								Mean ( $\pm$ SE) (hourly data only)
	10 Apr	11 Apr	12 Apr	13 Apr	14 Apr	16 Apr	17 Apr	18 Apr	
06:00-07:00	1,68	-	-	-	-	2,28	1,95	2,70	2,15 $\pm$ 0,22
07:01-08:00	2,55	-	-	3,80	3,12	2,93	2,93	3,25	2,92 $\pm$ 0,14
08:01-09:00	3,19	5,95	-	-	-	2,56	1,60	2,19	2,39 $\pm$ 0,33
09:01-10:00	1,92	-	-	-	4,21	2,27	1,92	2,08	2,05 $\pm$ 0,08
10:01-11:00	2,40	-	-	-	-	2,30	1,90	0	2,20 $\pm$ 0,15
11:01-12:00	1,97	-	-	-	4,72	-	2,08	2,55	2,20 $\pm$ 0,18
12:01-13:00	2,30	7,26	10,93	-	2,34	-	2,10	2,55	2,32 $\pm$ 0,09
13:01-14:00	2,50	-	-	-	-	-	2,11	2,13	2,25 $\pm$ 0,13
14:01-15:00	1,65	-	-	13,90	-	9,66	2,64	2,05	2,11 $\pm$ 0,29
15:01-16:00	2,05	-	-	-	-	2,70	2,45	2,75	2,49 $\pm$ 0,16
16:01-17:00	1,10	-	-	-	-	1,30	1,27	1,65	1,33 $\pm$ 0,12
17:01-18:00	0,40	9,16	8,10	3,85	-	0,50	0,77	0,83	0,63 $\pm$ 1,10
DAY TOTALS:	23,71	22,37	19,03	21,55		26,50	23,72	24,73	[MEAN/DAY: 23,09]



**Fig. 4.6** Variation in consumption of mealworms by captive Redchested Flufftails per hour throughout the day (one-way analysis of variance; means and 95% confidence limits).



**Fig. 4.7** Variation in consumption of mealworms by captive Redchested Flufftails by period of the day (one-way analysis of variance; means and 95% confidence limits). Periods:

#### 4.4.7 Other feeding-related behaviour

The birds drink daily, usually several times per day. Both wild and captive birds normally defaecate either in shallow water or on to liquid mud; often they pause to do so when first entering water. In captivity flufftail chicks, like those of other rallids, defaecate only in water (C.C. Wintle pers. comm.; Kaufmann 1977). Captive birds also defaecated regularly on a narrow concrete ledge low over the water, where they were completely hidden from view by dense sedges.

#### 4.4.8 Vocalizations and calling patterns

Redchested Flufftails are very vocal birds, in common with all the other flufftail species studied except the Whitewinged Flufftail (see Chapter 8). They respond very well to stimulation by taped playback throughout the year. As they live in very dense vegetation it is not surprising that they should rely greatly on vocal methods of communication, both for contact between individuals and for the maintenance of territories, including normal interactions between adjacent territory holders. I have frequently noted that when adjacent pairs approach each other, e.g. in response to taped playback at a territory boundary, they may be within 1 m of each other on the ground in dense vegetation but will still be invisible to each other; they may undergo a prolonged bout of calling and then retire from the scene without apparently having been in visual contact. The same situation occurs with adjacent pairs of Whitespotted Flufftails along streams in the dense forests of western Kenya (Taylor & Taylor 1986). It is therefore to be expected that these species will have an extensive vocal repertoire but, in comparison with other rallids which live in similar habitats, Redchested Flufftails possess an astonishing variety of calls. During this study I identified 113 recognizably different vocalizations made by this species (Table 4.1), which may be separated into eight groups on the basis of their functions (Table 4.3). In assessing the functions of calls I took into account other birds' reactions, the behaviour which accompanied the call and the stimulus which gave rise to the call, while as many calls as possible were recorded and played back to the birds, both in the wild and in captivity, to investigate their responses at different times of the year. The descriptions (Table 4.1) indicate that many of the calls are probably variants of a smaller number of basic call types; for example, 18 calls of the male appear to be derived from the basic *DUEH* and *KEVIC* notes, whereas the female has nine variants and the immature four. However each variant is distinctive, is given in a different situation or in response to a different level of stimulation, and indicates a different type or intensity of reaction. Furthermore, derivatives of any one basic call type may be used in different contexts, so that grunting notes, for example, are used in territorial, alarm, warning, courtship and contact vocalizations. A

TABLE 4.3

Different vocalizations of Redchested Flufftails described during the study, from South Africa and Zimbabwe. Abbreviations: A = adult; C = chick; F = adult female; I = immature (fully grown and less than one year old); M = adult male; U = unidentified adult; Y = young (i.e. C and I).

Vocalization function	Total calls	Total given by:					Total shared by:	
		M	F	U	I	C	M&F	A&Y
Advertising	9	8	2	1			2	
Territorial	33	24	13	1	4		7	2
Aggressive	23	17	10	2			6	
Alarm	13	7	6	1	4	1	4	2
Contact	20	5	13	2	5	3	3	3
Courtship	6	4	2					
Mating	3			3				
Court/mate	6				6			
<hr/>								
Grand totals :	113	65	49	13	13	4	22	7

detailed analysis of the call types, structure (with sonograms) and functions, will be made in due course but is not relevant to this thesis.

The advertising hoot (Table 4.1, calls M1 & M2) is well audible to the human ear at distances of 350 m or more in wetland vegetation and up to 550 m across water. The territorial DUEHs of males and females (Table 4.1, calls M10 & F3) carry less well and have been heard up to 200 m away in vegetation and 220 m across water. The common gulping calls (Table 4.1, calls M30 & F14) are usually audible only up to 30 m away. The advertising and territorial calls are audible over smaller distances than those of the Striped Flufftail (Chapter 7, Section 7.4.2), whose hooting and advertising calls are audible for 1.6-2 km and 400-700 m respectively, 3-4 times the distance of the Redchested Flufftail's calls. The differences are presumably related to the relative dispersion of the species in their breeding habitats: the Striped Flufftail has larger territories and the distances between pairs are greater (Chapter 7), so to communicate effectively it needs to make calls carry further. The lower frequency of the Striped Flufftail's hoot, its transmission through (normally) shorter vegetation (both species call from the ground), and the avoidance of background and interference noise by calling mainly at night, should all help to reduce signal attenuation and degradation, and assist propagation of the call over longer distances (Marten & Marler 1977; Marten, Quine & Marler 1977; Morton 1975; Wiley & Richards 1978). With regard to the territorial calls of the two species, that of the Striped Flufftail is of a higher frequency and thus may be expected to carry less far; why the opposite occurs is not clear but may be related to the vegetation height, the structure of the call and the atmospheric conditions (Krebs & Davies 1993; Wiley & Richards 1978). Thus sound transmission in strong or gusty winds (a characteristic feature of the grassland and wetland habitats studied) is improved by the very short, rapidly-repeated notes of this bird's territorial call.

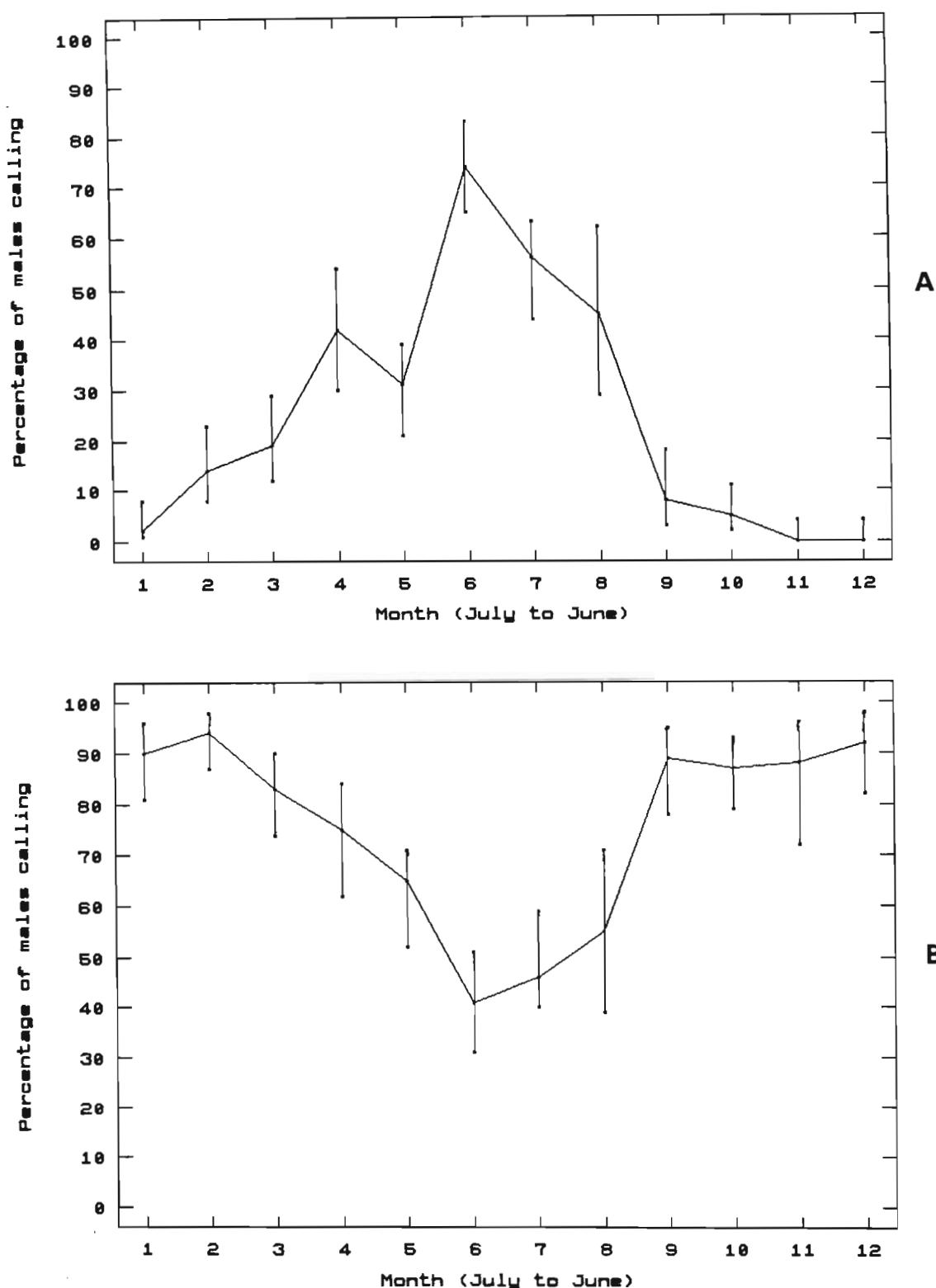
Territorial DUEH calls are given in response to stimuli other than the calls of conspecifics, either real or taped, examples being loud calls of other birds such as Little Bitterns *Ixobrychus minutus*, Hamerkops *Scopus umbretta*, Hadeda Ibises *Bostrychia hagedash*, Egyptian Geese *Alopochen aegyptiacus*, Helmeted Guineafowls *Numida meleagris*, African Rails, Moorhens, Redknobbed Coots *Fulica cristata* and Burchell's Coucals *Centropus burchellii*, as well as the territorial calls of Striped and Whitewing Flufftails. Calls are also given in response to loud noises such as hammering and human shouts, to the sight of large birds such as herons, geese and raptors flying overhead, and to human observers either approaching through dense vegetation or visible some way off, e.g. on a hillside overlooking the territory.

In view of the bird's permanently territorial existence it is not surprising that the largest groups of vocalizations should be those concerned with the maintenance of territory and agonistic behaviour: 56 (50%) of the vocalizations serve territorial and aggressive functions (Table 4.3). The

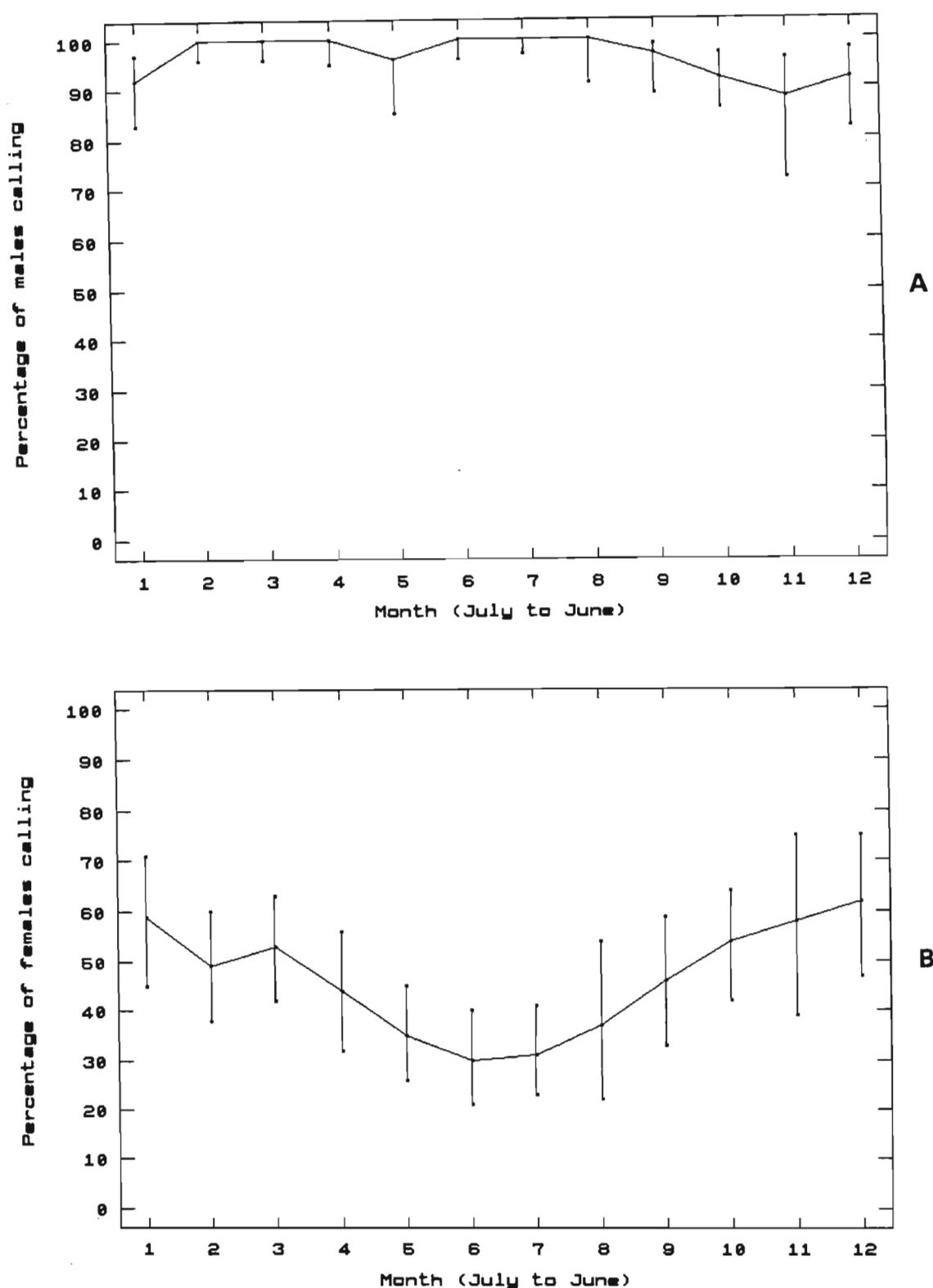
significant role of the female in territorial maintenance is indicated by her 23 different vocalizations covering these two functions. The high number (20) of contact calls attests both to the complexity of the bird's family life and to the problems of keeping in touch with other individuals in the dense vegetation. The female has 13 contact calls as opposed to the male's five, and the female of the captive pair made more frequent and varied calls to other members of the family group than they did to her. As in many other territorial species, vocalizations are probably enough to maintain territorial integrity after initial establishment, when most fights occur (Falls 1982).

To investigate seasonal variations in calling patterns, and thus to obtain an insight into variations in territorial behaviour, the vocal activity of all birds encountered at survey areas and study sites was noted and a monthly analysis was made of the proportion of birds calling either spontaneously or in response to taped playback. Only territorial and advertising calls were included in the analysis. It may be seen from Figs 4.8 and 4.9A, which show the percentage of adult males calling in each month of the year, that 88-100% of males made advertising and/or territorial calls every month, and that territorial calls were given by over 80% of individuals except between October and February, the peak breeding months when many males also gave the hooting advertising call (song). Females (Fig. 4.9B) rarely sang, but gave territorial calls throughout the year, over 50% of females calling during the non-breeding season. Females made fewest territorial calls during the breeding months, when the level of the male's territorial calling also declined. All flufftail species which I have studied make fewer territorial and advertising calls when nesting, and this behaviour is consistent with the statement by Skutch (1976) that in many species the time spent in territory defence is reduced during the period from egg-laying to the independence of the young.

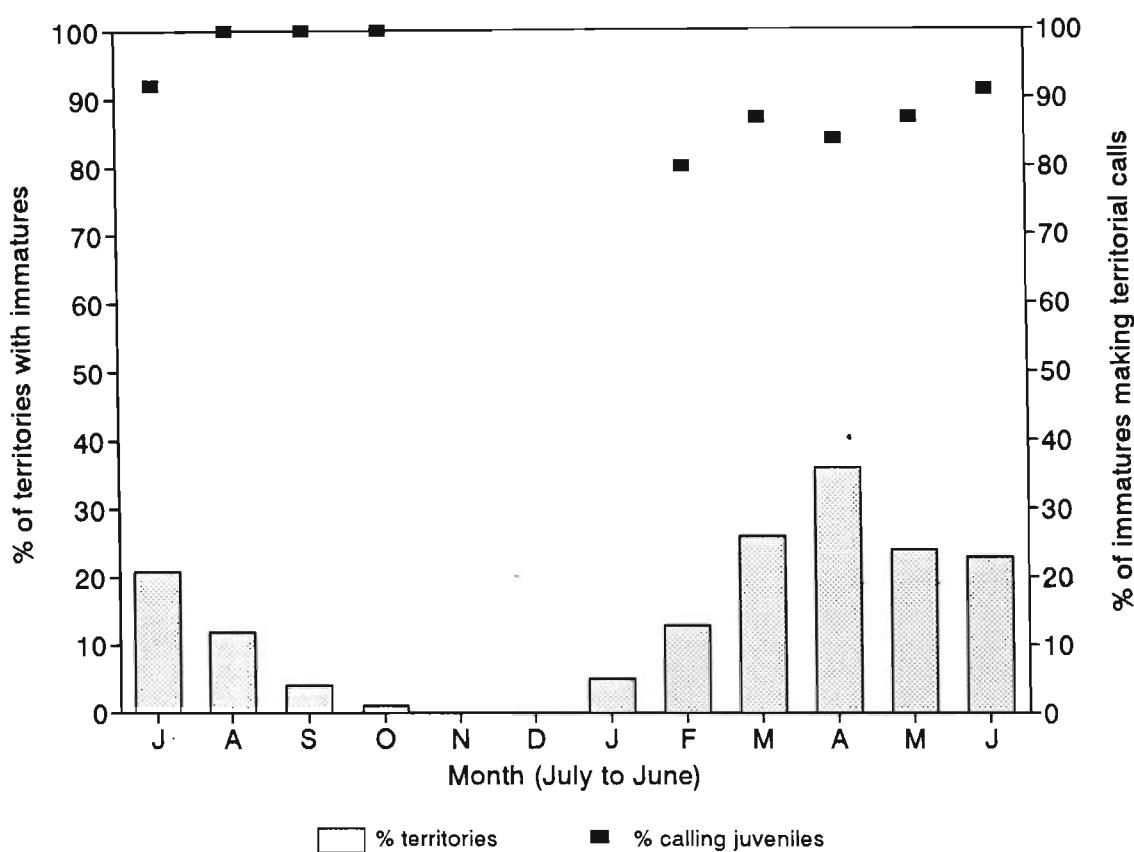
The marked resurgence in territorial calling of the adults in February-March coincided with the end of the breeding season, the cessation of advertising calls and the onset of territorial calling by immatures resident in parental territories (Fig. 4.10; see below). However, the overall percentage of calling males was at its lowest level from March to July, while from February many adult males did not make the normal *DUEH* territorial calls (Table 4.1, call nos. M10-M13) but instead gave a feeble, squeaky version of the *DUEH* call (call nos. M14 and M15), as did females at this time (call no. F6). These calls were heard commonly throughout March and April, especially in response to taped playback (but normal calls were given during experiments with models), and were replaced by more normal *DUEH* calls thereafter. This period of relatively low-intensity territorial calling coincided with the period when the highest percentage of territories contained calling young (Fig. 4.10) and presumably reflects a reduction in aggressive behaviour coincident with the sharing of territories with immatures. The percentage of territories containing young birds fell in May (Fig. 4.10), when some young were evicted at the end of the breeding season, and then remained fairly stable (representing



**Fig. 4.8** The monthly percentages of adult male Redchested Flufftails calling with advertising hoots (A;  $n = 249$ ) and territorial calls (B;  $n = 648$ ) in the period January 1990 to December 1992 inclusive. The total includes both spontaneous calling and that made in response to taped playback. No. of trials = 886; 95% confidence limits are shown.



**Fig. 4.9** The monthly percentages of (A) adult male ( $n = 860$ ) and (B) adult female ( $n = 393$ ) Redchesteds making either advertising or territorial calls in the period January 1990 to December 1992. The totals include both spontaneous calling and that made in response to taped playback. No. of trials = 886; 95% confidence limits are shown.



**Fig. 4.10** The monthly percentage of immature Redchested Flufftails ( $n = 100$ ) making territorial calls in parental territories and the monthly percentage of territories ( $n = 886$  trials) in which the presence of immatures was recorded. All but two samples do not exceed 25 units, so confidence limits are not shown as they make no useful prediction for the population.

the resident nonbreeding population) during June and July. It fell again in August and September when most immatures finally left, this coinciding with the start of the territorial males' advertising calling at some potential early-breeding sites and with habitat reduction due to burning at others.

The recorded vocalizations of fully grown juveniles and immatures (Table 4.1) included only contact, alarm and territorial calls. The territorial calls of young males resemble those of the adult female more than those of the male, and are often difficult to distinguish in the field; this may be an adaptation to reduce conflict with the adult male, which might react aggressively to birds giving typically male territorial calls. Fig. 4.10 shows the recorded pattern of territorial calling for those young birds encountered in parental territories during and after the breeding season. In the early part of the breeding season territorial calls of young birds were not apparent, while the presence of fully grown juveniles was first observed in January (Fig. 4.10). From February onwards, the territorial calls of the current season's offspring became noticeable in breeding territories, and the percentage of young birds calling in these territories remained at 80-90% until July, when calling increased (Fig. 4.10). After July, the number of territories containing immatures fell sharply as many young birds left or were ejected, this coinciding with an increase in the adult male's territorial and advertising calls (Figs 4.8 and 4.9A). Those immatures which did remain continued calling strongly until they finally departed; after October, when breeding was under way, all the last season's immatures appeared to have left the parental territories.

Most of the recognized immature calls have come from male birds and I have little definite evidence that the immature female calls as frequently, or takes as active a part in territory defence, as does the immature male.

#### **4.4.9 Breeding season**

It was difficult to establish precise breeding dates for Redchested Flufftails at the long term study sites, not only because I wished to avoid the disturbance caused by repeated systematic searches for nests (Section 4.3.6) but also because of the difficulties involved in observing young birds well enough to estimate their ages accurately. Despite these problems, 27 dated breeding records were obtained in Natal during the four breeding seasons of the study and a further seven were obtained from the captive pair at Bromley in the three breeding seasons following the birds' capture in November 1991. These records are summarized by month in Table 4.4. They include all records of young which could be aged accurately according to established criteria (see Sections 4.3.6 and 4.4.10). In Natal the breeding season extended from late September to late March and birds at coastal and low-altitude sites such as Danville and Allerton appeared to begin breeding up to two months earlier than those at high altitudes such as Mt Currie. This is shown by the comparison of breeding

TABLE 4.4

Redcheasted Flufftail breeding records obtained during the study for wild birds in Natal and captive birds at Bromley, Zimbabwe. The months are those in which the eggs were laid. Records include those of chicks and juveniles which could be aged accurately.

<b>Study area</b>	<b>Aug</b>	<b>Sep</b>	<b>Oct</b>	<b>Nov</b>	<b>Dec</b>	<b>Jan</b>	<b>Feb</b>	<b>Mar</b>	<b>Total</b>
Natal: Mt Currie				1	4	4	1	2	12
elsewhere		1	3	3	2	2	2	2	15
Zimbabwe: Bromley	1	2		2	1		1		7
<b>Totals</b>	<b>1</b>	<b>3</b>	<b>3</b>	<b>6</b>	<b>7</b>	<b>6</b>	<b>4</b>	<b>4</b>	<b>34</b>

months for Mt Currie and elsewhere (Table 4.4): laying at Mt Currie was recorded from late November and peak months were December and January, whereas in other areas seven (45%) of the records fell in the September-November period. It was not possible to compare mean first breeding dates for birds which had been resident all winter with those which had been forced to move after spring burning because, when breeding in either type of territory was first noted in mid-season (December-January), it was often possible that the pair concerned could also have made an unrecorded breeding attempt earlier in the season. However, as all September, October and November records involved undisplaced pairs, it is clear that such birds could theoretically begin breeding 1-4 months earlier than those which have been forced to vacate their territories until November or later. It is also probable that, at the higher altitudes, very early breeding may not usually occur even in unburned territories and the reason for this may be connected to the relatively low minimum temperatures experienced at sites such as Underberg and Mt Currie before November (see Discussion).

It was assumed that the hooting advertising calls (Table 4.1, calls M1-M3 and F1) are indicative of breeding activity, as has already been suggested (Chapter 1, Section 1.2.2.4), and males gave these calls from mid-August to early April (Table 4.5), principally from October to February with peak calling in December (Fig. 4.8A). The only instance of hooting outside the August-April period was of a wild male in Zimbabwe which made hoots when a captive caged female was temporarily placed in his territory on 25 July 1990.

The importance of early breeding may be related to factors other than the extended period available to make breeding attempts in the event of failures. In some small wetland patches it was noted that damage to breeding habitat by the trampling and grazing of indigenous large herbivores such as Blesbok *Damaliscus dorcas phillipsi* could be severe by February, and therefore that late breeding at such sites might be impossible. Such extensive late-summer damage was not seen to be caused by domestic stock, which normally are not grazed in wetlands after the spring and early summer, when they exploit post-burn new wetland growth while veld grassland is developing (for the effects of winter grazing, see Section 4.4.3).

#### **4.4.10 Breeding**

##### **4.4.10.1 Courtship and mating**

In the courtship display the male stands in front of the female and bobs up and down to her so that his lower breast almost touches the ground, with wings slightly raised above his back, wingtips crossed, head raised and body fluffed by raised plumage. He often utters quiet booming calls or other

TABLE 4.5

Earliest and latest dates on which the advertising calls (hoots) of male Redchested Flufftails were heard during each breeding season of the study. All localities are in Natal. An asterisk after a locality indicates a long-term study site (details in Chapter 2).

Breeding season	Earliest records		Latest records	
	Locality	Date	Locality	Date
1988-89	Kamberg	12 September	Allerton*	13 March
	Rosetta	18 September		
1989-90	Danville*	19 August	Danville*	21 March
	Mt Currie*	26 August	Allerton*	8 April
	Allerton*	30 August		
1990-91	Allerton*	14 August	Mt Currie*	12 March
	Mt Currie*	11 September	Allerton*	1 April
1991-92	Underberg	17 August	Mt Currie*	26 February
	Allerton*	3 September		
	Mt Currie*	4 September		

subdued notes (Table 4.1, calls M57-M60), and usually vibrates his tail rapidly from side to side during both courtship and mating. The female either stands still or walks around during this display, and when ready to mate crouches down with lowered head, giving very quiet calls (Table 4.1, calls F32 & F33). The male then walks round behind the female and mounts her, she raises her tail and they copulate for a period of 5-40 s, the male pecking at the female's head and neck and sometimes fluttering his wings to keep balance. The female may utter quiet calls during mating (Table 4.1, calls F34-F36). The birds then separate and resume normal activities, sometimes first standing side by side for a brief period. The male of the proven permanent pair at Allerton, and the male of the longterm resident pair at Danville (Section 4.4.5) both occasionally gave this courtship display to the female outside the breeding season (in May-July). Instead of the courtship display there may be a courtship chase, in which the male, sometimes with raised wings, vigorously chases the female; the birds may run round in circles while the male pecks at the female's head. If the female is receptive she crouches and mating takes place, but she may escape by flying up into the vegetation.

Breeding adults attacked model birds of the same sex (Fig. 4.3), and nonbreeding males sometimes attacked model females, but breeding males consistently displayed to, and attempted to mate with, model females. Captive males also mated with females of other pairs. These observations suggest that extra-pair copulations and sperm competition (Møller 1987) should be considered as possible factors in this species' breeding biology and territorial behaviour.

#### **4.4.10.2 Nest-building, laying, incubation and hatching**

Most aviary nests were well built, domed cups of typical construction (Chapter 1, Section 1.2.2.5), situated 20-30 cm above the substrate in a thick clump of grass or sedge, usually near the edge and facing water. Any available grasses were used, plus occasional dead leaves. Early-nesting birds sometimes built in dead grass tussocks. Only the male was seen to build in captivity, and only males were seen carrying nesting material in the wild. Aviary nests may be used for more than one brood and captive birds have also been recorded using the nests of two small passerine species, the Redthroated Twinspot *Hypargos niveoguttatus* and the Nyasa Seedcracker *Pyrenestes minor* (C.C. Wintle pers. comm.). In the aviaries the twinspot often nested on the ground, building a domed nest with an entrance tunnel, while the seedcracker built a domed nest on a branch over water. The flufftails once even ousted the occupants of one nest of each species, destroying the eggs of the twinspot in the process. The nests of these species, which are predominantly forest birds, normally would not be available to the flufftails in the wild.

Little information is available on clutch size in wild Redchested Flufftails, but during the study I only once saw adults with a brood of three chicks and once heard calls of a family of three young; other observations were of broods of two or one (when a second chick could have been present but not seen). During the study period the pair in the small aviary nested seven times (Table 4.4), once in the first (drought) season (February 1992), twice in the second (drought) season and four times in the third, when rainfall was normal. The number of eggs laid was not determined, but two chicks were hatched six times and three once. In previous years, birds in small aviaries such as this one usually laid clutches of 1-2 eggs three times per season, those in large aviaries (see Section 4.4.5) had larger broods (3-4 young) and laid up to five clutches per season, between September and March (C.C. Wintle *in litt.*).

One egg is laid per day. Incubation begins when the clutch is complete and takes 14-18 (usually 16-18) days (Wintle 1988; this study). Both sexes incubate, the male during the day and the female at night, with occasional short changes for feeding during the day. The incubating bird will come off the nest to attack a human intruder, running round his feet with open wings and lowered head, making hissing sounds (C.C. Wintle pers. comm.). After hatching, which may occur overnight, the eggshells are usually removed and are often eaten (C.C. Wintle pers. comm.; this study).

#### **4.4.10.3 Development and care of the young**

Observations of the development of young birds up to six weeks of age agreed with those given by Wintle (1988): see Chapter 1, Section 1.2.2.5 for details. At six weeks of age juveniles were fully grown and fully feathered, and some were just beginning the postjuvenile moult. At seven weeks young males had grown 10-20% of their red head, neck and breast feathers and 10-40% of their spotted/streaked body feathers (ventral feathers showed first). At eight weeks the relative percentages were 40-50% red feathers and 70-80% body feathers ventrally - often noticeably fewer dorsally. At nine weeks 90-100% of the red feathers had grown and all feathers were dark-tipped, rendering the colour dull. The body was 80-90% patterned, both above and below. Full subadult plumage was attained at 10-11 weeks of age. The major differences between immature males and adult males were that the immature's tail was an almost unpatterned plain black, while its greater upperwing coverts and the first row of median upperwing coverts remained unmoulted and were thus plain, contrasting with the adjacent patterned feathers.

Although chicks are capable of feeding themselves from the age of 4-5 days, they continue to solicit food from the parents until they are fully grown. If no other brood is produced, immatures may be fed occasionally by the parents until they are 8-9 weeks old. First- and second-brood young

normally help to feed the chicks of the subsequent one or two broods but, after the third brood has been reared the first-brood young are often ejected as they are then well advanced in their postjuvenile moult and are usually attacked by the parents (see Section 4.4.11). In captivity, it is frequently birds from the last brood which remain during the winter before being chased off in July or August.

#### **4.4.10.4 Breeding success and survival**

Little information on breeding success is available. Of the seven broods of two chicks hatched by the aviary pair between February 1992 and December 1993, only two young died: one chick was drowned when a week old and another was killed, probably by a rat. All the other young survived to maturity and were eventually released. Temporary deep flooding after heavy rain sometimes forces birds to abandon nests, while a severe hailstorm and subsequent flooding at Mt Currie in January 1991 also destroyed nests and eggs (Chapter 6, Section 6.4.2.3).

In view of the observations made of captive and wild birds (Section 4.4.5), and the apparently low level of predation (Section 4.4.12) it is probable that territory holders, at least, are long-lived. Some birds were probably killed by the severe hailstorm at Mt Currie but, in terms of pairs lost, the effect of the storm on the Redchested Flufftail population was much less (11 of 34 pairs lost) than on the Striped Flufftail population (23 of 33 pairs lost) of the Reserve (See Chapter 6, Section 6.4.2.3 and Chapter 7, Sections 7.4.10 and 7.4.12).

#### **4.4.11 Dispersal of young birds**

Most direct information comes from captive birds. Except for the last brood of the season, whose presence was often tolerated until July or August, young birds of both sexes might not be tolerated for long after they had completed their postjuvenile moult, i.e. after about 11 weeks of age. They were then chased by the parents and they actively tried to leave during the night, flying into the mesh sides of the aviary from about 20:00-21:00. Thus in 1993 birds hatched in early October 1992 were ejected by the parents in early February, when they were four months old (no further brood had been reared), and in mid-December 1993 the first-brood chick, hatched in late August, was also ready to leave at four months of age (when a fourth clutch was being incubated). In the aviary, the adults' rate of territorial calling increased noticeably at times when young birds attempted to depart, and the adults frequently called at night at such times. Resident adults never tried to escape from the aviaries at any time.

In April 1992, when the two captive male juveniles were 7-9 weeks old and undergoing their postjuvenile moult to adult-type plumage, the adult male made the occasional mild attack on the more

advanced immature (i.e. with more red on the head and neck, and more spots on the body), running at him and pecking at his head and neck. The young bird invariably adopted a crouched, submissive posture, with retracted head and fluffed-out plumage, when the male stopped the attack, looked at him for a few seconds and then continued with normal activities. Taped playback experiments were performed on these birds on 11 April 1992, when they were subjected to a 23-min playback of male territorial and aggressive calls. The result was dramatic: for 10 min the adult male vigorously chased and attacked the more advanced juvenile, which was often forced to escape by taking flight. The less well marked juvenile was ignored. Twenty minutes after playback had stopped, the adult male was again behaving normally, and after 30 min the male and the attacked juvenile were foraging together amicably.

The situation in the wild probably mirrors that in captive birds, although the extra space might permit longer residence of more young (but there was no evidence for this and food was always plentiful in the aviary). The patterns of occurrence given in Fig. 4.10 indicate that some young leave at the end of the breeding season (April-May), while others stay until August, rarely even into October. Table 4.6 shows the latest dates on which calling immatures were recorded in parental territories for each year of the study, and observations indicate that this final departure of immatures coincides with the reduction or destruction of territories by burning, or with the start of advertising calling. It was also thought possible that final departure dates might vary with the type of habitat so that, for example, the drier vegetation types might not be able to support both adults and immatures for as long as the wetter areas. However this is unlikely because the larger size of dry-habitat territories should compensate for a lower food availability, and a one-way analysis of variance showed that final departure dates did not vary significantly between territories of different Flooding Types ( $F_{3,18} = 0,157$ ;  $P > 0,9$ ;  $n = 22$ ): for a definition of Flooding Types, see Table 5.1 and Chapter 5, Section 5.3.1.

Occasional field observations were also indicative of the dispersal of young at the end of, or after, the breeding season. Near Gartmore, one immature male called on 9 April 1989 from marginally suitable habitat where no resident birds ever occurred. At Danville a pair of immigrant immatures appeared in the vacant territory on 19 April 1991. Three immature males were first heard calling from temporary territories in marginal habitat at Mt Currie on 1 and 3 May 1992, and one at Penny Park on 1 May 1992. On 30 March 1992 an immature male, about nine weeks old and therefore hatched in January, was killed at night by flying into a building in the Doreen Clark Nature Reserve, Pietermaritzburg, a forested area within the city and far from suitable habitat. Examination of museum skins provided further evidence in that the only southern African record of the Longtoed

TABLE 4.6

Last dates on which resident calling immature Redchested Flufftails were recorded in parental territories at the study sites. For descriptions of Flooding Types (FType), see Table 5.1. An entry in the "Burn date" column indicates that the juvenile(s) were, or (date in parentheses) may have been, resident until the date the territory was burned. In all cases the birds had been heard regularly from the end of the previous breeding season (February or March).

FType	Study site	Year	Last date recorded	Burn date
1	Allerton	1988	14 October	
		1989	13 September	13 September
	Danville	1988	16 July	
		1989	27 August	
		1990	26 June	
	Mt Currie	1990	10 June	
3	Gartmore	1989	17 July	
		"	3 August	
		1990	14 August	
	Mt Currie	1990	11 July	
		"	10 August	
		1991	30 June	
4	Gartmore	1990	13 August	(4 September)
		1991	22 May	
		"	2 July	
	Mt Currie	1989	26 August	
		1990	13 September	
		1991	29 July	
5	Gartmore	1989	28 August	(28 September)
			3 September	(28 September)
		1990	1 July	
	Mt Currie	1990	11 July	

Flufftail, a bird killed at night on 16 February 1966 at the Rhodes Inyanga Hotel, Nyanga, in the eastern Zimbabwe highlands, proved on examination to be an immature female Redchested Flufftail less than 16 weeks old, which was far from suitable habitat (Taylor & Hustler 1993). Such dispersals, which may be either short-distance or long-distance, possibly give rise to a relatively high mortality among immatures.

#### 4.4.12 Predation and mortality

The study produced no examples of predation under natural conditions and the only direct evidence of natural predation comes from R. Simmons (*in litt.*) who found the remains of one Redchested Flufftail among 707 dietary items of the African Marsh Harrier *Circus ranivorus*. This suggests that predation by the harrier is an uncommon occurrence and I found no evidence that any large raptorial bird preyed on wetland flufftails in the study area, although African Marsh Harriers, Grass Owls *Tyto capensis* and Marsh Owls *Asio capensis* were present at several sites, Marsh Owls mainly during the nonbreeding season. Examination of a small number of pellets of these three species from Redchested Flufftail sites produced no recognizable flufftail remains.

During my fieldwork in Natal, three species of mongoose were attracted to playback of Redchested Flufftail calls and to flufftail models: the Large Grey Mongoose *Herpestes ichneumon*, the Slender Mongoose *Galerella sanguinea* and the Water Mongoose, and it is probable that such mammals are occasional predators of flufftails. Whenever a Water Mongoose was in the vicinity at any observation site, flufftails fell silent and disappeared for some time, and the arrival of a Water Mongoose at Danville was followed by the permanent disappearance of the resident flufftail pair (Section 4.4.5.1). It is possible that Blackheaded Herons *Ardea melanocephala* are predators of flufftails immediately after burns, as was suggested by observations at Gartmore (Chapter 5, Section 5.4.6), and it is probable that direct and indirect effects of burning are the most significant cause of mortality in Redchested Flufftails (see Chapter 5, Sections 5.4.6 and 5.5.2). Rats and mice must be at least occasional predators of eggs and young in the wild, as they are in aviaries.

In general, the available evidence suggests that mortality among territorial adults is low, but the regular (and possibly long-distance) dispersal of immatures after the breeding season and during the following winter (Section 4.4.11) may result in relatively high mortality of these young birds.

In April 1992, an experiment was performed on the captive family to investigate their reactions to snakes, which are also potential predators. On two occasions a black rubber model snake, 25 cm long, was presented to the birds. Their reactions were very similar to those shown by wild Buffspotted Flufftails to a live snake (Chapter 9). Both adults and juveniles watched the snake

carefully, approaching cautiously to within 30 cm of it, walking round it, examining it from all angles and jumping quickly back if it was moved suddenly. When it was pulled slowly along by a concealed cord, the birds followed it with outstretched necks, the male giving little *CHEK-CHEK* calls, and they watched as it was pulled up into a tree. All birds vibrated their tails rapidly during encounters with the snake. For two hours after the snake was removed, a bird would occasionally return and look up into the tree where it had last been seen.

The available evidence suggests that Redchested Flufftails are normally long-lived. During fieldwork, some individually recognized adult males were still present in territories after four years (Section 4.4.4.1) and the adult pair captured in November 1991 were still alive in captivity at the end of 1993. Other captive birds at Bromley, obtained as adults in October 1978, were still alive and breeding successfully in December 1986, 8 years and 2 months later (C.C. Wintle *in litt.*).

## 4.5 Discussion

### 4.5.1 Distribution, status and habitat

The Redchested Flufftail's retiring habits mean that it is often overlooked and it is certainly greatly under-recorded, as is shown by comparing the distributional data from this study (Fig. 4.1A) with those recorded from the same area by atlassing projects (Fig. 4.1B). The species is undoubtedly resident all the year in suitable habitat throughout the southern-Natal survey area and the monthly occurrences plotted in Fig. 4.1A almost exactly reflect the monthly survey visits made to the squares concerned: in only two instances (July in square C11 and November in C12) did visits not produce records of the species. The lack of atlassing records from much of the northern Natal region is probably because of lack of coverage, the birds being overlooked rather than that they are absent: the 1:50 000 maps of South Africa (Government Printer, Pretoria) show that, of the 100 quarter-degree squares within the unsurveyed northern section, at least 83 contain potentially suitable wetland areas, but the species has been recorded in only 19 of them (Fig. 4.1B). In southern Natal the Redchested Flufftail is probably more widespread and numerous than in any area which I have surveyed in East and central Africa (Zambia, Tanzania and Kenya), while the southern-Natal survey area appears to hold a significant proportion of its South African population.

Although the Redchested Flufftail is widespread in Natal and appears to be a successful colonist of very small wet areas, the constant and ever-increasing threats to wetland habitats, both in Natal and elsewhere in South Africa (Begg 1986; Breen & Begg 1987; Kotze 1993) give no cause for complacency about the bird's long-term prospects. The species is continually losing habitat as a result

of the damming, drainage and overgrazing of wetlands and, although it colonizes wetland patches which have been created artificially (e.g. at seepage areas below dam walls, at dam intakes on flooded, shallowly sloping ground, and occasionally on moist ground which was previously deeply flooded), my observations in Natal show that the extent of such new habitats only partly compensates for the areas lost, a conclusion supported by Kotze (1993). Patches of wetland vegetation may develop along dam shorelines but such areas are usually too small and narrow, or of unsatisfactory substrate or vegetation types, to be suitable for permanent occupation by the flufftails.

The widespread distribution and apparent success of the Redchested Flufftail when compared to two of the three sympatric wetland *Sarothrura* species (Section 4.1) is undoubtedly associated with its wide tolerance of vegetation types (including alien plant species) and conditions of substrate saturation, and its ability to colonize small, isolated or artificially created wetland patches, as well as with its catholic diet, its sedentary territorial existence and other factors discussed hereafter. The available evidence from this study (Chapter 8) suggests that the rare Whitewing Flufftail has much more specific habitat requirements and is more sensitive to habitat loss and disturbance, while the uncommon Longtoed Flufftail apparently also occupies a much narrower range of vegetation types (Chapter 1, Section 1.2.2.2).

The Redchested Flufftail's occupation of atypical or marginal habitats, either very briefly during movements or dispersal, or for longer periods in temporary territories, is behaviour characteristic of the rallid family, any species of which is likely to make use of atypical habitats during local displacement or when migrating (Chapter 1, Section 1.1).

#### **4.5.2 General behaviour**

Although I observed pronounced crepuscular activity in Redchested Flufftails, I have no evidence for nocturnal activity other than breeding-season calling by males (which normally involves immobile birds), and dispersal movements by captive immatures with concomitant nocturnal territorial calling by adults. It would be very difficult to establish the occurrence of nocturnal activities such as foraging but, on the basis of the observed foraging activity throughout the daylight period, it is unlikely that the species also feeds at night. Furthermore, intensive observations of captive birds at Bromley failed to produce any evidence of nocturnal foraging or social activities, which would have been evident had they been of regular occurrence. I have no evidence that any *Sarothrura* species is nocturnal (see Chapter 9 for a discussion on the Buffspotted Flufftail), and most rallids are diurnal or crepuscular: statements that many are nocturnal (e.g. S.D. Ripley in Campbell & Lack 1985) probably refer mainly to breeding-season nocturnal calling, which I would not classify as true

nocturnal activity. Nocturnal foraging appears to be largely confined to species such as coots, moorhens and some gallinules, which eat much plant material and forage in open habitats where light conditions are better than in dense vegetation.

The birds' observed aversion to full sunlight may indicate an inability to withstand great degrees of heat, especially in the humid conditions of their wet habitats, but it may also be related to the hazards posed by predators. With the exception of the Whitewing Flufftail, which I have not observed on the ground for extended periods, adult flufftails of all the African species are very cryptic in shade and dense cover: females, with their dark, finely-patterned plumage, are extremely difficult to see, while in deep shade the bright red or orange head colours of males are toned down to inconspicuous dead-leaf shades and their body plumage is cryptic. However in full sunlight the males' head colours become very bright, rendering the birds extremely obvious, while the dull brown colour of the females becomes brighter and more obvious, even appearing golden-brown in the Buffspotted Flufftail.

Several different functions may be assigned to the observed activities designated as play in the Redchested Flufftail. Ficken (1977) summarizes three important functions of play in young animals, all involved in preparing the individual for adult life: (1) enhancing muscular development; (2) discovery and experimenting with the relationship between the animal's actions and the external world; (3) testing and adjusting important social relationships. The observed play behaviour probably fulfils all these functions but may be particularly important in the context of function (3) in that it helps the young to adjust their aggressive and territorial behaviour to a level which is acceptable within both the family group and the bird's later independent existence. Experiments on Whitespotted Flufftails, involving the reactions of adults and immatures to models (Taylor & Taylor 1986), show that immature flufftails of this species initially attack models much more strongly and violently than do adults. This observed high level of aggression, if not modified and reduced as a result of experience and social interactions, might eventually result in unnecessary injury or even death. Thus, play between immatures and adults could serve to establish acceptable levels of aggressive behaviour for the young birds. Play by adults is more difficult to understand than play by young (M. Bekoff *in* Campbell & Lack 1985), but in this species the social play may serve to consolidate relationships within the pair or family group, to establish acceptable levels of aggressive behaviour, and to provide a harmless outlet for the innate aggression of the adults towards any conspecific intruders within their territory.

These considerations may be important with regard to the longterm toleration by adults of fully grown young in the parental territory. As well as the possible beneficial effects of social play, several other factors seem to be involved in reducing the adult male's aggression to the male

offspring. Immature males make territorial calls when stimulated by taped playback, but such calls are more akin to those of the female than of the male (Section 4.4.8) and may thus be less likely to provoke an aggressive reaction from the parent, while still serving a useful function in territory defence. The red head and neck of the immature male are duller (because of dark feather tips) than in the adult, which may help to reduce possible aggressive behaviour in the adult. Furthermore the tail of the immature is, like that of the juvenile, unpatterned, and this may serve to moderate the adult's aggressive behaviour, especially as the tail is clearly visible to the aggressor during a chase. Reciprocal allopreening between adults and immatures must also serve to consolidate a good relationship, as it presumably does between the adults. It is also relevant that, during the period when immatures are most commonly recorded in parental territories, the calling patterns (Section 4.4.8) and aggressive behaviour (Section 4.4.5) of the adult male (Section 4.4.8) suggest a relatively low level of territorial activity.

Observations of both wild and captive birds have brought to light some aspects of behaviour which should serve to maintain and strengthen the permanent pair bond, especially during the nonbreeding season. These comprise reciprocal allopreening between pair members, occasional courtship displays by the male outside the breeding season, and occasional feeding of the female by the male throughout the year.

#### 4.5.3 Territoriality

Sufficient evidence has been accumulated to show that a pair of Redchested Flufftails will maintain a territory permanently whenever possible, in contrast to the other rallids which share the same habitats, which defend territories only in the breeding season. It is also clear that both sexes are active in territorial maintenance and that any immature males (possibly also females) which remain in the territory after the breeding season are also involved in territory defence. A full discussion on the selective advantage of holding permanent territories appears in Chapter 5.

Interspecific competition for nest sites has been suggested as a reason for the apparent failure of the Whitewing Flufftail to breed alongside the Redchested Flufftail in South Africa (Chapter 8, Section 8.5.4), but there is no clear evidence to support this hypothesis. The only observation suggestive of interspecific territoriality between the Redchested Flufftail and another *Sarothrura* species concerns a male Buffspotted Flufftail which foraged in a Redchested Flufftail territory at Danville on 14 May 1991 (Chapter 9, Section 9.4.1). While making typical aggressive *NÉ-NÉ* calls to taped playback of Buffspotted Flufftail calls, and even searching actively for their source, this bird subsequently reacted very differently to taped playback of Redchested Flufftail territorial calls, which

caused it to run into cover and not return. This suggests that the bird was wary of a possible attack by the resident male Redchested Flufftail. However captive Redchested Flufftails tolerate the close proximity of Streakybreasted Flufftails even in the breeding season, showing no aggression to them (C.C. Wintle *in litt.*).

Observations of the reactions of Redchested Flufftails to both living and model Black Crakes and African Rails, and the corresponding reactions of these two species to living and model flufftails, suggest that some degree of interspecific aggression occurs between the flufftail and the two larger species. Observations are too few to allow definite conclusions to be drawn, but it appears that in the breeding season Black Crakes are often aggressive towards Redchested Flufftails, while during the nonbreeding season the reverse applies. Thus when both species are territorial the larger one dominates, whereas the smaller flufftail dominates when the crane is not territorial. This behaviour was not seen frequently enough to suggest that strong interspecific territoriality is regularly practised and there was no evidence that either species was completely excluded from the territory of the other under natural conditions. Conflict between Redchested Flufftails and African Rails was never observed in the field and reactions to models were few and inconclusive. Both Black Crakes and African Rails are very aggressive towards other rallid species in aviaries during the breeding season and will attack and kill even species as large as themselves (C.C. Wintle pers. comm.).

Interspecific territoriality has been recorded in relatively few bird species and may arise most often in pairs of species which have been derived from a common ancestor and have recently come together by range expansion after a long separation (Skutch 1976). However it is easily overlooked and may occur more commonly than is realized (Orians & Willson 1964). Its existence presupposes that the species concerned exploit similar resources (Wittenberger 1981) and it often arises in situations where the environment imposes limitations preventing the evolution of adequate ecological divergence between species, for example in the structurally simple environment of wetlands (Orians & Willson 1964). Two hypotheses have been proposed to explain the occurrence of interspecific territoriality: (a) misidentification of other species as conspecifics and (b) competition for resources such as food and nesting sites, or to protect eggs from predators (N.B. Davies *in* Campbell & Lack 1985; Wiens 1989a; Wittenberger 1981). In the situation under consideration mistaken identity is unlikely to be the cause, so competition for resources must be assumed.

In all regions of southern, central and East Africa where I have found the Redchested Flufftail, the two larger species exist alongside it in permanently or seasonally shallowly flooded vegetation but they are predominantly found in permanently and more deeply flooded vegetation, including the interior of extensive reedbeds. Although in summer they both extend their activities into seasonally flooded sedge meadow and (especially the African Rail) hygrophilous grassland at the edge

of permanent reedbeds (P.B. Taylor *in* Keith 1986), they are rarely numerous in such habitats and do not occupy them permanently, in contrast to the flufftail. The African Rail feeds in mud and water and on floating vegetation, probing deeply with its long bill; it nests over water and climbs well in tall reeds (Keith 1986; pers. obs.). The Black Crake is very adaptable but prefers permanently flooded situations, usually with relatively tall vegetation and dense tangles of cover (Hopkinson & Masterson 1984; Keith 1986; pers. obs.), from which it emerges to feed at floating vegetation, in mud and shallow water, at the edge of open water and sometimes even on open dry ground (Keith 1986; Taylor 1985b). It often nests over water and is very adept at climbing in dense, tangled vegetation (Hopkinson & Masterson 1984; Keith 1986). Both species exploit aquatic food resources such as frogs, crabs and fish, both eat carrion, and the Black Crake takes plant material (Keith 1986); apart from seeds none of these resources is known to be exploited by the flufftail.

Thus, although all three species occur together, extensive spatial overlap during the breeding season probably occurs to a significant extent only in permanently flooded reedbeds, which represent only one of several habitat types occupied by the flufftail, so that in many situations spatial separation precludes interspecific competition. The flufftail's food requirements overlap to some extent with those of the other two species, but the flufftail usually takes smaller prey and also feeds more on seeds, while its foraging techniques and microhabitats overlap very little with those of the African Rail but more with those of the Black Crake. It is also possible that both the flufftail and the crake may feed their chicks on similarly sized invertebrate prey so that competition for food may arise in small habitat patches when the birds are breeding.

On the basis of these differences it may be expected that interspecific territoriality, probably resulting from competition for food resources, might occur to some extent in permanently flooded habitats, but is less likely to occur between the flufftail and the rail than between the flufftail and the crake. All observations, and the results of behavioural experiments, support these conclusions.

The only other secretive wetland rallids in which interspecific territoriality has been reported are the Sora *Porzana carolina* and the Virginia Rail *Rallus limicola* (Kaufmann 1989), which overlap completely in habitat requirements. However the recorded instances all involve pairs breeding in an aviary, when male Soras persistently chased Virginia Rails and excluded them from the Sora breeding territories. The Virginia Rails were also territorial but usually excluded only conspecific individuals from their breeding territories. Kaufmann (1989) interprets this behaviour as normal and proposes that, because the adults of the two species do not compete for food, interspecific competition has arisen because both species feed the young on similar invertebrate prey and the short-billed Sora (which normally eats seeds) is less efficient at collecting such prey. I have two principal objections to these conclusions. Firstly there is no evidence that comparable behaviour occurs in the wild and

two field studies of these species (Glahn 1974; Johnson & Dinsmore 1986a) produced results showing that the breeding territories of both species commonly overlapped. It is unwise to draw strong conclusions from captive birds, especially those forced to set up territories in restricted space (Kaufmann (1989) states that aviary territories were probably smaller than those of wild birds). Observations of captive Black Crakes and African Rails (C.C. Wintle pers. comm.) indicate that these birds are more aggressive to other species in aviaries than in the wild. Secondly, although nest-site and nest construction are identical in the two species (nests can be distinguished only by the eggs), Kaufmann (1989) considers neither competition for nest sites nor protection from predators as possible causes of interspecific territoriality. In addition he concludes that Soras defend their territory against all rail species, an assumption for which I can find no evidence.

#### **4.5.4           Vocalizations and calling patterns**

The seasonal variations in calling patterns recorded during this study agree with those noted in Zambia, where I made observations at Itawa, Ndola, from 1977 to 1980. Resident birds bred from November to March (possibly also in October), gave advertising calls from August to March (most frequently in December and January), and made spontaneous territorial calls throughout the year, fewest calls being recorded in May and June and most from July to September, i.e. before the rains and during the period when most wetland burning occurred.

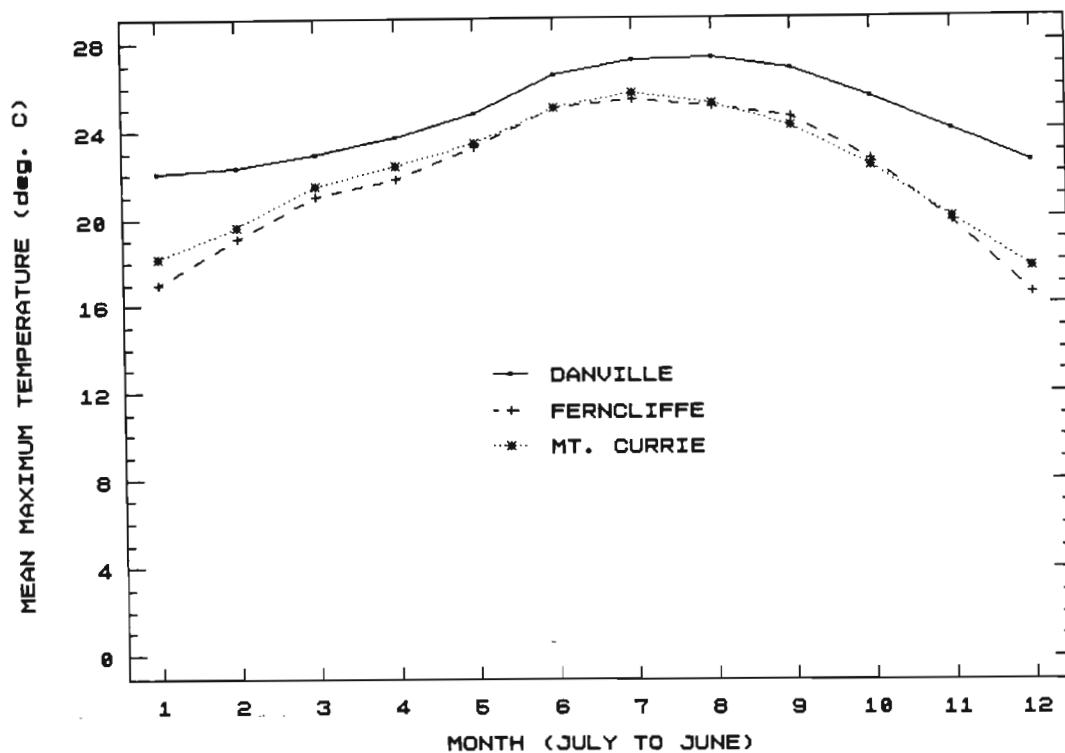
In studies of the vocalizations of the sedentary Light-footed Clapper Rail *R. longirostris levipes* in California (Massey & Zembal 1987; Zembal & Massey 1987) seasonal variations in calling patterns were observed, there being peaks in the occurrence of the common territorial call ("clapping") at the beginning and the end of the breeding season and of the advertising call ("kekking") during the breeding season. These observations are comparable to those made of the Redchested Flufftail's calling patterns except that Zembal & Massey (1987) attribute the peak in territorial calling at the end of the breeding season to the inclusion of juvenile calls, especially those resulting from observed aggression between fledglings. Clapper Rails are apparently territorial only in the breeding season, so one would not expect the adults to show a peak in territorial calling at the end of the breeding season. During each year of my study I noted a comparably great increase in the territorial calling of immature African Rails (not shown in Fig. 4.5) at the end of the breeding season, both spontaneously and in response to taped playback, when the adults were calling infrequently. Because the immature African Rail's version of the territorial call is easily distinguishable from that of the adult, the pattern was easy to detect.

#### 4.5.5 Breeding seasons

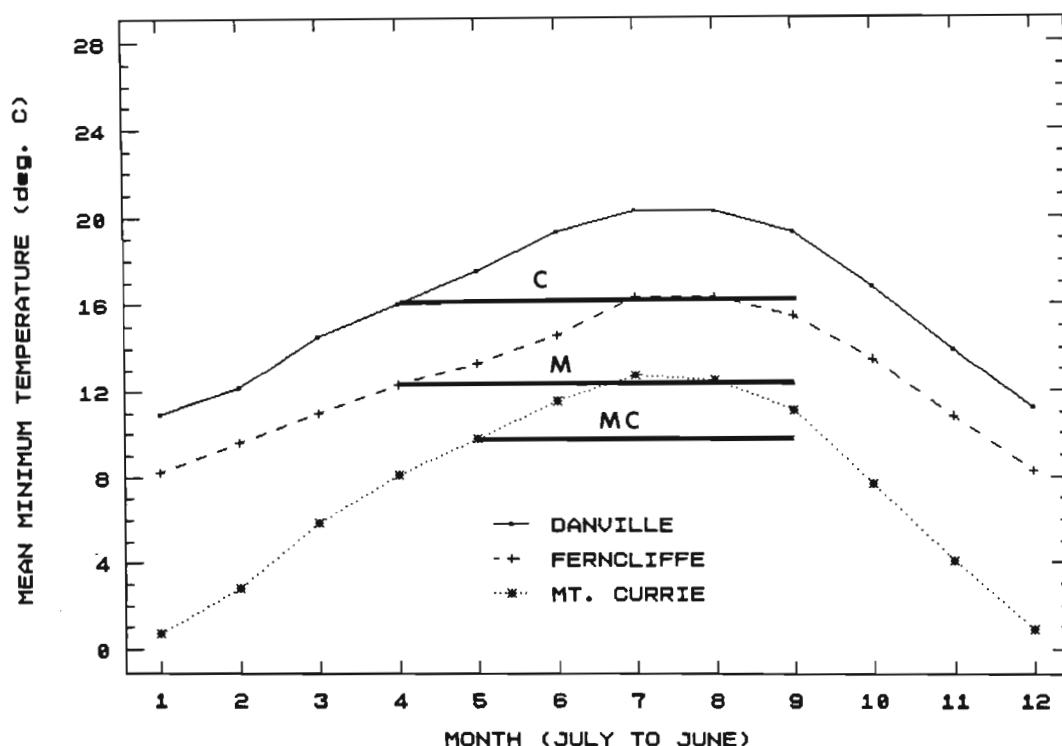
Although advertising calls, which are presumed indicative of the onset of breeding activity, appeared to begin at about the same time of year (from mid-August) throughout Natal (Table 4.5; Section 4.4.9), the first recorded breeding at Mt Currie was not until late November, up to two months later than at lower-altitude localities in Natal (Table 4.4). Breeding data are very few but the results do suggest a greater lag between the onset of advertising calling by males and of egg-laying in high-altitude areas. The mean monthly precipitation graphs for the four principal Natal study sites of the Redchested Flufftail (Chapter 2, Figs 2.7, 2.13, 2.18 and 2.29; Table 2.1) show that the rainfall pattern is similar in all localities, the rainy season running from September to March or April and a peak from November to March. Mean monthly temperatures (Table 2.2) are available for only two of these four sites (Danville and Mt Currie) but comparable figures for the Pietermaritzburg area are available from Ferncliffe (Fig. 2.10), where Redchested Flufftails also occur. At these three sites the mean maximum temperatures are all at least 21 °C in September and from 23-25 °C in November, the Ferncliffe and Mt Currie figures being very similar to each other (Fig. 4.11). The mean minimum temperatures differ more widely, and breeding at Mt Currie was noted only after the mean reached 9.8 °C, a figure which was exceeded in September at lower-altitude sites (Fig. 4.12; Table 2.2). To explain the apparently greater time lag between calling and laying at different sites I suggest that the onset of calling is triggered by day length, which would act similarly throughout the region, while egg-laying is delayed until the female has attained breeding condition as a result of the increased availability of invertebrate food. The increase in such food would probably be delayed in high-altitude areas by lower minimum temperatures in the early summer.

#### 4.5.6 Predation

The suggestion that the Blackheaded Heron may be at least an occasional predator of flufftails receives support from comments in the literature on the role of herons as predators of small birds in Africa. Stuart (1982) found unidentified bird remains in more than a quarter of 232 pellets from a breeding colony of Grey Herons *Ardea cinerea* in the western Cape, while in Kenya a Blackheaded Heron was seen to kill and eat an African Crake *Crex egregia* (R.A.M. McVicker in Taylor 1985a). Urban (1982) lists birds as a food item of the Purple Heron *A. purpurea* as well as of the other two species mentioned, and records instances of Blackheaded Herons killing birds up to the size of Cape Turtle Doves *Streptopelia capicola*.



**Fig. 4.11** Mean monthly maximum temperatures at three Redchested Flufftail study sites in Natal: Danville (coastal), Ferncliffe (mid-altitude, Pietermaritzburg) and Mt Currie (high altitude).



**Fig. 4.12** Mean monthly minimum temperatures at three Redchested Flufftail study sites in Natal: Danville (coastal), Ferncliffe (mid- altitude, Pietermaritzburg) and Mt Currie (high-altitude). The horizontal lines show the recorded breeding period of the flufftail in each area: C = coastal; M = mid-altitude; MC = Mt Currie.

## CHAPTER 5

### PERMANENT TERRITORIES AND SEASONAL MOVEMENTS: THE EFFECTS OF SEASONAL HABITAT CHANGES ON THE REDCHESTED FLUFFTAIL

#### 5.1 Introduction

One of the first things which became apparent when observing Redchested Flufftails in different habitats was that their dispersion apparently varied with the degree of flooding of the occupied vegetation: permanently flooded areas seemed to be more densely populated than seasonally wet ones. This study established that territory size varies with vegetation type and the degree of flooding, and the nature of these variations is documented in this chapter. The effects of burning on territory size and habitat suitability are discussed in Chapter 6.

The studies described in Chapter 4 show that Redchested Flufftails are territorial throughout the year and that territorial pairs tend to be entirely sedentary when conditions permit, most exceptions involving pairs which occur only in the summer in seasonally flooded vegetation not primarily wetland in character (Chapter 4, Section 4.4.2). However during winter and early spring the availability of habitat in permanent territories is often significantly affected by various environmental factors, including burning, which may so compress territories that the birds are forced to leave until the affected vegetation recovers, reoccupation often not occurring until December or January (Chapter 6, Section 6.4.1). The effects of burning and mowing on vegetation regrowth and food availability, and the relationships between habitat regeneration and the timing of recolonization by flufftails, are discussed in Chapter 6.

Nothing is known about the extent to which flufftails can tolerate severe habitat damage during the nonbreeding period, and a study of this is important in assessing the effects of natural and man-induced seasonal habitat changes on the birds' ability to survive and reproduce successfully in the habitat. Such studies are relevant not only to the relatively common Redchested Flufftail but also to rare flufftails, other rallids and ultimately to many other wetland birds which inhabit this threatened, severely modified and rapidly disappearing biome in Africa.

It is mentioned elsewhere (Chapter 4, Section 4.1 and Chapter 6, Section 6.1) that nothing is known about any movements which the flufftails might make in response to seasonal changes in their wetland habitats, and that no studies have previously been done to relate the effects of burning on vegetation regrowth to the timing of recolonization by wetland rallids. An investigation of these topics is essential to an understanding of the obviously successful Redchested Flufftail's adaptations to the frequent burning which has always been an environmental factor significantly affecting its

biome (Chapter 6, Section 6.1). Such an investigation is of particular interest in this species, which apparently maintains a permanent territory in habitats where other rallids do not (Chapter 4, Section 4.1).

The following topics were investigated in this part of the study:

- (a) the influence of habitat type on territory size;
- (b) seasonal variations in territory size in different habitat types;
- (c) the amount of winter or spring habitat reduction necessary to force temporary emigration;
- (d) the behaviour of flufftails during and after wetland burning;
- (e) the nature and extent of seasonal movements;
- (f) the size, location and habitat types of temporary nonbreeding territories;
- (g) alternative strategies to temporary emigration;
- (h) the hazards of enforced movements and the advantages of maintaining permanent territories.

## 5.2 Study areas

Most studies of seasonal variations in territory size were made at the three long term study sites where populations of Redchested Flufftails were monitored throughout the project, and at which controlled burning experiments were performed (Chapter 6). The sites, described in Chapter 2, are Gartmore, Howick (Section 2.2.5), Allerton, Pietermaritzburg (Section 2.2.7) and Mt Currie Reserve, Kokstad (Section 2.2.13). These three sites also provided most of the information relating to topics (c)-(g) in Section 5.1. Additional data on habitat types and territory sizes were also collected throughout the southern Natal survey area (Chapter 2, Section 2.1), at the Wakkerstroom and Dullstroom study sites in the Transvaal (Sections 2.2.2 & 2.2.3), and at the Bromley, Zimbabwe study site (Section 2.2.1).

## 5.3 Methods

### 5.3.1 Definition of habitat types

Investigations of preferred habitats showed that Redchested Flufftails occur in a wide range of vegetation types comprising many different wetland plant species (Chapter 4, Section 4.4.2) and it is difficult to attempt broad, simple definitions of habitat type based on plant-species composition. Overall vegetation type and structure differ most obviously in relation to the degree and permanence of flooding (Chapters 4 and 6) so, for the purpose of investigating the relationship between habitat

type and territory size, five habitat types were defined with respect to the degree of flooding in summer and winter, the range extending from total flooding throughout the year to complete dryness during the nonbreeding season. The definitions are set out in Table 5.1, which also summarizes (in simple terms) the dominant and characteristic types of vegetation associated with each Flooding Type (FT). The table shows not only that some vegetation types occur over a wide range of flooding conditions, but also that many or all of the vegetation types are present in some flooding conditions, and this is indicative of the complex mosaic of wetland vegetation which is often found. Types FT3 and FT4, which are predominantly moist to partially flooded for most of the year, are the richest in plant species. In Table 5.1 the vegetation types HG (hygrophilous grassland) and SM (sedge meadow) are generalized definitions covering plant communities transitional between marsh (i.e. reed- and sedge-dominated communities in permanently or semi-permanently wet areas) and dry grassland. Sedge meadow is a species-rich transitional zone between marsh and hygrophilous grassland, with sedges, rushes and hygrophilous grasses on seasonally moist to flooded ground. Hygrophilous grassland is transitional between wetland and dry grassland, occurs on temporarily flooded or moist ground, and is dominated by a mixture of hydrophytic grasses with some dry-land species. Examples of both vegetation types may be found in the vegetation descriptions for Wakkerstroom, Gartmore and Mt Currie (Chapter 2, Sections 2.2.3, 2.2.5 & 2.2.13).

### **5.3.2 Territorial mapping and censusing**

Territories were mapped using the taped-playback techniques described in Chapter 3, Section 3.4, supplemented by some direct observations, including those of colour-ringed birds. At the long-term study sites regular censuses were made to determine the periods of residence of as many pairs as possible, so that winter or spring emigrations could be monitored and the factors causing them assessed. Census techniques are described in Chapter 3, Section 3.4. From April to November inclusive, regular searches were also made for birds establishing temporary territories in marginal habitat at these sites. Regular checks were made on most temporary nonbreeding residents so that their departure times could be established and compared with the arrival of birds in the adjacent regenerating vegetation of abandoned permanent territories.

For each territory whose size was regularly calculated (often monthly), a representative summer (January) and winter (July) territory size was selected for use in comparisons and calculations involving (a) the relationship between habitat type and territory size, and (b) seasonal variations in territory size by habitat type. Depending on the prevailing conditions, winter sizes ranged from smaller than summer sizes (if there was post-breeding habitat reduction) to greater (if there was post-breeding expansion into vegetation where deep summer flooding had subsided). For territories mapped

TABLE 5.1

Flooding Types (FT) of Redchested Flufftail territories, with characteristic vegetation (D = dominant, f = frequent), as defined during the study. Abbreviations: *Ca* = *Carex*; *Cy* = *Cyperus*; *El* = *Eleocharis*; HG = hygrophilous grassland; *Ju* = *Juncus*; *Le* = *Leersia*; *Ma* = *Mariscus*; *Ph* = *Phragmites*; *Sc* = *Schoenoplectus*; SM = sedge meadow; *Ty* = *Typha*. See text (Chapter 5, Section 5.3.1) for definitions and examples of vegetation types HG and SM.

FT	Summer saturation (%)			Winter saturation (%)			Characteristic vegetation types											
	Flood	Moist	Dry	Flood	Moist	Dry	<i>Ca</i>	<i>Cy</i>	<i>El</i>	HG	<i>Ju</i>	<i>Le</i>	<i>Ph</i>	<i>Sc</i>	SM	<i>Ty</i>		
1	95-100	0-5	0	90-100	0-10	0	D	D	f		f		D	f		D		
2	90-100	0-10	0	60-90	10-40	0	D	D	D		D	D	D	D		D		
3	30-90	10-70	0	10-30	50-80	0-30	D	D	D	f	D	f	D	D	D	D		
4	10-30	70-90	0	0-30	10-50	0-50	D	D	D	D	D	f	f	D	D	f		
5	0-20	80-100	0	0-5	10-30	30-70				D	D	D			f	f		

only once per season summer sizes included estimates made in December and January, while winter sizes included estimates made in June and July. In all these cases, only one year's figures were included for each territory surveyed, while reductions in territory size were excluded if they were caused by events which were not part of the normal annual cycle of habitat changes described below.

The causes of reduction in the size of nonbreeding territories may be separated into two types: type A, regular and virtually universal events which do not normally cause emigration or displacement, and type B, irregular, often catastrophic, events which frequently cause emigration or displacement and may occur in winter or early spring. Type A includes normal winter changes in vegetation (dieback and structural collapse), and normal changes in substrate saturation (falling water levels and the drying out of seasonally wet substrates); the latter changes do not normally affect the permanently flooded FT1 territories. By definition, a permanent territory is one in which these regular seasonal events do not cause the resident birds to emigrate. Type B events include burning, mowing, grazing and trampling by domestic stock, large-scale deterioration of vegetation caused by severely reducing the water supply to permanent marsh or by the excessive accumulation of dead plant material, and encroachment by adjacent territory holders displaced by such events.

When investigating the birds' reactions to seasonal changes in the size of permanent territories caused by any event of type A or B, observations were included from all years at all sites and could involve more than one change per territory in the same nonbreeding season, e.g. a normal winter size reduction as a result of desiccation and a subsequent spring reduction caused by burning.

### **5.3.3 Behaviour and movements in response to burning**

Whenever possible, observations of behaviour were made during and immediately after controlled burns at the long-term study sites. Additional information was obtained from two Natal farmers who have encountered Redchested Flufftails during burns of wetlands on their farms. Whenever possible, immediately before a controlled burn, censuses were made in all habitat up to 1 km from the burning site to assess the local population so that any influx of post-burn immigrants might be noted. Censuses were then made as soon as possible after the burn, usually within 24 hours, to record changes in the resident population and to establish whether any birds had occupied the habitats up to 1 km away immediately after the burn (such birds could not be proved to have originated from the burn but their coincident appearance was regarded as strongly indicative of that origin). It was found that newly arrived or displaced birds sometimes might not respond to taped playback for at least the first day, so censuses were repeated locally for up to one week after the burn.

## 5.4 Results

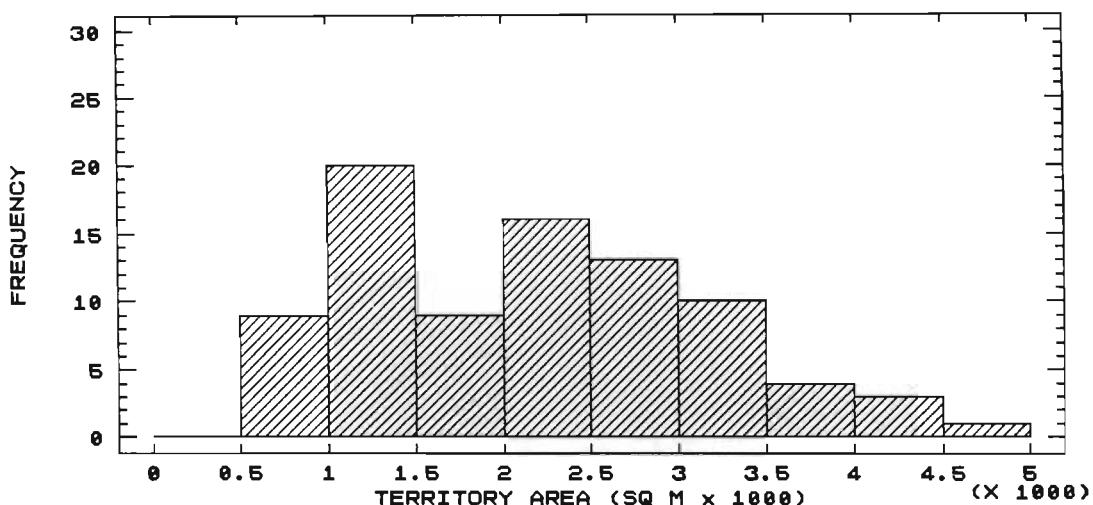
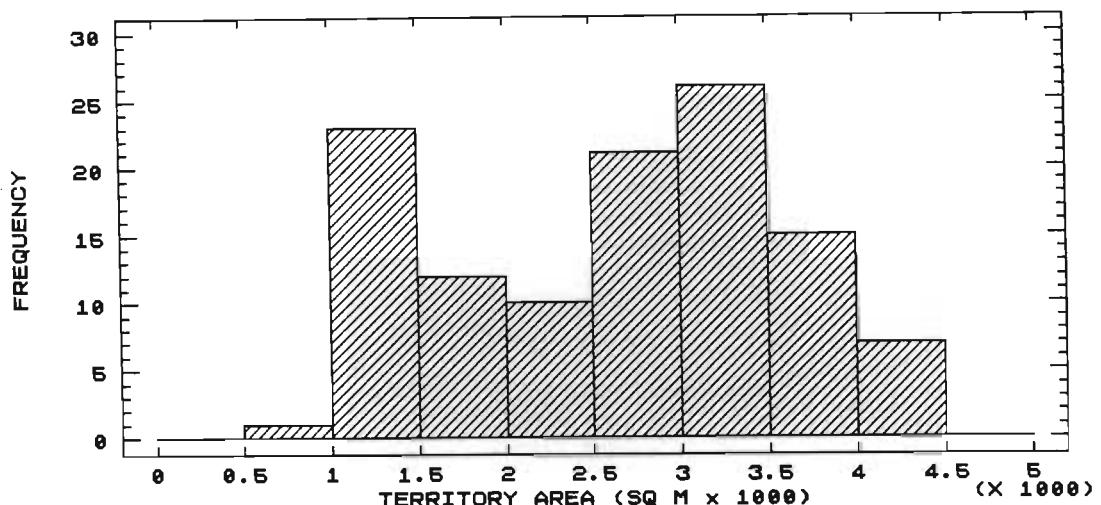
### 5.4.1 The permanence of territories

Chapter 4, Section 4.4 gives details of the results of investigations into the territorial behaviour of the Redchested Flufftail. Calling patterns, experiments with models and taped playback, long-term field observations, and studies of captive birds all indicate that Redchested Flufftails are monogamous, form a permanent pair bond and are strongly territorial throughout the year, whereas the other rallid species sharing their dense wetland habitats are territorial only during the breeding season. Most Redchested Flufftail territories are permanent, and the same pair may occupy a territory for several years.

### 5.4.2 The influence of habitat type on territory size

Figure 5.1 shows the frequency distribution in size of all summer ( $n = 115$ ) and winter/nonbreeding ( $n = 85$ ) territories which were accurately mapped during this study. Both permanent and temporary nonbreeding territories were included in this analysis, but nonbreeding areas occupied after reductions caused by events of type B (Section 5.3.2) were excluded. Summer territories were 960-4 488 m<sup>2</sup> in area, the smallest (all others were 1 200 m<sup>2</sup> or more) being a 1991-1992 territory at an unusually well flooded Mt Currie farm dam intake with vegetation consisting of *Eleocharis*, *Juncus*, *Schoenoplectus*, *Typha* and some grasses. This area was vacated at the end of the summer, after which it became almost completely dry and trampled by cattle. Nonbreeding territories were 530-4 860 m<sup>2</sup> in area, eight of the nine which were 1 000 m<sup>2</sup> or less being temporary territories (see Section 5.4.7).

Table 5.2 gives the range and mean of summer ( $n = 108$ ) and winter ( $n = 74$ ) sizes for all permanent territories of each Flooding Type (see Section 5.3.1), using territory sizes selected according to the criteria given in Section 5.3.2. Sizes of nonbreeding territories include those after type A reductions only; in some cases type B reductions (burning, grazing or trampling) subsequently occurred, sometimes great enough to force the occupants to leave. Table 5.2 shows that there is overlap in the range of territory sizes for some Flooding Types, both in summer and winter, but that the mean size of summer territories becomes progressively larger as the degree of substrate saturation decreases, while differences between mean winter sizes are less clear-cut for some Flooding Types. A one-way analysis of variance on the data for the sizes of breeding territories for FT1-FT5 showed that variances are equal ( $P > 0.05$ ) and that the differences between the sample means are highly



**Fig. 5.1** Frequency distribution of summer (A;  $n = 115$ ) and winter (B;  $n = 85$ ) Redcheasted Flufftail territory sizes ( $m^2$ ), including territories occupied both permanently and seasonally. Winter measurements include reductions to permanent territories caused only by type A events (see Section 5.3.2).

TABLE 5.2

Summer (breeding-season) and winter sizes ( $m^2$ ) of permanent Redchested Flufftail territories of different Flooding Types (FT) measured throughout the survey areas in South Africa and Zimbabwe. Seasonal territories are not included. Winter sizes include those after reductions caused by type A events (see Section 5.3.2). Winter redn. = mean % reduction in territory area in winter (a negative signifies an increase in area). For a definition of Flooding Types, see Table 5.1 and Section 5.3.1.

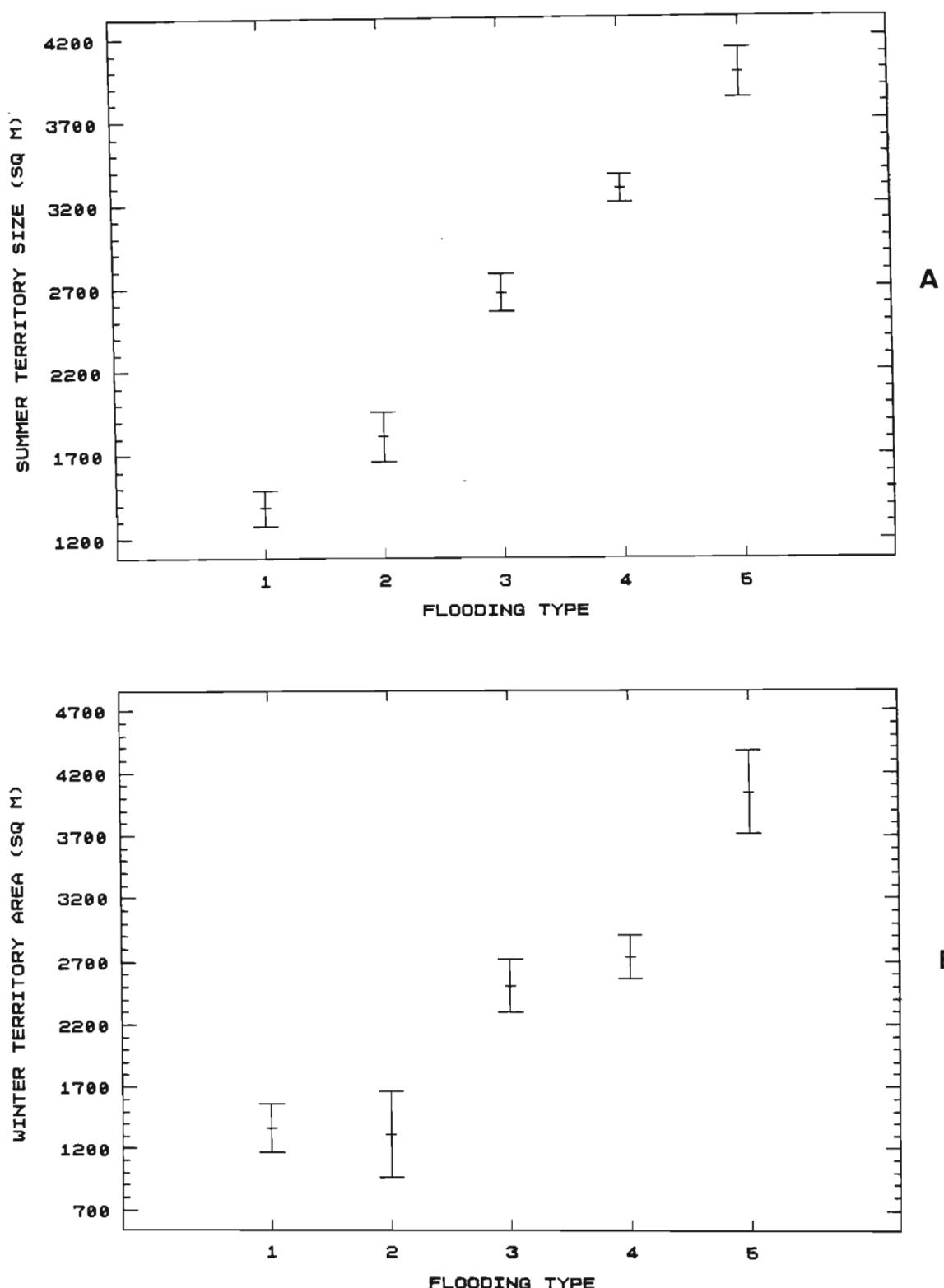
FT	Summer territory sizes			Winter territory sizes			Winter redn.
	n	Range	Mean (S.D.)	n	Range	Mean (S.D.)	
1	24	1200-1750	1382 (134,8)	19	1165-1690	1366 (145,1)	1,2
2	12	1550-2050	1807 (205,8)	6	970-1625	1315 (240,5)	27,2
3	22	2256-3768	2668 (299,1)	17	1700-3120	2509 (405,4)	6,0
4	38	2712-4100	3289 (303,5)	25	1210-3840	2740 (567,4)	16,7
5	12	3408-4488	3981 (331,9)	7	3120-4860	4046 (578,3)	-1,6

significant ( $P < 0,001$ ), confirming that the degree of flooding has a significant effect on the size of summer territories (Fig. 5.2A). A similar analysis on the data for the size of winter territories (Fig. 5.2B) showed that variances are equal ( $P > 0,05$ ) and that the data fall into three homogeneous and significantly different groups ( $P < 0,001$ ), FT1 + FT2, FT3 + FT4, and FT5. Thus the sizes of winter territories are similar in the two most extensively flooded habitats, and in the two predominantly moist to partially flooded habitats.

#### 5.4.3 Seasonal variations in territory size

Observations throughout the survey area indicated that, although in winter and early spring permanent territories were often reduced in area by burning, grazing, trampling, vegetation dieback and drying of the substrate, in some seasonally flooded wetlands more habitat was actually made available in winter by the partial drying out of dense vegetation too deeply flooded for occupation during the breeding season. Sometimes this more than compensated for loss of habitat so that territories were larger in winter than in summer.

Taking into account only winter size reductions caused by type A events (Section 5.3.2), Table 5.2 shows that in permanent territories the relationship between mean summer and winter sizes varies with Flooding Type. Thus FT1 territories, which are permanently almost completely flooded (Table 5.1), show a very small mean winter reduction; good examples of such territories are those at Allerton, described in Chapter 6, Section 6.4.2.1 and Table 6.7. In contrast, the larger FT2 territories are at least 60% flooded all the year but also contain areas which are only moist, and winter size reductions are regular, resulting in a mean winter area very similar to that of FT1 (see also Fig. 5.2B). Relatively few territories of this type were found, no examples being available from the Allerton and Gartmore study sites. FT3 territories show a small (6%) overall mean winter reduction in area but this includes both size reductions of 2-38% and size increases of 1-13%. These territories, which include nos 1, 2 and 6-9 at Gartmore (Chapter 6, Section 6.4.2.2 and Table 6.9) were often predominantly flooded in summer but in winter included large areas of moist to dry substrate (Table 5.2). A similar picture emerges for FT4, where the overall 16,7% winter reduction is derived from actual reductions of 18-36% and increases of 1-42%. These territories were largely moist in summer, with some flooding, while in winter they could be up to 50% dry (Table 5.1), and they included many of the Mt Currie Block V4 territories (Chapter 6, Section 6.4.2.3 and Figs 6.31-6.35). The driest territories (FT5) also showed large seasonal fluctuations, though the relatively small sample size gave a smaller range than for FT4. The overall mean 1,6% winter increase in area included actual reductions of 8-17% and increases of 2-28%; the impression gained was that winter



**Fig. 5.2** Variation in summer (A) and winter (B) Redchested Flufftail territory sizes with Flooding Type (one-way analysis of variance; means and 95% confidence limits). Temporary wintering territories are excluded, as are reductions in area caused by severe and irregular events (type B; see Section 5.3.2). For a definition of Flooding Types, see Table 5.1.

increases might be generally commoner than reductions in this habitat, which included the driest Gartmore territories, Nos 3 and 5 (Chapter 6, Section 6.4.2.2 and Table 6.9).

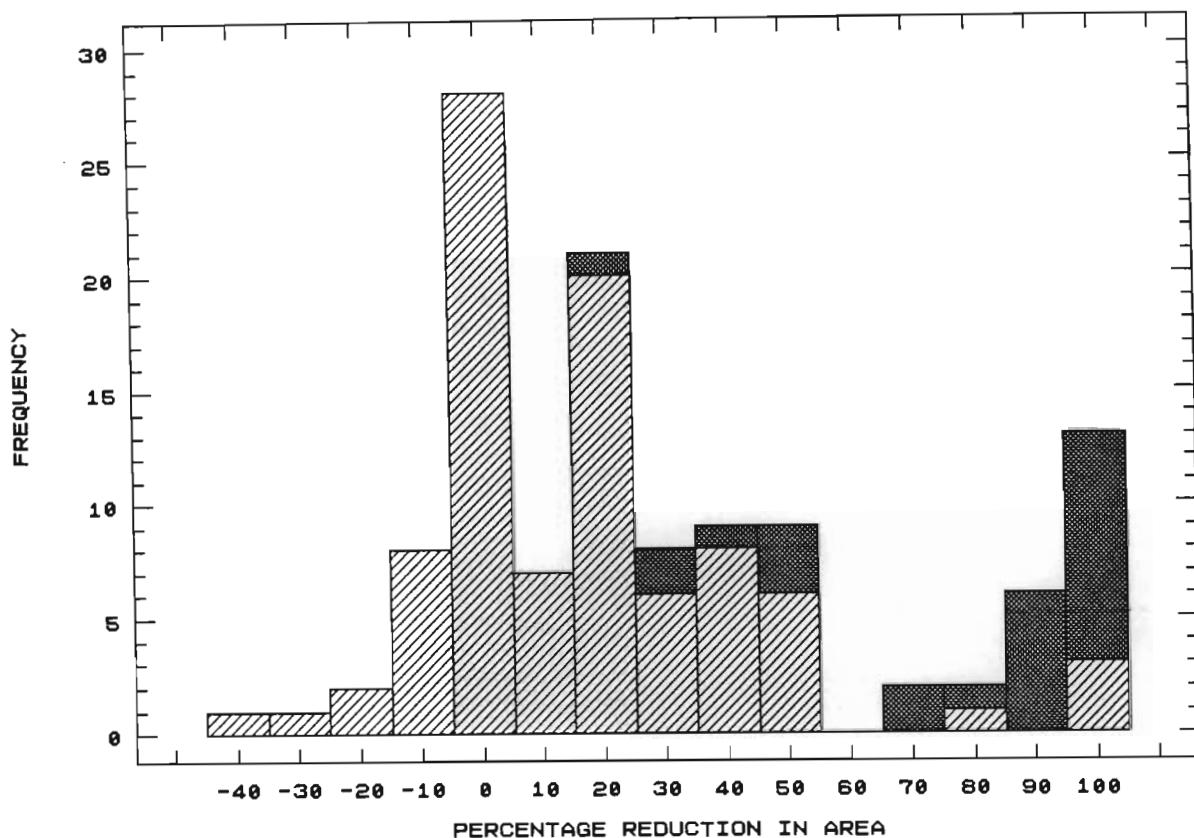
#### 5.4.4 The causes and effects of nonbreeding territory size reductions

During the study 117 measurements were made of changes in the areas of permanent territories during the nonbreeding season and these are summarized in Fig. 5.3. These results include measurements from more than one year in territories at long-term study sites, and in some cases include two (rarely three) events in one territory during a winter and spring period. They include two occurrences of a large accumulation of dead and moribund vegetation which resulted in emigration; these were assumed to cause 100% loss of habitat. Increases in nonbreeding area (i.e. negative percentage reductions) of 1-42% were recorded on 16 (14%) occasions. Overall, 28 (24%) of the changes involved an increase or decrease of less than 5%, while 63 of 88 reductions (72%) involved 55% or less of the summer area. Fig. 5.3 also highlights those changes which resulted from burning ( $n = 26$ , 22%) and it is clear that this factor is the most significant cause of large-scale reductions in territory area, being responsible for 19 (83%) of the 23 reductions of over 60%. Of the others, two (of 79% and 100%) were caused by spring mowing at Gartmore (Chapter 6, Section 6.4.2.2) and two by the accumulation of moribund vegetation.

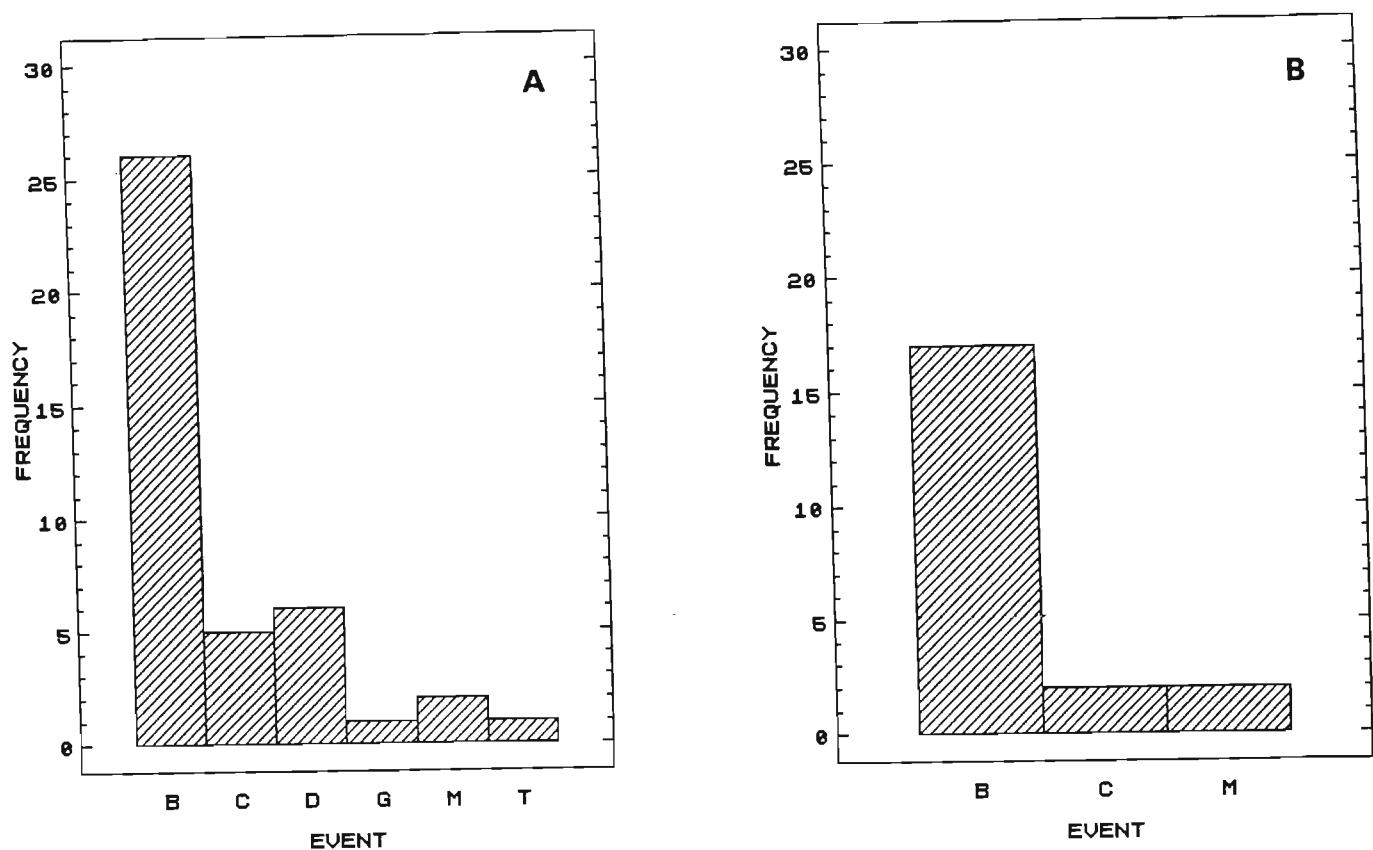
The frequency distribution of those events defined as irregular or type B (Section 5.3.2) is shown in Fig. 5.4A. Of the 41 occurrences recorded, 26 (63.5%) were burns, while six were displacements by adjacent territory holders (see Section 5.4.8). Fig. 5.4B shows that, of the 21 occurrences which resulted in emigration, 17 (81%) were burns.

The effect of reductions in the size of nonbreeding territories on permanently resident pairs is shown in Fig. 5.5, including the two occurrences of a large winter accumulation of moribund vegetation (event M in Fig. 5.4). No reduction in area of 70% or less ( $n = 64$ ) ever caused resident pairs to depart, although it is possible that some were responsible for the disappearance of immatures which had been present in some of the territories before the event but were not recorded afterwards. Only one of these 64 reductions was greater than 55%, that of 70% described in Section 5.4.5, example 3. Of the other 22 events, which caused reductions of 73-100%, only one did not result in the departure of the resident birds. This event occurred in the same Mt Currie territory as the 70% reduction was recorded and was tolerated because of the availability of adjacent foraging areas (for details see Section 5.4.5, example 3).

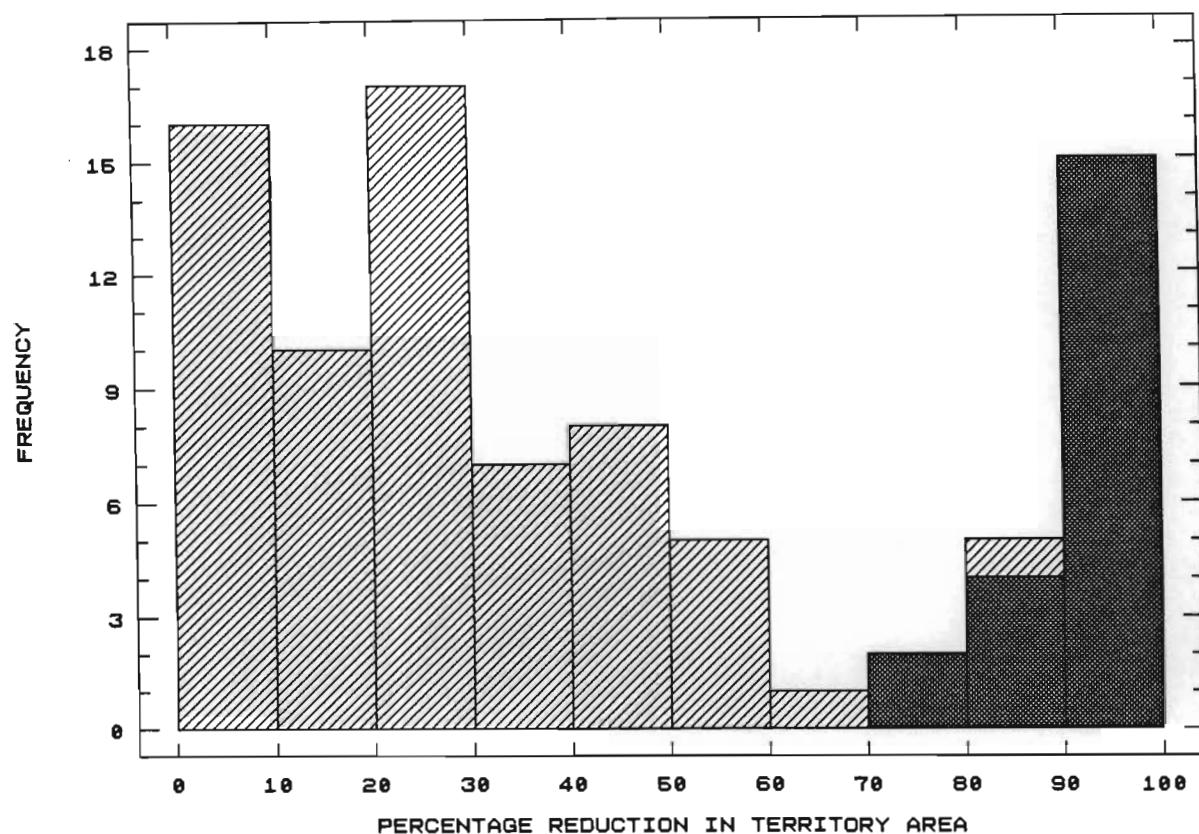
Fig. 5.6 summarizes the reductions in nonbreeding-season territory area measured in permanent territories of each Flooding Type. The histograms show that all large-scale reductions in



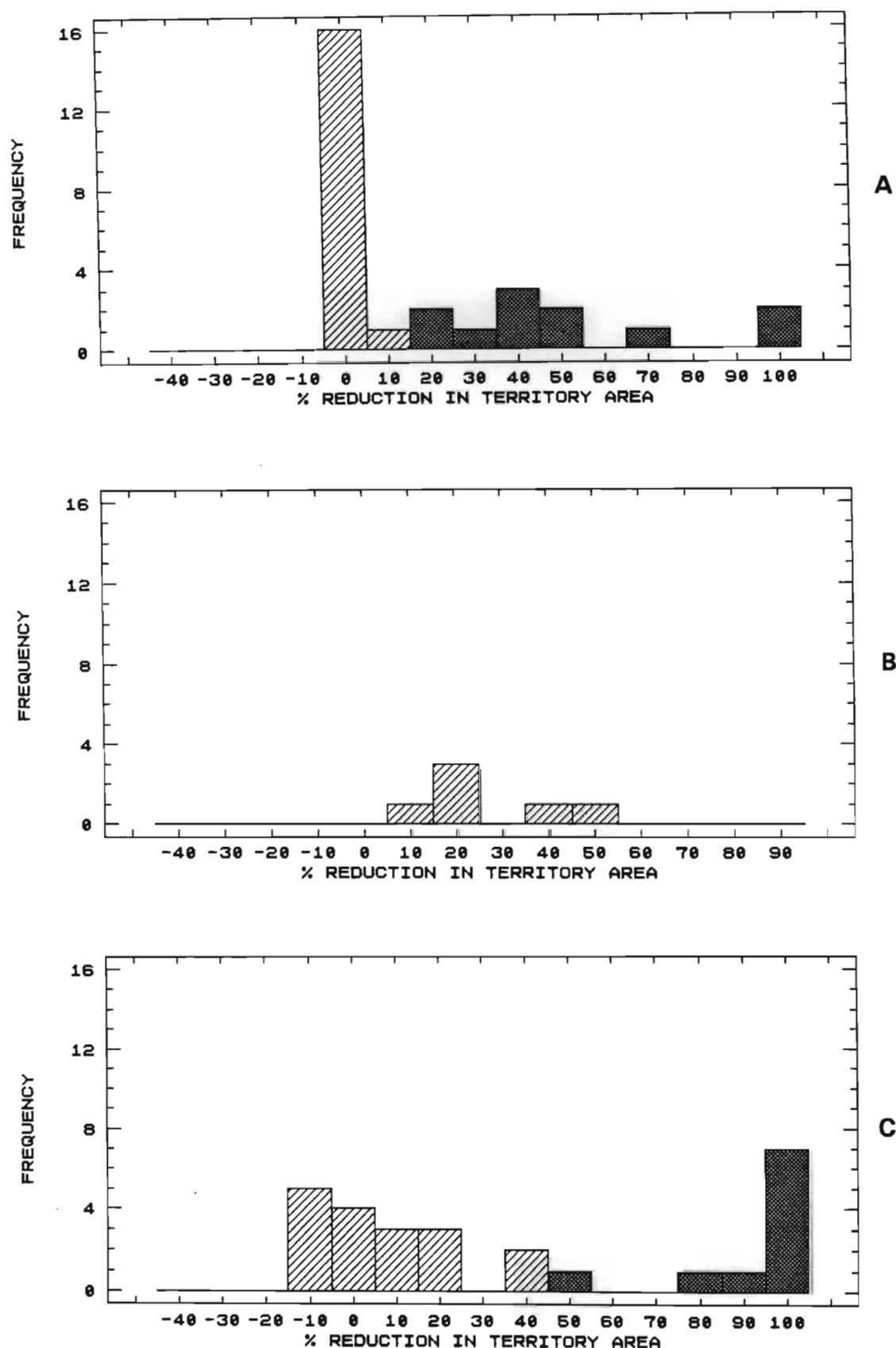
**Fig. 5.3** Frequency distribution of percentage changes in Redchested Flufftail territory areas ( $n = 117$ ) during the nonbreeding season, including reductions caused by event types A and B (see Section 5.3.2). Crosshatched = reductions caused by burning; hatched = all other events. A negative change represents an increase in territory area over that in summer.



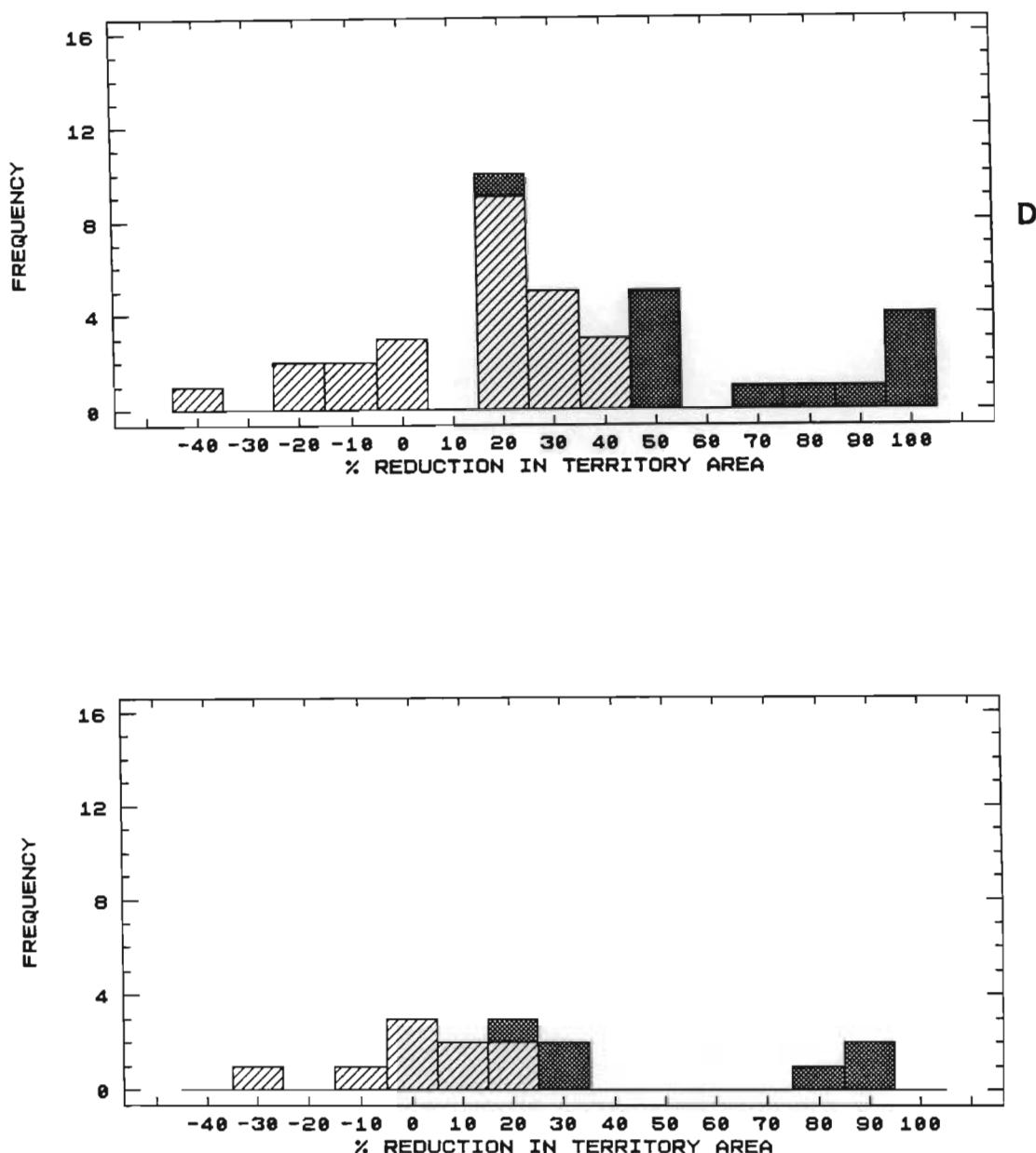
**Fig. 5.4** (A) Frequency distribution of Type B events (see Section 5.3.2) causing nonbreeding-season size reductions in permanent Redchested Flufftail territories ( $n = 41$ ). Events: B = burning; C = cutting or mowing; D = displacement by conspecifics; G = grazing by domestic stock; M = buildup of moribund vegetation; T = trampling by domestic stock. (B) Frequency distribution of Type B events causing nonbreeding territories ( $n = 21$ ) to be vacated by Redchested Flufftails. Events: B = burning; C = cutting or mowing; M = buildup of moribund vegetation.



**Fig. 5.5** Frequency distribution of nonbreeding-season reductions in the size of permanent Redcheasted Flufftail territories ( $n = 86$ ) caused by all events of types A and B (see Section 5.3.2). Crosshatched = reductions causing emigration; hatched = reductions not causing emigration.

**Fig. 5.6**

See following page for legend.



**Fig. 5.6 (continued).** Frequency distributions of the nonbreeding-season reductions in area of permanent Redchested Flufftail territories, including those caused by type A events (hatched) and type B events (crosshatched) by Flooding Type (FT). A: FT1;  $n = 28$ . B: FT2,  $n = 6$ . C: FT3;  $n = 27$ . D: FT4;  $n = 38$ . E: FT5;  $n = 15$ . For a definition of Flooding Types see Table 5.1).

the very stable FT1 (permanently flooded) territories were caused by irregular or severe events, i.e. fire, mowing and the accumulation of moribund vegetation, while irregular events were also responsible for the largest reductions in FT 3-5. Increases in nonbreeding territory areas were confined to FTs 3-5, which are predominantly moist to dry during the winter months.

The results suggest that any event causing a reduction of territory size greater than 70% usually forces resident birds to leave, but that the birds can tolerate smaller reductions, particularly those below 55%, for long periods, sometimes for the entire winter and early spring. This means that permanent territory holders must often defend nonbreeding areas which are up to 55% larger than the minimum needed to support a resident pair throughout the nonbreeding season.

#### **5.4.5      Conditions enabling Redchested Flufftails to tolerate severe winter and spring habitat modifications**

When assessing the responses of the birds to winter and spring area reductions, it is necessary to consider the length of time for which these reductions have to be tolerated before spring and early summer regrowth make more cover and foraging habitat available. In view of the relative sizes of territories in different Flooding Types, the type of habitat left undamaged is also important: the wetter the habitat the smaller should be the area needed for the birds to survive. It is also relevant that regrowth adjacent to unburned refuges often becomes available for foraging some weeks before it provides enough cover for permanent occupation.

Some large reductions were caused by spring burning, which at the study sites normally took place between late August and late September, and in these cases the birds were able to survive reductions of up to 70% for 1-2 months, until new foraging areas became available in October. In other cases, where large reductions took place earlier (sometimes as early as June) as a result of firebreak burning, other damage to vegetation, or displacement by conspecifics, pairs survived 20-53% reductions for as long as four months before habitat improved noticeably during spring regrowth.

Some examples of the circumstances under which Redchested Flufftails were able to tolerate severe nonbreeding habitat destruction will serve to illustrate the important environmental factors involved.

1. A territory in permanently flooded tall sedges at Underberg was reduced by burning to only 970 m<sup>2</sup> (52% of its summer area) in mid-July 1991 but was continually occupied by a pair for 13 weeks before the habitat began to improve in mid-October.
2. The area of a permanently flooded territory in sedges below a dam wall at Mt Currie was reduced by 20% to 2 050 m<sup>2</sup> at the end of April 1990 (by cattle damage) yet it continued to support

a pair of adults and two immatures until at least mid-August (15 weeks later), after which one immature was no longer recorded, while the second immature remained for another month, last being heard on 13 September.

3. At Mt Currie in the 1989 nonbreeding season one Block V3 territory suffered two severely damaging events which caused large reductions in territory area but did not force the resident pair to emigrate (Section 5.4.4). This FT4 territory comprised largely seasonally flooded sedge meadow and hygrophilous grassland but had an area of 1 000 m<sup>2</sup> (about 24% of its summer area) of permanently flooded reedbed vegetation dominated by tall dense *Typha* (some of this probably too deeply flooded to be used during the summer). The breeding area of 4 100 m<sup>2</sup> was reduced by 29% to 2 900 m<sup>2</sup> (measured on 24 June) as a result of drying out, vegetation dieback and firebreak burning. The burn of the adjacent Block V4 on 7 September resulted in the nonbreeding territory being reduced to 1 210 m<sup>2</sup>, only 30% of its breeding area, most of the territory's permanently flooded vegetation remaining intact. A mere 11 days later, on 18 September, the burn of Block V3 further reduced the area to 550 m<sup>2</sup> of flooded *Typha*, only 13% of the breeding-season area, but the birds then began to forage in an adjacent strip (6 m wide) of rather sparse tussocky wet grass which they did not normally occupy. This brought their total available foraging area to about 900 m<sup>2</sup> and the birds were able to survive until mid-October, when the firebreak-burned *Typha* had reached a height of 60-90 cm and made a further 250 m<sup>2</sup> of sheltered foraging area available. Subsequent rapid regrowth of burned vegetation assured the birds of adequate foraging and shelter.

4. In November 1991 at Bromley, Zimbabwe, in a spongy sedge and rush marsh with much *Carex*, *Schoenoplectus* and *Juncus* on black soil in miombo woodland, the territory of the resident pair had been extensively grazed by cattle during the drought and was reduced to a muddy watercourse with two bush clumps and small patches (each 0,25-2,0 m<sup>2</sup> in area) of sedges and rushes up to 5 m apart and separated by short grass, mud and grazed vegetation. The total cover was roughly estimated at no more than 900 m<sup>2</sup>, but an additional 200 m<sup>2</sup> of fragmented potential feeding areas with mud or short vegetation was also available. This is the most disturbed area in which I have ever found these birds resident during the dry season.

5. The Allerton burn on 4 September 1991 caused the pairs in Reedbed 3 (see Chapter 2, Fig. 2.12) to lose 45% and 48% of their permanently moist to flooded *Cyperus/Mariscus*-dominated territories, leaving them only 910 m<sup>2</sup> and 895 m<sup>2</sup> respectively. These areas were occupied for at least 2½ months before adjacent habitat developed sufficiently to be used extensively for feeding. Similarly, after the burn on 13 September 1989 one Reedbed 3 pair was left with only 850 m<sup>2</sup> of flooded habitat, in which the birds remained for about three months.

6. On a farm at Ashburton, near Pietermaritzburg, on 13 October 1990, a pair at a territory in the seepage from a dam wall, consisting of permanently flooded *Cyperus*-dominated vegetation with some flooded grass, had lost 41% of the summer area ( $1\ 248\ m^2$ ) to cattle damage during the winter; they not only survived in the remaining  $740\ m^2$  but had already started nesting in undamaged vegetation.

7. At Mt Currie on 25 July 1991 a firebreak burn almost completely destroyed one territory largely consisting of seasonally wet grass and sedge meadow. The resident birds emigrated, not being able to survive in the remaining  $275\ m^2$  of wet unburned sedges and *Typha*. The territory was reoccupied on 4 October and for the next six weeks the newly returned pair existed in shelter not exceeding the  $275\ m^2$  previously available, plus new feeding areas of up to  $1\ 535\ m^2$  in regrowing moist vegetation.

Further examples, involving territory extensions into marginal habitat and encroachment on neighbouring territories, are given in Section 5.4.8.

Considering the outcome of severe reductions in territory size, all birds which were able to remain in less than  $1\ 000\ m^2$  of habitat occupied areas which were either entirely or largely permanently flooded, and thus approximated to the nonbreeding habitat in Flooding Types 1 and 2, in which winter territory sizes are smallest. Of the six recorded instances, which include examples 1, 3, 5 and 6 above, the mean reduction on the summer territory size was 51% and the mean area occupied was  $878\ m^2$ .

#### **5.4.6 Behaviour in response to burning**

Observations made during controlled-burning experiments provided direct evidence of the responses of the flufftails to fire, and also of some of the burn and post-burn hazards to which they and small wetland-dependent mammals are subjected. The experimental burn of the southern half of the study site at Gartmore in September 1989 was a very hot, almost total burn in dry vegetation and was fanned by a wind which rose during the burn. The fire ran towards the road which borders one side of the site (Chapter 2, Fig. 2.6), i.e. away from the available cover in the unburned sector. The burned area included the entire territories of three pairs of Redchested Flufftails (Chapter 6, Fig. 6.22) and large parts of two others. Immediately before the fire the two pairs whose territories spanned the firebreak were both to the north of the firebreak (they responded to tape from there), so that six adults and three known resident juveniles were assumed to be within the burning vegetation and were thus completely deprived of cover. No birds were flushed during the entire burn until the fire was within 3 m of the road, when six individuals ran or fluttered from the edge of the burning

vlei on to the short grass verge and the road itself. Four were caught by hand as they reached the road: they were weak and confused, seemingly overcome by the heat and smoke, and one had singed its remiges by attempting to run back into the smouldering grass. The other two escaped, one by running across the road into a field, and the other by flying back through the smoke to the unburned northern section. All the captured birds recovered after being given water, and were released in dense cover. Had the observers not been there, these weak birds would have been at considerable risk from predators such as the Blackheaded Heron *Ardea melanocephala*: within 15 min of the fire being over the 2,4-ha burn was patrolled by 25 Blackheaded Herons which fed on animals disturbed or injured by the fire. Their prey included several large live vlei rats *Otomys* sp., which they retrieved from holes or minute patches of wet unburned vegetation and swallowed whole.

After this experience it was ensured that all other controlled burns at the study sites were cool and slow. Some were patchy, leaving some cover unburned (Plate 1B), but at Gartmore the Blackheaded Herons still caught several vlei rats in unburned vegetation after the patchy burn of September 1991. In all cases, most of the Redchested Flufftails were able to remain in cover and avoid the fire, while a few flew out to nearby cover without being affected by heat or smoke. At Gartmore a bird flew from a burning patch, circled and landed in the unburned basal dense cover of grass over which the fire had passed. Although no birds were retrieved from dense cover, either burned or unburned, after these fires, during the study I obtained evidence from farmers that the birds do shelter in such patches within a burned area. At Cedarville I. Sparg (pers. comm.) has picked up birds sheltering unharmed in unburned tussocks immediately after burns, while at Penny Park a resident pair in a permanently flooded territory dominated by *Typha* always remain during burns, crouching among the flooded *Typha* stems while the fire passes over them, and they have been caught by hand in such situations after burns (C. Adam pers. comm.). At Mt Currie, during the September 1990 burn, I watched the burning blocks from vantage points on the hillside immediately above the vlei. As the burn approached the stream, which here runs in a deep channel, a female Redchested Flufftail emerged from the grass ahead of the fire, ran down the stream bank and vanished down a rodent hole above the water line.

#### **5.4.7           Temporary nonbreeding territories and winter/spring movements**

Twelve temporary nonbreeding territories in marginally suitable habitat were located at Mt Currie and Penny Park, some of the examples at Mt Currie being documented with regard to arrival and departure dates, territory size and the possible origin and destination of the birds. The six examples not studied in detail involved four immatures which set up temporary territories in early

May 1992, three in *Hyparrhenia*-dominated grassland at Mt Currie and one in drying seasonally flooded *Cyperus/Typha* beds at Penny Park, and two males (or pairs) which occupied drying sedges and *Leersia* grass at Penny Park in late May 1992 and June 1991 (Chapter 4, Sections 4.4.2 & 4.4.11). The periods of residence of these birds were not determined.

As it was not possible to colour-ring and observe most permanently resident flufftail pairs, no unassailable proof could be obtained that the occupants of temporary territories were birds displaced by local burning, or that the birds reoccupying regenerating permanent territories had come from nearby temporary territories. However, circumstantial evidence from observations following the controlled burning at Mt Currie suggests that movements during the nonbreeding season are normally as short as possible, displaced birds sometimes occupying undamaged habitat adjacent or very close to the burned territory and returning to the permanent areas as soon as conditions are suitable (Chapter 6, Section 6.4.1). Detailed investigation of temporary residents provided the following information.

1. Two days after the Block V2/V4 burn on 7 September 1989 (Chapter 6, Fig. 6.32), which destroyed the territories of 15 pairs, two pairs were found in reedbeds at the edge of Crystal Dam, one in a narrow strip of flooded *Typha* 540 m<sup>2</sup> in area along the shoreline, the other in 530 m<sup>2</sup> of flooded *Typha* and *Phragmites* near the dam spillway. Both of these areas provided good-quality foraging habitat and shelter at this time but were normally too deeply flooded in summer for occupation. At the same time a large influx of Levaillant's Cisticolas *Cisticola tinniens* and Stonechats *Saxicola torquata* appeared in the dam margin reedbeds, obviously from the same burned blocks. The two flufftail pairs remained until November, the shoreline pair disappearing on 17 November, 10 weeks later and the day before a pair was found in a regenerating territory 550 m away in the vlei. The spillway pair appeared well settled, the male even making advertising calls from early October, but they disappeared on 15 December after 14 weeks, at a time when several vlei territories were reoccupied and when the rising dam water level began to flood their temporary area deeply.

2. The day after the 7 September 1989 burn a silent pair of flufftails was flushed (by dragging a rope) from 900 m<sup>2</sup> of dense grass with a *Typha* patch in Block V3, 200 m upstream of a burned Block V4 territory. These birds soon began calling, survived the subsequent burn of Block V3, and left about 10 weeks later in mid-November, at the same time that the burned Block V4 territory was reoccupied. On voice, the male of this pair was considered to be the displaced Block V4 individual.

3. Within two days of the 5 September 1990 burn at Block V2 (Chapter 6, Fig. 6.33) an adult male appeared in completely dry *Hyparrhenia*-dominated grassland on a slope above the stream at a drainage line in the adjacent Block V1. Two pairs had been displaced by the burn from the lower part of the same drainage line, 150 m and 250 m downstream. The area of ground occupied could not be

determined and the bird was not present in December, during which month both the vacated territories were reoccupied.

4. The day after the same 1990 burn a pair appeared in vegetation comprising *Hyparrhenia* with some *Carex* and *Schoenoplectus* along the other Block V1 drainage line, from the Block V2 part of which four pairs had been forced to emigrate (Fig. 6.33). These birds occupied about 1 000 m<sup>2</sup> of habitat for about 14 weeks until mid-November, when they disappeared at the same time that a burned territory 150 m downstream, adjacent to the firebreak, was reoccupied.

5. Immediately after the firebreak burn of 25 July 1991 a pair established a temporary territory of about 600 m<sup>2</sup> in flooded *Typha* along the Crystal Dam shoreline. These birds remained until 4 September, when the Block V4 burn destroyed their territory.

6. On 28 August 1991 a male, origin unknown, appeared in a 650-m<sup>2</sup> area of *Typha* wet grass in a small bay at Crystal Dam. This bird remained only until late September when it disappeared, possibly because the cover became inadequate after vegetation damage.

Other examples of apparently localized movements at Mt Currie were noted as follows.

1. A small burn on 25 June 1989 destroyed one territory within the wetland above the dam intake. The following day a calling male was located in flooded reedbeds at the dam intake 250 m away. This bird did not remain in the area, probably because the same fire caused a shift in the areas occupied by the three dam-intake territory holders (see Section 5.4.8) so that intake pair C subsequently occupied the vegetation in which the calling male had been heard.

2. On 21 November 1989 a calling male appeared in flooded *Typha* at the edge of Crystal Dam. The bird was not found after that date and was presumably moving, this occurrence being in the period when burned territories were being reoccupied elsewhere in the wetland (Fig. 6.32).

The six temporary territories whose areas were measured ranged from 530-1 000 m<sup>2</sup> in area, the four in permanently flooded habitat being 530-650 m<sup>2</sup> in area ( $\bar{x} = 593$  m<sup>2</sup>) and the other two 900 and 1 000 m<sup>2</sup> ( $\bar{x} = 950$  m<sup>2</sup>). The flooded habitat was considered good in terms of its shelter and foraging potential, and equated to habitat of Flooding Type 1, while the partially flooded habitat was most similar to that of Flooding Type 3. The mean sizes of the temporary territories were 57% and 64% less than the mean summer territory sizes (Table 5.2) of the equivalent Flooding Types, i.e. close to the maximum percentage nonbreeding-season reductions tolerated by the species (see Section 5.4.4); they presumably represent the absolute minimum territory sizes which will support a pair in winter or early spring.

The characteristics of the observed temporary territories may be summarized as follows: (a) they were very small, averaging 36-43% of summer territories in similar habitats; (b) the cover was good and the area provided either wet substrates for invertebrate prey or dense grass for (presumably)

seeds; (c) the areas were not suitable for summer occupation because they were too small, too dry or seasonally too deeply flooded.

#### 5.4.8 Post-burn territory extensions, displacement and sharing

Observations showed that pairs whose territories were significantly reduced by burning or other irregular events would sometimes incorporate adjacent, normally unoccupied, marginally suitable habitat into their nonbreeding territories until the damaged areas had regenerated. Such marginal areas might have been exploited occasionally for foraging before the burn, but were not defended until after the reduction. If this option were not available because all adjacent areas were occupied by other pairs, the affected birds either had to emigrate or had to encroach upon their neighbours' territories. An example showing a post-burn territorial extension which also included encroachment occurred at Allerton, where the Reedbed 3 resident pairs C and D (Chapter 6, Section 6.4.2.1 and Fig. 6.15) lost 73% and 26% respectively of their permanent areas to the burn on 13 September 1989. Both pairs adjusted their territorial areas to take in some previously unoccupied marginal habitat and in the process pair D relinquished to pair C some of its former territory on the common boundary (Fig. 6.16). In early December these pairs reoccupied breeding territories similar in position to those of the previous summer (Fig. 6.17).

Other examples of post-burn encroachment on an adjacent territory were obtained during the study, (the effect on the losing pair being designated "displacement" in Fig. 5.4A and Section 5.4.4). Most were from Mt Currie, where firebreak burns sometimes affected the three long-term resident pairs which occupied adjacent territories across the Crystal Dam intake. On 25 June 1989 a small burn deprived one pair (A) of almost its entire winter territory ( $2\ 575\ m^2$ ) and reduced that of the middle pair (B) by 16% to  $2\ 425\ m^2$ , with the result that pair A took over about  $1\ 500\ m^2$  of B's territory adjacent to its own area while the displaced pair B partly compensated by extending its territory across the opposite boundary into that of pair C. In response, pair C extended its own territory on the far side into some marginally suitable rather deeply flooded *Typha* beds near the intake stream. Pairs B and C occupied about  $1\ 800$  and  $1\ 700\ m^2$  respectively after the shift, representing 74% and 67% respectively of their pre-burn areas. This situation persisted until late October, when all three pairs shifted back into breeding territories in their normal areas. In late July 1991 a firebreak burn at the dam intake resulted in pair B losing  $1\ 725\ m^2$  (48% of its summer area and 65% of its post-breeding area); this pair again encroached upon the territory of pair C so that each pair subsequently occupied about  $1\ 700\ m^2$  of habitat until October.

The July 1989 firebreak burn at Mt Currie partially destroyed the territory of a pair in the Block V3/V4 drainage line and these birds encroached upon the adjacent downstream pair, which relinquished about 500 m<sup>2</sup> of its winter area.

The most extreme example of apparent displacement or sharing came from a small wetland at Nottingham Road, near Rosetta in the Natal Midlands. Two pairs occupied permanently wet *Cyperus* and *Typha* beds along a marshy stream, the boundary between the two territories being the dirt road which crossed the middle of the wetland. On 10 September 1988 the territory of the pair downstream of the road was completely destroyed by fire and later in the same day taped playback in the other territory revealed the presence of two calling males, which were still present in early October. Although the origin of the second male was not certain, and a second female was not found, it is very probable that the male came from the adjacent burned territory. No adjacent habitat was available for expansion so all the birds remained in the 1 340-m<sup>2</sup> area of the undamaged territory and both males called in close proximity to each other with no apparent segregation. Unfortunately it was not possible to follow developments at this site after early October.

## 5.5 Discussion

### 5.5.1 Territory sizes and habitat types

The only existing data on dispersion in the Redchested Flufftail are from Pakenham (1943), who found breeding pairs spaced at distances of 50-100 m or less in "extensive swamps". Calculating theoretical maximum territory sizes on the basis that territories should assume a hexagonal shape at high densities in a uniform environment (Barlow 1974), a size range of 2 200 m<sup>2</sup> (for birds 50 m apart) to 8 700 m<sup>2</sup> (for birds 100 m apart) is obtained; these are undoubtedly overestimates but in the lower half of the range are comparable to the measurements made in this study. Some information is available on the territory sizes of other wetland rallid species of dense vegetation in Africa and the Palaearctic region (Cramp & Simmons 1980; Taylor 1985a, 1987) but it is not possible to make detailed comparisons with these species because of interspecific variations in energy requirements, habitat types, food availability, breeding habits, the functions of territories and the duration of territorial behaviour.

Comparable variations in territory size with habitat type were recorded throughout the survey area, and territories of greatly different sizes may occur adjacently within a single wetland, especially if the area is a mosaic of permanently and seasonally flooded vegetation along drainage lines, as at Mt Currie, rather than a large, more uniformly-vegetated marsh. The variations in territory size

recorded during this study (Table 5.2), when the driest territories were sometimes 3-4 times the size of the wettest ones, are large but not unprecedently so; for example Skutch (1976) mentions that the size of Ovenbird *Seiurus aurocapillus* breeding territories ranged from 0.3 to 1.7 ha depending on vegetation quality and food supply.

In terms of the higher energetic costs incurred in defending large territories it is tempting to assume that the smallest territories on permanently flooded ground represent optimum habitat and that in areas where the substrate is drier the habitat may be less attractive to returning birds. Thus it follows that, after large-scale removal of birds by burning, the wettest areas should be recolonized first and the driest areas last. This has been shown to occur (Chapter 6) but the timing of recolonization is adequately explained by differences in the rate of regrowth of the vegetation and the corresponding delay in achieving equivalent levels of height and cover in drier vegetation types. Therefore the results of this study do not definitely indicate that the Redchested Flufftail has a preference for habitats of any type. Potential disadvantages of permanently flooded habitats in many areas are (a) the possibility that they may have to be shared with African Rails and Black Crakes, which may result in interspecific competition (Chapter 4, Section 4.5.3), and (b) that they may contain relatively few nest sites and be more liable to temporary flooding to a depth which would force brief emigration and result in failed breeding attempts.

No attempt could be made during this study to ascertain why the flufftails should defend larger territories in drier habitats, or whether there is any advantage in holding a territory in mixed vegetation types rather than vegetation dominated by one plant species such as *Carex*, *Cyperus* or *Typha*. Territory size is most likely to be related to the availability of an economically defensible resource (Brown 1964) such as food, shelter or nesting sites. Shelter is likely to be equally good in all habitats in summer, but subjective observations indicate that shelter in winter may be better and more continuous in permanently moist or wet reedbeds than in some sedge-meadow and tussocky-grass habitats, where dieback and wind damage may adversely affect the cover. No measurements were made of the relative availability of food in habitats of different flooding types, but it is clear that invertebrate food is much more abundant on wet or shallowly flooded ground than in dry grass (Chapter 6, Section 6.4.3). Conversely, seasonally wet tussocky grass for nest sites is more widespread and readily available in drier areas, and I consider this to be one reason why birds in permanently flooded vegetation often extend their territories into seasonally flooded peripheral areas during the breeding season; it may even explain why some pairs in winter apparently defended dry vegetation which, although providing cover, appeared to have little foraging potential but contained possible sites for early nesting in the following breeding season. A discussion of other factors related to territory size appears in Section 5.5.6. On the basis of the available evidence I suggest that

variations in territory size are principally related to the relative density of available invertebrate food, with an additional component relating to shelter and nest sites.

There are advantages in having some permanently flooded vegetation in any territory, even if it is too deeply flooded in summer for occupation, because in the winter it may provide not only a temporary refuge from burning but also useful foraging substrate and shelter. After a burn such flooded vegetation, if not fully destroyed, may be extensive enough to allow the resident pair to remain in the territory until spring regrowth occurs (see Section 5.4.5 for examples).

### **5.5.2 Behaviour in response to burning**

In grassland the direct and indirect effects of fire may cause considerable mortality among small terrestrial mammals (Tainton & Mentis 1984), but the few observations available from wetlands suggest that at least the adults of most wetland-dependent bird and mammal species are able to escape the direct effects of fire such as increased mortality, forced emigration and reduced reproductive effort (Kotze 1993). My observations do not support this view, at least with reference to the effects of some burns on flufftails and rodents. Although wetland burning is not normally regarded as a potentially lethal hazard to birds, which can escape by flying, under certain conditions burning may be very hazardous to flufftails, which prefer to run rather than fly when escaping from danger.

Those flufftails which shelter from fire in unburnt patches must emigrate very soon afterwards if insufficient unburned cover remains. Although no direct evidence was obtained, it was thought likely that such birds might remain hidden until nightfall, when they could move out of the area with less risk of being killed by predators such as herons.

### **5.5.3 Comparative effects of burning on sympatric rallids of dense wetland vegetation**

When assessing the comparative effects of burning on the Black Crake and the African Rail, the two sedentary rallid species which regularly share the Redchested Flufftail's permanent habitats, the precise habitat requirements of these other two species must be considered. These requirements (see Chapter 4, Section 4.5.3) show that both the larger rallids are normally associated with permanently flooded vegetation, which is more likely to provide refuges from fire than are the seasonally flooded areas permanently occupied by many flufftails. Also, as mentioned in Section 5.5.1, the chances of resident birds being able to remain after fire may be increased if the territory contains undamaged permanently flooded vegetation.

The rail and the crake are both more tolerant of sparse or very restricted cover than is the flufftail, the Black Crake in dry areas even managing to survive on tiny streams with only thin cover

(Keith 1986). After a severe fire at Mvoti Vlei both species were able to remain in areas of sparse cover which were unsuitable for occupation by Redchested Flufftails and both fed in open areas well away from cover, which are not available to the flufftails (Chapter 6, Section 6.4.3). Both are much larger than the flufftail and thus may be less vulnerable to predation in the more exposed conditions after a burn. Both exploit aquatic food resources such as frogs, crabs and fish, which are not only large and nutritious but are also little affected by fire and are thus always available, even immediately after a burn; both also eat carrion and the Black Crake takes plant material (Keith 1986). Thus they have access to a wide choice of foods not utilized by the flufftail, which feeds on small invertebrates more likely to be reduced in numbers immediately after a burn.

Thus both larger species are probably less affected by fire than is the flufftail because they are able to tolerate greater temporary habitat modification by burning, their habitat may provide more refuges and they can exploit open feeding substrates and different prey types.

#### **5.5.4           The hazards of enforced movements and the possible effects of recolonization timing on breeding**

In addition to the increased risk of mortality from burning, asphyxiation and predation at the time of a fire, those flufftails deprived of cover and forced to emigrate face additional problems. Firstly, they are deprived of living space at a time of year (winter or early spring) when suitable habitat is at its least extensive and when competition for unclaimed space is likely to be at its most intense, not only from birds hatched in the previous breeding season but also from other adults forced to leave their territories after burning. While searching for, and after colonizing, temporary habitat (which is often only marginally suitable), they must be at greater risk from predators than they would be in a permanent territory. Pairs may be split up or one member may die, so that survivors are faced with the necessity of acquiring a mate before breeding can commence in the following season. Finally the birds eventually will have to expend time and energy in either re-establishing themselves in their original territory or finding a new breeding territory.

Even if pairs survive the hazards of enforced emigration and manage to re-establish themselves in their original permanent territories, as may often be the case (Section 5.4.7), reoccupation of territories completely destroyed by burning may be delayed considerably past the date when breeding would normally commence. Thus, observed return times were 7-18 weeks after spring burning, in most habitats 10-15 weeks (Chapter 6, Table 6.2), and estimated return times were 10-20 weeks, in most habitats 10-16 weeks (Chapter 6, Section 6.5.2; Table 6.4). Assuming returns of 10-16 weeks ( $2\frac{1}{2}$ - $3\frac{1}{2}$  months) after burning during September, this places return time between mid-

November and mid-January. As breeding is recorded from late September but usually begins in October-November (Chapter 4, Section 4.4.9; Table 4.4), burning may delay the start of breeding for 1½-3½ months.

Despite its obvious adverse effects on the flufftails, burning has some beneficial effects. It is obviously an essential factor in maintaining both the quality of the wetland vegetation and the availability of an adequate and accessible supply of food (these factors are discussed in Chapter 6). A complete lack of burning results in habitat deterioration and the eventual invasion of woody shrubs and a transition to a hydrophytic woodland community (Downing 1966; Tainton & Mantis 1984).

### **5.5.5 Neighbour recognition, post-burn displacement and territory sharing**

The observed instances of neighbour displacement and territory sharing (Section 5.4.8) raise some interesting questions about the relationships between adjacent territory holders and the relative degree of aggression shown by territorial birds to neighbours and strangers. It appears that, under some circumstances in the nonbreeding season, some territorial birds will allow neighbours to encroach extensively on their territories whereas there is no evidence that incursions by strange intruders are tolerated.

Vocalizations are an important factor in the maintenance of Redchested Flufftail territories (Chapter 4, Sections 4.4.5 & 4.4.8). Falls (1978) notes that birds are able to recognize other individuals by their songs and shows (1982) that, among species which occupy large territories, neighbour-stranger discrimination by song is widespread. In many species males respond much less to the songs of neighbours than to those of strangers and my observations of the flufftails' reactions to taped playback showed that territorial pairs responded less strongly, less frequently and less quickly to the calls of neighbours than to those of strangers (these results are not analyzed for this thesis). Neighbour recognition therefore occurs, while observations at many sites showed that short-term incursions by neighbours were tolerated by residents, especially when all birds were responding to the playback of strangers' calls.

On the limited evidence available it is difficult to explain the apparently altruistic behaviour involved in displacement and sharing. It may imply that neighbours whose encroachment is tolerated are related to the territory holders, and thus that the holders are motivated by indirect (kin) selection; if the neighbours are not related it may imply that the behaviour has been selected for on the basis of reciprocal exchange of benefits (Wittenberger 1981).

Neighbour recognition by vocalizations may help birds to re-establish themselves in permanent territories after temporary emigration, because they will presumably incur a lesser degree of

aggression from established neighbours than would strangers trying to establish themselves (Falls 1982).

#### **5.5.6 Permanent territories**

It is now generally accepted that territoriality has evolved because competition exists for limited resources and, when such resources are economically defensible (when individuals defending them leave more progeny than those which do not defend them, and when the energetic costs of defence are less than the benefits), territorial behaviour is advantageous (Brown 1964; Wittenberger 1981). The Redchested Flufftail defends a multipurpose Type 1 breeding territory, as defined by Nice (1941), which encompasses all the resources required for survival and reproduction, namely food, shelter and nesting sites (Falls 1978; Wittenberger 1981).

Many birds defend territories during the nonbreeding season (Wittenberger 1981). Some may defend or establish winter territories to reserve a breeding territory for spring (Davies & Houston 1984; Lack 1954, 1968), others to defend food resources which are scarce and patchily distributed during the winter (Wittenberger 1981). As far as the flufftails are concerned, it is probable that winter defence of some vegetation types ensures the availability of nesting sites (Section 5.5.1) and it is also likely that the birds are defending food resources and shelter which are at a premium in winter because of seasonal changes in many of the occupied habitats, and particularly in view of the increased competition for resources at this time of the year (Section 5.5.4). Thus I suggest that Redchested Flufftails defend winter territories to ensure adequate supplies of food and shelter, plus potential breeding sites for the next season, and that nonbreeding-season territoriality confers the additional advantages of allowing the birds to remain in familiar areas where they are at a lower risk from predation than elsewhere and where they are in a position to begin breeding as early as possible in the next season.

On the basis of the cost-benefit explanation of territoriality proposed by Brown (1964) it is generally accepted that a feeding territory is of a size just sufficient to satisfy its owner's needs (Davies 1980). If one accepts that Redchested Flufftail territory sizes are principally related to food supply (see also Section 5.5.1), it should follow that the winter territories should be of a size sufficient to support the resident pair, with some minor variation to account for the inclusion of adequate shelter and potential nesting sites. However, in view of the reductions in territory size tolerated after catastrophic events such as burning (Sections 5.4.4 & 5.4.5) it is quite clear that pairs regularly defend winter territories up to 55% larger than the minimum required. What is the selective advantage of defending such apparently unnecessarily large areas? Considering breeding territories, if territory size is selected in relation to food supply, one might expect it to be adapted to

periods of minimal food availability (Falls 1978) and this could explain observations that territories often contain excess food (Carrick 1972; McLaren 1972; Skutch 1976). An apparent surplus may be defended as insurance against sudden and unpredictable periods of resource depression (Wittenberger 1981), both in the breeding season (Skutch 1976) and to ensure survival over a whole winter in a fluctuating environment (Davies 1980).

It is not clear to what extent the sizes of Redchested Flufftail breeding territories may exceed the normal requirements of the birds, but these arguments provide an explanation for the defence of excessively large nonbreeding territories by the flufftails: the extra space is an insurance against being forced to vacate the permanent territory as a result of severe reductions in area during the winter or early spring. There are great advantages in being able to remain permanently in the territory, such as: (a) avoiding the increased risk of mortality incurred during and after emigration, (b) removing the necessity to expend time and energy in acquiring a breeding territory (and possibly also a mate) in the following spring, (c) enabling breeding to begin as early as possible and giving time for more breeding attempts if some fail and (d) providing extra resources to accommodate offspring until the following breeding season, thereby increasing the chances of these young surviving to maturity and increasing the individual fitness of the parents (Wittenberger 1981).

There is an additional advantage in having resources large enough to accommodate immatures during the winter: the energetic costs of defending the resources will be shared by the immatures, which thus help the parents as well as helping themselves. In the event of a significant reduction in territory size the immatures can be ejected so that the parents can then remain in the territory and survive on the reduced resources.

It is also clear that, having defended a summer territory of a size adequate for breeding, if the resident pair were to reduce the area in winter to that just sufficient for its own requirements, this would incur the risk that other individuals would establish themselves in the undefended areas, from which they would have to be ejected when the territory was again expanded for breeding.

One further reason for the existence of excessively large territories should be considered. Verner (1977), proposing the superterritory concept, suggested that animals defend territory areas larger than those necessary for survival and reproduction because, as selection acts on an individual's performance relative to that of others, an animal can potentially increase its own fitness by decreasing that of others in the population. One way of achieving this goal would be to defend a superterritory and thus deprive others of resources. This theory is now generally rejected because the conditions under which spitefully large territories can evolve are restricted (benefits would be very small in large populations), the magnitude of the effect of spite on territory size will usually be small, and the strategy would be unlikely to spread when the costs of defending extra resources are high (Davies 1980; references reviewed by Davies & Houston 1984). In view of the flufftails' tolerance of

displacement and territory sharing (Section 5.5.5) it is unlikely that they are also behaving selfishly by excluding others from their territories before the occurrence of habitat reductions.

#### **5.5.7 Territoriality in the Black Crake and the African Rail**

The defence of permanent territories by Redchested Flufftails forms an interesting comparison with the behaviour of the Black Crake and the African Rail, which defend only breeding territories (Chapter 4, Section 4.4.5; Keith 1986; Schmitt 1975, 1976). The rail and the crake are probably not subjected to the environmental pressures which have encouraged the development of permanent territoriality in the flufftail. Their habitat (Chapter 4, Section 4.5.3), being largely permanently flooded, is probably more stable than much of that in flufftail territories, and provides more food during the winter than drier areas; it is also perhaps less likely to be drastically reduced by burning. During the nonbreeding season, because of their less rigid requirement for dense cover and because of their ability to exploit a wider range of food items and foraging substrates (Section 5.5.3) these two species are less likely to be displaced from burned areas and, if forced to move, can make use of feeding areas in relatively exposed and temporary habitats such as the open shorelines of ponds, lakes and rivers, floating vegetation, and short grass and the edges of cultivated lands near water (Keith 1986; pers. obs. from Zambia and Kenya). They therefore probably suffer less from the effects of habitat loss and enforced movement than do the flufftails.

#### **5.5.8 Immatures and floaters**

Little evidence is available for the permanent existence of a floating population of Redchested Flufftails unable to hold territories because of competition for limited resources, but the increase in the number of breeding pairs at Gartmore and Mt Currie after habitat improvement, and the occurrence of two summer-only territories at Mt Currie (Chapter 6), shows that surplus birds were present. Most of the immatures which are ejected from breeding territories each year must, if they survive the winter, contribute to a floating population of nonbreeding adults.

Non-territorial floaters would be very difficult to find (presumably they do not advertise their presence by calling) but it is possible to suggest locations in which they regularly occur. The most likely places are areas of marginally suitable or isolated habitat normally too small to hold breeding territories, and large, diverse, seasonally flooded habitats where resident flufftails hold large territories. On the assumption that territorial defence becomes more costly the further one goes from the central "core" area, birds holding the largest territories in seasonally flooded habitats may have more difficulty in locating intruders, and excluding them from peripheral areas, than may those

holding small territories in permanently flooded areas. It would be advantageous for floaters to occupy undefended home ranges on the periphery of territories in large seasonally flooded areas because, in years of good rainfall or after habitat improvements, some of these areas will provide enough additional habitat to accommodate extra territories. Likewise, in years of good rainfall some small areas of marginal habitat might become large enough to accommodate a breeding territory.

It is advantageous for a floater to live in one restricted area; it benefits from intimate knowledge of the terrain and it possibly knows a potential mate and establishes dominance relations with other floaters (Smith 1978). There are many examples of floaters living singly and spending at least some time in the breeding territories of others (Brown 1969 and references reviewed therein). Also, given the observed tendency of male Redchested Flufftails to attempt extra-pair copulations (Chapter 4, Section 4.4.10.1), male floaters might be able to obtain occasional matings with the females of established pairs.

## CHAPTER 6

### SOME EFFECTS OF BURNING AND MOWING ON THE WETLAND HABITATS AND DISPERSION OF THE REDCHESTED FLUFFTAIL IN NATAL

#### 6.1 Introduction

Fires have always occurred naturally in both grasslands and wetlands and have influenced many ecosystem properties, including the structure and composition of vegetation, the availability of nutrients and the substrate microclimate (references reviewed by Chambers 1992, Kotze 1993 and Schmalzer & Hinkle 1992). Lightning is the most significant cause of natural fires (Edwards 1984; Goudie 1989), while anthropogenic fire has a long history in both grassland and wetland (Chambers 1992; Schmalzer & Hinkle 1992). Prescribed burning of wetlands is now widely practised for wildlife management, the enhancement of stock grazing value, the reduction of fire risk and the control of alien plants (Kotze 1993). In Natal many wetlands are burned (annually, biennially or irregularly), either for the above reasons or simply because they are not specifically protected from fires in the regularly burned grasslands within which they occur.

Wetland fires are basically of two types, surface and subsurface fires, and this study considers only the effects of surface fires i.e. those that do not consume organic soil material or the underground parts of plants. After surface fires wetland plants usually grow rapidly from undamaged underground parts and little physical change in vegetation or soil results (Ellery *et al.* 1989). An important indirect effect of burning is the removal of surface and standing dead plant material, which favours the growth of new vegetation (Kotze 1993).

The overall effect of burning on wetland plant communities is partly dependent on the response of the dominant species to the timing of the burn. Most wetland plants are well adapted to the direct effects of fire but vary in their relative responses, and burning may favour species that die back in winter (Kotze 1993). Of the little quantitative work which has been done on the effects of burning on wetland vegetation, most studies are of plants such as *Typha*, *Phragmites* and *Scirpus* species, or of coastal *Juncus* and *Spartina* marsh communities in temperate regions. In Florida, Vogl (1973) found that a winter burn produced an earlier, more rapid and more productive growth of "wet-prairie" shoreline plants, including *Typha latifolia* and *Panicum* grass. A Canadian study (Mallik & Wein 1986) showed that cover increases in flooded *Typha* after burns in spring, summer and autumn, while in Utah Smith & Kadlec (1985) found that fire had no significant effect on the total annual production of *Typha* and Smith *et al.* (1984) noted that protein increased in *Typha* shoots after fire

treatment. Spring burning enhances the performance of *Phragmites australis* in Canada (Thompson & Shay 1984) and the Netherlands (Mook & van der Toorn 1982), whereas burning during growth results in the death of most shoots (van der Toorn & Mook 1982). In coastal *Juncus* and *Spartina* marshes winter burning in Mississippi increased the net primary production of the aerial portions of the plants (Hackney & de la Cruz 1981) and increased the ratio of live to dead biomass, while in Florida total cover was re-established one year after burning but at least three years would be required to re-establish preburn biomass (Schmalzer *et al.* 1991). In Kansas freshwater wetlands *Spartina pectinata* in annually burned areas had significantly greater aboveground biomass production, inflorescence density and plant height than that in biennially burned wetlands (Johnson & Knapp 1993). No detailed work has been done on the effects of fire on sedges such as *Cyperus*, *Carex* or *Mariscus*, or on complex and species-rich wetland plant communities such as those which exist in Natal, including seasonally flooded sedge meadow and hygrophilous grassland communities.

In Natal, wetland vegetation is usually spring-burned (September–October), with a small amount of winter burning (July–August); autumn burning (May–June) of wetland patches is normally practised only in forestry areas, where the risk of runaway fires increases later in the dry season. Little is known about the relative effects of burning wetland vegetation in autumn, winter and spring, except that the performance of *Phragmites australis* appears to be similar after both spring and autumn burns (Mook & van der Toorn 1982; Thompson & Shay 1985), but it is likely that growth rates will be similar after burns occurring at any time within the vegetation's dormant period, as is the case in Natal Tall Grassveld (Tainton *et al.* 1977; Tainton & Mentis 1984).

The effects of mowing have been studied mainly in saltmarshes and in wetland vegetation dominated by harvestable grasses. In such areas, mowing has been shown to result in a higher plant-species diversity than in unutilized wetland (Kotze 1993). Winter mowing of stands of *Phragmites australis* on wet ground was found to have no damaging effect (van der Toorn & Mook 1982).

The effects of fire on wetland-dependent animals are complex, ranging from direct effects such as increased mortality, forced emigration and reduced reproductive effort to indirect effects such as those resulting from changes in the quality and quantity of food and cover, availability of nest sites, predation pressure and competition (Kotze 1993). Information on the effects of fire on wetland-dependent birds is very limited, being confined largely to direct effects such as the high mortality of Wattled Crane *Bugeranus carunculatus* chicks due to winter burning (Kotze 1993), and those indirect effects involving post-fire improvement of habitat and food availability for cranes and waterfowl. Thus, ducks nesting in Mississippi *Juncus* marshes prefer areas burned at least three years previously (Hackney & de la Cruz 1981), while surface burns of Florida coastal marshes favour waterfowl by producing short vegetation, accelerating the production of food and increasing the availability of food

after the removal of dense growth (Lynch 1941) and the numbers of two crane species feeding in wetlands (in the USA and South Africa) have been seen to increase after fires (Cypert 1961; Kotze 1992a). During four months of observation after a burn at a Florida freshwater pond, Vogl (1973) found that over three times as many birds were recorded on a burned shoreline as on a comparable unburned shoreline, while 30 of the 35 bird species encountered were seen more often along the burned shoreline. These species included the Moorhen *Gallinula chloropus* and the American Purple Gallinule *Porphyrula martinica*, both of which established territories, and possibly nesting sites, more commonly on the burn. This isolated example of the response of rallid species to wetland burning highlights the lack of any information on the effect of fire on the more secretive wetland-dependent rails and crakes. There have been no studies on the effect of burning on the quality of the dense vegetation in areas inhabited by such birds and how this might affect the birds' dispersion, or of the effects of post-burn vegetation growth on the timing of recolonization of breeding territories.

In Natal the Redchested Flufftail is a common and widely distributed, secretive, wetland-dependent species. It is more catholic in its choice of habitats than are other wetland rallids, is not restricted in its range by altitude or climate, and is obviously a very successful generalist in terms of its habitat and food requirements within that part of the wetland biome which comprises dense vegetation not prone to deep permanent flooding (Chapter 5). Therefore it may be expected to be well adapted to the frequent burning which occurs in its wetland habitats, and its complete dependence on wetlands makes it an ideal species on which to study the effects of wetland burning. Like most other flufftail species which I have studied it is permanently territorial in suitable habitat, a characteristic not shared by any other African rallid genus and one which suggests that it should be capable of accommodating large seasonal changes in habitat quality and extent within the framework of its territorial system. Thus its reactions to burning should be of considerable interest, especially as the fate of individual pairs may be monitored over several years (see Chapters 4 and 5).

The principal aim of this part of the study was to investigate the effects of fire on the habitats and dispersion of the Redchested Flufftail in Natal. For this it was necessary to compare the regeneration of different vegetation types after burning, and to relate these to the recolonization patterns shown by the birds at the start of the breeding season. It was hypothesized that, as the most essential requirements of recolonizing birds are shelter and food (and later, nesting sites), the major factors affecting recolonization time are the height and density of the vegetation, the supply of invertebrate food, and the moisture content of the substrate (which itself must affect the vegetation and the food supply). The following topics were investigated.

- (a) Comparative rates of vegetation regrowth after burning (and mowing when possible) in existing occupied areas of various vegetation types, including stands of pure or predominant

*Typha*, *Carex* and *Cyperus/Mariscus*, and of mixed sedge and hygrophilous-grass communities. This included comparisons between rates of growth on substrates of different degrees of saturation, ranging from seasonally moist to permanently flooded, and involved basic measurements of height and cover.

- (b) The effects of burning on the dispersion and territory sizes of the birds. This was intended to show whether biennial burning improves habitat quality to the extent that, after burning, birds can either (i) exist at an increased density, or (ii) utilize more of the available wetland habitat.
- (c) The effects of partial burning as opposed to complete burning in terms of the provision of spring refuges and any improvement in breeding numbers likely to have resulted from a reduced level of forced winter/spring emigration.
- (d) The availability of invertebrate food in burned and mown vegetation and its possible effect on recolonization times.

## 6.2 Study sites

Chapter 2 gives details of the three Natal sites at which the effects of controlled burning were studied: Allerton, Pietermaritzburg (Section 2.2.7), Gartmore, Howick (Section 2.2.5) and Mt Currie Reserve, Kokstad (Section 2.2.13). Allerton and Gartmore are small wetland sites at which only wetland rallids, including Redchested Flufftails, were studied, and comprise wetland patches which are very stable at Allerton and which have well defined maximum limits at Gartmore, such features making it relatively straightforward to calculate territory sizes and available habitat at these sites. Mount Currie Reserve, however, is a large area, comprising principally upland grassland and being the main site for studies of the Striped Flufftail. It has some wetland patches, most of those large enough to accommodate Redchested Flufftails being confined to the low-lying ground of the valley floor at the Reserve's southwestern boundary (Fig. 2.28) and falling within Burning Blocks V1-V4, which cover an area of 109 ha (Table 2.5). This area was established as a study site for the Redchested Flufftail in December 1988 and Fig. 2.32 shows its major features, including the approximate extent of the Redchested Flufftail habitats, both permanently wet and seasonally inundated, which were located along the three major drainage lines and at the intake of Crystal Dam.

### 6.3 Methods

Regular observations of Redchested Flufftails were made at the three study sites throughout the research period, and controlled burning experiments were performed according to the schedules described in Chapter 2. All burns were spring burns, taking place in late August and September, and involved surface fires, only the aerially exposed parts of the wetland plants being burned. Subsurface effects, such as the combustion of both soil material and the subterranean parts of plants, did not occur to an appreciable extent in any burn undertaken during this study. The effects of three burns (1989-1991) were monitored at Gartmore (Section 2.2.5.3) while two (1989 and 1990) were monitored at Allerton (Section 2.2.7.3), where the third year's burn (1991) was uncontrolled and spread to the wrong area. At Mt Currie, observations ran from December 1988 to January 1992 and covered one year with no burn (1988), one with a complete burn of the study area (1989) and two years (1990 and 1991) of controlled partial burns (Section 2.2.13.3). At Allerton and Gartmore the effects of mowing were also observed on an irregular basis.

Vegetation regrowth was measured at all three study sites after one season's spring burn: from October 1989 to January 1990 at Allerton and from October to December 1990 at Gartmore and Mt Currie. Table 6.1 gives details of the vegetation type, defoliation method and soil saturation at each sampling site. Supplementary observations were made at these sites in other years, and if any birds' precise return date after a burn could be established (a rare occurrence) an attempt was made to estimate the height and canopy cover of the newly occupied vegetation. Full details of such observations are given in the Results section and in Table 6.2. Vegetation sampling and measurement were carried out in accordance with the methods described in Chapter 3, Sections 3.6.1-3.6.3.

The populations of Redchested Flufftail at all three sites were censused at least once per month throughout the study period, and territorial mapping was done at intervals of 1-2 months. Both operations were performed more frequently during critical periods, i.e. immediately after a burn, when displaced birds were attempting to re-establish themselves, and early in the breeding season, when birds were reoccupying vegetation which had grown up after burning, mowing, or recent inundation. Censusing and territorial mapping were done as described in Chapter 3, Section 3.4. The results were plotted on territorial maps and were used to assess the effects of habitat management on dispersion, recolonization times, territory size and habitat quality. At all three sites the amount of suitable habitat was assessed according to three criteria: (1) a substrate which was moist to shallowly flooded at least during the rains, (2) the presence of wetland vegetation (sedges, rushes, reeds and hygrophilous grasses) of sufficient height and density to provide cover for the birds, and (3) lack of major disturbance from grazing and trampling, which fragmented and destroyed vegetation cover. The

TABLE 6.1

Vegetation type, defoliation method and soil saturation of the Redchested Flufftail territories in which vegetation regrowth was measured. F/B = firebreak.

Study site	Vegetation type	Defoliation	Soil saturation
Allerton	<i>Cyperus/Mariscus</i>	Burn 13 Sept 89	Dry to moist
		Burn 13 Sept 89	Moist to flooded
		Mown 13 Sept 89	Dry to moist
		None	Moist to flooded
Gartmore	Mixed grass & sedge	Burn 4 Sept 90	Dry to moist
		Burn 4 Sept 90	Moist to flooded
		F/B burn 17 Aug 90	Dry to moist
		None	Dry to flooded
Mt. Currie	<i>Carex acutiformis</i>	Burn 5 Sept 90	Dry to moist
		Burn 5 Sept 90	Moist
		Burn 5 Sept 90	Flooded
	<i>Typha capensis</i>	Burn 5 Sept 90	Moist to flooded

TABLE 6.2

Return dates of Redchested Flufftails to different vegetation types at three study sites following spring burns, 1989-1991. Abbreviations: Cy = *Cyperus*; El = *Eleocharis*; Fu = *Fuirena*; Is = *Isolepis*; Ju = *Juncus*; Ma = *Mariscus*; Py = *Pycreus*; Sc = *Schoenoplectus*. \_ = in summer breeding territories (all others are in permanent territories). Height and canopy cover are mean values (see text).

Study site	Vegetation type	Date of burn	Date return noted	Days after burn	Height (cm)	Canopy cover (%)
MT CURRIE	<u>Carex</u> - moist (2 sites)	5 Sept 1990	23 Oct 1990	48	75	82
	<u>Carex</u> - dry	5 Sept 1990	24 Nov 1990	80	78	72
		4 Sept 1991	25 Nov 1991	82	77	79
	-----					
	<u>Typha</u> - moist/flooded	7 Sept 1989	19 Nov 1989	73	150	60
		5 Sept 1990	24 Nov 1990	80	147	55
	-----					
	Flooded tall sedges: <u>Cy, El, Ju, Ma, Sc</u>	7 Sept 1989	19 Nov 1989	73	90	75
		" "	20 Nov 1989	74	85	70
		4 Sept 1991	25 Nov 1991	82	88	70
	-----					
	Flooded short sedges: <u>El, Fu, Is, Py</u>	7 Sept 1989	25 Nov 1989	79	60	75
	-----					
	Hygrophilous grasses'	7 Sept 1989	17 Dec 1989	101	60	80
		" "	21 Dec 1989	105	65	80
	-----					
ALLERTON	Flooded sedges: <u>Cy, Ma</u>	13 Sept 1989	2 Dec 1989	80	136	72
	Dry to moist <u>Cyperus</u>	21 Aug 1990	24 Dec 1990	125	129	68
	-----					
GARTMORE	Flooded sedges & hygrophilous grasses	28 Sept 1989	15 Dec 1989	78	56	65
		4 Sept 1990	23 Nov 1990	80	56	64
	-----					

structure, height and density required to render any vegetation potentially suitable for occupation were usually first assessed subjectively, on the basis of measurements and observations made both during this study and in many vegetation types throughout eastern, central and southern Africa from 1974 to 1986. Observations of colour-ringed birds at Allerton, and the identification of other birds (at all sites) by their regular use of distinctive variants of common calls, showed that at least some of the birds at all three sites were resident throughout the study period (Chapter 4). Each such individual was always found within its original territory area, to which it returned if burning forced temporary emigration (see Chapter 4).

No satisfactory method was found for accurately sampling the invertebrate populations of dense wetland vegetation (see Chapter 3, Section 3.7.2, for a discussion of the problems involved), but samples were taken at Allerton on two occasions in October 1989, after the mid-September burn and before vegetation growth made sampling impossible. The sampling method used was that employed in grassland, i.e. visual sampling by direct counting of invertebrates within randomly positioned 50-cm-square quadrats (see Chapter 3, Section 3.7.1). Counts of 20 quadrats were attempted at each sampling site (Table 6.1) but the impenetrable, dense, moribund vegetation of the unburned site made sampling impossible, while on the second sampling visit it was found that the invertebrates in the wet burned vegetation were too numerous to count accurately, so sampling was discontinued after this visit.

## 6.4 Results

### 6.4.1 The effects of burning and mowing on vegetation regrowth and recolonization times

All sampling techniques except the light-meter method (Chapter 3, Section 3.6.3.1) yielded acceptable results. The logarithmic scale of the light-meter resulted in less accuracy in the brightest conditions, when more frequent and larger errors were obtained, and results were not always comparable over the sampling period. To obtain acceptable results with this method would have required ideally a very large number of readings in each sample, constant incident light throughout each sampling session and an incident light of approximately the same intensity on each sampling visit. The other sampling techniques gave sufficient indication of vegetation development, and it was concluded that the light-meter method would be of the most practical value in measuring differences between vegetation types at the same time, rather than over a period of months.

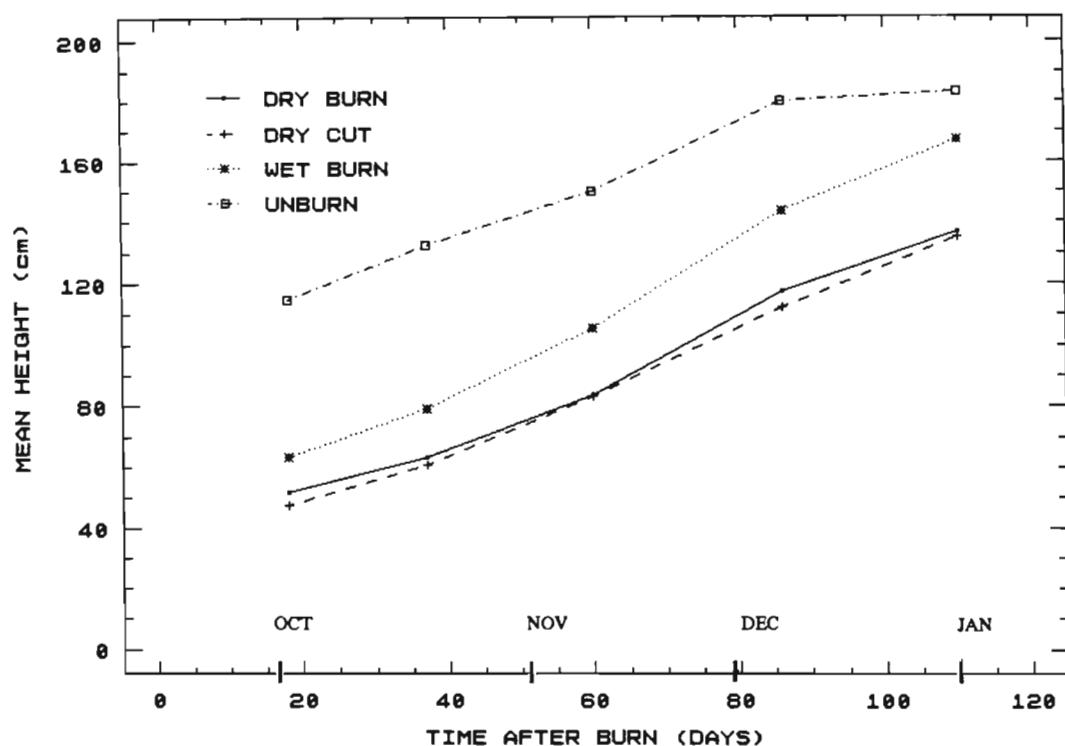
Sampling results for the three sites are summarized graphically in Figs 6.1-6.8. Standard errors of the means are not shown on these graphs because their values are very small (between 0,42 and 3,03) for all types of measurement made at the sites. On all graphs the differences between any month's means for different substrate saturations or defoliation types are usually greater by an order of magnitude than the variations in height or cover within an individual sample, as is obvious from the wide separation of most growth curves.

#### 6.4.1.1 Allerton, Pietermaritzburg

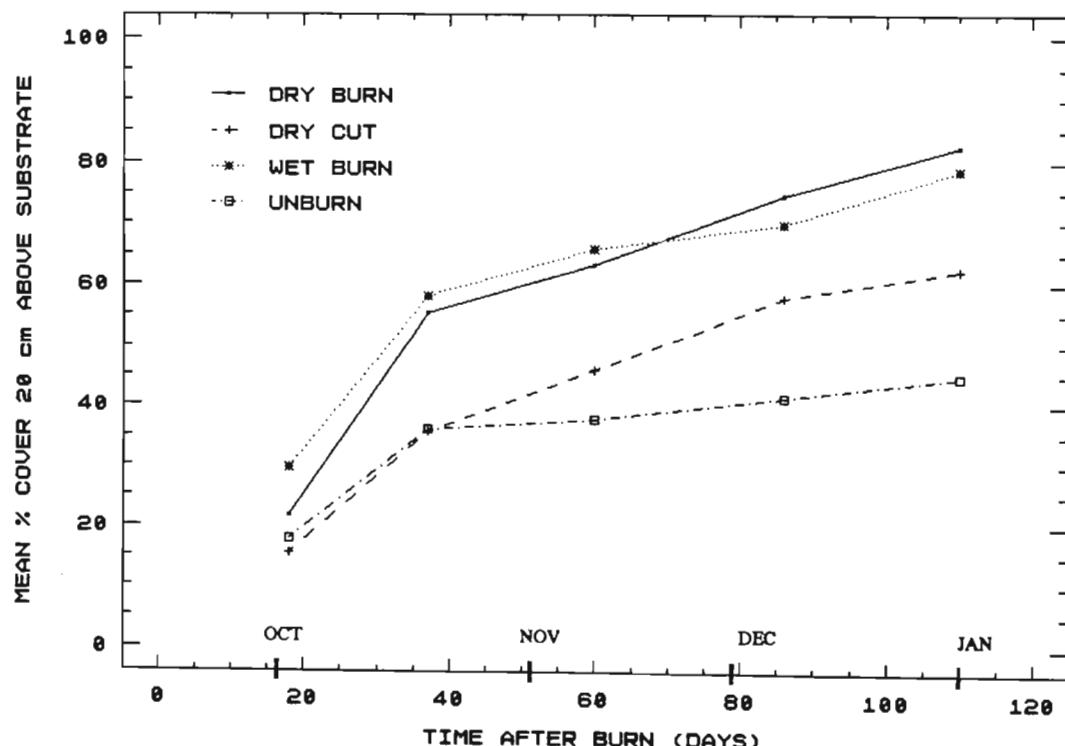
The burn on 13 September 1989 (Fig. 6.16) was slow and thorough, resulting in the almost complete removal of aerial vegetation from both wet and dry areas. Vegetation on the firebreak was cut to a height of 5-10 cm immediately before the burn and was largely unaffected by the fire. Vegetation sampling began on the 18th day after the fire (1 October) and ended on Day 110 (8 January 1990). The total rainfall for this period was very close to the long-term mean but rainfall timing was irregular, twice the mean falling in November and about half the mean in October and December (Fig. 2.13B).

Results are summarized graphically in Figs 6.1-6.3. Measurements were made only in Reedbed 3, in areas dominated by the tall sedges *Cyperus dives* and *Mariscus solidus*, which both showed a similar overall size, structure and growth pattern at this site. The unburned vegetation sampling site was on wet ground. Although two of the sampling sites were dry at the beginning of the sampling period, after the heavy rain in November all sites were moist to flooded (Table 6.1). By Day 18 there was already considerable regrowth at all sites and growth continued throughout the sampling period. At all sites cover increased most rapidly during the early growth period in October (Fig. 6.2) while height increased most rapidly in November and December (Fig. 6.1), during which period recolonization by rallid species occurred. The sedges came into flower from late December and on 8 January 1990 the percentage of plants in flower at the four sites was estimated as: dry burn 90%, dry cut 80%, wet burn 10% (flowering was just beginning) and unburn 1%. Less than 5% of the unburned plants flowered during this summer.

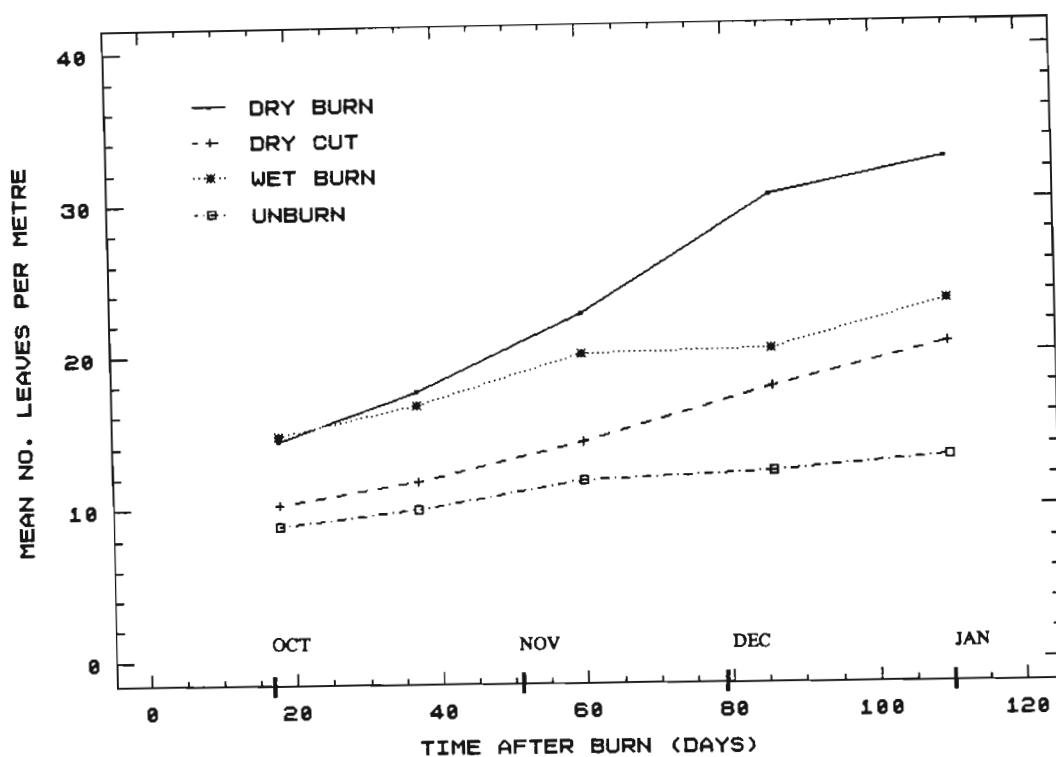
Because of the thoroughness of the burn no old growth remained in the sampling area and measurements refer entirely to new growth. On the burn (Fig. 6.1) the vegetation at the wet site averaged 22-26% taller than that at the dry site, which maintained a similar mean height to the dry cut vegetation throughout the sampling period, reaching 135 cm on Day 110 compared with 167 cm at the wet site. The unburned vegetation was always the tallest type, averaging 115 cm tall on Day 18 and 183 cm on Day 110. The percentage cover, measured 20 cm above the substrate, was similar



**Fig. 6.1** Growth (mean height) of burned and cut *Cyperus dives* and *Mariscus solidus* sedge beds on different substrates at Allerton after the burn and cut on 13 September 1989. The unburned sampling site was on wet ground.



**Fig. 6.2** Growth (mean percentage cover) of burned and cut *Cyperus dives* and *Mariscus solidus* sedge beds on different substrates at Allerton after the burn and cut on 13 September 1989. The unburned sampling site was on wet ground.



**Fig. 6.3** Growth (mean no. of leaves per metre) of burned and cut *Cyperus dives* and *Mariscus solidus* sedge beds on different substrates at Allerton after the burn and cut on 13 September 1989. The unburned sampling site was on wet ground.

in both wet- and dry-burned vegetation, the wet burn averaging slightly denser early in the season, but the situation was reversed after the onset of the good November rains (Fig. 6.2). The unburned sedges, growing through the dense mat of dead vegetation, achieved an early cover development similar to that of the dry-cut sedges but, from mid-October, very little extra cover was developed (Fig. 6.2). Measurements of the number of leaves per metre (Fig. 6.3) confirm the relative lack of growth in the unburned area, where very few new leaves were produced after the initial early spring growth. Leaf production was somewhat higher in the dry-cut vegetation, continuing throughout the sampling period, while the wet-burn vegetation produced most leaves in early spring and relatively few from November onwards and the dry burn produced leaves at the greatest rate during the period of best rainfall in November.

The measured growth patterns confirmed my subjective observations of vegetation development over the whole site. In areas with much moribund plant material the sedges grew and flowered very poorly, producing little new cover, despite their growth being allowed to proceed uninterrupted throughout the spring and summer; the most obvious effect of the lack of a spring burn was the development of taller vegetation. The densest new cover was produced by sedges which had been burned, whether the substrate was dry or wet at the start of the season, but plants on ground which was wet in the spring produced the tallest vegetation. The most leaves were produced by burned plants on ground which progressed from being dry to moist during the summer (the overall density of plants in both wet and dry patches was similar) and in January these plants gave the densest cover. Leaves in dry areas tended to be more numerous, and thinner (not measured), than those in wetter conditions. Almost complete flowering was seen in burned and cut sedges, plants on wet ground flowering later than those in drier areas.

These results show that both spring burning and cutting stimulated good growth in these sedges, burning somewhat more so than cutting, the best growth being in moist to shallowly flooded conditions. Prolonged use of the regenerating vegetation by rallids was first noted on 12 November 1989 (Day 60), when both African Rails *Rallus caerulescens* and Black Crakes *Amaurornis flavirostris* foraged for periods of over one hour in the wettest new growth but returned across the firebreak to shelter in unburned vegetation. By 15 November (Day 63) they were continually present in new growth averaging 109 cm tall with 67% cover (Figs 6.1 and 6.2). The Redchested Flufftails reoccupied the burned area only on 2 December (Day 80) when the cover, at 72%, had increased relatively little but the mean height had risen to 136 cm (Figs 6.1 and 6.2). In 1990, moist *Cyperus* at Reedbed 5 was occupied on 24 December, 125 days after the burn, when cover and height were similar to those attained by the flooded burned vegetation when reoccupied in early December 1989 (Table 6.2).

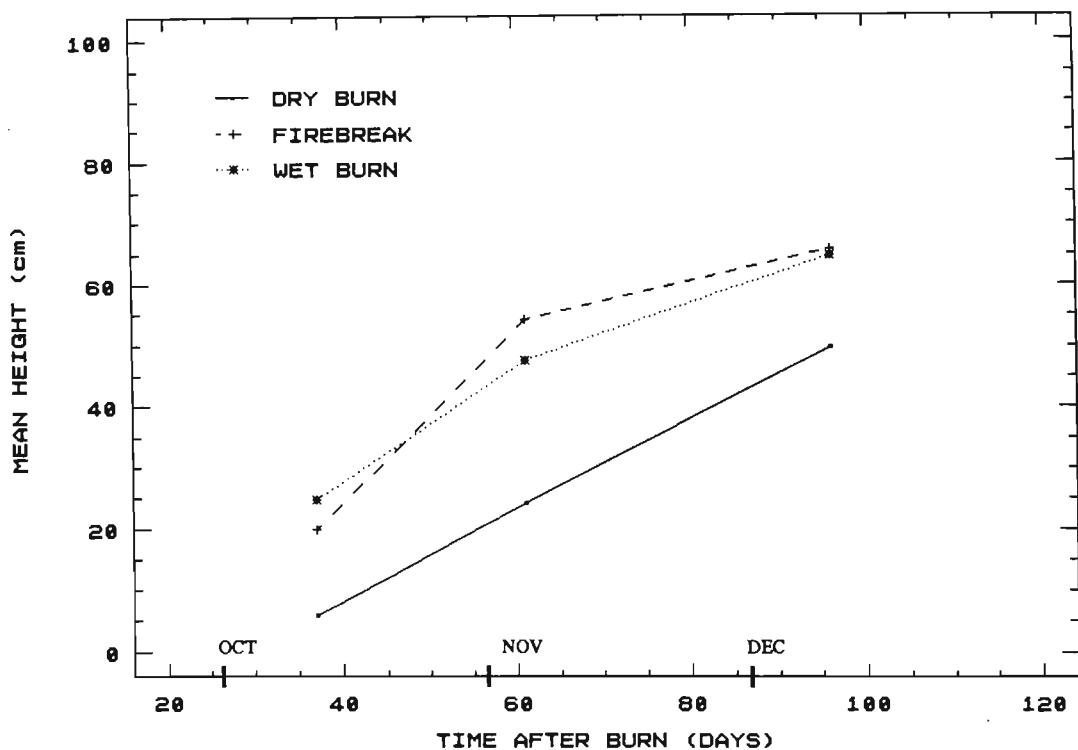
#### 6.4.1.2 Gartmore, Howick

The burn on 4 September 1990 was fast and cool, taking place after a 12-day period in which over 50 mm of rain fell. Much tussocky and other dense vegetation was burned down to about 20 cm above the ground, allowing small animals to shelter within it and leaving patches of ground cover intact. The firebreak (on predominantly wet substrate) had been burned 18 days previously (Table 6.1) and on the day of the burn it showed some new growth, which was not tall enough to increase the overall height above that of the burned vegetation remnants. Sampling began on the 37th day after the fire (11 October) and ended on 9 December (Day 96). During this period the rainfall was variable, being average in October, low in November and very high in December (Fig. 2.8A).

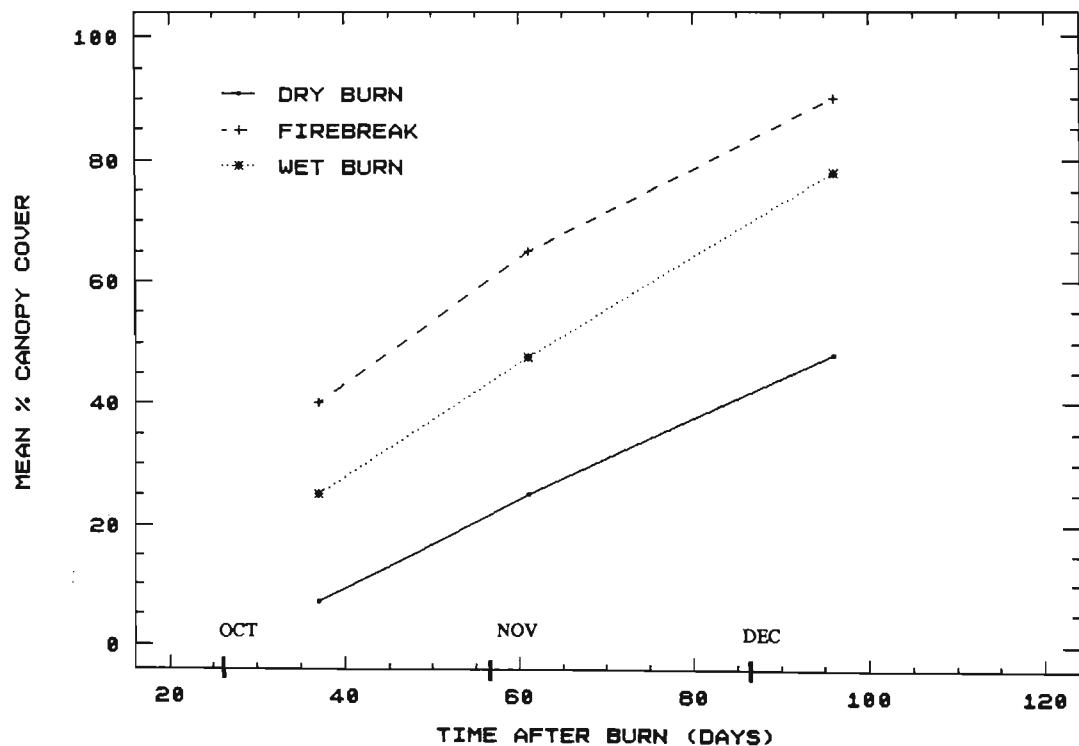
Results are summarized in Figs 6.4 and 6.5. Measurements were made in areas of mixed sedge and hygrophilous grass on ground where more or less all aerial cover had been removed by the burn, and on Day 37 were made in all the four vegetation types specified in Table 6.1. However after this it was found that the unburned vegetation developed too patchily and variably to give consistent results, the taller tussocks showing a much greater growth than the more open areas, which became flattened by rain and Reedbuck *Redunca arundinum*, grew poorly and became extensively flooded in December. By the end of the sampling period all sampling sites were moist, some being shallowly flooded in patches.

Vegetation regrowth in September was most marked on the firebreak and the wet burn, which showed similar mean heights throughout the period (Fig. 6.4). The driest area began growing noticeably only from early October and, although having the greatest height development in November-December (when it became moist), it had attained a mean height of only 49.8 cm by Day 96, 76% of the 65.9 cm attained on the firebreak. Overall vegetation cover developed at similar rates on all burned sites throughout the sampling period (Fig. 6.5), the firebreak always having more cover than the wet burn and the initially dry vegetation attaining only 48% cover at the end of the sampling period, when the firebreak had 90% cover. On Day 37 the unburned vegetation averaged a 5% cover of new growth in flattened sedges such as *Eleocharis*, 30% in tussocky patches and up to 80% in a few small areas of unflattened level grassy vegetation; the overall new cover was poor.

Thus the firebreak vegetation, burned in mid-August, achieved the best overall growth, while the driest areas never produced very dense cover. The firebreak was too narrow a strip to accommodate Redchested Flufftails and the birds' first return to the burned section was in the wet burn on 23 November (Day 80), when vegetation height averaged 56 cm and cover 64% (Figs. 6.4 and 6.5); this was a territorial extension of Pair 6 from the unburned southern block (see Fig. 6.26 for territorial maps). Before this date, birds from unburned territories 5 and 6 had been venturing



**Fig. 6.4** Growth (mean height) of mixed sedge and hygrophilous grassland at Gartmore after the burn on 4 September 1990. The firebreak was on predominantly wet ground.



**Fig. 6.5** Growth (mean % canopy cover) of mixed sedge and hygrophilous grassland at Gartmore after the burn on 4 September 1990. The firebreak was on predominantly wet ground.

occasionally into adjacent firebreak vegetation for about three weeks, i.e. after the firebreak had attained a similar overall height and cover to that in the wet area at the time of reoccupation.

These results, although few, show that, in mixed sedges and hygrophilous grassland, vegetation growth after a burn was greatest if the vegetation were burned slightly earlier than normal, i.e. in mid-August rather than in September. As at Allerton, the greatest growth was noted in moist or wet areas.

Comparative observations at Gartmore in other seasons confirmed these results and impressions. In 1989 a hot and thorough burn took place on 28 September and 60% of the burned area was green after seven days, shoots averaging 6 cm in height. Rainfall in October was normal but was very high in November and December and the first reoccupation of burned ground was on 15 December 1989 (Day 78), in wet vegetation averaging 56 cm high and having 65% mean cover: almost exactly the same measurements as those obtained in 1990. In 1991 the burn took place on 4 September, October rainfall was more than twice the mean (Fig. 2.8B), resulting in extensive temporary flooding, and the vegetation developed well, the mean height and cover in a wet burned area on 25 October (Day 51) being estimated at 51 cm and 65% respectively (compared with about 35 cm and 40% at the same time in 1990). No birds had permanently reoccupied the burn on this date, although adjacent pairs were very close to the burned area (the earliest return date was not established in 1991).

The mowing of part of the northern study block at Gartmore in mid-October 1989 (Fig. 6.23; Chapter 2, Section 2.2.5.3) took place about 2½ weeks after the burn of the southern study block, and covered an area of predominantly hygrophilous grassland which is dry in winter. Although precise return dates could not be established, the two territories in the mown area were reoccupied in early January 1990 (Fig. 6.24), 2½ months after the mowing and at about the same time as those burned southern territories which showed similar vegetation development. In the following season, one of the northern territories was reoccupied in December, about 3.3 months after the burn, the other in January (Fig. 6.26). Although vegetation measurements were not made, it was noted that the vegetation in the December-occupied territory provided tall dense cover at least four weeks earlier than in adjacent areas, principally because it contained a large proportion of exotic brambles, which grew more rapidly than the surrounding grasses and provided good impenetrable cover at canopy level despite being quite open at ground level.

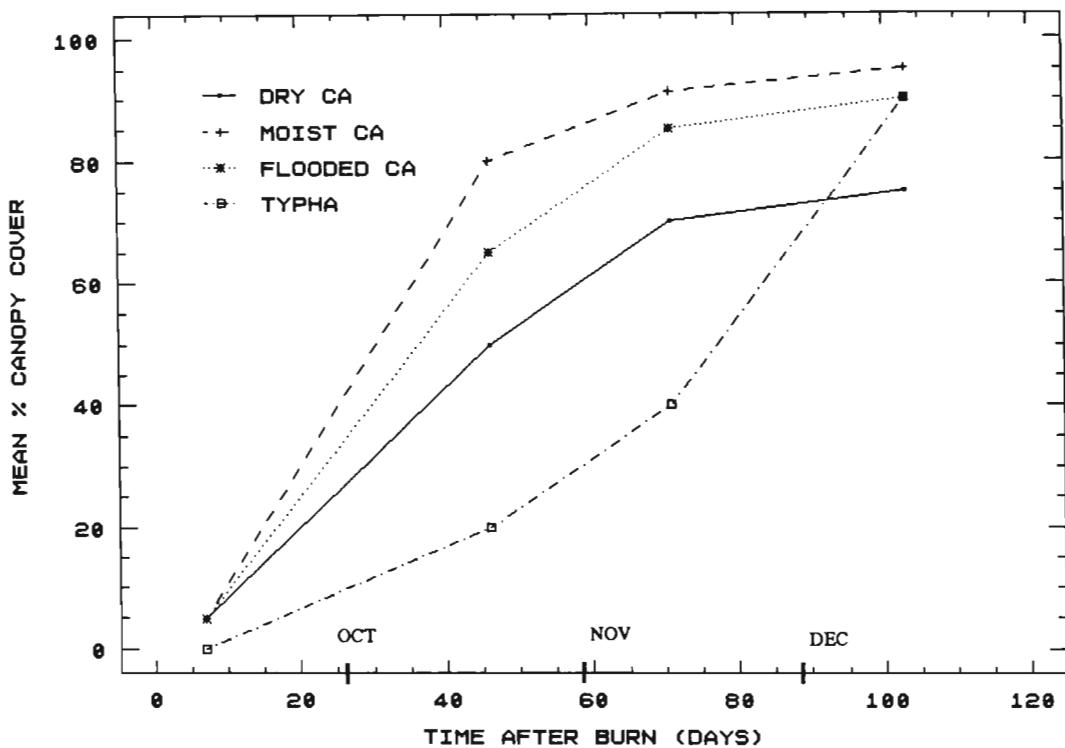
## 6.4.1.3

## Mt Currie, Kokstad

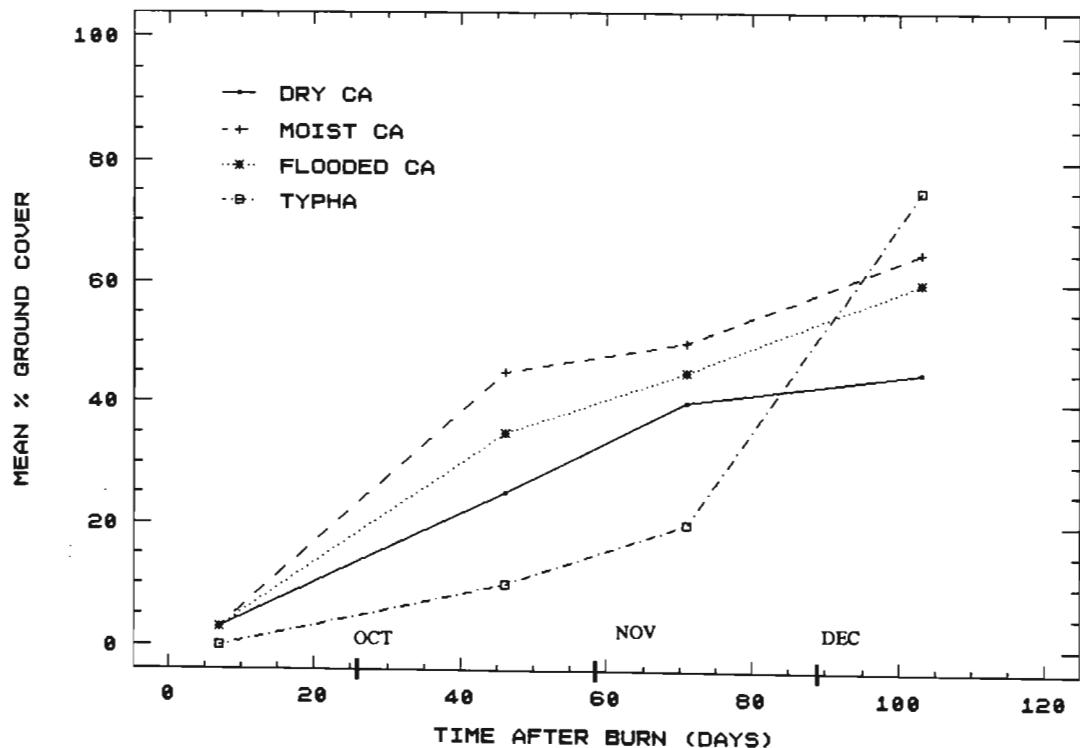
The burn on 5 September 1990 was hot and rapid, burning down to the ground in dry areas but only burning down to 15-20 cm above the surface in *Carex* on ground which was either moist or flooded to a depth of 5 cm. The burn removed virtually all stems of *Typha* from wet ground, the aerial parts of these plants being dead. (Much of the *Carex* remains green at the base of the leaves throughout the winter, even though it may die at the tips, and it may also produce some new growth at low levels in August-September, in contrast to *Typha* and *Phragmites*, the aerial parts of which die back completely during the winter.) Observations began on 12 September, 7 days after the burn, and ended on Day 103 (17 December 1990). The total rainfall for this period was somewhat below the mean, being very low in September and November (Fig. 2.31A).

Results are summarized in Figs. 6.6-6.8. Measurements were made in two vegetation types: pure *Carex acutiformis* and almost pure *Typha capensis* (Table 6.1). The two driest sites, lying on relatively well drained ground near a sunken stream channel, remained only moist during the sampling period. The unburned *Carex* stems accounted for the small amount of cover and the mean heights recorded on Day 7, when the *Typha* sampling site was virtually bare (Figs 6.6 and 6.7). The *Carex* in the dry area remained lower and less dense than that in the moist and wet areas throughout the sampling period, the greatest height and cover being attained by the plants on moist ground and the wettest vegetation being almost as tall but developing cover intermediate between that on the moist and dry substrates (Figs. 6.6-6.8). At the end of the sampling period the tallest (moist) vegetation averaged 97,4 cm in height with 95% canopy cover, and the shortest (dry) vegetation 85,4 cm and 75%. In the flooded area, comparable figures were 95,1 cm height and 90% canopy cover and it was noted that the leaves of the moist-substrate *Carex* plants were more folded back at the tips than those of the slightly less developed plants in flooded areas, this contributing to the greater canopy cover in the moist vegetation. The ground cover, measured 5 cm above the substrate, (Fig. 6.7) was considerably less than that at the canopy, reaching 60-65% in moist to flooded areas and only 45% at the dry site. Thus, although the vegetation was almost completely closed at canopy level, much open space remained at ground level in all areas. The growth rate at all three sampling sites was greatest in September-October and decreased in November-December except at ground level, where an increased growth rate was noted in the final month at the moist and wet sites and the greatest growth rate was in October-November at the dry site (Fig. 6.7). On 17 December (Day 103) the first flowers were visible on plants in the wettest areas.

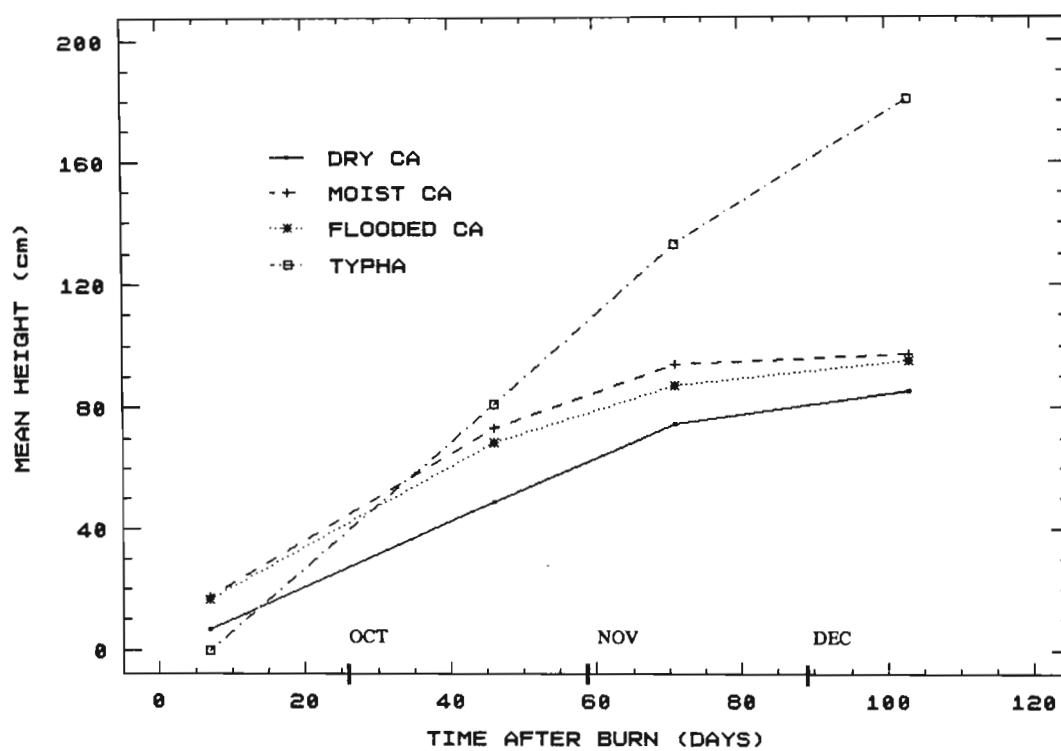
Growth and flowering patterns in other situations were observed in October-December 1991, during which period the rainfall was well above the mean (Fig. 2.31B). The sampling site was not



**Fig. 6.6** Growth (mean % canopy cover) of burned *Carex acutiformis* and *Typha capensis* beds on different substrates at Mt Currie after the burn on 5 September 1990.



**Fig. 6.7** Growth (mean % ground cover) of burned *Carex acutiformis* and *Typha capensis* beds on different substrates at Mt Currie after the burn on 5 September 1990.



**Fig. 6.8** Growth (mean height) of burned *Carex acutiformis* and *Typha capensis* beds on different substrates at Mt Currie after the burn on 5 September 1990.

burned, and thus retained good cover throughout the winter, although the distal parts of most *Carex* leaves were dead by July. On 1 October there was 100% canopy cover in the wettest unburned *Carex* beds, about 80% of this being provided by dead vegetation and the rest being new growth, while only 15-20% of the growing plants were flowering. On flooded ground which was burned for a firebreak about 25 July (68 days previously), the *Carex* averaged 40 cm in height with 40% canopy cover (i.e. less than half-grown) and was almost all in flower. In contrast, in a nearby wet area burned on 4 September (27 days previously), the *Carex* averaged 35 cm tall with only 20% canopy cover and no flowers: these plants began flowering in mid-December, as in 1990. By 25 November growth in the unburned vegetation had improved and almost all the plants were flowering, while the flooded *Carex* at the firebreak was tall and had almost finished flowering. Near Crystal Dam small beds of *Carex austroafricana* were burned for a firebreak on 24 July; on 4 October (Day 72) they averaged 52 cm in height with 25% canopy cover, and 80% of the plants were flowering.

The increase in height of the *Typha* followed a similar pattern to that of the *Carex* at the sampling site in 1990 (Fig. 6.8), with a decreased growth rate in the last month; this vegetation grew rapidly and attained a mean height of 158 cm on Day 103. The pattern of increase shown by cover measurements, however, differed from that in the *Carex* (Figs 6.6 and 6.7), the *Typha* showing an increasing rate of cover development with time as the upper leaves grew longer and broader and more leaves and shoots developed at lower levels. At the end of the sampling period the *Typha* had the densest ground cover (75%) and a canopy cover equivalent to that in the flooded *Carex*. Both burned and unburned *Typha* beds were coming into flower in late December and early January, the seedheads were ripe in March and almost all the aerial growth was dead by the end of April.

These measurements again confirmed my subjective assessment of the growth pattern of both vegetation types, both at Mt Currie and elsewhere. The densest, tallest monospecific growths of *Carex* were associated with moist conditions rather than with deeply flooded or very dry substrates, while burned pure *Typha* provided poor cover early in the growing season but developed good tall, dense cover by mid-December. In contrast to the situation observed in *Cyperus* and *Mariscus* sedges at Allerton, where unburned sedges flowered poorly and the wet burned sedges flowered later than those on drier ground, the unburned *Carex* at Mt Currie was flowering well by late November, while the wet burned plants flowered in mid-December, somewhat earlier than those on drier ground.

All precise return dates of Redchested Flufftails to burned vegetation at Mt Currie are given in Table 6.2. In late 1990 the birds returned first to moist *Carex* on Day 48, when a mean height of 75 cm and a mean canopy cover of 82% had been attained, but were not found until Day 80 in dry vegetation with corresponding means of 78 cm and 72%. The precise date when the flooded *Carex* was reoccupied could not be determined but was 70-80 days after the burn. The first return to *Typha*

at the sampling site was noted on Day 80, when this vegetation had a mean height of 147 cm and canopy cover of 55%, while in 1989 a return after 73 days was noted in *Typha* of similar height and density (Table 6.2). Occupation of flooded mixed-species sedge beds, both in permanent and summer territories, was also noted after a similar period (73-82 days), these observations agreeing well with those of the reoccupation of wet sedge beds at both Allerton (80 days) and Gartmore (78-80 days). In contrast, seasonally flooded summer territories of virtually pure hygrophilous grassland were not occupied until much later (101-105 days after the burn in late 1989); in these areas the vegetation was relatively short but the cover dense (Table 6.2).

#### **6.4.1.4 Relationships between return time and habitat variables**

Statistical analyses were done to determine the relationships between the observed return times and the major habitat characteristics of the reoccupied territories. The habitat variables used in these tests are described in Table 6.3, and the results of the analyses are tabulated in Table 6.4. In view of the limited number of observations of recolonization times the analysis variables were made as few as possible, so they are of necessity broad subdivisions which do not fully reflect the complexity of the wetland vegetation and substrate conditions.

Using the 16 precisely recorded return dates (Table 6.2), a multifactor analysis of variance (MANOVA 1) was done to investigate the effects of three different vegetation types, two substrate saturations, and vegetation height and cover, as shown in Table 6.3. The first two groups were entered as factors and the height and cover variables as covariates. All variables had a significant effect on the return date ( $P < 0,05$  in all cases). The return dates were significantly different for each of the three vegetation types (Fig. 6.9), the mean date for return to short continuous vegetation being 7 weeks after the burn (day 49), to tall sparse vegetation a month later (day 83) and to short tussocky vegetation after a further three weeks (day 105). The dates were also significantly different for the two saturation types (Fig. 6.10), averaging 65 days in moist to flooded conditions and four weeks later (day 94) in initially dry conditions.

A stepwise regression on return date as a function of these variables revealed confounding effects between the variables, as is to be expected in such a complex system. A regression model (Model 1) was constructed on the basis of cover and substrate saturation, which together accounted for most of the variance ( $R^2 = 60\%$ ). This model provides a good explanation of the observed effects ( $P = 0,01$ ; standard error of estimate = 11,87 days) and may be expressed as follows:

TABLE 6.3

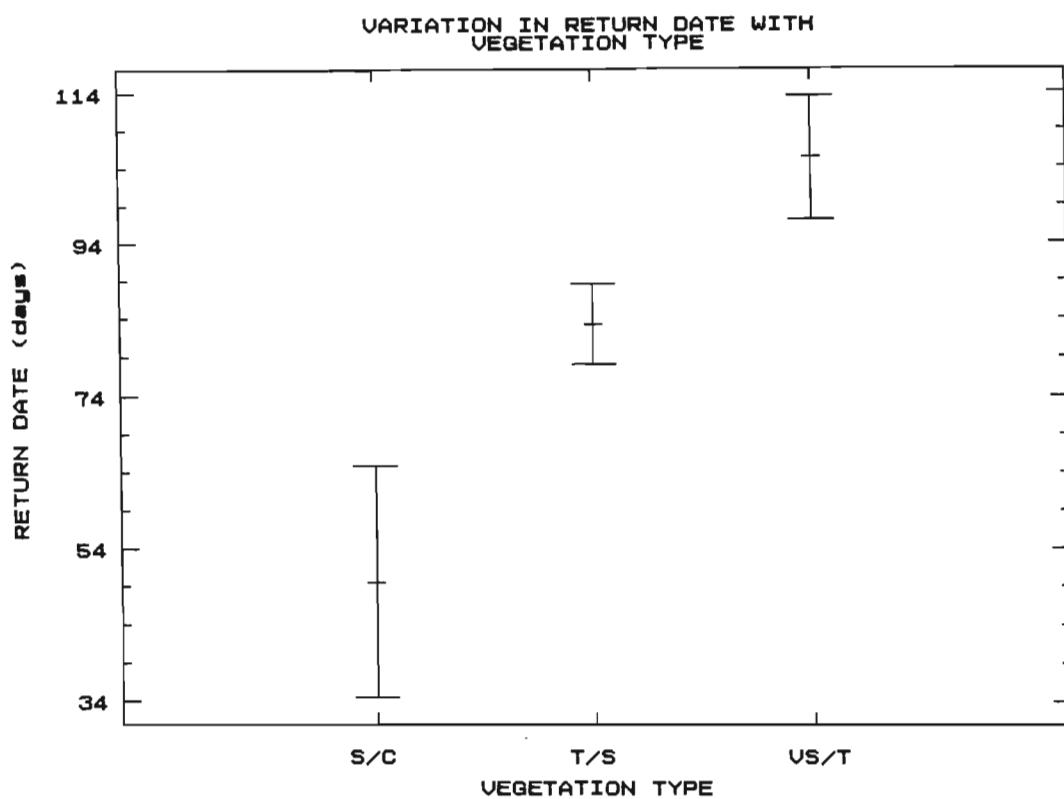
Definitions of vegetation types and substrate-saturation factors recorded in Redchested Flufftail territories, and the statistical analyses in which they were used to investigate the relationship between return time after burning and habitat variables. See text for details of the analyses used. R Model = Regression Model; Sat. = Saturation; Veg. = Vegetation; X = used in analysis. Saturation Factors (a) and (b), used in MANOVA 2, R Model 2 and ANOVA, are subdivisions of Saturation Factor M/F, which was used in the MANOVA 1 and R Model 1 analyses.

Habitat variable	Description	Analysis				ANOVA
		MANOVA		R Model		
		1	2	1	2	
<u>Veg. Types</u>						
T/S	Tall, relatively sparse cover, dominated by <i>Typha</i> .	X	X	X	X	X
S/C	Short continuous cover, such as that dominated by <i>Carex</i> , <i>Cyperus</i> or <i>Mariscus</i> .	X	X	X	X	X
VS/T	Very short, tussocky or continuous cover, such as sedge meadow and hygrophilous grassland.	X	X	X	X	X
<u>Sat. Factors</u>						
D/M	Dry, becoming moist during the summer.	X	X	X	X	
M/F	Permanently moist to flooded. (Includes both types PM/SF and PF below).	X		X		
(a) PM/SF	Moist to seasonally flooded.		X	X	X	
(b) PF	Permanently saturated or flooded.		X	X	X	
<u>Veg. height</u>						
Canopy cover		X		X		

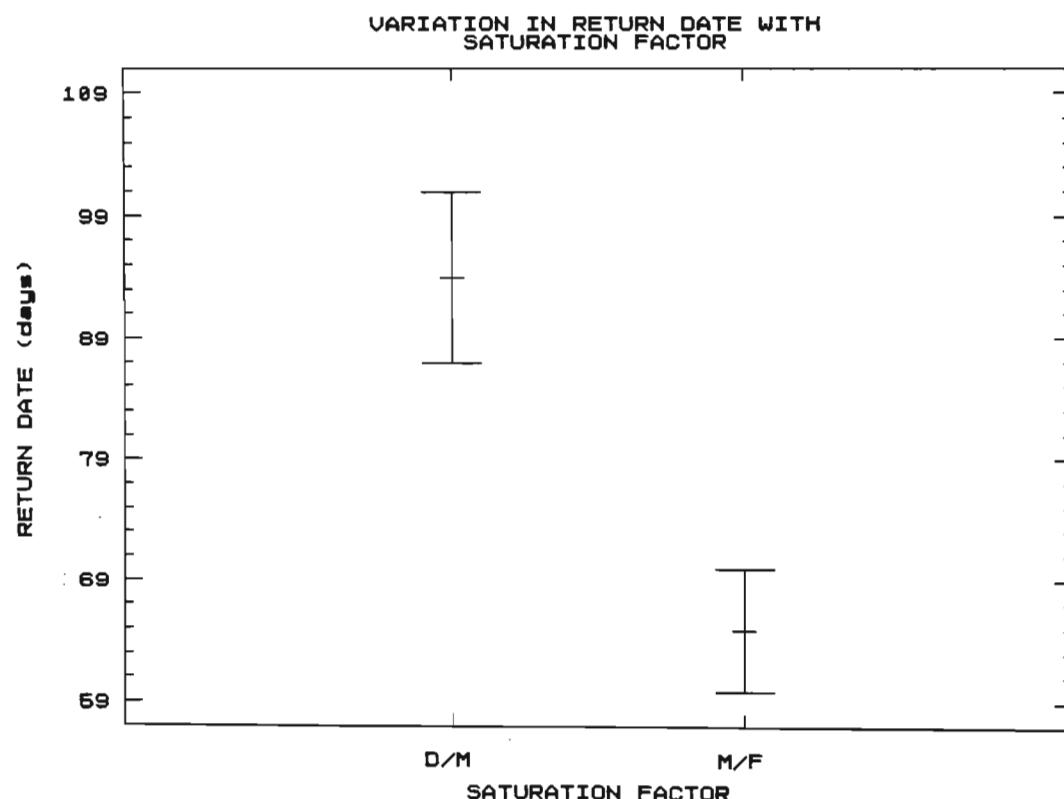
TABLE 6.4

Mean return dates ( $\pm$  1SE), expressed as days after the burn, of Redchested Flufftails to different vegetation types and soil saturations, as predicted by the analyses described in Section 6.4.1.4. For definitions of the variables used, see Table 6.3. R Model = Regression Model; Sat. = Saturation; Veg. = Vegetation; <sup>1</sup> = assuming 65% canopy cover; <sup>2</sup> = see Table 6.5 for a breakdown of return times by unique combinations of vegetation type and saturation factor.

Habitat variable	<u>Predicted mean return date (days) from each analysis</u>				
	MANOVA 1	MANOVA 2	R Model 1	R Model 2	ANOVA <sup>2</sup>
<b>Veg. Types</b>					
T/S	83 $\pm$ 3	94 $\pm$ 5	-	-	75 $\pm$ 1
S/C	49 $\pm$ 10	100 $\pm$ 7	-	-	67-94 $\pm$ 4-8
VS/T	105 $\pm$ 5	112 $\pm$ 4	-	138 $\pm$ 14	86-114 $\pm$ 5-3
<b>Sat. Factors</b>					
D/M	94 $\pm$ 5	128 $\pm$ 10	110 $\pm$ 12 <sup>1</sup>	104 $\pm$ 14	-
M/F	65 $\pm$ 3	-	77 $\pm$ 12 <sup>1</sup>	-	-
PM/SF	-	104 $\pm$ 4	-	97 $\pm$ 14	94-114 $\pm$ 8-3
PF	-	76 $\pm$ 3	-	69 $\pm$ 14	67-86 $\pm$ 4-5



**Fig. 6.9** Variation in return date with vegetation type (multifactor analysis of variance; means and 95% confidence limits: MANOVA 1 - see text), for precisely-dated returns to burned vegetation.



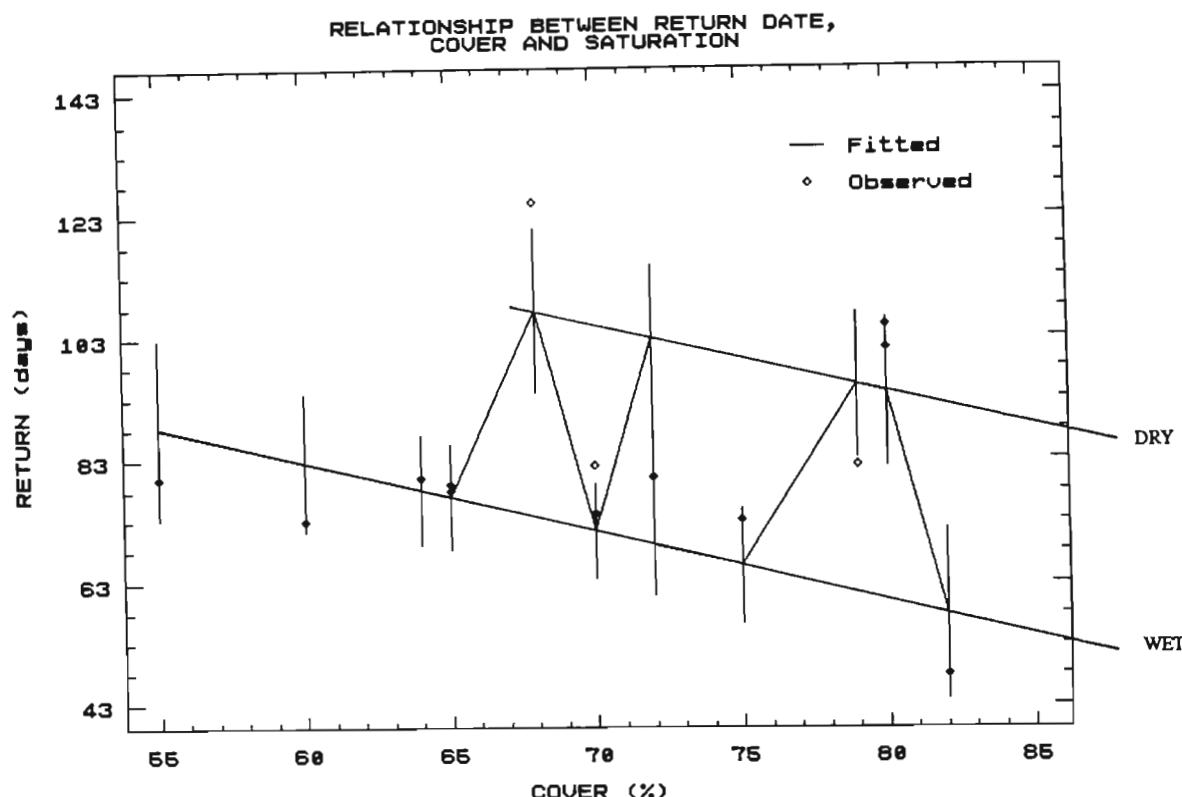
**Fig. 6.10** Variation in return date with substrate saturation factor (means and 95% confidence limits: MANOVA 1 - see text), for precisely-dated returns to burned vegetation.

Return after the burn = 150,16 days  
 less 1,127 days for every 1% of canopy cover  
 plus 33 days if substrate is dry initially. .... **Model 1**

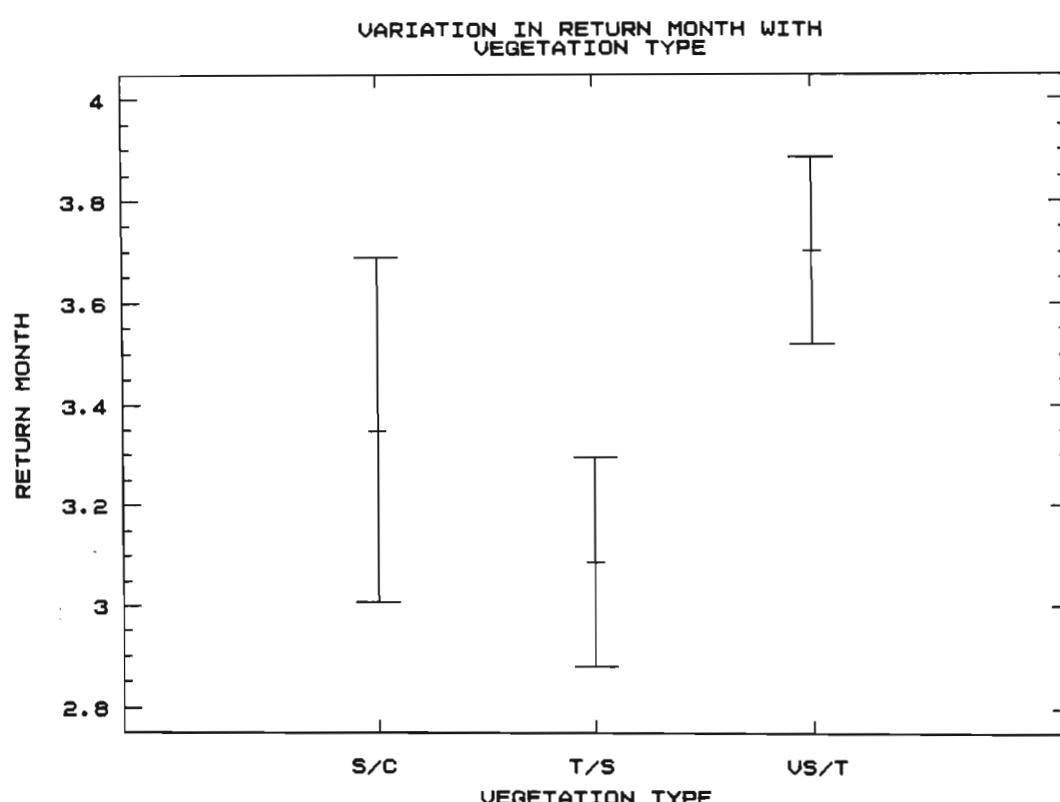
Thus in any vegetation type early return is dependent on the development of good cover, while the average return date to seasonally moist habitat should be 33 days later than to permanently moist or flooded habitat. These effects are shown in Fig. 6.11, which is an interval plot of the relationship between return date, cover and saturation. It is clear from Table 6.2 and other observations that birds do not return to wetland vegetation if the cover is less than 55% (it was usually over 65%), so that estimates for cover of less than 55% may be disregarded. The model predicts, for example, that in initially dry conditions at 68% canopy cover return should take place after about 101 days ( $\pm$  12 days), and thus that the return date of 125 days under these conditions at Allerton in 1990 (Table 6.2) is exceptional. This observation was flagged as influential, and the late return probably resulted from factors such as prolonged early-season dryness and slow development of vegetation height. An observation from Mt Currie in dry *Carex* in September 1990 (Table 6.2), was flagged as an outlier, the return at day 80 to 72% cover lying outside the predicted range for both substrate types at this cover level. This also suggests that the relatively early development of vegetation height in that season may have been responsible for the early return date.

Although there were great practical difficulties in establishing the precise return date to any territory, the regular census and mapping work always gave the month in which the birds returned after a burn, while sometimes a return could be estimated to within 3-15 days. All such returns were recorded as a fraction (0,1-0,5) of the month, 63 such observations being made at the three study sites. Measurements of vegetation cover and height at the time of the birds' discovery were not made in this situation, because the vegetation often developed considerably during the estimated period. The variables measured were vegetation type and substrate saturation, the latter being split into three categories instead of the previous two (Table 6.3). Five vegetation types were initially defined, in terms of the dominant plant species present, but exploratory analysis produced considerable overlap in return periods and the original three types were found to be the most effective for analysis purposes. It was clear that the overall structure of the vegetation was more significant than were the plant species involved.

A multifactor analysis of variance (MANOVA 2) on these variables (defined in Table 6.3) showed that both variables had a highly significant effect on the return date ( $P < 0,001$  in both cases). For the three vegetation types two homogeneous groups emerged from the analysis, there being a significant difference in return time between the tallest and shortest vegetation types, T/S and



**Fig. 6.11** Interval plot of the relationship between return date (days after the burn) and substrate saturation (MANOVA 1).

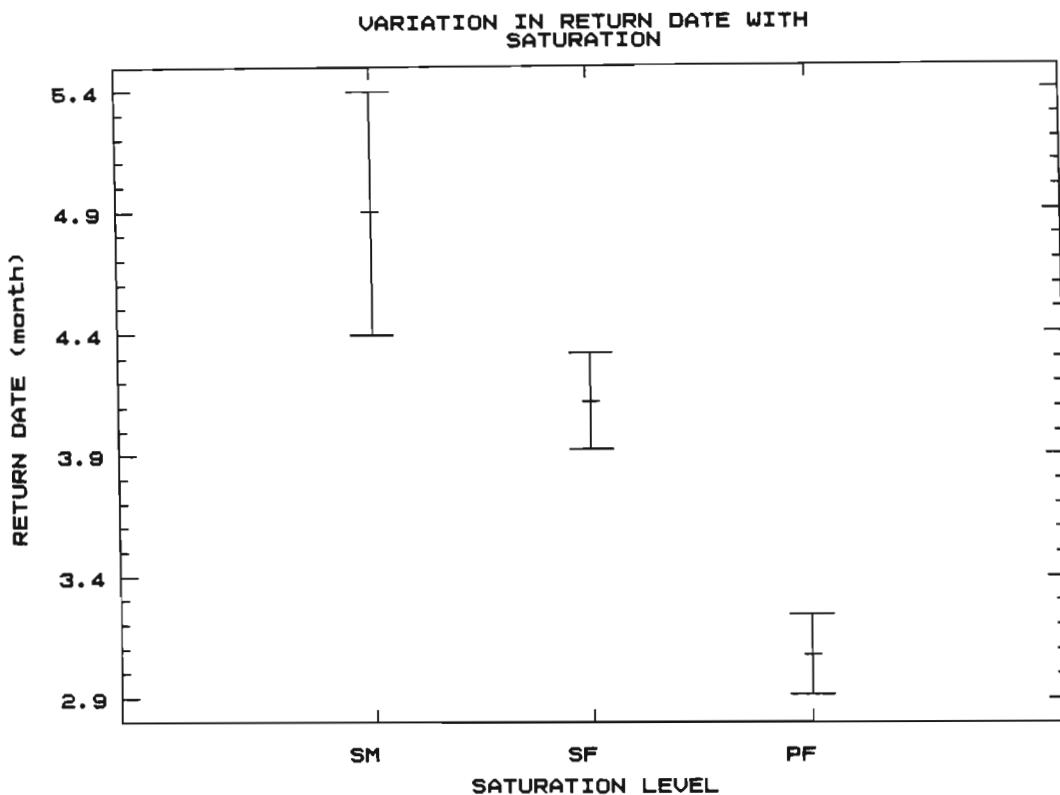


**Fig. 6.12** Variation in return month with vegetation type (multifactor analysis of variance; means and 95% confidence limits: MANOVA 2 - see text), for estimated returns to burned vegetation. Return month is relative to the burning date.

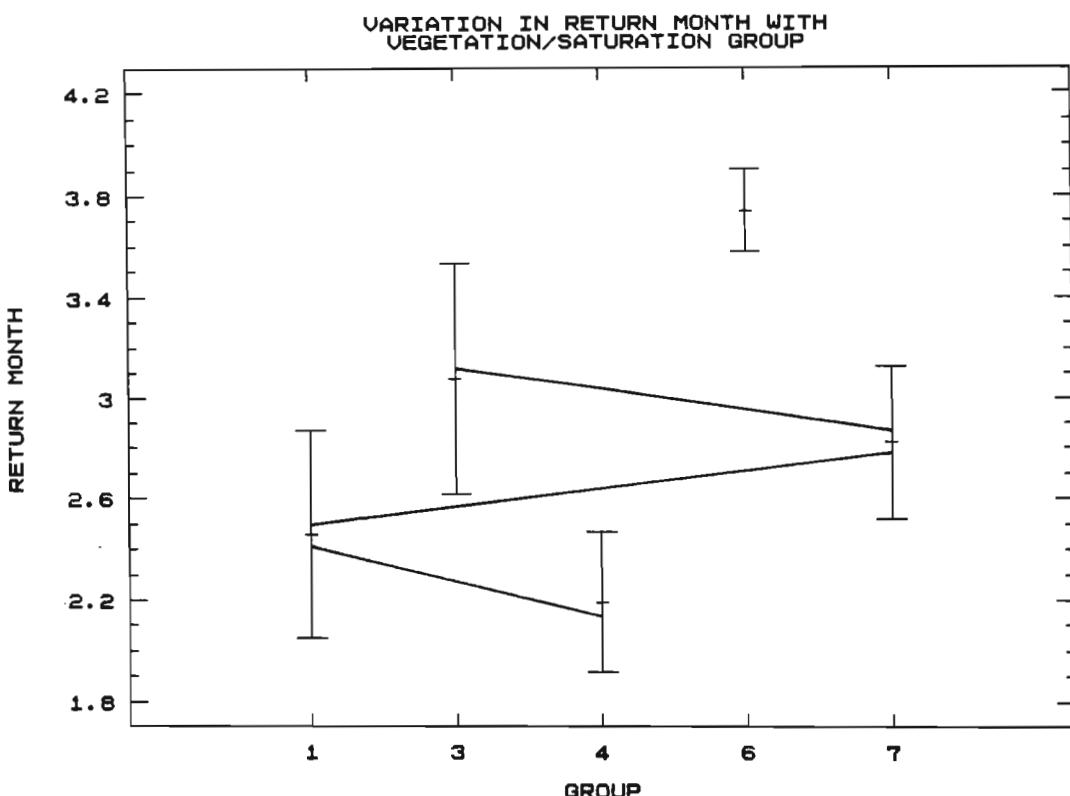
VS/T respectively; mean dates were 3,1 months (94 days) and 3,7 months (112 days) respectively (Fig. 6.12 and Table 6.4). Type S/C had a mean of 3,3 months (100 days) and overlapped both the others. The means for T/S and VS/T were fairly close to those obtained in the analysis of precise return dates, but type S/C showed a great difference from the mean early return (49 days) previously calculated. This is because the second analysis included a much wider range of vegetation and substrate conditions than did the first analysis, which included some exceptionally rapidly developing *Carex* beds at Mt Currie (Table 6.2) and also included the effects of measured vegetation height and cover. Mean return months differed significantly for all three saturation factors (Fig. 6.13), being 2,5 months (76 days) in permanently flooded habitats, 3,4 months (104 days) in permanently moist areas and 4,2 months (128 days) in seasonally moist areas. These return times averaged later than those obtained in the first analysis, again presumably because of the wider range of conditions, and the less precise timings, included in the second analysis.

Because there must be an interaction between the vegetation type and the saturation factor it is not clear which of the two is the more important, so to clarify this a one-way analysis of variance (ANOVA) was done on five of the seven unique combinations of vegetation type and saturation factor (Groups 1-7) as shown in Table 6.5. Groups 2 and 5 were excluded from the analysis because they each contained only one observation. For the remaining five groups the variances were equal ( $P > 0,05$ ) and there was a real difference between the groups ( $P < 0,001$ ). The analysis showed (Fig. 6.14) that four homogeneous groupings exist (Groups 1 and 4, 1 and 7, 7 and 3 and 6), with overlap. The three groups with permanent flooding (1,4 and 7) all overlapped, and averaged earlier return dates than the two with only seasonal flooding, of which Group 3 (including sedge beds dominated by *Carex*, *Cyperus* and *Mariscus* sedges) showed a return period overlapping with two of the permanently flooded groups; these sedges usually grew rapidly and provided good cover relatively early (see Sections 6.4.1.1 to 6.4.1.3). The shortest vegetation (Group 6), seasonally flooded hygrophilous grassland, had the latest return period, not overlapping with that of any other group.

A stepwise regression on return date as a function of the vegetation types and substrate saturations revealed confounding effects, and a regression model (Model 2) was constructed on the basis of three factors (saturation factors SM/PF and PF, and vegetation type SM/HG), which together accounted for most of the variance ( $R^2 = 67\%$ ). This model provides a good explanation of the observed effects ( $P < 0,001$ ; standard error of estimate = 0,45 months), and is expressed as follows:



**Fig. 6.13** Variation in return month with substrate saturation factor (means and 95% confidence limits: MANOVA 2 - see text), for estimated returns to burned vegetation. Return month is relative to the burning date.



**Fig. 6.14** Variation in return month with vegetation type/substrate saturation group (means and 95% confidence limits: MANOVA 2 - see text) for estimated returns to burned vegetation. See Table 6.4 for definitions of groups. Return month is relative to the burning date.

TABLE 6.5

Unique combinations (Groups 1-7) of vegetation type and saturation factor recorded for the wetland territories in which post-burn return of Redcheasted Flufftails was observed at three study sites, together with estimates of the mean return time ( $\pm 1SE$ ), in days after a burn, for the five groups included a one-way analysis of variance. See Table 6.3 for an explanation of symbols.

<b>Group:</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>	<b>6</b>	<b>7</b>
<b>Vegetation Type:</b>	T/S	S/C	S/C	S/C	VS/T	VS/T	VS/T
<b>Saturation Factor:</b>	PF	SM	PM/SF	PF	SM	PM/SF	PF
<b>Return (days)</b>	75 $\pm 1$	-	94 $\pm 8$	67 $\pm 4$	-	114 $\pm 3$	86 $\pm 5$

**Return after the burn = 3,97 months**

less 1,7 months for saturation PF (permanent flooding)

or less 0,8 months for PM/SF (permanently moist/seasonally flooded)

plus 0,57 months for vegetation VS/T (very short and tussocky).

#### .... Model 2

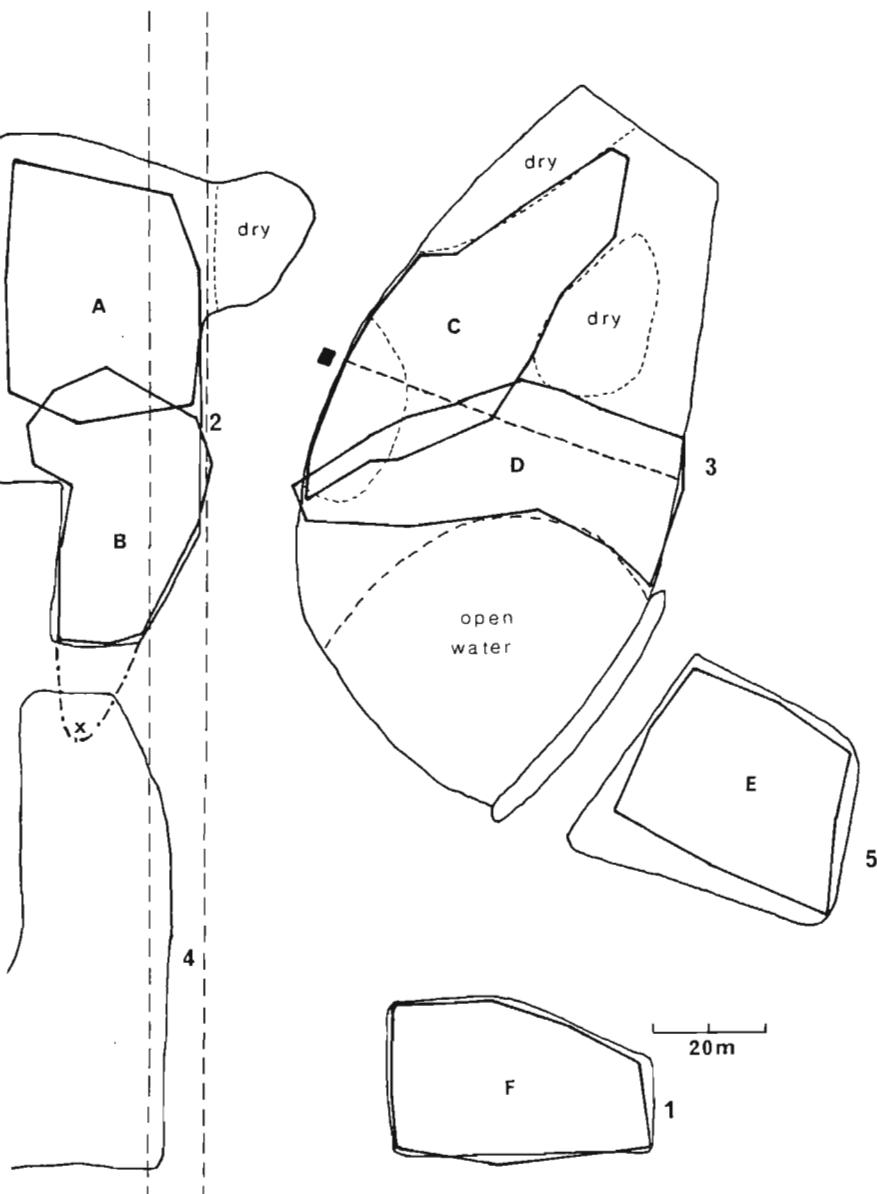
Thus the wetter the substrate the earlier should be the return, as was also indicated by Model 1 (derived from the precise return dates), while return is later in the shortest vegetation, which usually comprised tussocky hygrophilous grassland and short sedges. Other observations consistently led me to regard this vegetation type as the least favoured by the birds, in view of the relatively late development of acceptably tall, dense cover (see Sections 6.1.4.2 and 6.1.4.3). The very long return time of 134 days predicted by this model (Table 6.4) for vegetation type VS/T reflects the inclusion of some very late-flooding (January) and thus late-developing areas.

#### **6.4.2           The effects of burning and mowing on habitat quality and the dispersion and territory sizes of Redchested Flufftails**

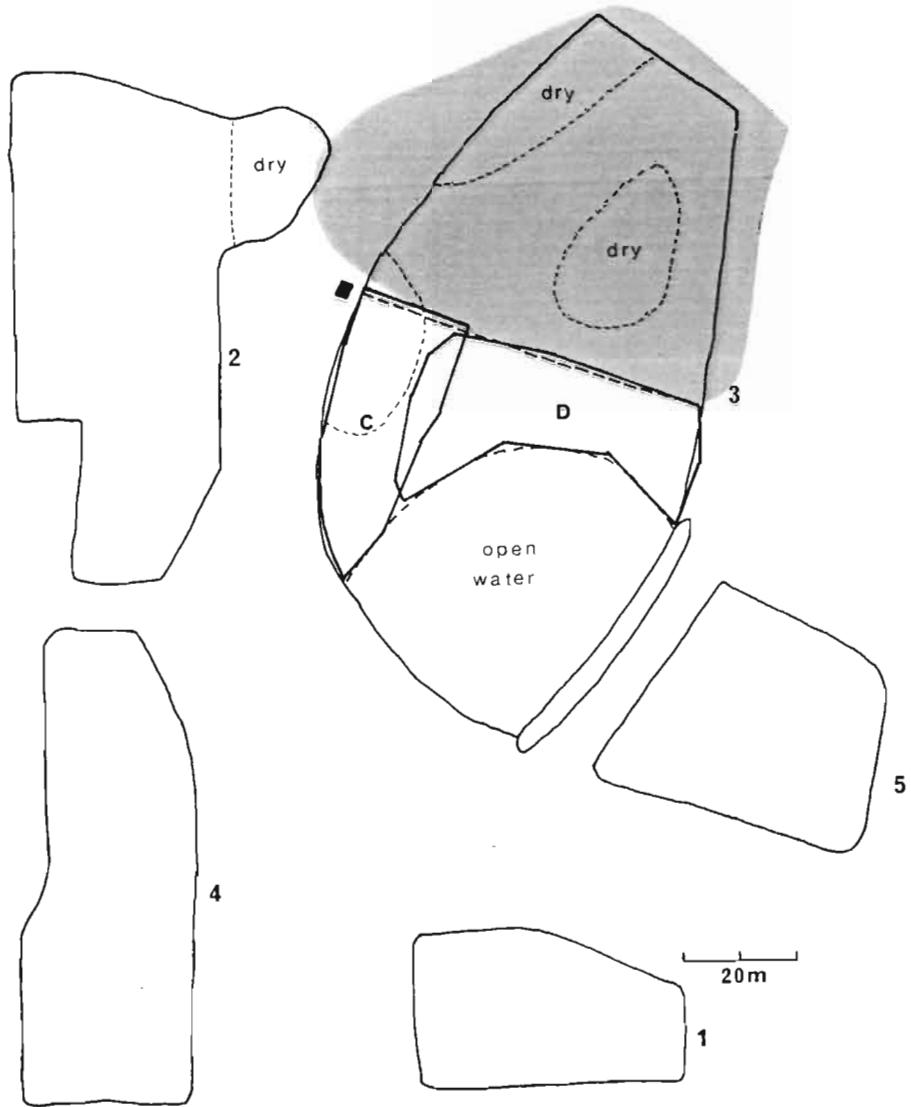
When considering the effects of burning, it is hypothesized that any post-burn territory size increases take place because there is more suitable habitat available for occupation. However it is theoretically possible that the converse is true, i.e. that birds need to expand their territories because the overall suitability of the habitat is diminished by burning. This second hypothesis is unlikely to be true, primarily because burning has been shown to increase plant productivity (Section 6.1) and thus (presumably) the abundance of invertebrate food (Section 6.5), while providing adequate cover and nesting sites and allowing increased mobility for foraging.

##### **6.4.2.1       Allerton, Pietermaritzburg**

Results are shown in Figs 6.15-6.20 and Tables 6.6 and 6.7. The Allerton site is characterized by some of the smallest permanent Redchested Flufftail territories that I have found anywhere in Africa, the four most stable of these (Territories A-D, Fig. 6.15) occurring in predominantly permanently flooded sedge beds (Chapter 2, Section 2.2.7). All are in wetland patches which show little variation in size throughout the year (Table 6.6) because they occur in depressions surrounded by elevated grassy areas which are not significantly inundated during the summer. Seasonal variations in habitat quality and area are largely confined to the depth of flooding and to the small decreases in



**Fig. 6.15** Redcrested Flufftail territories at Allerton, January 1989. 1-5 = reedbed numbers; A-F = flufftail pairs, x = October 1988 extension of Pair B. The pipeline track was mown in March 1989. Pairs E and F disappeared in April 1989 and March 1989 respectively.



**Fig. 6.16** Extent of the burn (shaded area) at Allerton, 13 September 1989, at Reedbed 3, and positions of this reedbed's flufftail territories (C & D) in October 1989.

TABLE 6.6

Areas ( $m^2$ ) of reedbeds comprising potentially suitable habitat for Redchested Flufftails at the Allerton study site, 1988-1991. These areas exclude open water, permanently dry substrates and peripheral short grass, and (for winter areas) seasonally dry substrates.

<b>Reedbed No.</b>		<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>
<b>Habitat area:</b>	<b>summer</b>	1240	3115	3550	1500	1530
	<b>winter</b>	1165	3115	3550	1350	1225
<hr/>						
<b>% loss in winter</b>		6	0	0	10	20
<hr/>						
<b>% summer area used by flufftails:</b>	<b>1988-89</b>	98,0	86,7	82,5	0	86,3
	<b>1989-90</b>	0	78,7	77,5	0	0
	<b>1990-91</b>	0	82,2	95,8	0	100,0

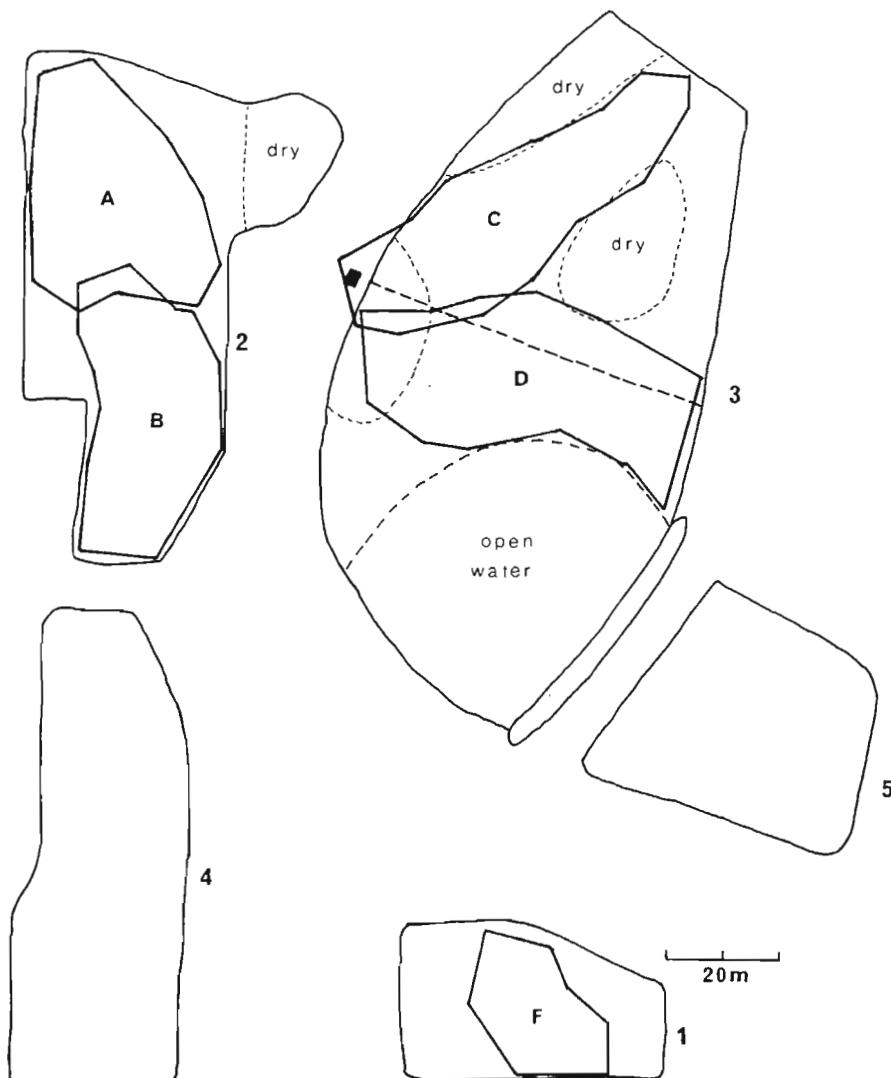
cover produced by the drying of peripheral substrates and the dieback of vegetation in winter. This situation, unique among the Redchested Flufftail habitats which I have studied, gives rise to very small seasonal variations in the size of territories (Table 6.7). It is probably significant that the three reedbeds (Nos. 1, 4 and 5) in which permanent territories were not maintained throughout the study period were the driest (Chapter 2, Section 2.2.7) and showed noticeable seasonal variations in the area of suitable habitat (Table 6.6). In the period October 1988 to September 1989 six pairs (Pairs A-F, Fig. 6.15) of Redchested Flufftails held territories at this site, occupying all reedbeds except No. 4. However the male of Pair B temporarily extended his calling range into Reedbed 4 in early October 1988 (Fig. 6.15), when the strip of grass and sedge between this and his permanent territory (in Reedbed 2) temporarily provided new growth and feeding substrate after slight disturbance during the winter. Fig. 6.15 shows the extent of the six territories in January 1989; their shape and area varied very little during the period. The only events significantly affecting the habitat during the period were: (1) the mowing of the pipeline track in late March 1989, which reduced the areas of Territories A and B (Table 6.7) but did not force emigration, and (2) repairs to the dam wall which reduced the amount of water flowing into Reedbed 5. This reedbed was already choked with dead vegetation and was not occupied by the flufftails after May 1989. Fig. 6.16 shows the displacing effect of the September 1989 burn on the territories of Pairs C and D, which are plotted as they appeared in October 1989. During the 1989-1990 summer these two pairs reoccupied areas very similar in extent to those occupied before the burn (Figs 6.15 and 6.17; Table 6.3), the birds returning to the burned section in early December (Section 6.4.1.1). Only four pairs of flufftails were present in the 1989-1990 summer, the territory areas A-D plotted in Fig. 6.17 representing the January 1990 situation. Reedbed 1 was very moribund and was vacated by its Redchested Flufftails in June 1989, being temporarily occupied by a pair of African Rails in early December 1989 (Fig. 6.17).

The burn on 21 August 1990 (Fig. 6.18) was primarily of Reedbeds 1 and 5, but a dry part of No. 3 was also burned in error, this not affecting the areas occupied by pairs C and D, whose nonbreeding territories were similar in extent to those occupied in the previous summer (Figs 6.17 and 6.18; Table 6.7). The burn resulted in good regrowth of Reedbed 5, which was reoccupied by a pair of flufftails on 24 December 1990 (after an absence of 18 months); good rain in early 1991 (Fig. 2.14A) kept this reedbed moist thereafter. Good regrowth was also apparent in Reedbed 1 but no flufftails reappeared there, possibly because the reedbed was occupied on 26 November 1990 by a pair of African Rails which then nested and probably excluded all other rallids from this very small area. Thus five Redchested Flufftail territories were present in the 1990-1991 summer (Fig. 6.18), when the areas occupied by Pairs C, D and E were larger than those defended during previous breeding seasons (Table 6.7).

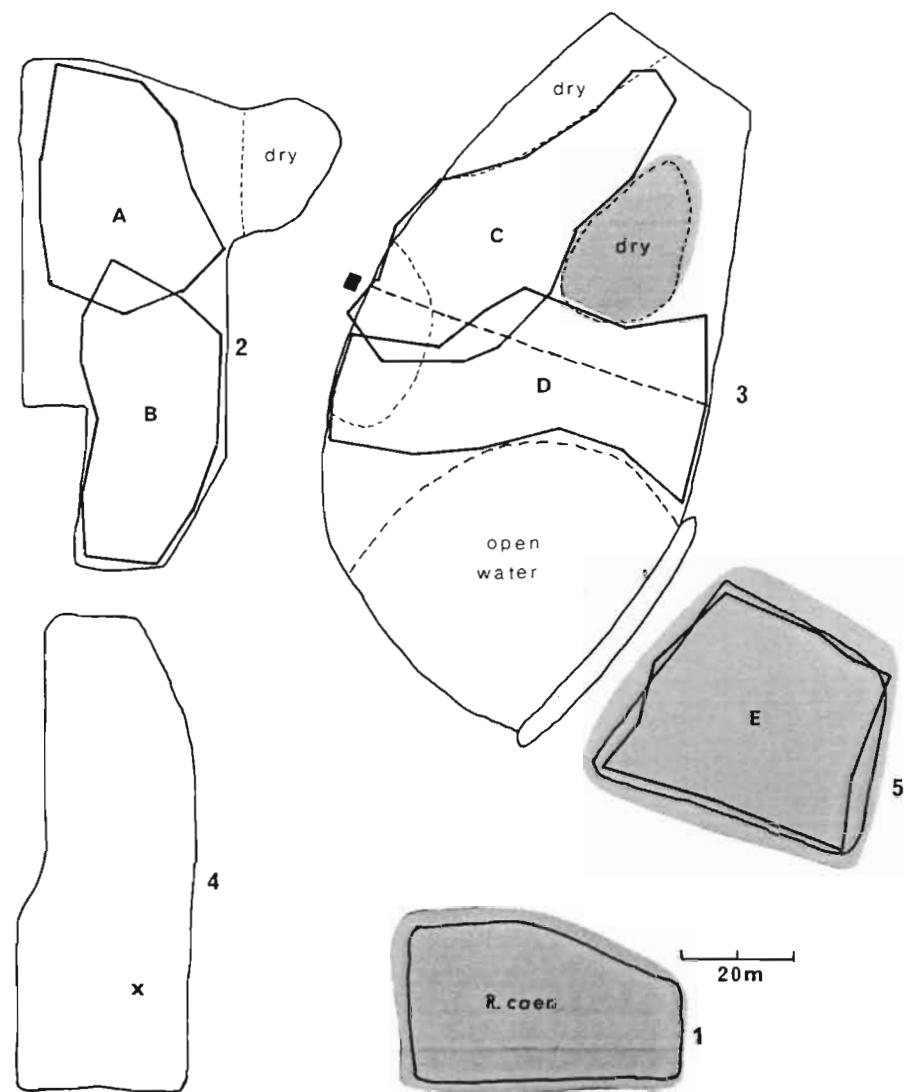
TABLE 6.7

Sizes ( $m^2$ ) of Redchested Flufftail territories A-F at the Allerton study site, 1988-1991, with notes on significant events which occurred during the periods concerned. Periods: 1 = Oct 1988 - Nov 1989; 2 = Dec 1989 - Aug 1990; 3 = Sep 1990 - Aug 1991. See Table 6.6 for areas of suitable habitat in Reedbeds 1-5.

Flufftail pair	Reedbed No.	Period	Max. territory area ( $m^2$ ): Dec - Feb      Jun - Aug	% loss in winter	Notes
A	2	1	1400	1050	25,0
		2	1200	1200	0
		3	1260	1250	0,8
B	2	1	1300	1050	19,2
		2	1250	1200	4,0
		3	1300	1300	0
C	3	1	1480	1480	0
		2	1350	1310	3,0
		3	1650	1580	4,2
D	3	1	1450	1330	8,3
		2	1400	1350	3,6
		3	1750	1690	3,4
E	5	1	1320	0	- Territory vacated May 1989.
		3	1530	1530	0 Territory reoccupied 24 Dec 1990.
F	1	1	1215	1165	4,1 Territory vacated Jun 1989.



**Fig. 6.17** Allerton territories in January 1990. Pairs C and D reoccupied the breeding areas in mid-December 1989. Pair F was present from 7 to 14 December 1989 only; thereafter Reedbed 1 was occupied by a pair of African Rails.



**Fig. 6.18** Extent of the burn (shaded areas) at Allerton on 21 August 1990, and positions of Redchested Flufftail territories in January 1991. x = an isolated flufftail record, 10 August 1990. Pair E reappeared on 24 December 1990; Reedbed 1 was occupied by African Rails from 26 November 1990.

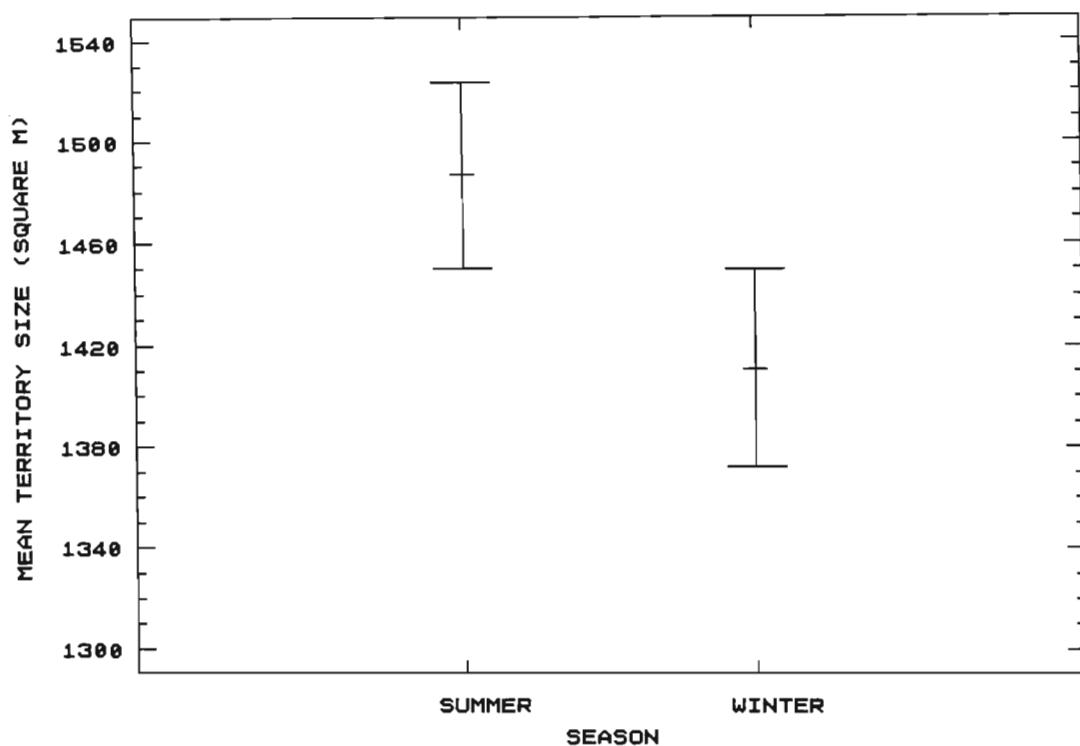
The burning at Allerton thus did not increase the number of resident pairs in any reedbed, its only obviously beneficial effects being the reduction of dense, tangled, dead vegetation and the stimulation of new growth, with the consequent reoccupation of the whole of Reedbed 5 in 1990 and the extensions of Territories C and D into previously unoccupied vegetation in the western sector of Reedbed 3, i.e. an increase in the percentage of habitat occupied (Table 6.6). It is probable that, in these very small areas of habitat, extra pairs of flufftails cannot be accommodated because territory sizes are already close to the minimum for the species in permanently flooded habitats, and the improvement in quality presumably brought about by the removal of moribund vegetation would have to be accompanied by a significant increase in the area of available habitat before further pairs could be accommodated.

A multifactor analysis of variance was done on the territory size data (Table 6.7) to determine the effects of two variables: season (summer and winter) and burning treatment (no burn, one burn, and a burn followed by a year with no burn). The three large temporary winter/spring reductions resulting directly from burning or mowing were excluded from the analysis. There was a significant difference between summer and winter territory sizes ( $P < 0,05$ ) even though the summer and winter means differed by only  $76 \text{ m}^2$  (Fig. 6.19). This highlights not only the very small winter reductions in territory sizes at this site but also the consistent nature of the annual variations under normal conditions. The burning treatment had a highly significant effect on territory size ( $P < 0,001$ ), the mean increasing from  $1\,273 \text{ m}^2$  with no burn to  $1\,405 \text{ m}^2$  after a burn and  $1\,667 \text{ m}^2$  a year later (Fig. 6.20). This confirms that burning can make more habitat available in predominantly permanently flooded reedbeds, and that a year's rest after a burn may allow even more to be used.

#### **6.4.2.2 Gartmore, Howick**

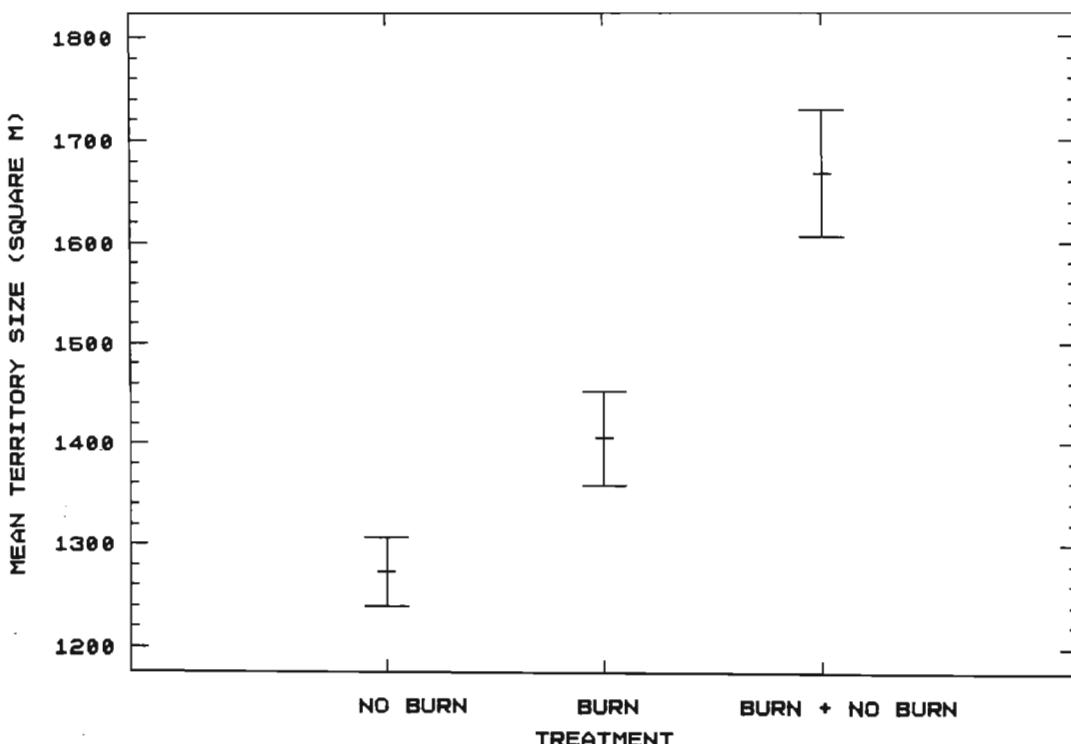
Results are shown in Figs 6.21-6.28 and Tables 6.8 and 6.9. Compared with the habitat at other long-term study sites, and almost all other areas surveyed during this project, Gartmore showed two unique features. First, the vegetation permanently inhabited by Redcrested Flufftails is primarily sedge meadow and hygrophilous grassland, and includes no permanent tall reedbeds such as those of *Typha*, *Carex*, *Cyperus*, *Mariscus* or *Phragmites* which were often an important part of the birds' territories at other sites. Second, at least half of the inhabited area is only seasonally inundated, so that the nonbreeding habitat in the territories of some pairs, especially in the north study block (Fig. 2.6), was largely dry grass with short sedges. At other study sites, birds breeding in seasonally wet hygrophilous grassland tended either to retreat in winter to wet ground and permanent reedbeds within their territories, or (occasionally) to vacate their breeding territories at the end of the summer. All

**ALLERTON: VARIATION IN TERRITORY SIZE  
WITH SEASON**



**Fig. 6.19** Allerton: multifactor analysis of variance showing variation in mean territory size (with 95% confidence limits) between summer (January) and winter (July) territories.

**ALLERTON: VARIATION IN TERRITORY SIZE  
WITH BURNING TREATMENT**



**Fig. 6.20** Allerton: multifactor analysis of variance showing variation in mean territory size (with 95% confidence limits) with burning treatment.

the Gartmore pairs, however, are permanently resident and the site is characterized by the large territory sizes typical of sites with much seasonally flooded grassy habitat (for a discussion of this, see Chapter 5).

In contrast to the situation at Allerton, the Gartmore territories showed considerable variation in size and position, both in consecutive summer and winter seasons and over longer periods (see Figs 6.21-6.28 and Table 6.9). Gartmore was also unique among the study sites in regularly having the majority of territories larger in winter than in summer (Table 6.9), this being in marked contrast to the normal situation in mixed-vegetation habitats, where territory sizes often decrease in winter as the birds abandon drying areas. The Gartmore birds did not abandon grassland which dried out in winter, as long as the cover remained suitable, and were often able to extend their territories into vegetation (particularly that dominated by *Cyperus*, *Eleocharis*, *Isolepis*, *Leersia* and *Rhynchospora*) which had been too deeply flooded in summer for occupation, but which dried out at the end of the rainy season.

The amount of habitat available (Table 6.8) in the southern study block was quite variable and depended principally on the degree of summer flooding and its effects on the development of cover: deep flooding often resulted in sparse cover. In winter, habitat was usually slightly more extensive than in summer. In the northern block the extent of summer habitat varied little from year to year, in very wet seasons loss of habitat due to flooding being compensated for by the creation of new habitat in peripheral areas usually too dry for occupation in summer. Winter habitat availability varied somewhat more, depending primarily on the extent to which summer-flooded areas could be used in winter.

In the 1988-1989 season, rainfall was about 10% less than the mean (Fig. 2.7A) and summer flooding was approximately normal. As the study area had not been burned for four years it contained a considerable amount of moribund vegetation, especially in the drier northern block. Eight pairs of birds were present, occupying about 79% of the available habitat (Table 6.8). All these pairs remained throughout the winter, when the territories averaged slightly larger than in the summer (Figs 6.21 and 6.22; Table 6.9). After the September 1989 burn of the southern block and the October mowing of part of the northern block, only two pairs remained in residence in late October (Fig. 6.23). Five more pairs returned in December 1989 and January 1990 but exceptionally heavy rain in November and December (Fig. 2.7B) had caused widespread deep flooding in regions adjacent to the dam and this reduced the amount of habitat (Table 6.8) by rendering unsuitable the area normally occupied by Pair 8 and displacing the territories of other birds near the dam (compare Figs 6.21 and 6.24); this accounted for the reduction of the 1989-1990 breeding population to seven pairs. However the percentage of available habitat occupied in the southern (burned) block was greater, in both summer and winter, than that in the previous season (Table 6.9), suggesting some improvement in habitat

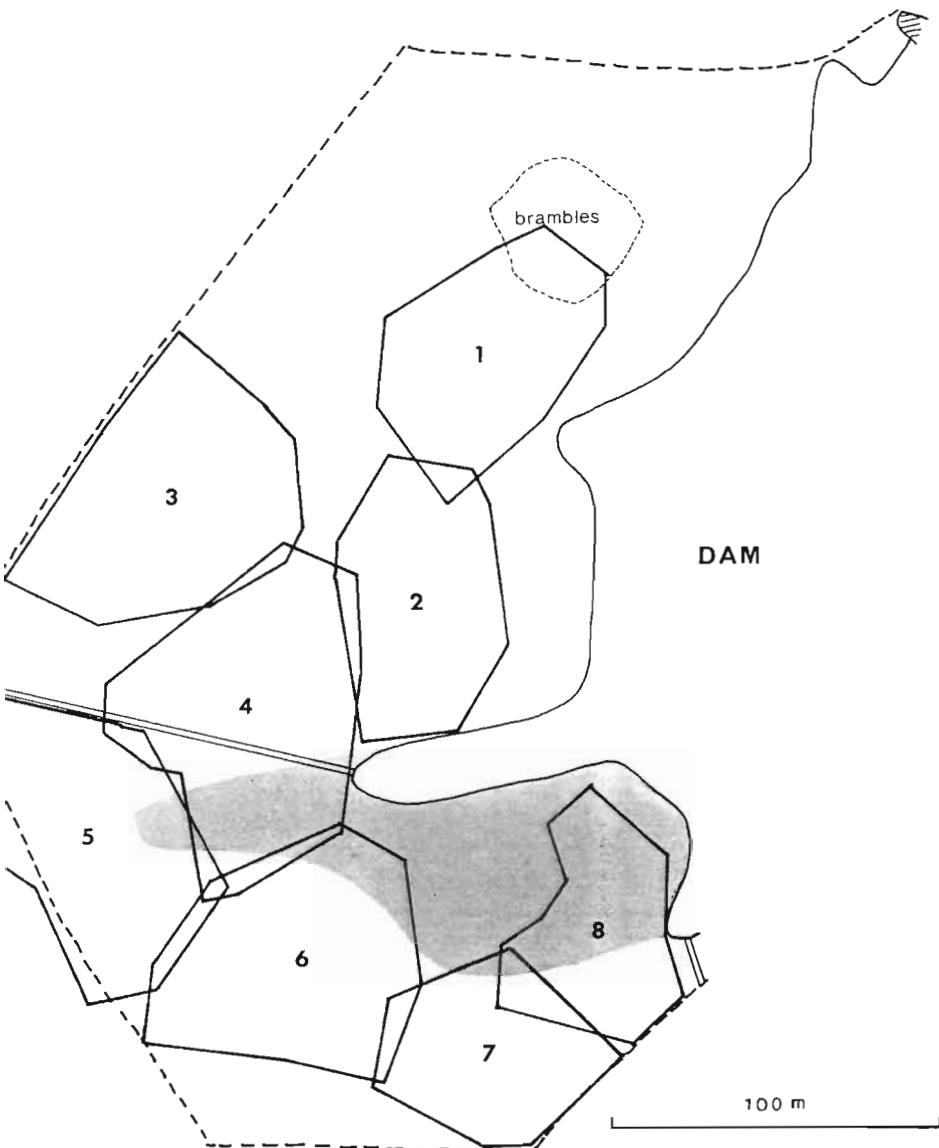
TABLE 6.8

Redchested Flufftail habitat availability and usage, and mean territory sizes, at the Gartmore Farm study site, December 1988 to July 1992. All winter habitat and territory measurements refer to July, before firebreak or block burns, while all summer measurements refer to late January, when the total breeding population was present and habitat was normally at its maximum extent. A = total habitat available ( $m^2$ ); B = total habitat used ( $m^2$ ); C = % habitat used; terr. = territory.

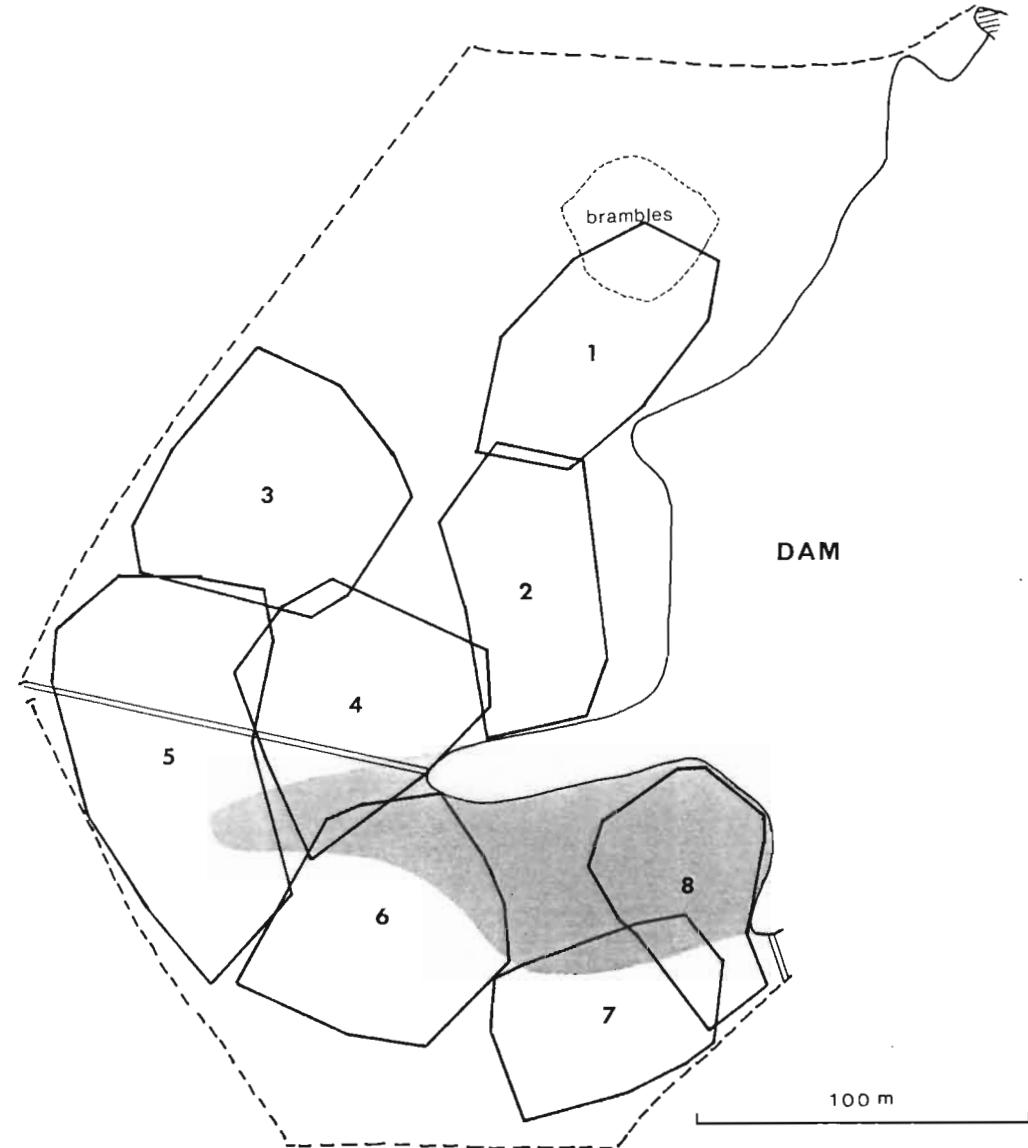
Season		Total habitat			North study block			South study block			Total terrs	Mean terr-size ( $m^2$ )
		A	B	C	A	B	C	A	B	C		
1988-89	Summer	30 600	24 216	79,1	15 600	11 136	71,4	15 000	13 080	87,2	8	3027
"	Winter	32 760	25 350	77,5	17 280	12 762	73,9	15 480	12 588	81,3	8	3173
1989-90	Summer	26 640	21 840	82,0	15 360	11 256	73,3	11 280	10 584	93,8	7	3120
"	Winter	27 570	22 008	79,8	15 840	11 544	72,9	11 730	10 464	89,2	7	3144
1990-91	Summer	29 904	26 958	90,1	15 552	14 670	94,3	14 352	12 288	85,6	9	2995
"	Winter	31 704	28 468	89,8	16 752	15 412	92,0	14 952	13 056	87,3	9	3163
1991-92	Summer	28 968	26 424	91,2	16 008	15 192	94,9	12 960	11 332	87,4	9	2936
"	Winter	30 768	28 610	93,0	17 928	17 328	96,7	12 840	12 120	94,4	9	3179

TABLE 6-9

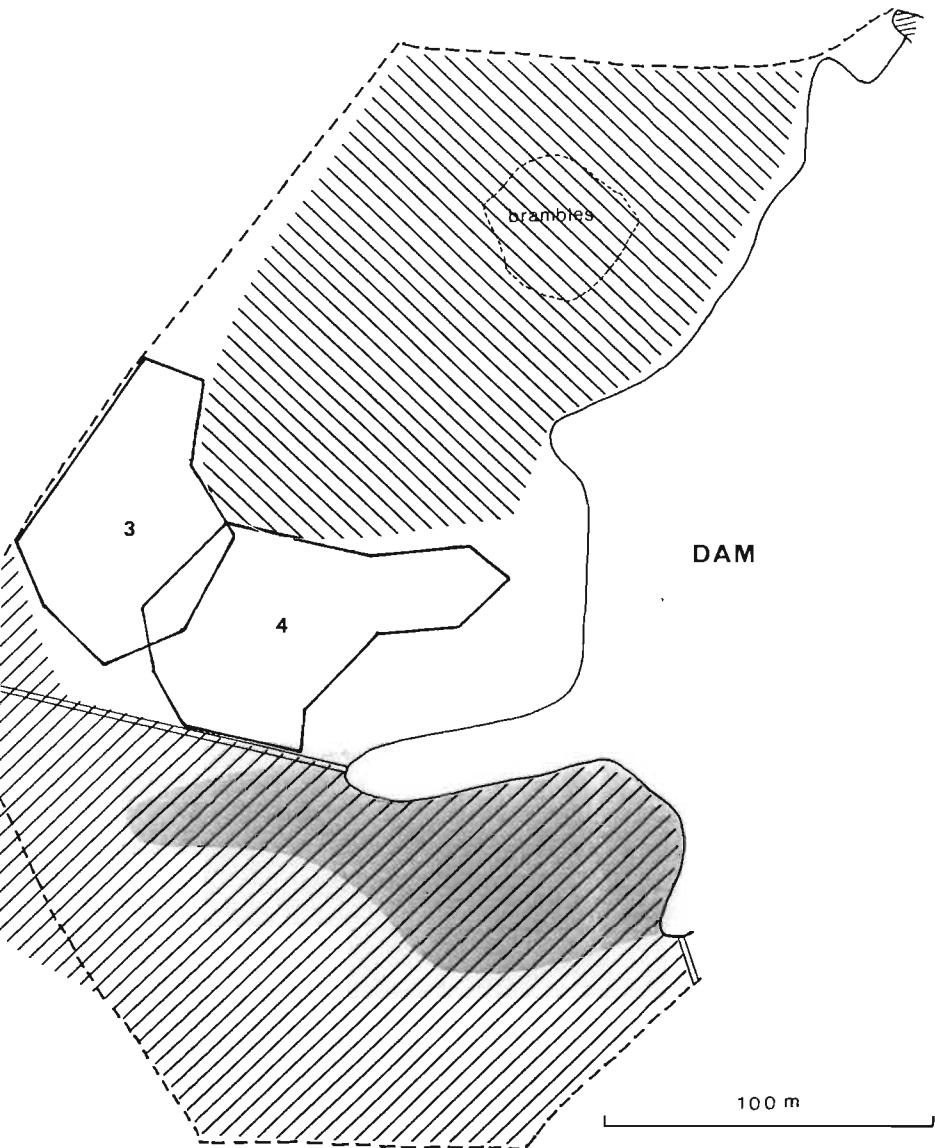
Sizes ( $\text{m}^2$ ) of Redchested Flufftail summer and winter territories at the Gartmore Farm study site, December 1988 to July 1992. All summer territory measurements refer to late January, when the total breeding population was present, and all winter territory measurements to July, before firebreak or block burns. See Figs. 6.21-6.28 for corresponding territory maps. Codes: S = summer; W = winter; % = percentage change i.e. the winter increase/decrease on the summer territory size. Exact winter territories were not plotted in July 1992 but an estimate of the total occupied area was obtained.



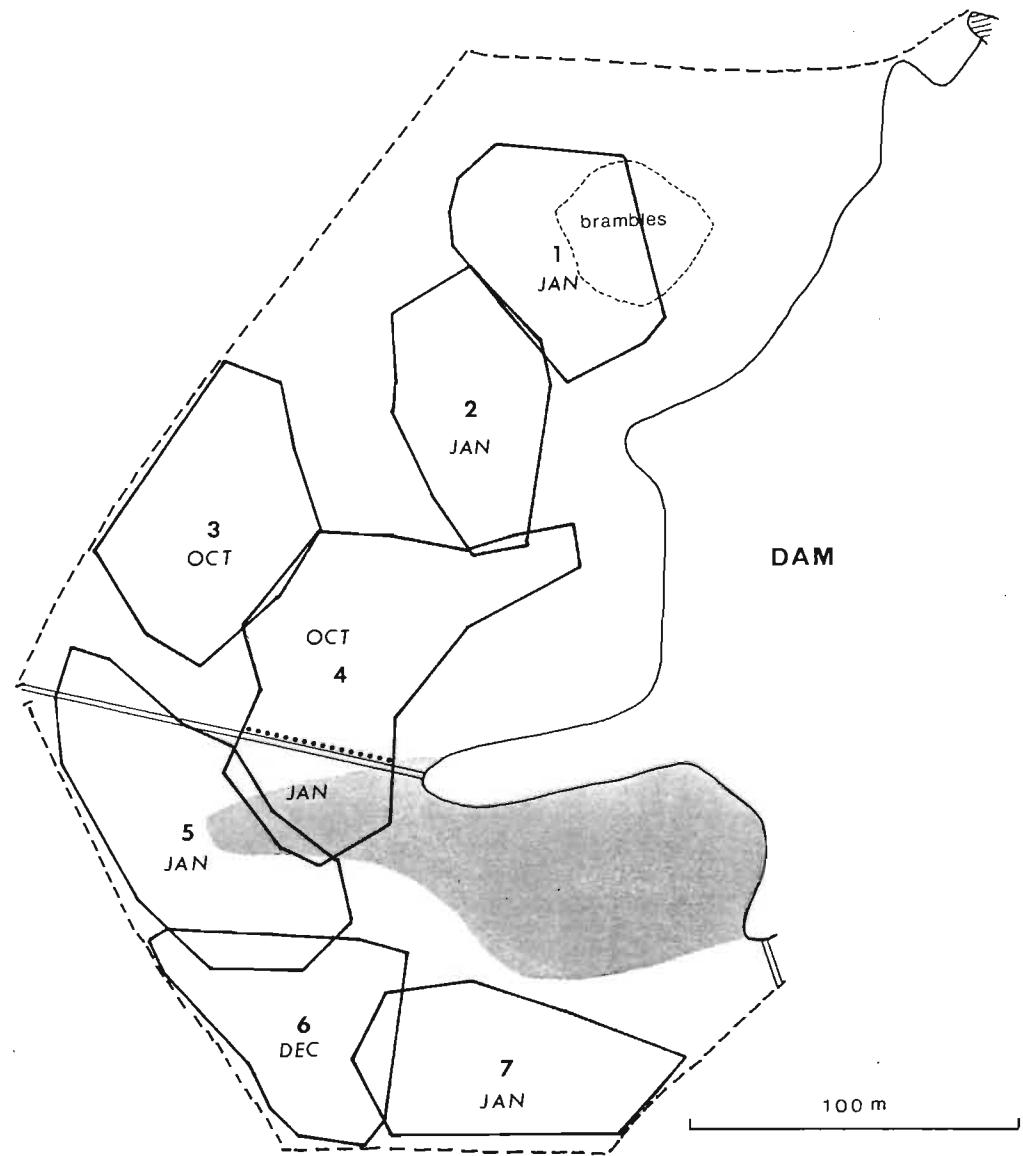
**Fig. 6.21** Redcrested Flufftail territories (1-8) at Gartmore, January 1989, after four years with no burn. Shaded area gives the approximate extent of permanently moist vegetation.



**Fig. 6.22** As for Fig. 6.21, winter territories, July 1989 (pre-burn).



**Fig. 6.23** Position of the Redchest Flufftail territories (3 and 4) remaining at Gartmore, October 1989, after the burn of 28 September 1989 and the mow of mid-October 1989.



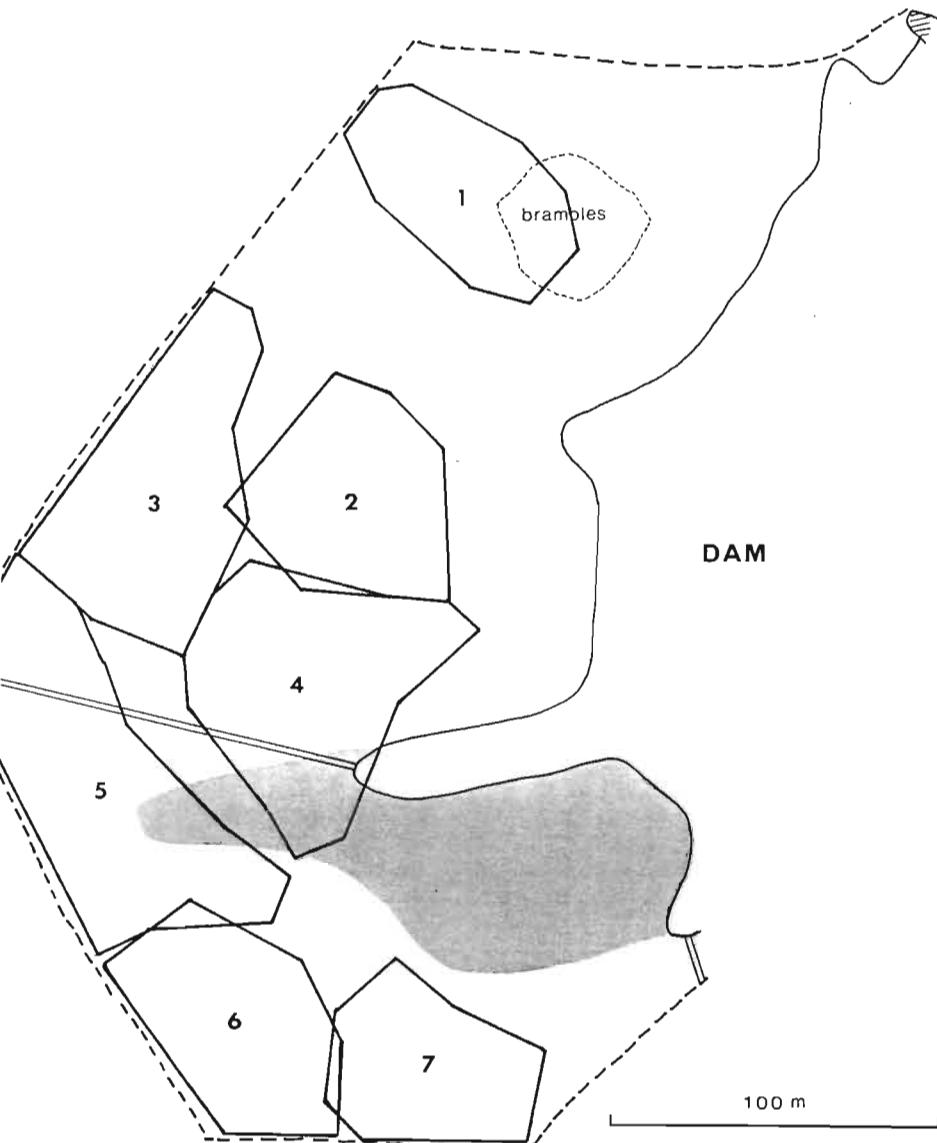
**Fig. 6.24** Redchest Flufftail territories (1-7) at Gartmore, January 1990. Months represent the month of reoccupation of each territory or part of a territory (No. 4). Oct = birds did not leave after the burn.

quality. The amount of suitable habitat increased during the winter but much of the deeply flooded area, although drying out, had very sparse vegetation and was not occupied, so the total available habitat was still less than in the previous winter (Figs 6.22 and 6.25; Table 6.8).

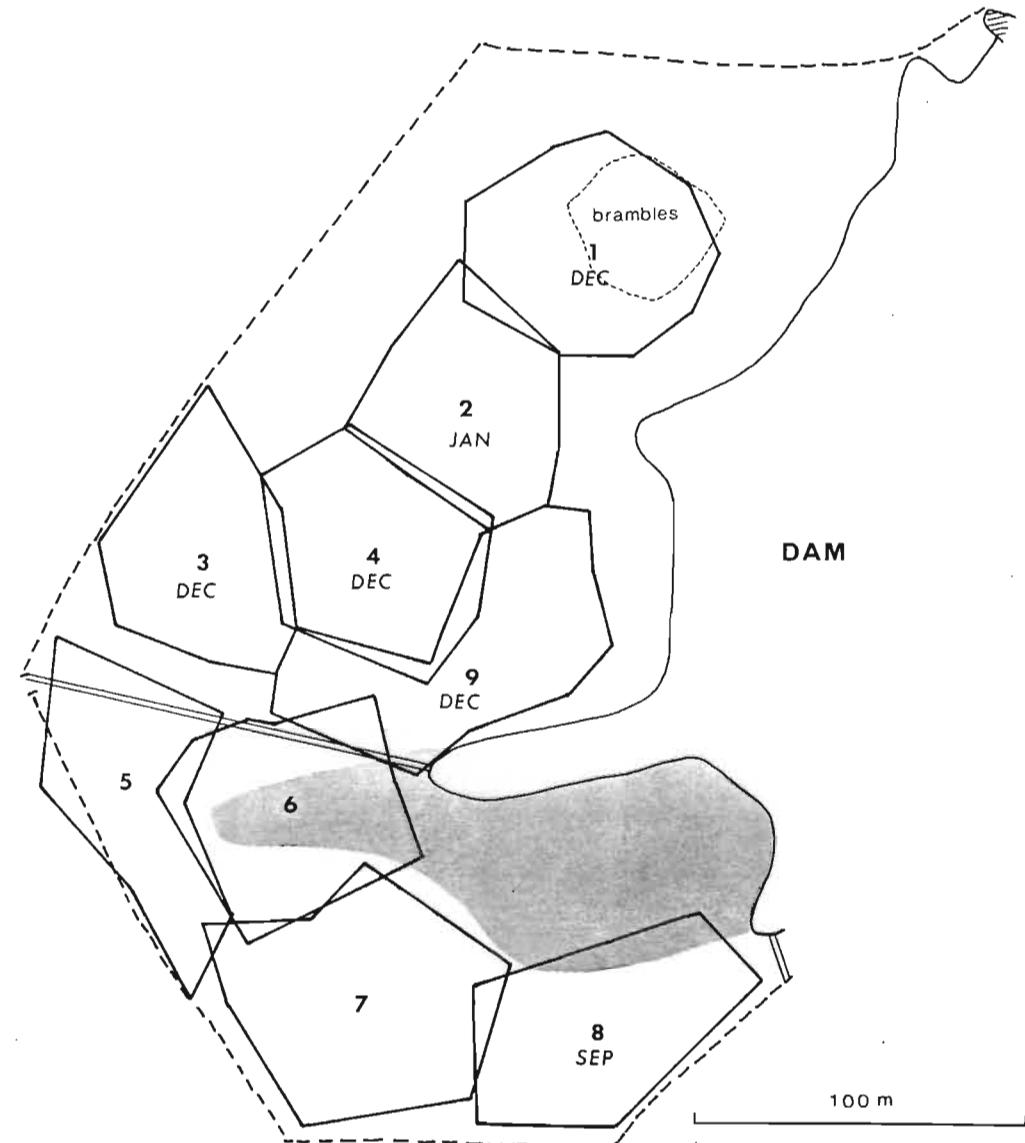
The 1990-1991 season saw a very different situation. After the September burn of the northern block regrowth was good, rainfall was slightly above average (Fig. 2.8A) and flooding normal. The amount of habitat increased, approaching that available in 1988-1989 (Table 6.8), and the unburned southern block held four breeding territories, pair no. 8 (origin unknown) appearing in September after the burn (Fig. 6.26). The northern block was reoccupied in December and January, holding five territories in a slightly smaller area than that which supported four in January 1989 (Figs 6.26 and 6.21). Compared with the situation in the 1988-1989 season, the mean territory size was slightly reduced and 90% of the habitat was occupied instead of 79% (Table 6.8). All nine pairs wintered in 1991, the northern block again holding five pairs in a smaller area than that which had previously held four, and the mean winter territory size being almost the same as that in the 1989 winter (Fig. 6.27; Table 6.8).

The burn of the southern block in September 1991 was followed by good spring rain and below-average rain from December to March, giving a total slightly below the long-term mean (Fig. 2.8B). The southern block was reoccupied by four pairs in December 1991 and January 1992 (possibly at least one territory in November; precise dates were not established), while the northern block continued to support five (Fig. 6.28). The total breeding habitat in the southern block was less than that in 1988-1989 and 1990-1991, principally because of the early deep flooding of the permanently wet area adjacent to the dam. The mean territory size was less than that in any other season and the percentage of habitat used increased slightly over that of the previous breeding season (Table 6.8). Precise winter-territory boundaries were not plotted in July 1992 but an estimate of the total occupied area was very close to that obtained for the previous winter and gave a mean winter territory size close to that of all other years; percentage usage of available habitat was high (Tables 6.8 and 6.9).

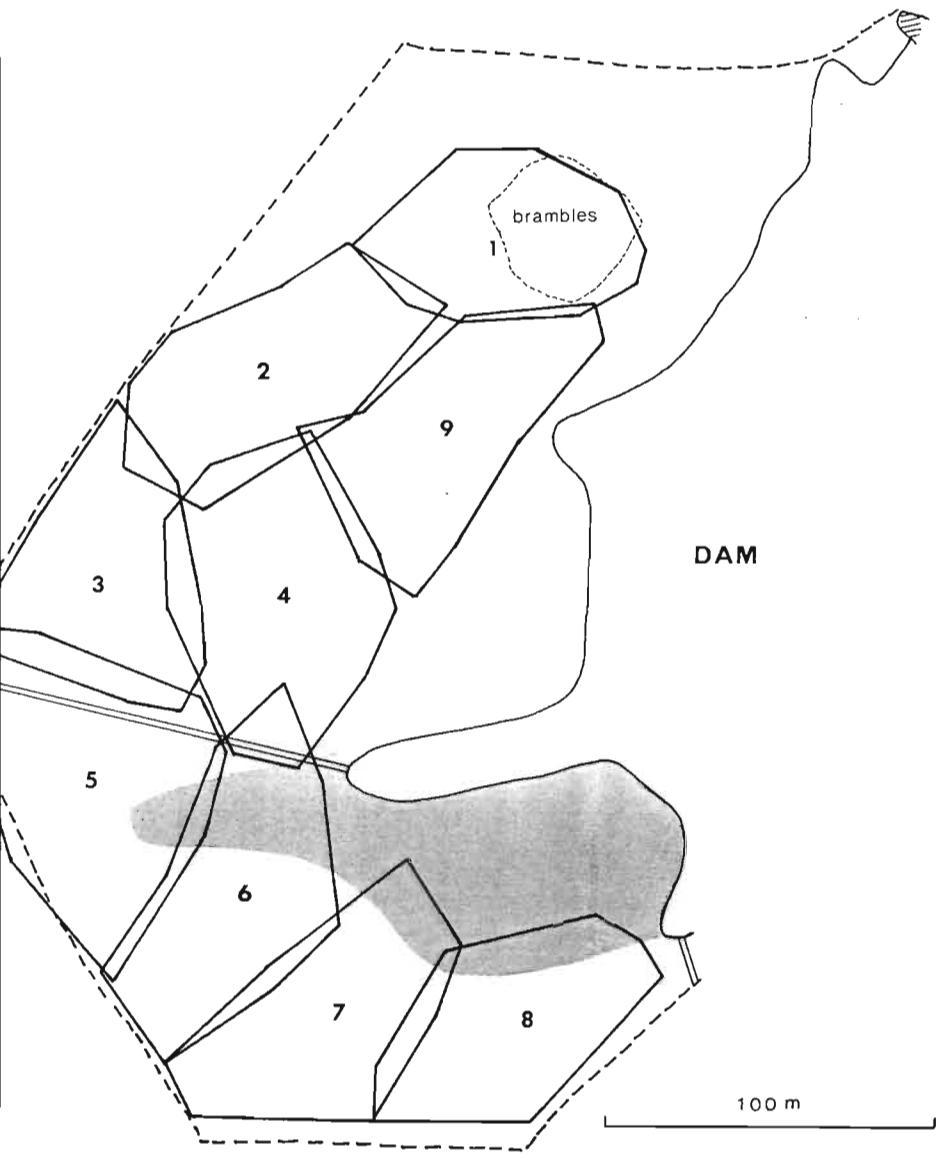
The observed effects of biennial burning at Gartmore may be summarized with reference to Table 6.8 and Figs 6.21-6.28. Apart from the 1989-1990 and 1991-1992 seasons, when flooding reduced the available habitat in the southern block, climatic factors apparently did not significantly influence the amount of habitat available or the population density of the birds. The burning operations are thus the only major factor likely to have been responsible for the differences in dispersion noted in the other two seasons in the southern block, and in the northern block throughout the study period. It appeared that the 1990 burn of the relatively dry northern block resulted in the immediate improvement of the block's vegetation to the extent that a much greater percentage of it



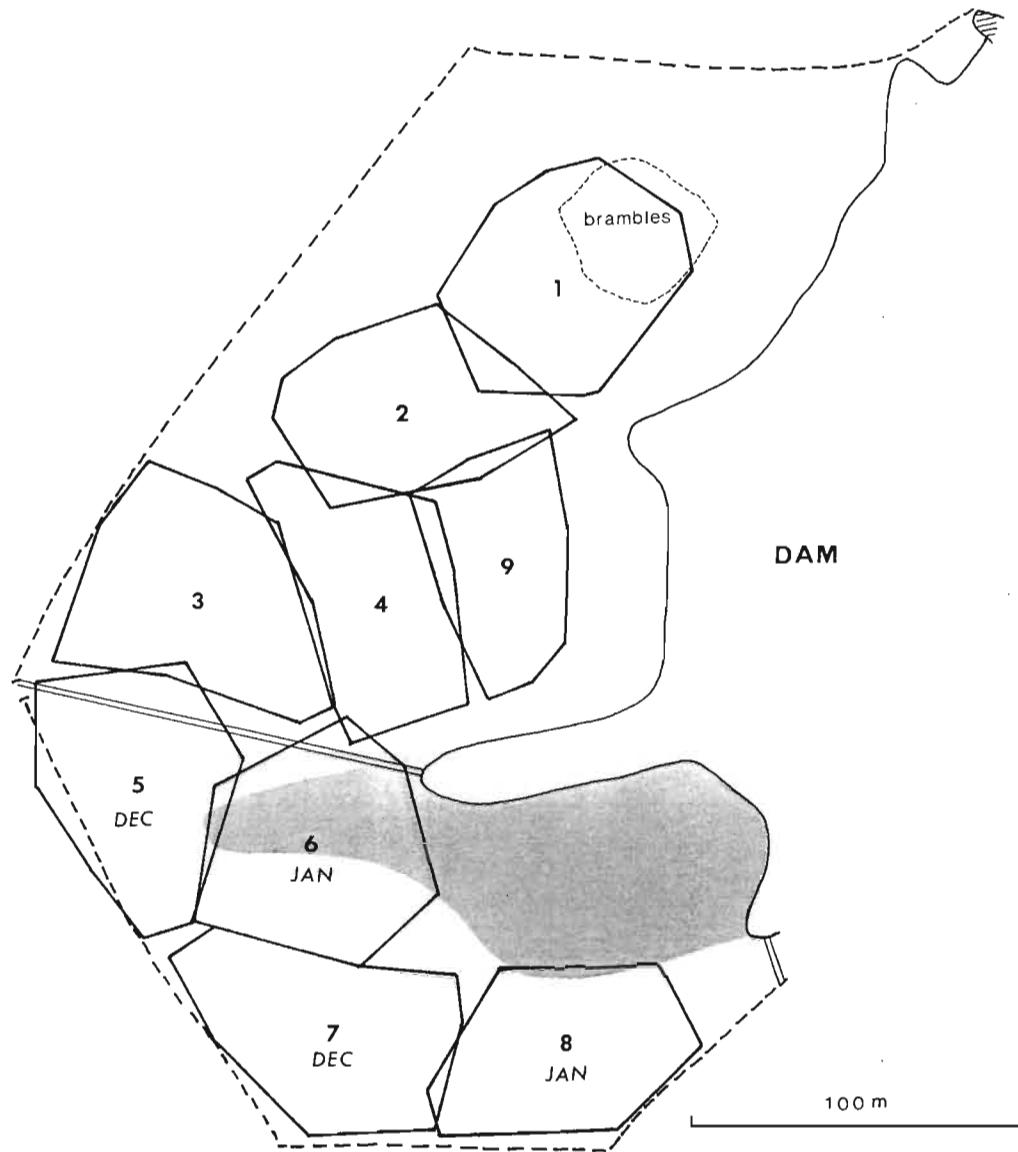
**Fig. 6.25** Redcheasted Flufftail winter territories (1-7) at Gartmore, July 1990.



**Fig. 6.26** Redcheasted Flufftail territories (1-9) at Gartmore, January 1991, after the burn of the northern study block on 4 September 1990. Months represent months of reoccupation of territories vacated after the burn.



**Fig. 6.27** Redcheasted Flufftail winter territories (1-9) at Gartmore, July 1991.



**Fig. 6.28** Redcheasted Flufftail territories (1-9) at Gartmore, January 1992, after the burn of the southern study block on 4 September 1991. Months represent reoccupations of territories vacated after the burn.

was habitable, so that the block was able to accommodate five territories instead of four. This situation persisted for two summers after the first burn. The burns of the smaller, wetter southern block failed to increase the number of resident pairs, or to make available an appreciably greater percentage of the habitat in summer, but the southern block suffered a relatively large annual variation in habitat area during the study period and it is possible that, in years when as much breeding habitat is available as there was in 1988-1989, the improvement in vegetation quality produced under the biennial burning regime might allow a fifth breeding pair to be accommodated. There was an improvement in the percentage of nonbreeding habitat occupied in all years after burning was introduced, and this should favour an increased number of wintering birds in a season when most of the block's vegetation is tall and dense enough for occupation.

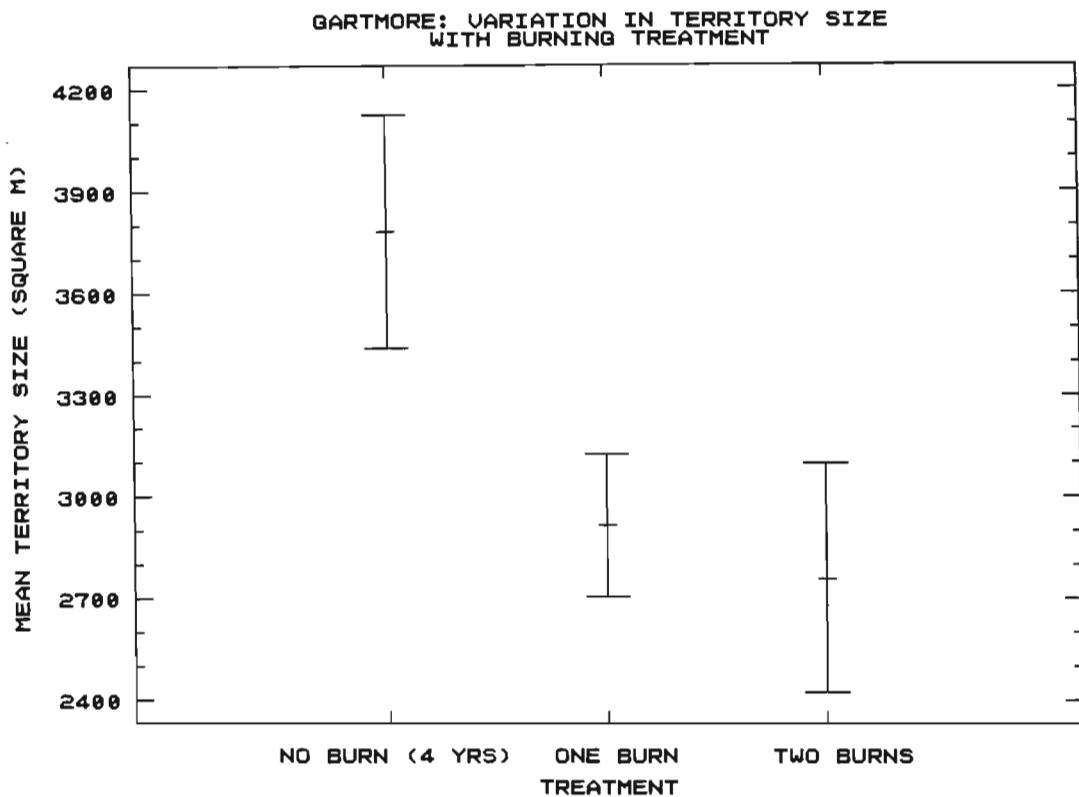
To investigate the effects of burning on territory size, a multifactor analyses of variance was done on the data in Table 6.9, excluding territories 8 and 9 which were not present in all years. Between-territory size variations were not relevant to this analysis and the variables used were year, season (summer or winter), and burning treatment (no burn for at least four years, one burn or two burns). Mowing was assumed to be equivalent to burning and the two mown territories (Nos. 1 and 2; see Table 6.9) thus experienced "burns" in two consecutive springs, while all other twice-burned territories came under the biennial burning regime; all these territories were included in the two-burn treatment type. After correcting for the small, non-significant ( $P > 0,05$ ), effects of season and year, there was a significant variation between treatments ( $P < 0,05$ ). Two homogeneous groups were recognized (Fig. 6.29), there being a significant difference in territory size before (mean 3 780 m<sup>2</sup>) and after (means 2 760 and 2 915 m<sup>2</sup>) the start of the burning treatments (Fig. 6.29). There was little difference between the territory sizes after one burn or two burns (Fig. 6.29). The analysis clearly shows the immediate beneficial effects of burning this seasonally flooded habitat type.

To investigate variations in habitat usage, the proportions of habitat occupied in each block during each season (from Table 6.8) were transformed via logit (McCullagh & Nelder 1989), using the formula

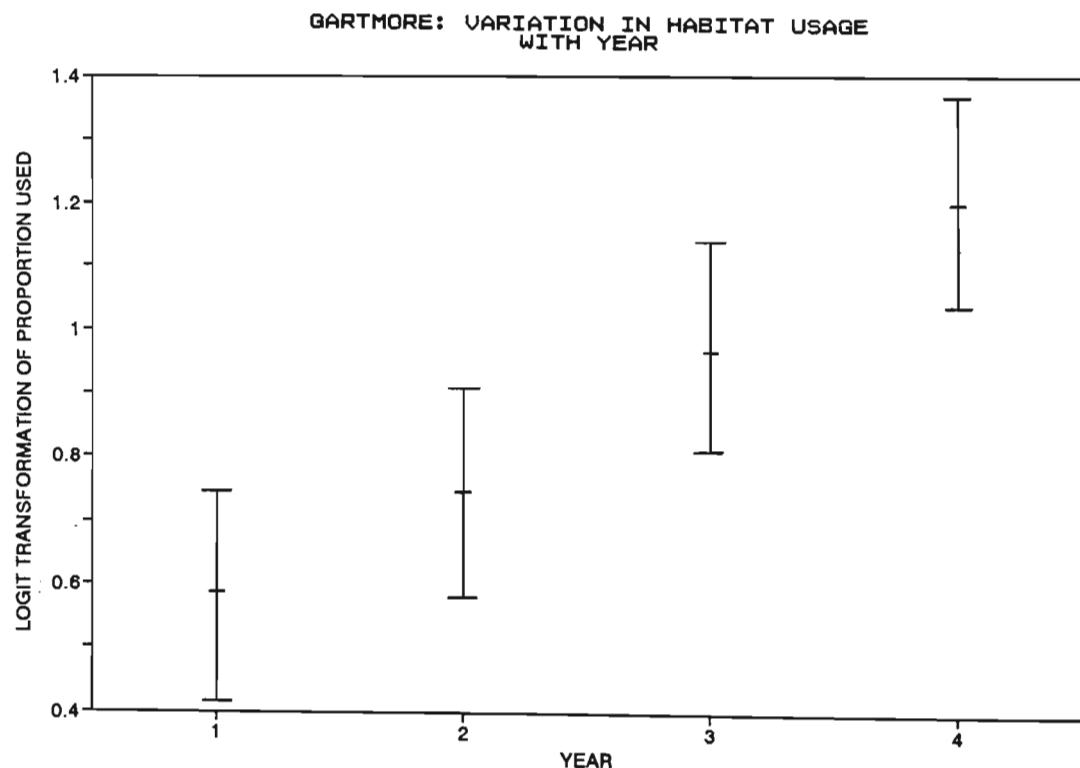
$$\text{logit} = \log_e \left( \frac{a}{1-a} \right)$$

where  $a$  = proportion of available habitat used.

A multifactor analysis of variance was then performed on the transformed data, when  $\text{logit}(a)$  was found to be a function of the year only ( $P < 0,05$ ), plus an interaction between season and study block. A generalized linear model (McCullagh & Nelder 1989) was then created to show the logit values as proportions and Fig. 6.30 shows that, in every year of the study, there was an increase in the proportion of available habitat occupied. Interactions of year were significant ( $P < 0,05$ ) only



**Fig. 6.29** Gartmore: multifactor analysis of variance showing variation in mean territory size (with 95% confidence limits) with burning treatment.



**Fig. 6.30** Gartmore: generalized linear model from logit transformation of proportions of habitat (means and 95% confidence limits) used in each year of the study.

in the north study block, where the proportions used in years 1 and 2 (1988-89 and 1898-90) were much lower than those used in years 3 and 4 (see Table 6.8), when habitat in this block had improved sufficiently to support one extra territory. Thus at this site it appears that conditions continued to improve throughout the study period and, as discussed above, further improvement might allow the southern block to accommodate an extra territory. Considering the habitat type, ten territories are probably all that this site could carry under optimum conditions.

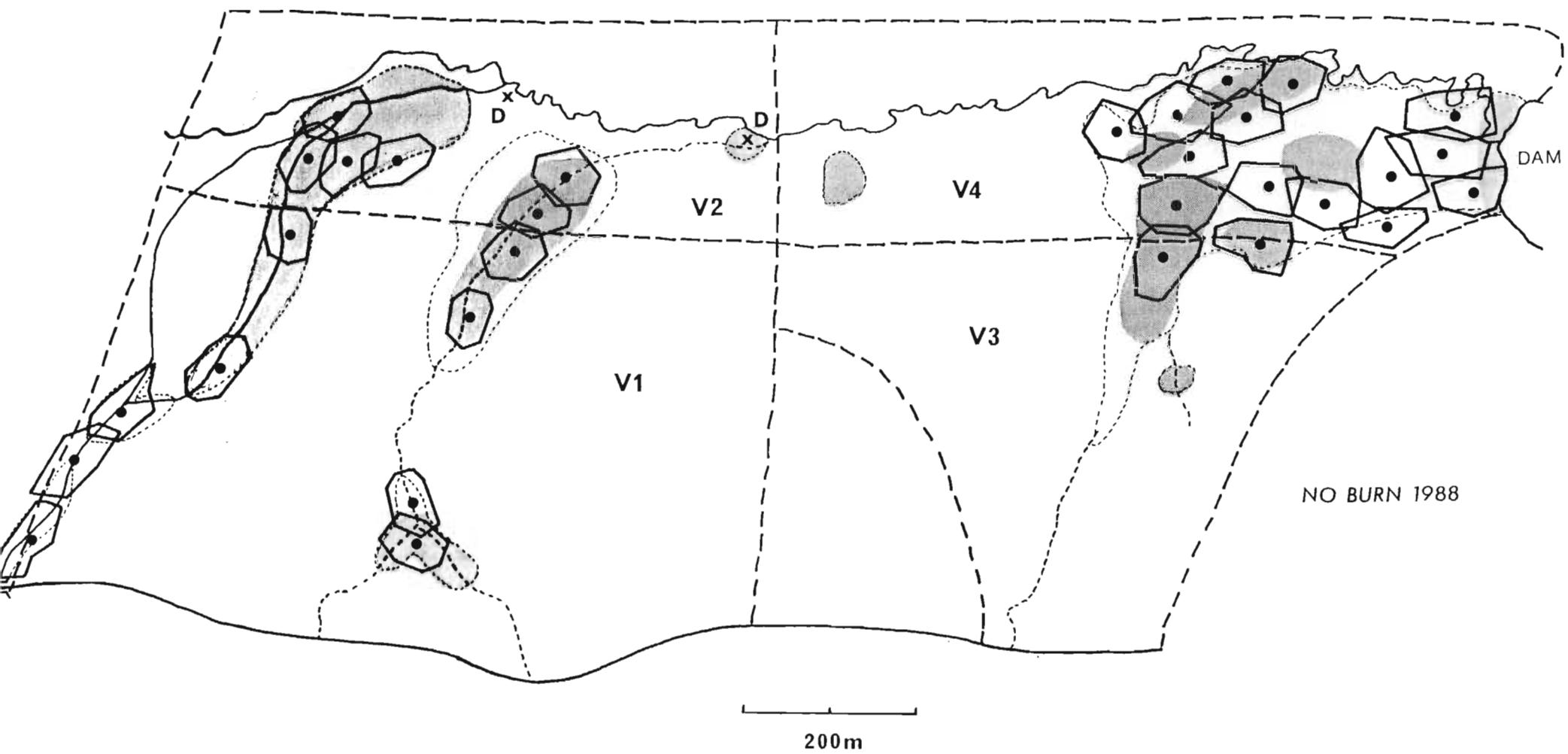
#### **6.4.2.3      Mt Currie, Kokstad**

The study site's Redchested Flufftail habitats are fragmented and comprise both permanently wet and seasonally inundated areas (Fig. 2.32). As at Gartmore, the extent of suitable habitat varies from year to year as a result of differences in annual precipitation, such variations usually being most marked in seasonally inundated areas. During the study period it also became apparent that the permanent reedbeds (comprising principally *Phragmites*, *Typha*, and the larger sedge species) along the three drainage lines showed annual variations in their overall shape and size, these being recorded during aerial surveys and by observation and mapping from the adjacent mountain slopes. Such changes were presumably linked to annual variations in the depth and extent of flooding, and to differences in the burning schedule from year to year. In such an extensive area of diverse vegetation types the overall situation with respect to variations in habitat availability is complex and dynamic, and could not be clarified during this project. However, taking into account the obvious effects of annual variations in precipitation and burning (the two most important agents of flufftail habitat change at this site), it was possible to suggest explanations for the observed changes in the numbers of Redchested Flufftail territories at the site.

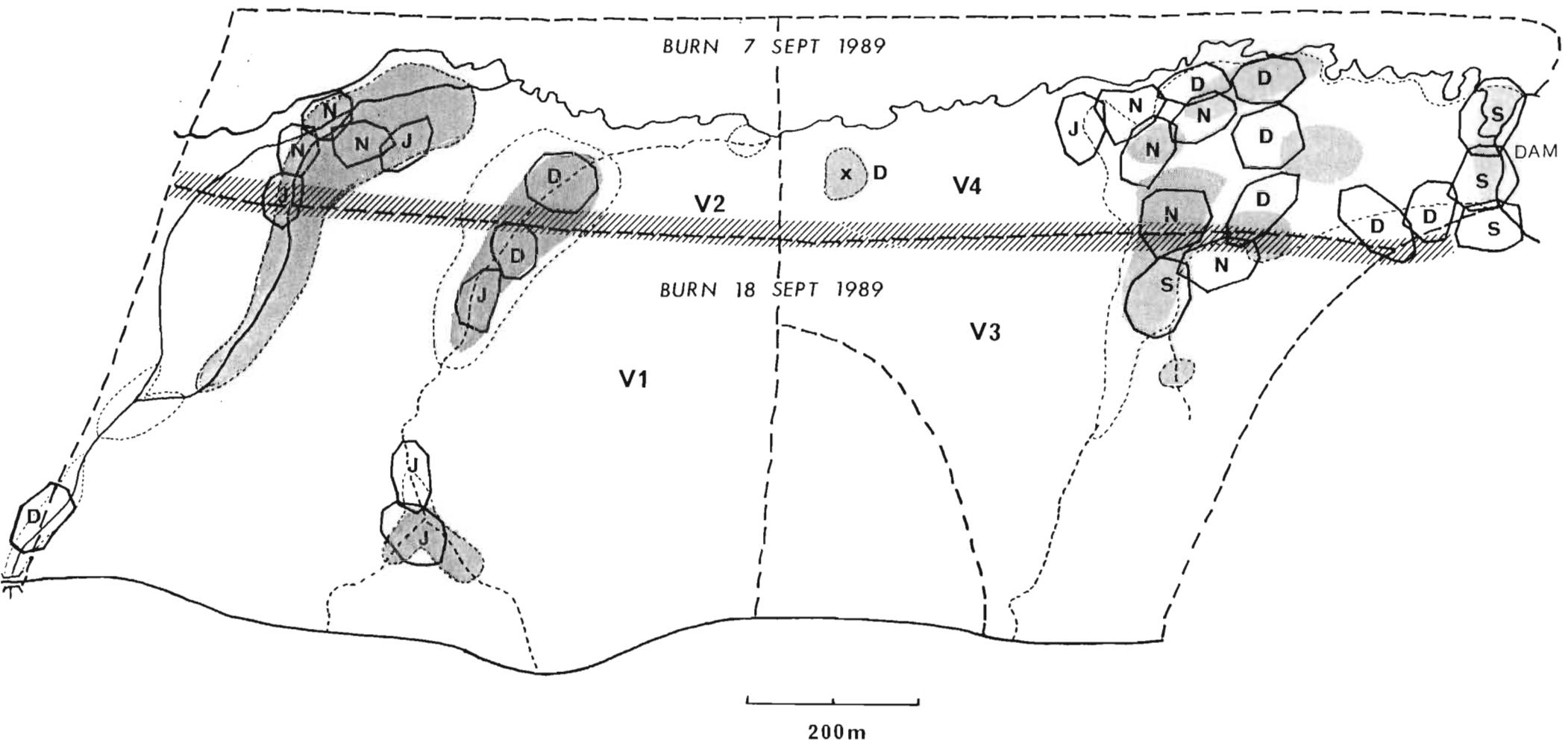
Results of the study are summarized in Figs 6.31-6.37. Most Redchested Flufftail territories were permanent but in the 1988-1989 and 1989-1990 breeding seasons two breeding territories in seasonally inundated hygrophilous grass and sedge meadow were vacated in April and June. The sizes of the territories ranged from some of the largest recorded during the study (comparable in area and habitat type with those at Gartmore) to relatively small areas in extensive permanent reedbeds (see Chapter 5, Table 5.2). In view of the time and difficulties involved in the frequent mapping of the many territories, and especially of the varying amounts of habitat, in this relatively large and complex wetland system, detailed comparisons between territory sizes and available habitat areas could not be made for all wetland patches in all years. The overall effects of burning were therefore assessed on a broader scale than at the other two study sites, principally with reference to the number of territories which the area supported from year to year.

The 1988-1989 breeding season was notable for its high rainfall (Fig. 2.30A) the July-June total being 30% above the long-term mean. High summer rainfall at this site, if spread over the whole breeding period, has the effect of increasing the amount of available breeding habitat (by more extensive waterlogging and inundation of grassland) but, if very high, may also produce flooding deep enough to reduce the available habitat in some permanently wet areas. In this season these two effects were both felt, more extensive habitat being available in Block V4 after good early summer rain, but January floods making some parts of this block temporarily uninhabitable, so the overall breeding habitat availability was probably about that of a more average rainfall summer. Before 1990 the entire study area was spring-burned biennially, the last burn having been in September 1987, so in late 1988 the area had good vegetation cover, having enjoyed the maximum period normally allowed for its development. The July 1987 to June 88 period had exceptionally high rainfall, 1 293 mm being recorded (66% above the mean), 602 mm (47% of the total) falling from January to March, and the resulting high water levels must have reduced breeding habitat availability, while flooding possibly had some adverse effect on breeding success. Taking these factors into consideration, it was judged that the habitat in the 1988-1989 summer was of good quality and average extent, but that the resident flufftail population had probably been unable to attain its potential maximum in the previous season and thus that the 31 breeding territories mapped in January 1989 (Fig. 6.31) did not represent the maximum number which the site was able to support under the biennial total-burning schedule. Of these 31 territories, 29 were still occupied during the 1989 winter (Fig. 6.36).

The 1989-1990 spring burn was also total, but the area was divided into two blocks by a firebreak, and one block was burned 11 days after the other (Fig. 6.32); the only beneficial effect of this was apparent in one territory on the V4/V3 border, which was partially burned twice, neither burn reducing its area sufficiently to force the birds to leave (see Chapter 5). This was one of only four territories remaining after the burn, the other three being at the reedbeds of the dam intake. The 1989-1990 rainfall was 3% above the mean, being very high in November and December and very low in January and February (Fig. 2.30B); this resulted in good vegetation growth early in the season but some reduction in seasonal flooding later, so that in January slightly less breeding habitat was available than in the previous summer. Recolonization took place from November to January, as shown in Fig. 6.32, 27 breeding pairs were present in January 1990, and 25 remained into the 1990 winter. The reduction in breeding numbers from those in 1988-1989 was attributed to the somewhat less extensive and poorer-quality habitat available in January 1990, this probably being a result of the combined effects of the lower rainfall and the time needed for cover to develop after the burn. Block V1 suffered the greatest reduction in numbers (Fig. 6.37); in comparison, the situation there in the following season (when it was not burned) shows a doubling of the breeding population by January



**Fig. 6.31** Redchested Flufftail territories at Mt Currie, January 1989. x = isolated occurrence, with month initial (December). V1-V4 = vlei burning blocks. Total no. of territories = 31.



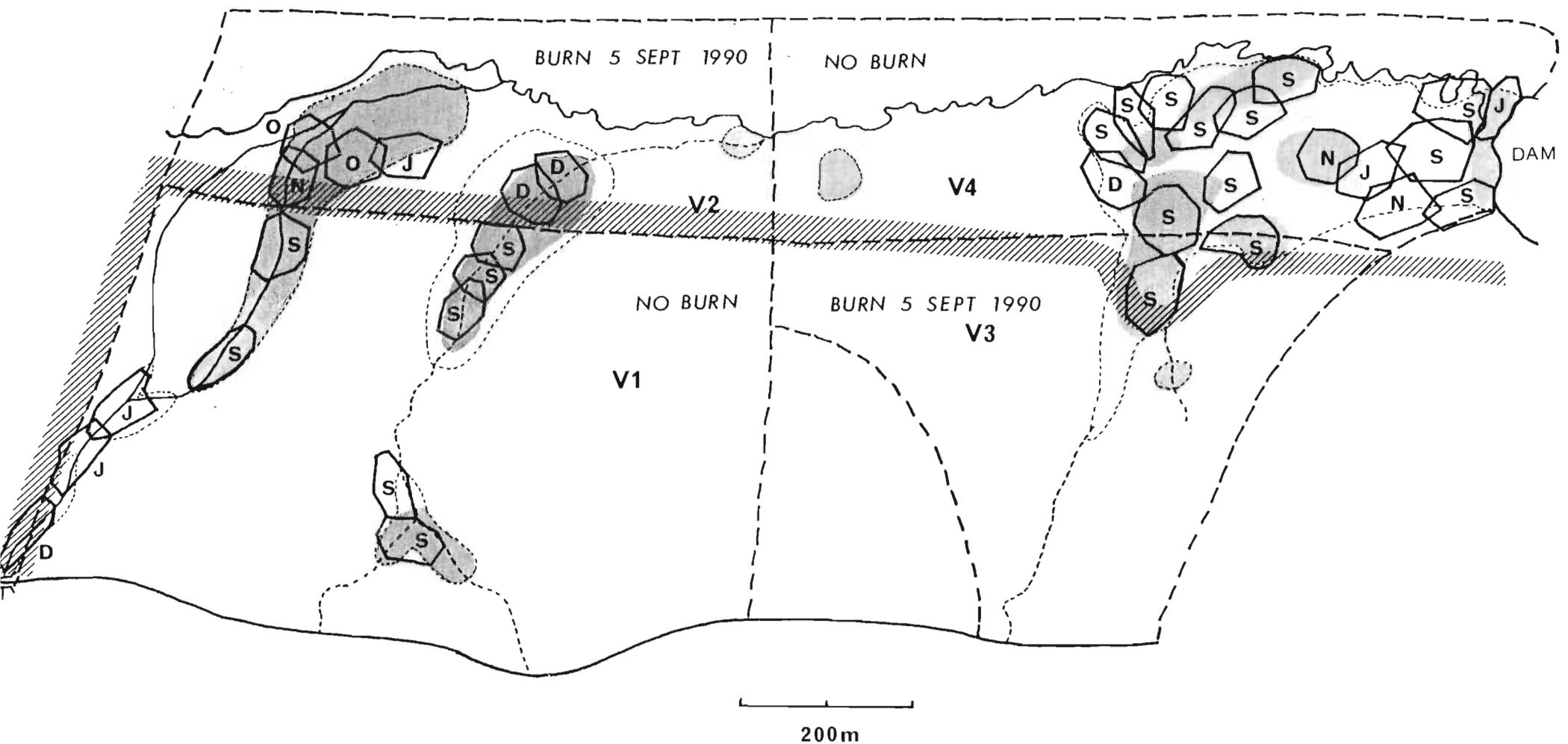
**Fig. 6.32** Redchested Flufftail territories at Mt Currie, January 1990. Return month is indicated by the month letter initial within each territory (D = December; J = January; N = November; S = September i.e. the birds did not vacate the territory after the burn). Hatched line = firebreak. Total no. of territories = 27.

1991, the population buildup during the 1990-1991 period beginning as a result of good winter-habitat availability (see next paragraph).

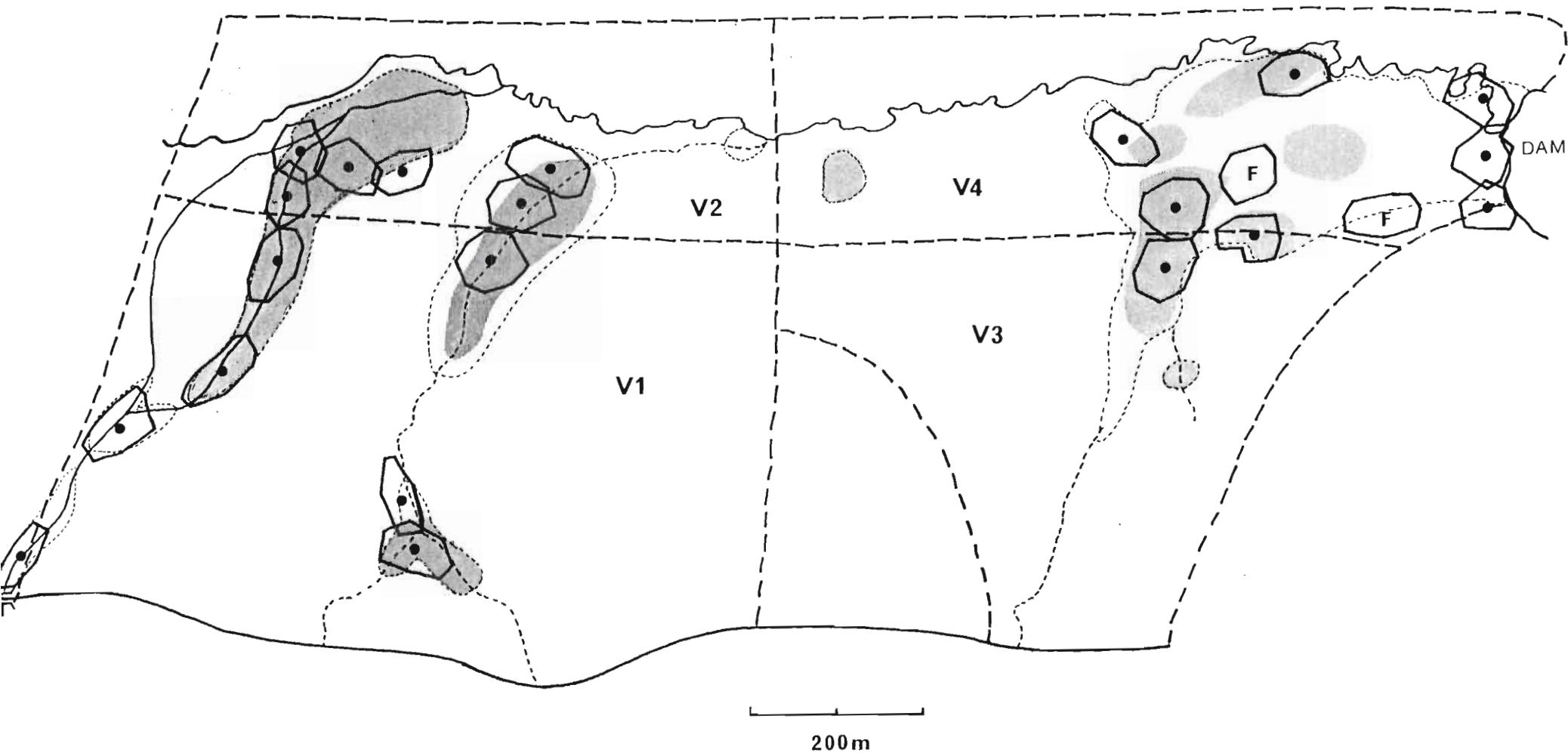
In 1990 the study site was divided into four burning blocks (V1-V4), of which two were burned in September (Fig. 6.33). This resulted in only the six pairs in Block V2 being forced to vacate their territories, at least one of these pairs moving into the adjacent unburned Block V1, which had plenty of good winter/spring habitat and was able to support three extra pairs during September. The unburned Block V4 lost two pairs in September, from areas which had dried out and become extensively flattened in July and August, so that 20 pairs were in residence after the burn. Total precipitation in 1990-1991 was 91.5% of the mean, being poor in November and very high only in January (Fig. 2.31A). By mid-January 1991 flooding conditions were judged to be normal and the site held 34 breeding pairs of Redchested Flufftails (Figs 6.33, 6.36), the highest recorded during the study. More pairs were present in three areas than in January 1989 (Fig. 6.37), when the previous highest total of 31 pairs was recorded and when habitat availability was at least as great and no areas had been burned in the spring. Compared with January 1990, when Blocks V1 and V4 supported 18 pairs after the spring burn, in January 1991 these blocks supported 24 pairs after not being burned; the extent of flooding in these blocks was judged to be similar in both seasons. Block V2 held the usual six pairs, while the dam intake accommodated an extra pair in January as a result of the normal residents' movement out into good-quality seasonally flooded grassland in the vlei (Fig 6.33).

Despite this excellent start, the 1990-1991 season ended disastrously, for the birds and for this aspect of the study. A severe hailstorm on 18 January (described in Chapter 7, Section 7.4.12) reduced the number of pairs to 23 (Fig. 6.34), seven pairs being lost from Block V4 alone, which was particularly badly damaged. Some Redchested Flufftails may have been killed, as probably were some Striped Flufftails in nearby dry grassland on the mountain slopes; although more shelter may have been provided by the wetland vegetation than by this dry grassland, the Block V4 reedbeds were very badly damaged, the *Typha* and *Phragmites* plants being broken down to half their previous height and large expanses of sedges and hygrophilous grasses being flattened. No Redchested Flufftail corpses were found, but broken Redchested Flufftail eggs were washed out by the heavy rain and floods which immediately followed the hail. No population recovery took place during the remainder of the summer, numbers being further reduced in March, when two more pairs disappeared from Block V4 (Fig. 6.34). The remaining birds wintered undisturbed until the spring burn in September 1991 which, covering Blocks V2 and V4 which held the most birds, reduced the number of pairs to eight (Fig. 6.35).

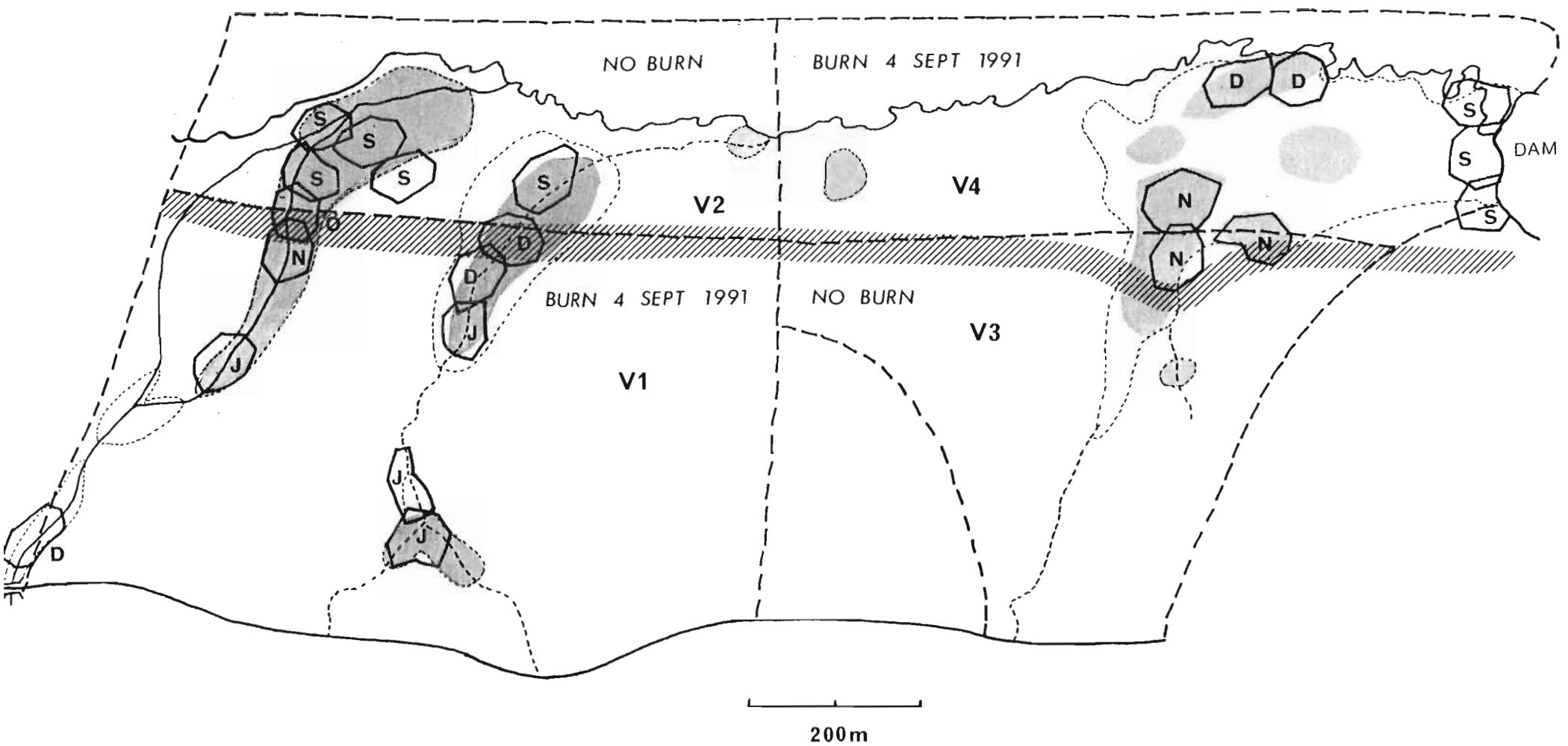
Rainfall in 1991-1992 was average (Fig. 2.31B) but in the early summer apparently was not high enough to produce the extent of habitat available in previous seasons, while January rainfall was



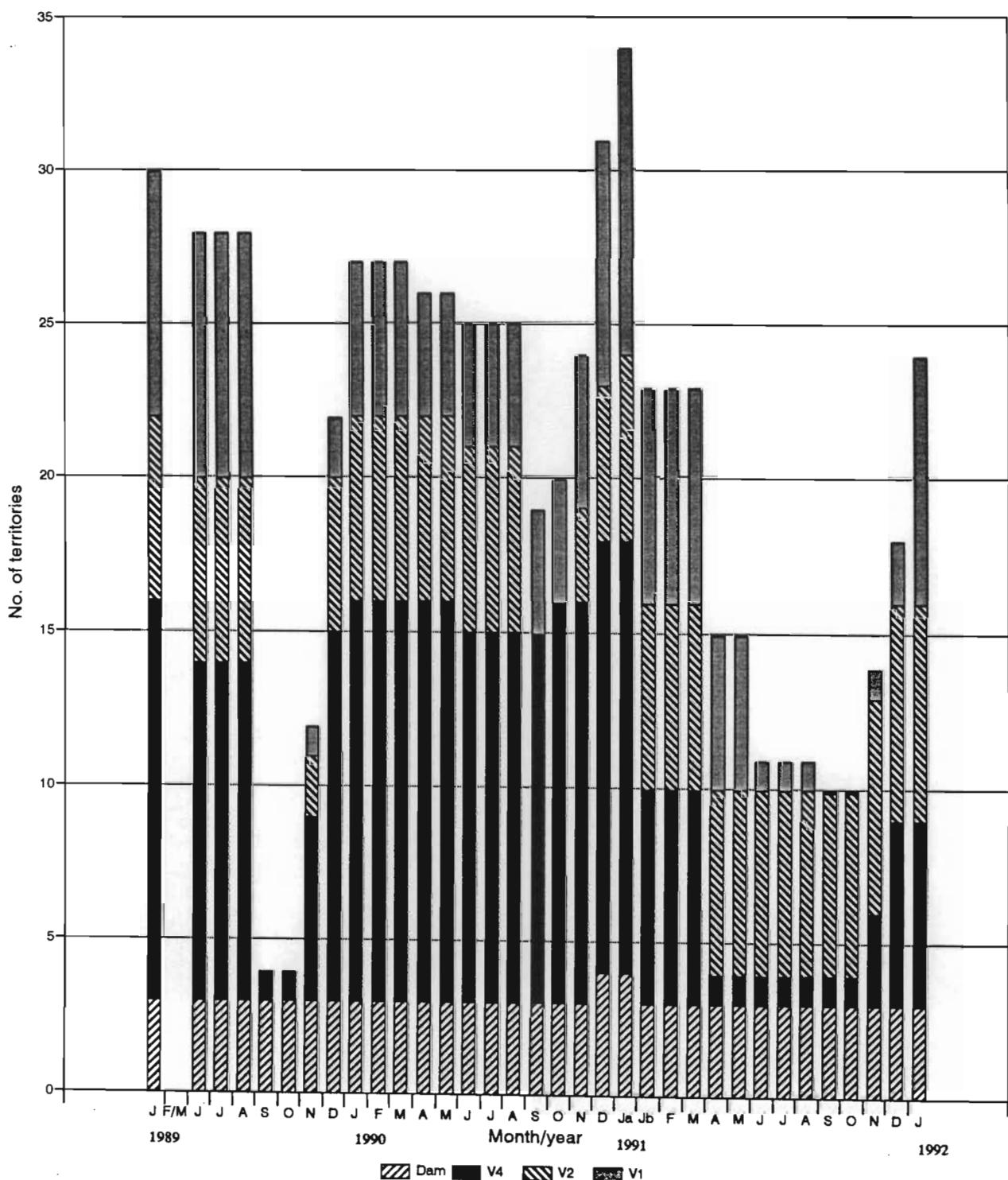
**Fig. 6.33** Redchedest Flufftail territories at Mt Currie, January 1991, before the hailstorm on 18 January. Return month is indicated by the month initial within each territory (D = December; J = January; N = November; O = October; S = September i.e. the birds did not vacate the territory after the burn). Hatched line = firebreak. Total no. of territories = 34.



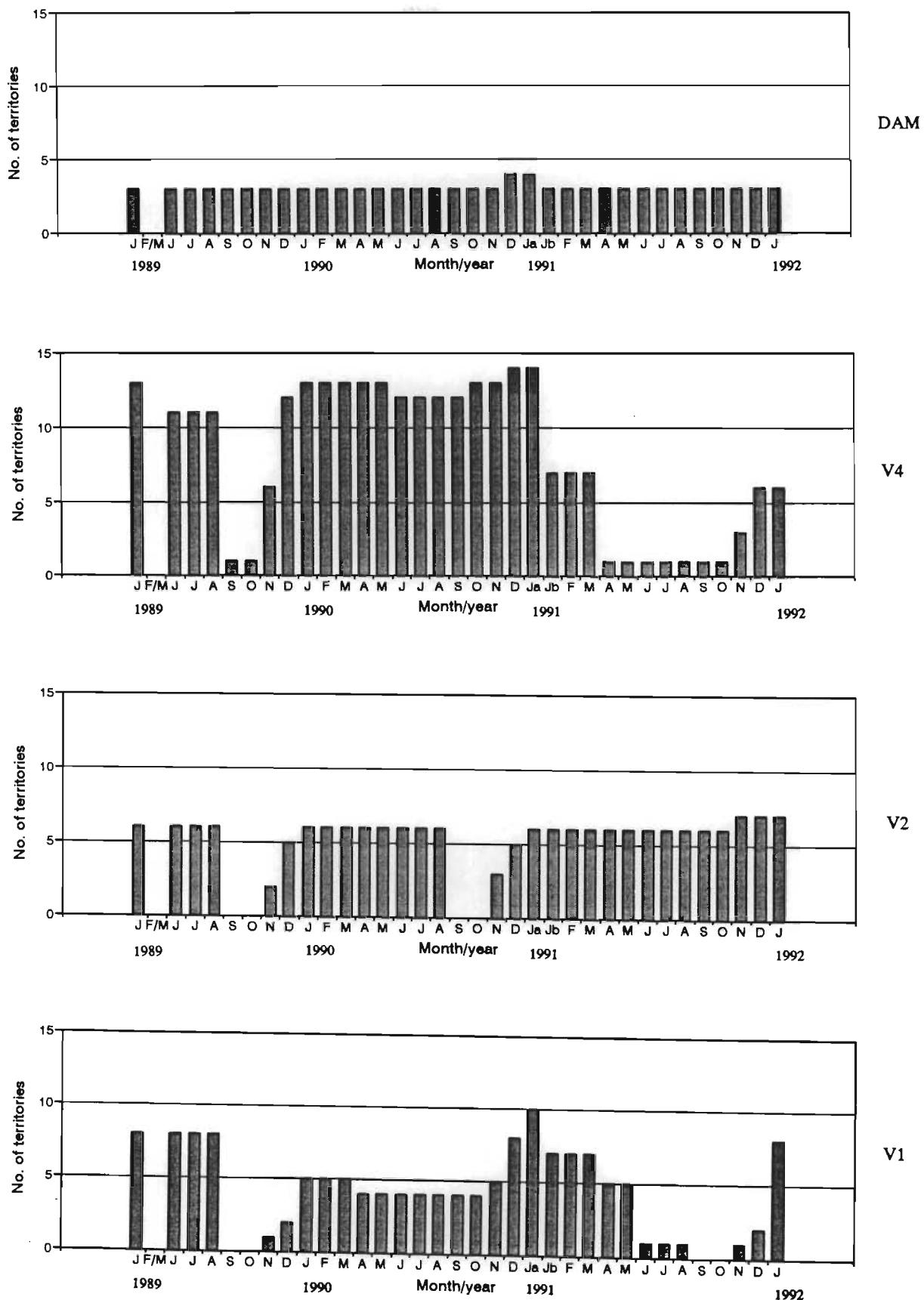
**Fig. 6.34** Redchested Flufftail territories at Mt Currie, January 1991, after the hailstorm on 18 January. F = territory vacated in February 1991. Total no. of territories = 23 in February.



**Fig. 6.35** Redchested Flufftail territories at Mt Currie, January 1992. Return month is indicated by the month initial letter within each territory (as for Fig. 6.29). Hatched line = firebreak. Total no. of territories = 22.



**Fig. 6.36** Monthly total number of Redchested Flufftail territories at Mt Currie, January 1989 to January 1992 (excluding February-May 1989). Totals for the dam intake and the vlei blocks V1, V2 and V4 are shown.



**Fig. 6.37** Monthly total number of Redchested Flufftail territories at Mt Currie, January 1989 to January 1992 (excluding February-May 1989), by survey block (dam intake and vlei blocks V1, V2 and V4).

relatively poor. In January the vlei habitats were drier than they had been in any previous season of the study and strong winds had flattened large patches of hygrophilous grass and sedge meadow habitat. Birds returned to burned areas from November to January and the last detailed mapping exercise was undertaken in January 1992, when 22 pairs were present (Fig. 6.35). This total compares poorly with that in 1989-1990: neither of the burned blocks recovered the high numbers of birds present in January 1991, nor did they even attain the relatively low numbers present in January 1990. The January 1992 numbers certainly reflect the poor quality of the breeding habitat, but it is not clear to what extent they were also influenced by the long-term effects of the hailstorm and the subsequent burn of two densely-populated areas.

Leaving aside the situation in the 1991-1992 summer it is clear that, after the introduction in 1990 of the biennial partial burning schedule, there was an overall small increase in the number of pairs of Redchested Flufftails. This increase, giving January 1991 numbers higher even than those in January 1989 when no burn had taken place, could not be fully explained by any increase in habitat extent, but is suggested to have been the result of an improvement in the quality of the habitat which had not been burned for one year coupled with a greater population buildup due to the presence of extensive wintering habitat and a successful previous breeding season. However, the significance of this increase is difficult to determine in the absence of detailed measurements of habitat availability and territory sizes. A multifactor analysis of variance was done to show the effects of burning treatment on the number of territories in each block during each year of the study, excluding the post-hail data. Three burning treatments were defined: a total burn, no burn and a partial burn (two blocks out of four). The analysis showed that neither year nor treatment had a significant effect on territory numbers ( $P > 0,6$  in both cases), and there is no statistical substantiation for my impression that habitat and conditions were improving as a result of the partial burning schedule. Although one could not expect as much improvement at Mt Currie, where a biennial burning schedule was already in operation, as at the other two study sites, which had not been burned for several years, the noticeable improvement in January 1991 suggested that a continuation of the experiment might yield significant results. However the January 1991 hailstorm had a severe negative impact on the flufftail population and its effects appeared to be long-lasting. A multifactor analysis of variance showed that there was a highly significant difference ( $P < 0,01$ ) in the effects of the hailstorm on territory numbers in the southeastern block (V4) and the two northwestern blocks (V1 and V2; see Figs 6.33 and 6.37), V4 showing a much greater reduction in numbers than the other blocks; observations of vegetation damage indicated that it was the block most severely affected by the storm.

#### 6.4.3 The effects of burning and mowing on invertebrate availability

The Allerton samples (Table 6.10), though few and taken only on two visits, show that food availability is unlikely to be a factor influencing the time of recolonization in burned or mown wetland vegetation. The majority of arthropods encountered were either small flies (especially on wet substrates) or small ants (on dry substrates), with some spiders and a few adult individuals of other groups, such as Coleoptera, Hemiptera, Cercopidae and Acrididae (grasshoppers); all except Cercopidae and grasshoppers are known to be eaten by Redchested Flufftails (Chapter 1, Section 1.2.2.3; Chapter 4, Section 4.4.6). Invertebrates were most numerous in the wet-burned vegetation and least in the dry-cut sedges (Table 6.10), and numbers increased greatly at all sites between the two sampling dates, so that on 20 October (day 37) the invertebrates were too numerous to sample at the wet site. On this day even the lowest recorded density ( $17,3/m^2$ ), at the dry site, considerably exceeded the maximum summer density ( $12,8/m^2$ ) measured in the dry-grassland habitats of the Striped Flufftail (Chapter 7, Section 7.4.8). It was considered that, in late October, lack of food was unlikely to have been responsible for the absence of Redchested Flufftails from the wet areas, which they did not occupy until early December (about day 80), but rather that the vegetation height and cover, which averaged 79 cm and 58% at the wet site (Figs 6.1 and 6.2), were insufficient to allow recolonization. Furthermore, at both this and other burned sites Redchested Flufftails were sometimes seen foraging in extremely short, sparse wet vegetation at the edge of denser cover in which they lived, obviously exploiting the abundance of invertebrates which were relatively easy to find in the open regenerating growth. Other rallid species exploited burned wet ground more extensively: for example at Mvoti Vlei on 15 July 1992, just after a very extensive burn, Black Crakes and African Rails were able to remain in the vlei by foraging in very open, wet, burned areas adjacent to patches of unburned *Typha* and *Phragmites* along streams where the birds could shelter; obviously the food supply was sufficient, even on very open burned ground. When disturbed the birds flew to cover up to 100 m away. Redchested Flufftails were not present in the burned areas, because they require denser cover than the other species and never feed far from cover on open ground. At Allerton, Black Crakes and African Rails made brief foraging trips into wet burned areas throughout the regrowth period, although they did not spend long periods in the growing sedges until mid-November, 60 days after the burn (Section 6.4.1.1).

TABLE 6.10

Number of invertebrates per square metre in burned and mown *Cyperus dives/Mariscus solidus* sedge beds at Allerton, October 1989. Day = number of days after burning and mowing (both on 13 September 1989). No attempt was made to count invertebrates in shallow water and mud at the wet site. Sample size was 20 50-cm-square quadrats per site. See text for further details of invertebrate groups.

Sampling site	Day	Invertebrates/m <sup>2</sup> :				Total
		flies	ants	spiders	other	
Dry burn	18	4,4	3,2	1,6	0,8	10,0
	37	4,0	23,9	2,7	6,7	37,3
Dry cut	18	1,2	0,4	1,2	0,8	3,6
	37	4,7	10,6	1,3	0,7	17,3
Wet burn	18	29,2	0	0,4	0,8	30,4
	37	(Too numerous to sample accurately)				
No burn	18	(Dead vegetation too dense to be sampled)				

#### 6.4.4 Substrate conditions at recolonization time

These are fully dealt with in Sections 6.4.1 and 6.4.2. Throughout the study and survey areas, no birds were ever found to recolonize vegetation on dry ground at the start of the breeding season and every territory, when reoccupied after a burn, had a significant proportion of its substrate at least moist (and often saturated to shallowly flooded), this apparently being a prerequisite of good vegetation growth. Recolonization of any type of burned vegetation at the sampling sites was always earliest in areas with the best cover, which were often on the wettest substrates, although at the Mt Currie *Carex* site (Section 6.4.1.3) moist ground had the greatest vegetation growth and was occupied first.

### 6.5 Discussion

#### 6.5.1 Vegetation regrowth and reoccupation times

This study provides the first comparative assessment of wetland vegetation regrowth on substrates of different degrees of saturation and most of the results are not comparable with those from other studies, which have followed growth patterns for much longer periods (usually at least one year) and which have usually compared overall productivity after a burn with that of an unburned control area. The aim of my sampling was only to establish differences in early vegetation development which might affect the timing of reoccupation by Redcrested Flufftails.

Considering the observed regrowth rates it is clear that soil moisture affects the development of the burned vegetation. All the vegetation types developed taller, denser vegetation more rapidly on ground which was saturated or shallowly flooded than on ground which was dry, while at Allerton and Gartmore the vegetation on the driest ground grew more rapidly after the substrate had become moist. This accords with observations made during a study of a Canadian *Typha* marsh community (Mallik & Wein 1986), where the cover and frequency of unburned *Carex* species increased when ground was flooded and decreased when it was drained. My measurements at Allerton provide a striking example of the great increase in new growth which is encouraged by burning sedge beds and this, as well as producing better conditions for movement and foraging (by removing low, dense, dead vegetation), must provide a greatly increased food supply for many of the arthropods upon which the flufftails feed. An analogous growth situation was observed in *Phragmites* beds by Thompson & Shay (1985), who attribute the higher shoot density after burning to the effect of the removal of litter, while Sharow & Wright (1977) found that grassland herbage production in the early growing season was

considerably higher where litter had been removed by fire. Burning is known to stimulate tiller production in perennial grasses and one of the most important factors influencing this tillering is light intensity (Everson 1985; Tainton & Mentis 1984; Thompson & Shay 1985), so the increased light reaching the soil surface after a burn should result in a higher shoot density in *Phragmites* (Thompson & Shay 1985).

Burning in grassland is known to affect the soil moisture content as a result of increased evaporation and more rapid drying out of the soil (relevant references are reviewed by Tainton & Mentis 1984). These effects may also apply to burning in seasonally dry hygrophilous grass and sedge communities and it is necessary to consider whether they might affect the regrowth of this vegetation type. It is thought unlikely that post-burn loss of surface moisture would adversely affect growth: not only are the surface soils in these areas often already very dry when burned, but the deep roots of the plants should obtain moisture from levels unaffected by the burn.

The *Carex* sedges showed different growth patterns and flowering periods from those of the *Cyperus* and *Mariscus* species, both in burned and unburned stands and on wet and dry substrates, while the growth pattern of *Typha* differed from those of all the sedges studied. The *Carex* developed most rapidly on moist ground and was reoccupied comparatively soon after burning (48 days), when it was relatively short but dense, while the *Cyperus/Mariscus* vegetation grew most rapidly on flooded ground and was reoccupied after a much longer period (80 days) when it was taller but less dense. The more rapid development of vegetation on the firebreak at Gartmore suggests that flufftail habitat might be further improved, at least in the mixed sedge meadow/hygrophilous grass communities, by a somewhat earlier burn, in August rather than early September.

The burned wet *Cyperus/Mariscus* sedge beds flowered a month later than the dry beds, in contrast to the *Carex* beds where the burned wet plants flowered slightly earlier than the drier plants. In the unburned sedges the difference in flowering was very striking, the Mt Currie *Carex* flowering early and almost completely while the Allerton sedges flowered over two months later and very poorly. The reasons for these differences are not clear, but it may be unwise to compare the flowering patterns of *Carex*, a predominantly temperate genus, with the more tropical *Cyperus* and *Mariscus* (K.D. Gordon-Gray pers. comm.). Both the observed early flowering and the increased flowering-shoot production in some sedges at my study sites may have been directly stimulated by fire: flowering of some plants has long been known to have an obligate dependence upon fire and the production of flowers in the South African fire-lily *Cyrtanthus ventricosus* is rapidly stimulated by smoke (Keeley 1993). Spring burning has been shown to improve flowering-shoot density in *Phragmites australis* (Thompson & Shay 1985), but to a much lesser extent than it did in the burned sedges at Allerton. Baijnath & Getliffe (1977) observed the effects of fire on three *Cyperus* species

of dry ground in Natal and found that one (*C. prolifer*) responded by undergoing rapid vegetative growth, while the others (*C. sensilis* and *C. x turbatus*) responded by an increase in flowering.

At Ntabamhlope Vlei, Natal, Downing (1966) found that *Typha capensis* plants grew most rapidly in November and December, flowered from late December (when growth almost ceased) and died back in April. These observations agree well with those of growth and flowering patterns made on burned and unburned *Typha* at Mt Currie during this study.

A regrowth period of 70-80 days appeared to be the norm for most wetland vegetation types to become suitable for reoccupation after a spring burn (Table 6.2), by which time they ranged from being relatively short but dense (most sedges) to very tall and less dense (*Typha*). The hygrophilous grassland at Mt Currie took longest to become suitable, and was short but very dense when occupied, and this vegetation type was presumably sub-optimal breeding habitat both because of the late occupation date and the fact that some of it was unsuitable for permanent territories, being vacated at the end of the summer. This contrasts with the situation at Gartmore, where mixed sedges and hygrophilous grassland supported permanent territories and were occupied after an 80-day period, when they were still relatively short and sparse (Table 6.2). The reason for these differences is probably related to the structure of the vegetation: that at Gartmore is tussocky and robust, with a mosaic of patches of permanently dense cover and more open areas, while that at Mt Currie is more continuous and much more prone to become flattened at the end of the summer. The different species of sedges and grasses in these two vegetation types (see Chapter 2, Sections 2.2.5.1 and 2.2.13.1) appear to be at least partly responsible for this situation.

Mowing at Allerton promoted less development of leaves and cover in the sedges than did burning, on a substrate which progressed from dry to moist. In contrast, spring mowing of local grassland (tall sourveld) produced slightly higher yields of living material, and more leaves, than did burning (Tainton *et al.* 1977), this being a result of the greater destruction of tillers in the burning treatment. This situation is probably not comparable with that in marsh vegetation, where the destructive effect of spring surface burns on the protected buds and underground perennial parts of sedges should be negligible, as it is in *Phragmites* (Thompson & Shay 1977). The mown sedges at Allerton appeared to produce relatively few new leaves, but the cut leaves continued to grow, and it is possible that there was less stimulus for regrowth after the mow than after the burn (K.D. Gordon-Gray pers. comm.). In hygrophilous grassland at Gartmore the mowing, although two weeks later than the burn in equivalent habitat, apparently produced an equal or greater growth since both areas were occupied at about the same time; however (as was the case after the following year's burn) the presence of rapidly-growing exotic brambles may have enabled the mown area to be occupied earlier than if it had contained only grass.

### 6.5.2 Relationships between return time and habitat variables

The results show that the time of return to burned vegetation is related to the development of the vegetation and to the substrate water content. It is clear that birds return only when virtually all the substrate is moist to flooded, and also that the availability of invertebrate food is not a factor influencing return time: food is abundant early in the summer, when vegetation is still relatively poorly developed, and the food resources of burned ground are exploited (by brief forays from adjacent cover) before that ground is reoccupied. Moist to flooded substrates encouraged better development of vegetation height and cover in all the habitat types investigated, and the most critical factors influencing return time seem to be the development of a suitable density of canopy cover (at least 55% and usually over 65%) and the concomitant attainment of a suitable vegetation height. The analysis of precise return dates (MANOVA 1) suggests that return time is less affected by vegetation height than by cover, but the height effect is important, as is shown in the analysis of return months (MANOVA 2) and the ANOVA analysis (Tables 6.5 and 6.4), which both give an early return time for the tallest vegetation. It is clear that the effects of height and cover are complementary, and birds will return to vegetation such as *Typha* when cover values are still relatively low but height is exceptionally great, while the very shortest vegetation types are correspondingly very dense (Table 6.2).

In a complex mosaic of plant species and substrate saturations such as that of the wetlands studied here, it is difficult to explain recolonization timing adequately in terms of the few broad habitat variables which were used in this study. However the analyses and models, both of precise dates and of return months, do provide a reasonably comparable measure of the effects of vegetation type and substrate moisture on the birds' return times. Using the values in Table 6.4 it is reasonable to state that return time to the tallest *Typha*-dominated permanently flooded vegetation should be 11-13.5 weeks (75-94 days) after a spring burn, and 15-20 weeks (105-138 days) to the shortest vegetation on seasonally dry substrates. The largest difference in predicted return times is that for the flooded tallest sedges of vegetation type S/C (*Cyperus*, *Mariscus*, *Carex*, etc.) and this has been discussed earlier (Section 6.4.1.4). This vegetation type includes many different sedge species occurring on both moist and flooded substrates; it is an over simplified classification, necessitated by the small number of observations available for most of its recognizable subdivisions. The MANOVA 1 time of 49 days applies to the quickest-developing moist *Carex* habitats and the MANOVA 2 time of 100 days is not close to that observed in any Table 6.2 territory falling within Type S/C. Return times of about 100 days (14 weeks) were observed mainly in mixed-species sedge beds at Gartmore and Mt Currie, on ground which was at first moist and sometimes became flooded as the season

advanced. When considering the majority of sedgebed vegetation types falling within this category, it is better to predict return dates on the basis of the degree of saturation, using the estimates from the ANOVA and Model 2, where three saturation factors were recognized. These predict that sedges on permanently flooded ground should be reoccupied after 67–69 days (10 weeks) and those on moist to seasonally flooded ground after 94–97 days (14 weeks). The latter figure agrees well with the MANVOA 2 estimate for this vegetation type.

The timing of return to initially dry substrates, which predominantly hold vegetation of type VS/T, is consistently estimated at 14–16 weeks (94–112 days), January-flooding areas not being suitable for 18 weeks (Section 6.4.1.4). The ANOVA breakdown (Table 6.5) into 86 days (12 weeks) for permanently wet, very short vegetation and 114 days (16 weeks) for seasonally flooded vegetation gives an idea of the differences in return time imposed by seasonal flooding in this habitat type.

A discrepancy occurs between the observed and predicted return times for mown vegetation at Gartmore. Return was noted in this vegetation after about 75 days (Section 6.4.1.2), whereas the estimates for vegetation of type VS/T and seasonally wet substrates range from 86 to 114 days. Comparisons with the burned vegetation may not be valid, however, not merely because the vegetation was mown 2½ weeks after the burn but also because of the presence of exotic brambles, which provided quick-growing dense cover (Section 6.4.1.2).

### **6.5.3 Dispersion, territory size and habitat quality**

When assessing the effects of burning on flufftail dispersion, a factor to be considered is the theoretical possibility that sequential settlement in fixed locations can produce a lower-than-optimal density of birds (Maynard Smith 1974). Experiments have shown that more birds will occupy an area if all territory holders are removed simultaneously than if they are removed and replaced individually (Falls 1978; Knapton & Krebs 1974). Thus, increased density after total removal by burning could rather reflect a more optimal arrangement of pairs than an improvement in habitat quality. However the other removal situations differ from that involving flufftails in one important respect: removal is not accompanied by any major habitat change. The possible operation of an optimum density adjustment after total removal by burning is difficult to assess, especially in wetland habitats where several factors may contribute to a considerable year-to-year variation in habitat quality and extent, but it is considered unlikely to occur because (a) no increase in the number of pairs occurred in the southern study block at Gartmore after two experimental burns, and (b) the maximum numbers of pairs in Blocks V1 and V4 at Mt Currie did not occur until the second summer after a burn, following (in Block V1) initially low breeding numbers and a buildup during the intervening winter (Section

5.4.2.3). Even if this effect did operate, it would still provide justification for periodic burning to encourage an optimal utilization of space in the available habitat.

At Allerton the impermanence of territories 1 and 5 indicates that in small permanent reedbeds dry habitat is not favoured, especially when it is choked with moribund vegetation. In such habitat the birds would probably need to expand their territories in winter, which was not possible in the circumscribed area of these reedbeds. Although they were never burned, territories 2 and 3 were always permanently occupied, presumably because of their almost complete permanent flooding and the less moribund vegetation which they contained.

The increase in suitable habitat after burning at Allerton was not sufficient to allow more pairs of birds to be accommodated, but did allow the existing pairs to extend their territories and thus may have had a beneficial effect in providing a greater foraging area both in summer (for rearing young) and in winter (for supporting resident immatures), as well as being an additional safeguard against enforced emigration as a result of extensive habitat reduction (see Section 6.5.4 and Chapter 5). In captivity, Redchested Flufftails in large aviaries laid larger clutches and nested more frequently than those in small ones (Chapter 4, Section 4.4.10.2.).

At Gartmore the effects of post-burn improvement in habitat quality are shown by the increase in the carrying capacity of the northern block, while the overall reduction in territory size and increase in the percentage of habitat occupied were both significant.

At Mt Currie most territories are permanent and the results showed that the number of territories did not vary significantly in any season (before the hailstorm), whatever the burning treatment. However the 45% reduction in the number of territories in block V1 after the complete burn in September 1989 suggests that complete burns may sometimes have a marked effect and, even though recovery was complete after the year with no burn (Fig. 6.37), a series of annual complete burns might have a cumulative adverse effect on the flufftail population. It is reasonable to assume that a biennial complete burn is preferable to an annual one and, as no wetland-dependent animal species in Natal have been shown to have a recovery period longer than two years after a burn (Kotze 1993), a biennial cycle is probably adequate for overall wetland management. It is also possible that, in many Natal wetlands occupied by Redchested Flufftails, a triennial cycle might also work well, although this has not been tested, but my observations suggest that wetlands which have not been burned for at least four years (such as Allerton and Gartmore at the start of this study) develop an amount of moribund dense vegetation which significantly reduces the quality of the habitat, in terms of vegetation regrowth, food production and the flufftails' mobility. Some additional advantages of partial burning are discussed in Section 6.5.4.

Although the territory sizes of some pairs, and the overall variations in habitat availability, were not measured accurately at Mt Currie it is noticeable from the territorial maps (Figs 6.31-6.35) that a greater part of the wetland habitat was used when a block had been allowed to recover for a year after a burn. It is also clear that the beneficial effects of increased habitat availability were most felt in those parts of the wetland in which seasonally inundated habitats were most widespread (i.e. Blocks V1 and V4), and least where the birds occupied permanently wet reedbeds such as the *Carex* in Block V2 (where constraints on the accommodation of extra pairs would be similar to those at Allerton, for similar reasons).

#### **6.5.4 Partial and complete burns**

Results from this part of the study, and observations made during the work on seasonal movements of Redcrested Flufftails (Chapter 5), show that partial or patchy burns of occupied wetlands are always preferable to complete burns because (a) they leave some nonbreeding habitat undamaged, and thus reduce the number of birds forced to emigrate after a burn, and (b) they provide a greater variety of microhabitats as a result of the presence of vegetation in at least the first- and second-year stages of redevelopment. The advantages of pairs being allowed to remain in permanent territories, or of being displaced by only a very short distance, have been discussed fully in Chapter 5, and include a lower risk of mortality, less chance of pairs being split up, and an opportunity to begin breeding earlier in the following season. At Mt Currie in 1990 the unburned Block V1 provided a spring refuge for three extra pairs of birds (at least one of which came from the adjacent burned block), while in the following summer, by virtue of its improved habitat after one year without a burn, it was able to support twice as many breeding pairs as in the previous summer. To have a mixture of vegetation in different developmental stages means that at least some territory holders will enjoy the benefits conferred by both young and old vegetation, including the possibly greater food supply (and easier foraging) in young growth and the better cover and higher number of potential sites for early nesting provided by the older vegetation.

#### **6.5.5 Food availability**

It is very unlikely that a lack of invertebrate food would be a factor affecting recolonization time in burned wetland vegetation. The sampling at Allerton, and my observations of rallids feeding on burned ground, showed that there was no shortage of food in burned areas, even very soon after the burn. The numbers of arthropods recolonizing aerial (above-ground and emergent) vegetation in

burned areas may be higher than those in unburned vegetation of the same type, as is the case in burned and unburned grassland both at Natal study sites (Chapter 7, Section 7.4.8) and elsewhere (Warren *et al.* 1987). No sampling was attempted of invertebrates in mud or shallow water at burned sites but the burns may not have had a great effect on such organisms, relatively few of which are likely to be killed by a surface fire. Schmalzer & Hinkle (1992) found that burning in marshes was followed by an increase in the amount of organic matter and nutrients, probably as a result of the addition of ash and partially burned residues to the water and soil, and this could be beneficial both to plant regrowth and to organisms at higher trophic levels. Freshwater wetlands are physically complex environments with an abundance and diversity of aquatic vegetation which provides a wide range of microhabitats and food resources for a high density and variety of invertebrates (Murkin & Wrubleski 1988), and it seems unlikely that surface fires will have a severe or long-lasting effect on the invertebrate populations of such areas.

## **6.6 Conclusion: burning wetlands to maintain optimal habitat for Redchested Flufftails**

With regard to the habitats of Redchested Flufftail studied in Natal, periodic burning is obviously advantageous because it removes moribund vegetation, promotes vigorous new growth and maintains the wetlands in the fire-modified states to which both birds and vegetation are obviously well adapted. Although the effects of annual complete burns were not studied, repeated annual total burning is not recommended because of its short-term effect on vegetation structure and density (i.e. the destruction of dense clumps which provide shelter and early nesting sites) and because of the increased risk of flufftail mortality as a result of repeated emigrations. A biennial or triennial complete burn is better for the birds than an annual one because it allows the resident flufftail population to recover for 1-2 years between burns, but a triennial regime may reduce vegetation productivity significantly: three years of protection from defoliation is usually sufficient to cause a marked deterioration in the structure and species composition of moist grasslands (Edwards 1984). It is known (Johnson & Knapp 1993) that one wetland grass species (*Spartina pectinata*) is well adapted to annual burning, under which regime it has a greater productivity than when biennially burned. If the dominant wetland plants in flufftail habitats react similarly, annual burning would be advantageous in maintaining high productivity, and a compromise could be achieved by burning some parts of the wetlands annually, within a partial burning cycle.

The advantages to the birds of partial burns have already been discussed (Section 6.5.4) and, in the light of our current knowledge, partial burning on a two-year cycle would seem to be a good option. The Gartmore results also suggest that regular burning is more important in maintaining

optimal habitat quality in seasonally flooded hygrophilous grassland and sedge meadow than in permanently flooded reedbeds. Mowing probably confers no advantage over burning, and seems not to encourage such vigorous regrowth.

With regard to the timing of burns, the principal consideration is the length of time which must elapse before the vegetation can be reoccupied. The earlier the reoccupation date, the longer the potential breeding season and the greater the chance for repeated nesting after failed attempts. The little evidence from firebreak burning suggests that an earlier burn (in August instead of September) could encourage the earlier development of suitable conditions. As the driest areas take longest to develop conditions suitable for reoccupation, earlier burning in these areas would be advantageous. A theoretical disadvantage of autumn (May-June) burning is the longer period over which displaced birds must survive away from their permanent territories, sometimes in only marginally suitable habitat; this is a significant consideration in view of the fact that autumn burning of wetland patches, being practised in forestry areas (Section 6.1), will become more widespread as afforestation increases in Natal (Chapter 7, Section 7.1).

The preferential inclusion of wetland plant species when burning could be advantageous if seed production is thus improved. If the seeds of the taller dominant sedges such as *Carex*, *Cyperus* and *Mariscus* are important to the flufftails as a late summer or winter food supply, then my observations of increased flowering in burnt areas suggest that selective burning of these plants could be useful, even if done only on a small scale with patch burns. This consideration would be relevant only if the seeds are eaten by invertebrates on which the birds may feed, or if the birds themselves eat sedge seeds. In view of the birds' frequent consumption of grass seeds (Chapter 4, Section 4.4.6) it is quite possible that they also eat sedge seeds; Cramp & Simmons (1980) mention that three Palaearctic rallids (the Water Rail *Rallus aquaticus*, the Little Crake *Porzana parva* and the Spotted Crake *P. porzana*) of dense wetland habitats are known to eat *Carex* seeds.

Reviewing all these factors, it is clear that the optimum management strategy is one which incorporates burning to remove dead vegetation, variations in timing of the burn to encourage some early development of vegetation, years without burns to reduce the frequency of emigration and to allow early nesting, and some annual burning to improve productivity of the vegetation. The best strategy to achieve all these goals appears to be annual patch burning at irregular times between autumn and spring, or failing that a biennial partial cycle of controlled, low-intensity winter or spring burns which leave sufficient unburned patches to provide temporary shelter during and immediately after the burn. Patch burning gives the advantage of creating a mosaic of burned and unburned vegetation so that birds will be able to remain in refuges from which they can exploit the food resource associated with early spring post-burn growth in adjacent patches.

## CHAPTER 7

### THE DISTRIBUTION, STATUS AND GENERAL BIOLOGY OF THE STRIPED FLUFFTAIL IN SOUTH AFRICA

#### 7.1 Introduction

Throughout its entire range the Striped Flufftail's distribution is discontinuous and poorly known, and its status uncertain (Chapter 1). Its precise habitat requirements, and the nature of its seasonal movements (if any), are also unclear (Chapter 1). The nominate race is confined to South Africa, where it is of very restricted distribution in grassland habitats which have been much reduced in area during the recent historical past by continuous selective grazing, erosion, agriculture and forestry (Acocks 1988; Rowe-Rowe 1988), and which are under continual threat of greater reduction, especially by afforestation (Bainbridge 1991; Morty 1992). It is therefore imperative to investigate the distribution, numbers, habitat requirements, movements and breeding of this race (Brooke 1984), so that threats to its survival can be assessed and conservation measures proposed.

The aims of the present study were to investigate the following aspects of the Striped Flufftail's biology and ecology in South Africa:

- (a) the bird's past and present distribution and status;
- (b) vocalizations, including the pattern and seasonality of calling (particularly important as most birds were located by sound);
- (c) times of breeding throughout South Africa;
- (d) habitat preferences, particularly at the Natal study sites;
- (e) territory size and dispersion;
- (f) the effects of burning on vegetation structure and food availability in the Natal study areas;
- (g) the relationship between seasonal movements in the Natal study areas and critical environmental variables such as vegetation cover and food availability;
- (h) the nature and extent of post-breeding dispersal;
- (i) general biology, including food and feeding methods, territorial and agonistic behaviour, breeding, predation and mortality.

## 7.2 Survey area and study sites

The survey area comprised the southern part of Natal (see Chapter 2, Section 2.1., and Fig. 2.1). Long-term study sites were potentially difficult to pinpoint because of (a) the restricted nature of the bird's distribution, (b) its apparent scarcity even in areas where it was thought to occur regularly, and (c) the logistical problems of combining work in relatively remote upland grassland areas with concomitant studies of wetland and forest flufftail species elsewhere. Fortunately a convenient study site was found at Mt Currie Nature Reserve, East Griqualand, where preliminary observations indicated the presence of a substantial breeding population, and where detailed studies were also possible of a population of Redchested Flufftails. A second study site was established at Vernon Crookes Nature Reserve, Umzinto, near the Natal South Coast, for comparative observations of status and movements in a less climatically severe, lower-altitude grassland area. These two study sites are described in detail in Chapter 2, Sections 2.2.11 and 2.2.13).

## 7.3 Methods

The difficulties involved in locating and studying flufftails are described in Chapter 3, Section 3.1. The paucity of our existing knowledge of Striped Flufftail (Chapter 1, Section 1.2.3) suggests that it is one of the most difficult species to locate and observe, especially as there is no evidence that it calls regularly outside the breeding season. Preliminary studies indicated that the species is particularly difficult to observe on the ground, but that it is not completely silent outside the breeding season. Although I was not able to observe the birds' normal activities for the prolonged periods which were possible with Redchested and Buffspotted Flufftails my occasional observations, both from hides and when not concealed, yielded some information on food, feeding methods and agonistic and territorial behaviour, including threat displays and attack behaviour to mirror images and models.

### 7.3.1 Surveys

Almost all surveys were based on auditory information. Surveys were made at irregular intervals and concentrated on the Natal Drakensberg Park and East Griqualand areas. All surveys were made in the December-February period, during which the advertising call of this species is most frequently heard in Natal, and most searches were undertaken at night, when calling is most persistent and easier to detect because of the lack of confusing background noise. Clear, moonlit and windless nights were the most productive. The usual technique was to drive on roads through areas of potentially suitable habitat, stopping frequently to listen for calls. In Natal Parks Board reserves

suitable habitat was traversed by both driving and walking. Lack of time usually prevented more than one repetition of a drive over any survey route, and surveys were sometimes limited to areas where potentially suitable habitat had been observed during the day. Small areas of suitable habitat, such as those on farms, was also surveyed during the day using playback techniques. Farmers and birdwatchers in the survey area were approached for information, but very little was forthcoming from such sources because of the scarcity and unobtrusiveness of the bird, its general absence from regularly grazed areas and the relative infrequency of daytime calling. The bird lists for all Natal Parks Board reserves were examined and, in areas where the species had been recorded, Natal Parks Board field staff were contacted for further information.

### **7.3.2 Collection of data from other sources**

Chapter 3, Section 3.11, gives details of the sources consulted for additional data, both current and historical. The most valuable sources of information on Striped Flufftail were the Southern African Bird Atlas Project (SABAP), a few important literature sources, personal contacts (details are given in the relevant sections of this chapter), museum collections of skins, and egg collections.

### **7.3.3 Censusing and territorial mapping**

These were largely accomplished by plotting the positions of calling birds in response to taped playback (see Chapter 3, Sections 3.4 and 3.5). At Mt Currie a census of the entire reserve was made at least once a month during the study period, by night drives and walks during the summer months (November-March) and by daytime taped playback in all months. The approximate positions of calling birds located at night were marked on a map and, if possible, the birds were approached immediately (this was easily accomplished on moonlit nights) to pinpoint their exact calling positions. The areas were visited the next day to establish, if possible, the extent of the birds' territories (bearing in mind the caveat given in Chapter 3, Section 3.4 (k) regarding birds with no near neighbours). In addition daytime taped playback was regularly performed over as large an area as possible and an attempt was made to monitor the presence of established territory holders throughout the breeding season. Given favourable weather conditions, a census of all the reserve's grassland habitats in summer took 3-4 days to complete. At Vernon Crookes, mainly daytime census work was undertaken.

### **7.3.4 Mapping home range**

Estimates of home ranges were made as described in Chapter 3, Section 3.2., normally only for those pairs whose breeding territories could be reliably established (see Chapter 3, Sections 3.2 and 3.4 (k)). In addition, for six isolated pairs whose territories could not be properly mapped, the number of visual and unstimulated vocal registrations was sufficient to permit an estimate to be made of the home range.

### **7.3.5 Habitat preferences, movements, vocalizations, territorial behaviour and breeding**

The study period at Mt Currie extended from December 1988 to July 1992, intermittent observations being continued to the end of 1992. At least one study visit was made in every month up to July 1992, with the sole exception of March 1989, and 324 days were spent at the reserve during the study period. I was resident at the reserve for most of the three-month period January-March 1991.

To investigate breeding-season habitat preferences at Mt Currie, topographical and environmental variables were measured at each location where the presence of a breeding territory was confirmed by censuses, territorial mapping and calling behaviour. For those territories whose boundaries could not be delimited accurately (see Section 7.3.3), measurements could always be made in a central area which was known to be regularly occupied by the birds. The following variables were measured.

- (a) Vegetation type:
  - (1) grassland (G): predominantly grass species, with or without patches of forbs sufficiently abundant or tall to affect the physical character of the vegetation;
  - (2) mixed (M): grassland, with trees or bushes of any type;
  - (3) bracken-briar (B): predominantly a mixture of *Rubus pinnatus* and *Pteridium aquilinum*.
- (b) The dominant grass species (for vegetation types G and M only).
- (c) Any other grasses or forbs constituting 20% or more of the ground cover.
- (d) Presence of *Leucosidea* and/or *Buddleja* bushes, which provide cover at ground level.
- (e) Presence of *Protea caffra* and/or *P. roupelliae* trees, which do not provide ground-level cover.
- (f) Presence or absence of a drainage line within the territory.

- (g) Aspect of the territory, in degrees (north-facing = 0°, west = 90°, east = 270° etc.).
- (h) Altitude (m a.s.l.) at the upper and lower limits and midpoint of the territory.
- (i) Overall slope between upper and lower altitude limits, in degrees (minutes converted to tenths of a degree).
- (j) Percentage of ground covered by rocks (and therefore usually bare of vegetation cover).
- (k) Mean percentage of ground vegetation cover (see Chapter 3, Section 3.6.1.1, for the sampling method used).
- (l) Mean height of ground vegetation (see Chapter 3, Section 3.6.2, for the sampling method used).

The mean vegetation height and cover were measured as soon as a territory was found to be occupied, and only measurements from the first season of occupation were included in subsequent analyses.

The total amount of the different habitat types available to Striped Flufftails was calculated from measurements of the areas of all habitat types (Table 7.1) in the reserve, using information from surveys and vegetation maps made during the study period supplemented with details from aerial photographs from (a) my four survey flights over the reserve (27 December 1989, 2 August 1990, 10 October 1990 and 26 March 1991), and (b) a June 1975 survey (Chief Surveyor General, Department of Regional and Land Affairs). Ground and aerial surveys after spring burns provided an estimate of the area of the reserve having more than a 20% cover of rocks; anything above this percentage was assumed to render habitat unsuitable, preliminary observations having indicated that no birds occurred on ground where the total vegetation cover was less than about 80%. Altitudes and aspects were determined from the 1:5 000 map of the reserve produced by the Department of Surveying and Mapping, University of Natal.

Dates of the first and last visual and vocal records of all birds at all locations were noted throughout the study period and, although I was not continually present at the reserve during the main arrival and departure periods of November-January and May-June, I was able to establish accurate arrival dates at territories in which birds appeared during my visits. Departures were more difficult to ascertain because very localized movements away from breeding territories occurred some weeks before the birds finally left the reserve, while all birds were much more difficult to locate after they had ceased spontaneous calling in February and were much less responsive to taped playback; however final occurrence dates recorded within a prolonged survey visit were taken to indicate departure times.

Details were noted of all vocalizations made by all birds, whether spontaneous or in response to playback, during the study period, and all variations in the types and frequency of calls were noted. Calls were tape-recorded whenever possible, using the equipment described in Chapter 4, Section

TABLE 7.1

Total areas of the major habitat types at Mt Currie Reserve. The three habitat areas marked with an asterisk constitute suitable habitat for Striped Flufftails and total 693 ha.

Habitat type	Area (ha)	% of Reserve
Highland sourveld, no woody vegetation	478*	27,5
Highland sourveld with trees or bushes ( <i>Protea/Leucosidea/Buddleja</i> )	211*	12,1
Bracken-briar	4*	0,2
Wetland and hygrophilous grassland	133	7,6
Indigenous forest and exotic plantations	131	7,5
Ground with > 20% cover of rocks	736	42,3
Open water	21	1,2
Other (buildings, campsite, disturbed ground, verges etc.)	27	1,6
 Total	1 741 ha	100%

Section 4.3.5. The functions of calls were assessed by noting the behaviour which accompanied the call, the stimulus which gave rise to the call, and the reactions of birds to taped playback of the calls. Any evidence of breeding, whether from behaviour, calls or observations of young birds, was recorded. The reluctance of the birds to emerge from cover made it very difficult to study their reactions to models and mirrors, but in April 1990 some observations were made from a hide of the threat display and attack behaviour of a territorial male. Attempts were made to locate nests each season but this proved extremely difficult and almost all indications which I obtained of breeding dates were indirect in nature.

### **7.3.6 Measurements of the effects of burning on vegetation structure and food availability**

Two sites were selected for measurements of vegetation structure and invertebrate abundance, one in Block 3 at 1 440 m a.s.l. and one in Block 2 at 1 470 m a.s.l. (Fig. 2.28). Both sites were within known Striped Flufftail territories, in tracts of grassland which were occupied between November-January (depending on the burning schedule) and April, were in *Themeda triandra*-dominated grassland of approximately equivalent plant species composition, were largely west-facing (aspect 90°) and had slopes of 9-11°. The sites were burned in alternate years (Chapter 2, Table 2.7). At each site measurements were made in vegetation of each of the three normal stages of the burning cycle (see Chapter 3, Section 3.6.1.1). Measurements of mean vegetation cover and height were made according to the methods described in Chapter 3, Sections 3.6, 3.6.1.1 and 3.6.2. Measurements of invertebrate abundance were made according to the methods described in Chapter 3, Section 3.7.1. All sampling was repeated at approximately monthly intervals from October 1990 to July 1992. At Vernon Crookes Nature Reserve comparative vegetation and invertebrate measurements were made at one site in *Themeda triandra*-dominated grassland, and one in an area of mixed tussocky taller grass and forb species (not identified), in July 1992. Both sites were at an altitude of 340 m a.s.l. in known Striped Flufftail permanent territories, the *Themeda* site being on an open west-facing slope and the other being 200 m away in a small sheltered south-facing valley and adjacent to a patch of scattered trees on the central drainage line. Both sites had been burned in the previous spring.

## 7.4 Results

### 7.4.1 Distribution, status and habitat

Distributional data for South Africa are summarized in Tables 7.2-7.5. The date selected for the arbitrary division of records into two groups, those before 1969 (Tables 7.3 and 7.5) and those from 1 January 1969 to 31 December 1992 (Tables 7.2 and 7.4), results from 1969 being the earliest year for which observers supplied unpublished records with details of dates and localities.

#### 7.4.1.1 Natal and Transkei

Distributional data are summarized in Tables 7.2 and 7.3, and mapped by quarter-degree square in Figs 7.1 and 7.2. These summaries show that the known distribution of the species has been extended considerably in the last 33 years, despite there being no recent records from squares I13 and A15. Distribution in the Natal Drakensberg Park (Table 7.2) has been particularly well highlighted by the present study.

With the exception of four squares (G13, I13, F14 and H15) the past and present Natal and Transkei distribution of Striped Flufftail lies entirely within the region of highland sourveld vegetation (compare Figs 7.1 and 2.3), most of which occurs at altitudes above 1 200 m a.s.l. (compare Figs 2.3 and 2.2), and only two (Ixopo and Vernon Crookes Nature Reserve) of the 15 recent localities for which altitudes are known (Table 7.2) lie below 1 200 m a.s.l. In both of these localities the birds are found in *Themeda triandra*-dominated tussocky grassland, that at Ixopo being designated Natal Mist Belt 'Ngongoni Veld by Acocks (1988) and that occupied at Vernon Crookes being tall sourveld (Chapter 2, Section 2.2.11.2); the physical characteristics of the vegetation in these areas are very similar to those of the highland sourveld in which the species was found elsewhere in Natal during this study.

Although the grassland habitats in which the birds occur in the Natal Drakensberg Park extend up to 2 240 m a.s.l. (Table 7.2), Striped Flufftails were recorded only up to 2 040-2 060 m (Cathedral Peak and High Moor) and 2 100 m (Giant's Castle). The lowest altitudes recorded were at Vernon Crookes (250 m) and Ixopo (900 m).

The records of other observers suggest that the Striped Flufftail is sparsely distributed and uncommon in Natal, most observations referring to only 1-5 birds at any locality. My own observations support this estimate of the bird's status in farming areas, but in Natal Parks Board reserves, where grazing pressure is low and burning is on a biennial schedule, the species can exist

TABLE 7.2

Records of Striped Flufftail *Sarothrura affinis* in Natal and Transkei by locality and month for the period 1 January 1969 to 31 December 1992. When locality is not known, the SABAP atlas square name is given in brackets. See map (Fig. 7.1) for a monthly summary of Natal records by quarter-degree square. The altitude range is that approximated for suitable habitat, not necessarily all occupied by the birds. NDP = Natal Drakensberg Park; NR = Nature Reserve; (T) = Transkei locality; ? = altitude not known. Sources: C&R = Cyrus & Robson (1980); SABAP = Southern African Bird Atlas Project data; PC = P. Clowes; GK = G. Keet; ML = M. Lawes; RL = R. Little; GM = G. Maclean; PL = P. Lowry; JM = J. Morford; DO = D. Osborne; AR = A. Rennie; BS = B. Stuckenbergh; ES = E. Smith; WS = W. Small; BT = B. Taylor; RT = R. du Toit; CV = C. Vernon; JV = J. Vincent; PW = P. Walker.

SABAP square(s)	Locality	Altitude range (m)	Months of occurrence												Source(s)	Fig. 7.1 map refs
			J	F	M	A	M	J	J	A	S	O	N	D		
2829 CC	Cathedral Peak, NDP	1370-2100	X	X	X		X				X	X			RL,BS,WS,BT	B9
2929 AB	Monk's Cowl, NDP	1360-2000	X								X	X	X		RL,DO,BT	C10
2929 AD-BC	Giant's Castle, NDP	1700-2200	X	X	X										BT,CV	C11, D11
2929 BB-BD	Firle, Mooi River	1400-1500	X								X	X	X		JV	E10, E11
2929 BC	High Moor, NDP	1700-2080	X	X											ML,BT	D11
2929 BC	Kamberg, NDP	1750-2240	X								X	X			C&R,SABAP	D11
2929 BC	Loteni, NDP	1370-2110			X										RT	D11
2929 CB-DA	Cobham, NDP	1020-2000	X	X							X	X	X		RL	C12, D12
2929 CC	[Bushman's Nek]	?		X	X	X									SABAP	B13
2929 CD	Underberg	1500-1620	X										X		PC,SABAP	C13
2929 DC	Pevensey	1600-1980	X		X	X						X	X		C&R,AR,SABAP	D13
2929 DC-DD	Bulwer Mt	1460-1900	X												GK	D13, E13
2929 DD	[Donnybrook]	?			X							X	X	X	SABAP	E13
2930 AC	Karkloof NR	1200-1700							X						PL,PW	F11
2930 CC	West of Richmond	?							X						C&R,SABAP	F13
3029 AD-CB	Mt Currie NR	1420-2200	X	X	X	X	X	X				X	X		BT	C15, C16
3029 DA	Ngele, Weza	1580-1650	X									X			BT	D16
3030 AA	Ixopo	900-1200	X	X	X	X	X	X	X	X	X	X	X		GM,JM,BT	F14
3030 BC	Vernon Crookes NR	180-520	X	X	X	X	X	X	X	X	X	X	X		GM,ES,SABAP,BT	H15
3129 DA	[Port St. Johns] (T)	?				X									SABAP	-

TABLE 7.3

Records of Striped Flufftail *Sarothrura affinis* from Natal and Transkei before 1969. S = south; SABAP = Southern African Bird Atlas Project; (T) = Transkei locality; W = west; ? = date not known. Sources: BM = Bulawayo Museum; BMNH = British Museum (Natural History); TM = Transvaal Museum.

SABAP square(s)	Locality	Date or period of occurrence	Source	Fig. 7.1 map refs
2929 BB	Brynbella, south of Estcourt	10 April 1925	Notes on painting by H Millar (P Burdon pers.comm.)	E10
2929 BB-BD	Firle, west of Mooi River	From 1930s	J Vincent ( <i>in litt.</i> ) - see text	E10, E11
2929 BB-BD	Firle " " "	17 March 1946	BMNH specimen	E10, E11
2929 BB-BD	Firle " " "	26 March 1946	" "	E10, E11
2930 AC	Balgowan	6 January 1921	4 eggs, BM (collected Cottrell) - see Table 7.8	F11
2930 DD	Pinetown	14 June 1875	BMNH specimen	I13
3028 BD	Matatiele	17 April 1910	Davies (1911); TM specimen	A15
3028 BD	Matatiele	3 March 1912	TM, 2 specimens	A15
3030 BC	Ifafa	?	Stark & Sclater (1906)	H15
3129 AB	Flagstaff (T)	September 1904	Davies (1907)	-

TABLE 7.4

Recorded occurrences of Striped Flufftail *Sarothrura affinis* in Transvaal and Cape Provinces by SABAP atlas square and month for the period 1 January 1969 to 31 December 1992. SABAP = Southern African Bird Atlas Project. Where records are from bird club magazines, details of the publication are given followed by the observer's name in parentheses.

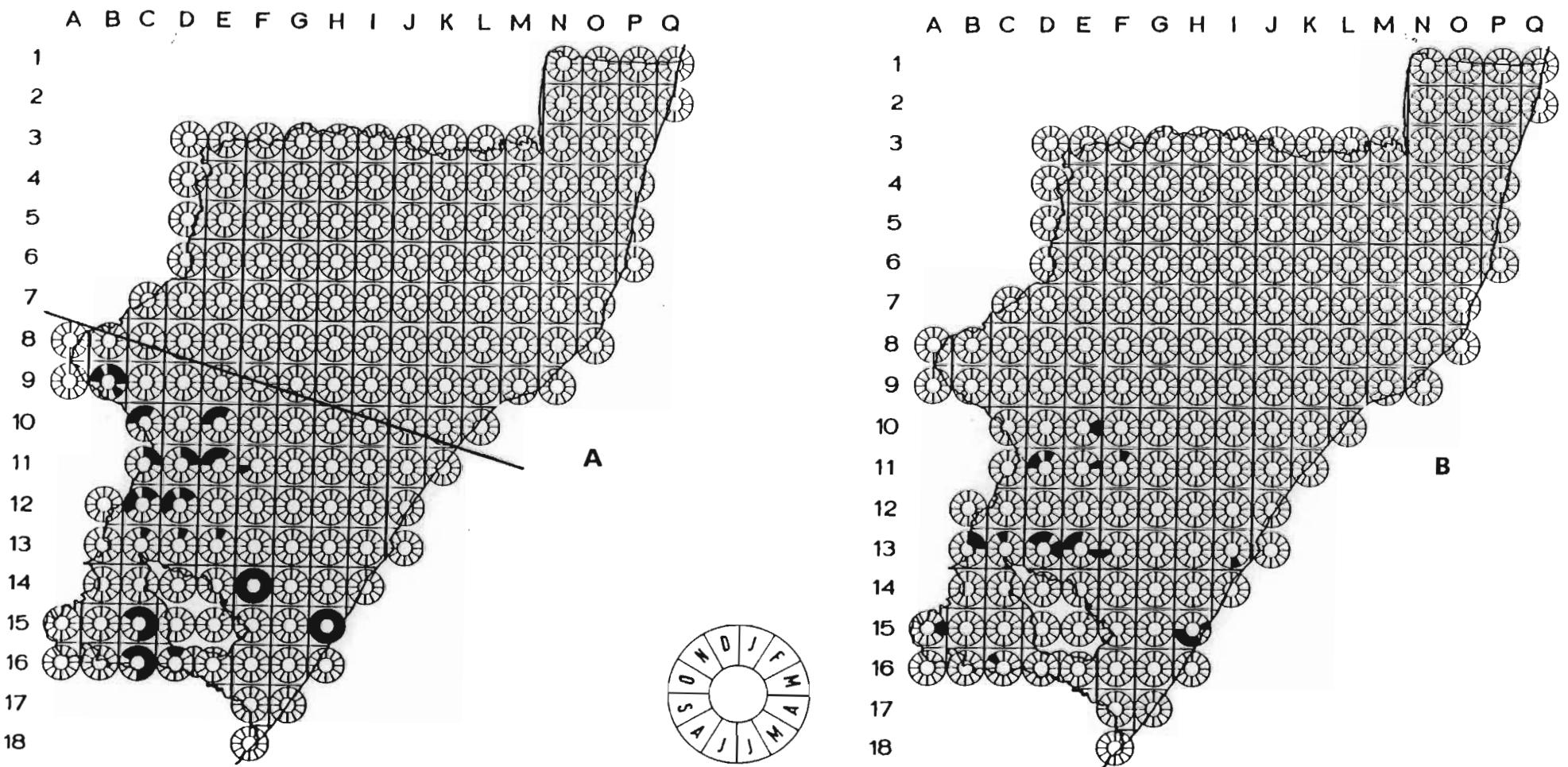
Region	SABAP square(s)	Square name	Months of occurrence												Source(s)
			J	F	M	A	M	J	J	A	S	O	N	D	
Transvaal	2330 CC	Tzaneen			X										Allan (1988)
	2430 AA	The Downs			X										Allan (1988)
	2430 DB	Vaalhoek				X									Porter (1970) - see Table 7.8
	2430 DD	Graskop				X									Hornbill 1986, 5:9
	2530 CA	Belfast				X									Tarboton et al. (1987)
	2530 DA	Ngodwana				X							X		Allan (1986); Hornbill 1988, 13:6
	2530 DB	Kaapsehoop		X	X	X							X		SABAP
	2630 BA	The Brook								X	X				SABAP
	2631 AA	Malalotja		X						X	X	X			SABAP
	2730 AD	Vredefhof							X						SABAP
Cape	3126 BC	Brosterlea	X	X											C Vernon (in litt.); SABAP
	3128 AA	Ugie			X										SABAP
	3226 CA	Bedford							X						SABAP
	3227 BC	Bolo			X										C Vernon (in litt.)
	3227 CB	Stutterheim					X			X					SABAP; C Vernon (in litt.)
	3227 DA	Kei Road						X		X	X				C Vernon (in litt.)
	3227 DD	Cambridge	X												C Vernon (in litt.); SABAP
	3228 CB-CD	Kei Mouth	X												SABAP
	3322 DC &	Wilderness		X				X		X	X	X			SABAP
	3422 BA														
	3324 CD	Kareedouw						X							SABAP
	3326 BC	Grahamstown									X				SABAP
	3418 AB-AD	Cape Peninsula	X	X	X	X	X	X	X	X	X	X	X		SABAP; Graham & Ryan (1984)
	3418 BB	Somerset West				X	X	X	X	X	X	X	X		SABAP; Promerops 1984, 166:13
	3418 BD	Hangklip	)												Martin (1985)
	3419 AA	Grabouw	)												Martin (1985)
	3419 AC	Hermanus	)												Martin (1985)
	3422 AA	Mosselbaai										X			SABAP
	3424 AA	Oubosrand						X							C Vernon (in litt.)

TABLE 7.5

Records of Striped Flufftail *Sarothrura affinis* from Transvaal and Cape Provinces and Lesotho before 1969. SABAP = Southern African Bird Atlas Project. ? = date or square not known. Sources: AM = Albany Museum; BMNH = British Museum (Natural History); ELM = East London Museum; TM = Transvaal Museum.

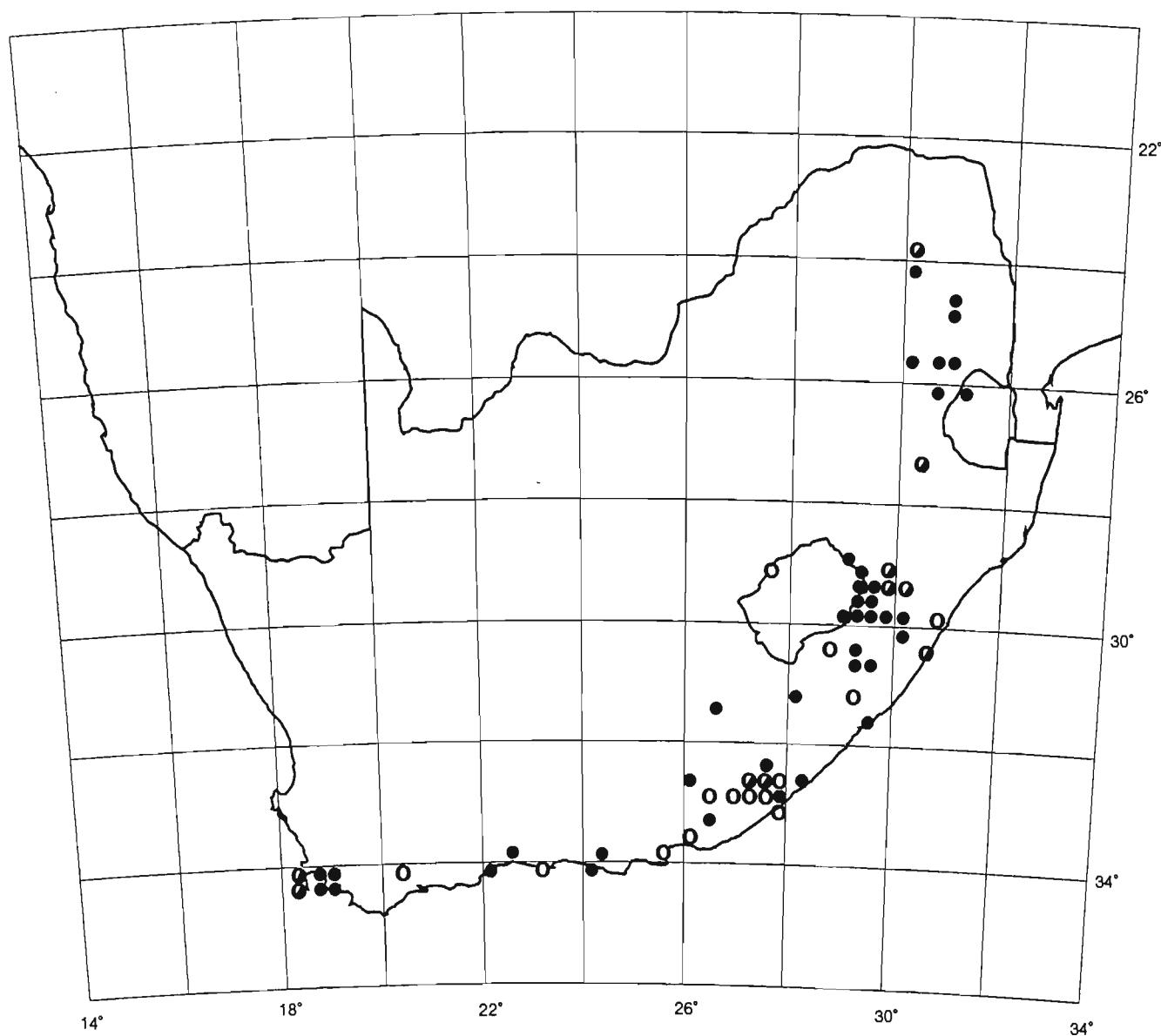
Region	SABAP square(s)	Locality	Date or period of occurrence	Source
Transvaal	2330 CC	Woodbush	14 December 1905	BMNH specimen
	2730 AD	Zuurbron, east of Wakkerstroom	27 May 1904	BMNH specimen
Cape	3226 DC	Kat River	1929 (?)	Keith et al. (1970)
	3227 CB	Stutterheim	27 July 1939	ELM specimen
	3227 CC	Pirie Mission	15 November 1911	AM specimen
	3227 CC	" "	12 March 1912	C Vernon (in litt.)
	3227 CC	Pirie Forest, King Williams Town	11 August 1939	ELM specimen
	3227 CD	King Williams Town	1870 - 1875	Stark & Sclater (1906)
	3227 DA	Brooklyn, Kei Road	2 August 1909	C Vernon (in litt.)
	3227 DA	Gleniffer, Kei Road	6 March 1950	Keith et al. (1970)
	3227 DA	" "	September 1950	" "
	3227 DA	" "	12 February 1958	" "
	3227 DA	" "	30 August 1964	" "
	3227 DA	" "	December 1965	" "
	3227 DB	Komga	1899	C Vernon (in litt.)
	3227 DB	Draaibosch, Komga	September 1906	" "
	3227 DB	" "	25 February 1912	" "
	3227 DC	Berlin	21 August 1964	ELM specimen
Lesotho	3325 DC	Port Elizabeth	October 1867	" "
	3326 DA	Lower Albany	1900	" "
	3327 BB	East London	26 July 1869	ELM specimen
	3327 BB	Mt Gulu, south of East London	9 June 1961	ELM specimen
	3418 AB-AD	Cape Town	1839	Smith (1839)
	3420 AB	Swellendam	?	Stark & Sclater (1906)
	3420 AB	Swellendam	12 November 1977	R K Brooke (in litt.)
	3423 AA	Knysna	1838	Grant & Mackworth-Praed (1935)
	?	Fish River	1891	TM specimen
	2927 BA	Teyateyaneng	?	Winterbottom (1964); see text.

Monthly distribution of records, Cape: J0, F2, M2, A0, M0, J1, J2, A4, S2, O1, N1, D2 (n = 17)



g. 7.1

Monthly distributional data for the Striped Flufftail in Natal, by quarter-degree square. A: data collected during this study, plus unpublished information covering the period 1 January 1969 to 31 December 1992. B: Combined data from Cyrus & Robson (1980) and the Southern Africa Bird Atlas Project, plus 1875-1947 records as summarized in Table 7.3. Data presentation follows the mapping system used by Cyrus & Robson (1980), described in Chapter 4, Section 4.4.1. Inset: monthly information, (January to December) recorded clockwise within each quarter-degree-square symbol.



**Fig. 7.2** Recorded distribution of the Striped Flufftail in South Africa, by quarter-degree square, showing pre-1969 records (open circles), 1969-1992 records (filled circles) and records from both periods (half-filled circles). Outline map courtesy of the Southern African Bird Atlas Project.

in larger numbers. The maximum breeding population at Mt Currie Reserve was 33 pairs in the 1990-91 summer, giving a density of 1 pair/21 ha of grassland-*Protea*-savanna habitat (1 pair/53 ha over the reserve as a whole). At Vernon Crookes Reserve a complete census was not achieved, this having been scheduled for the 1991-92 breeding season, when drought conditions and extensive 1991 burning rendered counts unrepresentative. However partial surveys in previous seasons indicate that the reserve could support at least 41 breeding pairs, depending on the timing and extent of the burns in any year.

The sourveld vegetation in which Striped Flufftails have been recorded in Natal is largely dominated by *Themeda triandra* but with grasses such as *Tristachya leucothrix*, *Hyparrhenia* spp. and *Cymbopogon* spp. also present locally. At Karkloof birds were found in *Themeda*, *Cymbopogon* and *Festuca* grassland (P. Walker pers. comm.), *Festuca* here occurring at the higher elevations in seepage areas (I. Gordon pers. comm.), and at Bulwer one was in *Hyparrhenia* grass (G. Keet pers. comm.). At two Ixopo sites the birds have been found in areas of tall rank grass near streams and moist areas (J. Morford & G.L. Maclean pers. comms.) and the 1925 Estcourt record (Table 7.3) was of a bird in "grass 4 feet (1.2 m) high". My general observations suggested that the birds usually occur in dense tussocky grass up to 60 cm tall, often close to a small stream or seepage, but not in rocky or stony areas. More detailed investigations of such habitat preferences were made at Mt Currie (Section 7.4.5). Occurrence in *Protea* savanna was noted at Mt Currie and Loteni, in bracken at Karkloof, in bracken-briar and tall forbs at Mt Currie, in grassland at forest edges at Karkloof, Cathedral Peak, Vernon Crookes and Bulwer, and in grassland with clumps of *Leucosidea* and *Buddleja* bushes at Mt Currie. The Corncrake was recorded alongside the Striped Flufftail in January 1989 and January 1991 in the open *Themeda* grassland territories on the western slopes of Mt Currie, the grassland height (35-40 cm) being within the range of 30-200 cm recorded at wintering territories in Zambia (Taylor 1984).

During this study Striped Flufftails were never found in close association with wet areas whose size, physical characteristics or vegetation allowed them to be classified as proper wetlands (e.g. such as those which might contain Redchested Flufftails) or which were large enough to accommodate a territory. Regular monthly surveys throughout the study period of large and small wetlands in Striped Flufftail breeding areas in the Natal Midlands, East Griqualand and elsewhere produced no evidence whatsoever that the birds moved into wetlands at any time of the year. However, many breeding territories at Mt Currie contained a drainage line (Section 7.4.5) with a small stream or a spongy seepage area where the birds were sometimes found, while at Cathedral Peak a bird was found in a spongy depression with a small stream (B. Stuckenberg pers. comm.) and at Karkloof and Ixopo the birds were recorded near streams (see preceding paragraph). J. Vincent (*in*

(*litt.*) gives old records from near Mooi River (see Discussion), where birds were found in hay or millet fields "especially if the field was near a swamp", but there was no evidence that the birds entered the wet areas. Only once at Mt Currie was a bird found in a wetland reedbed: on 12 November 1990 a newly-arrived male called from moist ground in a patch of *Carex glomerabilis* 80 cm high, near the river at the foot of a grassy hillside which always held breeding territories; it was not seen or heard in the *Carex* subsequently.

At Vernon Crookes, where Striped Flufftails are present in every month of the year (Table 7.2), no difference was found between the habitat occupied in the breeding and non-breeding seasons, the birds tending to hold permanent territories unless forced to move by burning.

The two coastal localities from which there are old records (Table 7.3), Ifafa in 1906 and Pinetown in 1875, are within Acocks's (1988) Veld Type 1 (Coastal Forest and Thornveld) and, in the periods when the birds were found, must have contained *Themeda* sourveld similar to that occurring today at Vernon Crookes Reserve. Urban development and intensive agriculture probably eliminated long ago any suitable habitat for the Striped Flufftail in these areas and I found no evidence of their recent occurrence there.

The study produced relatively few records of Striped Flufftail in the farming areas of the Natal Midlands and East Griqualand, where I never found birds in grassland which was kept relatively short and sparse by regular or intensive grazing and/or by regular annual burning. Most records in farming areas were from grassland which was lightly and irregularly grazed, was burned biennially or less frequently, and had not been grazed or burned for at least one year before the birds were located. The only exception was at Ixopo where the species was found in midsummer in grassland which had been mown in the spring but not grazed thereafter (J. Morford pers. comm.).

The months of occurrence summarized in Table 7.2 show that the Striped Flufftail has been recorded in every month of the year only at Vernon Crookes Reserve and Ixopo. The indications from this study are that the birds are permanently resident at Vernon Crookes, holding territories throughout the year. This low-altitude coastal site has a mild climate (Chapter 2, Section 2.2.11) and it is worth noting that another dated record of this species from a coastal hinterland locality (Pinetown, 1875; see Table 7.3) is from June, a month in which the species is rarely recorded further inland. At Ixopo, another relatively low-altitude site, the birds are also probably permanently resident. In contrast, in the high-altitude colder Natal interior localities, occurrences are recorded only between October and May, suggesting some movements (possibly altitudinal) in the cold winter months. At Mt Currie Reserve, where occurrence periods were closely monitored, the birds were absent in July–October, being recorded between 12 November and 25 June during the study period (Table 7.6). September occurrences are recorded at Karkloof and Cobham, two sites at which the lowest habitat

(1 000-1 200 m a.s.l.) is intermediate in altitude between the coastal/Ixopo and highland sites. The September record near Richmond is probably from a locality with a relatively mild climate.

#### 7.4.1.2 Transvaal and Cape Provinces

Tables 7.4 and 7.5, and Fig. 7.2, summarize the data for these provinces. Increased observer coverage in the Transvaal has resulted in the bird being recorded from eight new quarter-degree squares since 1 January 1969. New distributions have also been mapped in the Cape Province during this period, involving 15 squares from which there were no previous records, while there have been no recent records from 10 squares in which the bird was recorded before 1969 (Tables 7.4 and 7.5). The bird's recently mapped overall distribution in Cape Province (SABAP data) differs little from that before 1969, except that it is more extensive in the eastern Cape at 31-32°S (Fig. 7.2).

In recent years very little new information has been gained on status, habitat preferences and altitude range in these provinces, other than the published details summarized in Chapter 1, Sections 1.2.3.1-2. For the Cape Province C.J. Vernon (*in litt.*) provides the following unpublished details of habitat (see Table 7.5 for full details of the records): in August 1909, square 3227 DA, a pair in long *Cymbopogon* grass on dry ground near a trickle of water, and in November 1911, square 3227 CC, a male in cultivated land bordering an overgrown stream. The birds at Helderberg Nature Reserve, Somerset West (B. Kakebeeke *in litt.*), are not found in completely dry areas but occur in fynbos near small mountain streams at around 230 m a.s.l. and also on dry to moist ground at 90 m a.s.l. in a seepage area below a reservoir, where they bred in 1992 (Kakebeeke 1993). The nest was in a dry patch of *Pycrus* and *Juncus* surrounded by taller *Mariscus* sedges on marshy ground which was inhabited by Redchested Flufftails, these birds being recorded within 20-40 m of the Striped Flufftail nest (B. Kakebeeke *in litt.*).

Although no altitudes are given for the Transvaal records, all are from localities within the high-altitude escarpment and highveld regions defined by Tarboton *et al.* (1987) and all records fall within the period October-March except for an August occurrence at Vredefhof, for which no further details are available. The monthly distribution of records from the Cape Province spans the whole year, with occurrences at the Cape Peninsula in all months and from the adjacent Somerset West region in March-June and August-November.

C.J. Vernon (*in litt.*) gives the only South African examples, all from the Cape Province, of Striped Flufftails obtained in situations which suggest that the birds were making either dispersal or migratory movements. In 1986, at Stutterheim (square 3227 CB), a dead bird was picked up by

TABLE 7.6

First arrival and final departure dates of Striped Flufftails at Mt Currie Nature Reserve, 1989 to 1992.

Season	First date	Last date	Comments
1988-89	-	25 June 1989	First visit 27 December 1988.
1989-90	17 November 1989	10 June 1990	-
1990-91	12 November 1990	1 March 1991	Early departure after January hailstorm.
1991-92	25 November 1991	29 May 1992	-
1992-93	28 November 1992	-	No observations in mid-1993.

K. Fennell near his house but the date was not recorded and the specimen has been lost. In October 1988 an injured male was found by H. Scott next to his house, which is only 1 km from the previous locality; a colour photograph shows the bird to be an adult. In July 1989 at Skuitbaai, Eerste River (square 3424 AA), J. Smith and J.B. Richie found a dead male which appeared to have flown into a wall; from a colour photograph, the bird also appears to be an adult.

#### **7.4.2      Vocalizations and calling patterns**

Compared with the wide range of vocalizations recorded for the two common flufftail species studied (Chapters 4 and 9), relatively few different calls were heard from the Striped Flufftail during this study. This is at least partly because opportunities for detailed studies of behaviour were very limited. Of the 23 different vocalizations described for Striped Flufftail during this study (Table 7.7) only three are significant with regard to location of individuals for censusing and mapping: the advertising hoot (call no. M1), the territorial *KI-KER* (call nos M4 and F1) and the alarm bark (call nos M16 and F4).

The advertising hoot was apparently given only by males and, in the migratory population at Mt Currie, calling started immediately after arrival in November-January and continued for varying periods up to late February, after which it ceased completely. After 1-4 weeks most males called much less frequently, when territories had probably been established and breeding started, but some birds continued intermittent hooting for several weeks, 64 days being the maximum recorded period over which an individual gave this call. Calling after the start of breeding was probably stimulated by the hoots of birds arriving in adjacent areas, and sometimes could be induced by taped playback of hoots, but hoots were not given in response to playback of *KI-KER* calls and alarm barks. In clear weather most hooting took place between about 18:00 and 08:00 but intermittent calling could persist, especially in cloudy weather, until almost midday and start from 17:00. In November-January occasional hoots were given throughout the day, especially in response to taped playback. Strongly calling males usually called in bouts lasting up to 10 min and often continued intermittently throughout the night. Hooting males normally do not move in response to playback at night but occasionally, on brightly moonlit nights, a strongly calling male which continued hooting on my approaching to within 20 m would in turn approach almost to my feet, continuing to call from dense cover. Birds did not hoot in strong wind or heavy rain, but were occasionally heard briefly in very light rain.

After the hailstorm at Mt Currie on 18 January 1991 displaced birds began hooting again in new territories, prolonged calling continuing until at least 19 February but not into March. At Vernon

TABLE 7.7

Striped Flufftail vocalizations described during the study. All calls are repeated as a sequence unless otherwise specified. The column headed F or M gives the equivalent call of the female or male: see relevant section of table for details. Contexts: A = advertising; G = aggression; T = territorial; X = warning/alarm; Z = contact; ? = context uncertain. Secondary or possible contexts are placed in parentheses.

## ADULT MALE

No.	Description & phonetic rendering	Context	F
M1	Advertising hoot, occasionally rising in pitch	A	
M2	Very rapid deep short hoots: OO-OO	A	
M3	Low-pitched GOOP	T	F2
M4	Rapid KI-KI sequence, usually followed by KER-KER sequence; sometimes KER-KERs only	T	F1
M5	Irregularly-repeated KUK	T(G)	
M6	Faint rapid DUK-DUK after call M4	T/Z	
M7	Quiet KEE-ker when attacking mirror image	G	
M8	Single hard KER notes when attacking mirror image	G	
M9	Rapid stuttering K-K-K	G	
M10	Sharp quiet KIP-KIP or KI-KI during attack on mirror	G	
M11	Quiet KI-DIK after attack on mirror	G	
M12	Quiet TIK on retiring after aggressive display to mirror	G/X	
M13	Plaintive TEE-TEE, context as for call M12	G/X	
M14	ZEEP-ZEEP during aggressive display to mirror	G	
M15	Gulps: GUG-GUG, sometimes preceding call M4	G/T	
M16	Gruff single bark: KEH or KAH	X	F4
M17	Very quiet, almost sneezing, KER-CHI or KER-CHOO	Z(T)	
M18	Quiet rapid bubbling call DU-DU	Z/X	
M19	Quiet GRK to chicks	Z	F6

/continued

TABLE 7.7 (continued)

## ADULT FEMALE

No.	Description & phonetic rendering	Context	M
F1	Rapid <i>KI-KI</i> sequence followed by <i>KER-KER</i> sequence, quieter, more rapid and higher-pitched than in male	T	M4
F2	Low-pitched <i>GOOP</i>	T	M3
F3	Quiet grunt: <i>GRG</i>	T/G	
F4	Gruff single bark: <i>KEH</i> or <i>KAH</i>	X	M16
F5	Sharp <i>CHK-A-CHK</i> when flushed from nest	X	
F6	Quiet <i>GRK</i> to chicks	Z	M19

## DOWNY CHICK

No.	Description & phonetic rendering	Context
C1	Plaintive cheeping: <i>PEE-PEE</i>	Z
C2	Quiet <i>IP</i>	Z

Crookes hooting was heard from late October, and at Karkloof a male hooted briefly on 12 September 1990: this bird was possibly re-establishing itself in a new area after the previous day's burn.

At Mt Currie the male's *KI-KER* territorial call was given, both spontaneously and in response to hoot and *KI-KER* playback, throughout the period of occurrence as long as birds were within their breeding territories. After vacating the territories at the end of the breeding season the birds did not make this call. It was never heard during the night, even after prolonged tape stimulation, being given only between dawn and dusk. Females have a quiet version of the call (Call F1) which was heard occasionally. At Vernon Crookes territorial males and females made *KI-KER* calls throughout the year.

The alarm bark was made by both sexes and was heard throughout the period of occurrence at Mt Currie and throughout the year at Vernon Crookes. At Mt Currie it was the only call given by non-territorial birds which congregated in favourable habitat outside territories in May-June (see Section 7.4.10). The call was made in response to playback of all Striped Flufftail calls and also to the playback of the alarm and territorial calls of Redchested Flufftail, African Rail *Rallus caerulescens* and Baillon's Crake *Porzana pusilla*. It was usually made infrequently and it was never heard at night. It is very similar to the snort given by Grey Rhebok in response to disturbance (Smithers 1977) and care had to be taken not to confuse distant calls of these two animals. The barks of adjacent individuals usually differed sufficiently in frequency (pitch) to be easily distinguishable.

The hoot call is well audible over at least 1,6 km on a still night, and the maximum distance at which I heard a traceable call at Mt Currie was exactly 2 km over mainly level ground but behind a belt of pine trees, the bird being about 80 m higher than my position when I first heard it. The *KI-KER* call is well audible from 400 m and faintly up to 700 m in still weather, but the bark is audible for only up to 200 m and can be difficult to pinpoint exactly.

Calling patterns indicate that the male is much more active in territory defence than is the female, whose territorial calls (Table 7.7) were heard only very occasionally. The female probably takes a much less active part in territory maintenance than does the female Redchested Flufftail, which has a wide range of territorial calls and utters some of them very frequently (Chapter 4, Section 4.4.8).

During this study I discovered three aspects of the Striped Flufftail's calling behaviour which have a bearing on censusing and mapping work. First, recently arrived male Striped Flufftails when presented with taped playback frequently ceased their advertising hoots instead of responding to the tape. During the day such birds, which were not yet closely tied to a defended area, often moved

away from the observer instead of approaching him. If playback were continued and the flufftail followed by tracking its intermittent alarm calls, the bird would frequently move a considerable distance (up to 500 m, over a hilltop into the next valley, etc.). Mapping such birds was impossible until they had properly established a territory, before which continued playback might have caused them to leave the area. This behaviour was also noted in both Buffspotted and (occasionally) Redchested Flufftails which had just moved into suitable habitat. Second, Striped Flufftails in fairly short (i.e. 35–45-cm-high) grassland at a higher elevation than the observer, could see an observer approaching from a considerable distance and would often spontaneously give alarm or territorial calls when I was up to 700 m away from them. This behaviour was often helpful in daytime census and mapping work but birds in short grass usually would not approach an observer as closely as would those in taller vegetation. Third, wherever several hooting males could be heard from one point, the pure note emitted by each bird was always recognizably different in frequency (pitch) from that emitted by all others. In general it could be assumed that the calls of all other birds audible to any territory holder would be recognizably different in pitch from each other and from its own call. This was very useful, especially in night census work, and individuals could be identified by this character during subsequent censuses.

#### 7.4.3 Aggressive behaviour

In early April 1990 at Mt Currie the reactions of a territorial male to models and mirrors (see Chapter 4, Section 4.3.2) were observed from a temporary hide. The bird was attracted to the vicinity of the hide by taped playback of territorial and advertising calls, and playback of territorial calls was continued during most of the bird's display and attack behaviour. When presented with a lifelike model male Striped Flufftail (with glass eyes) and a mirror, the bird ignored the model and attacked the mirror. In attack sequences the bird walked out of cover with the plumage raised on its body, neck and head (giving it a very swollen appearance), its head up, its throat distended to show the white feathers prominently, and its red tail raised and fanned out into a prominent fluffy "powder puff". It approached the mirror with a crouching run, drooped and spread its wings and made jumping attacks at its reflection, with vicious pecks. Sometimes it flapped its wings or even raised them above its head to buffet the mirror with their leading edge (Plate 2A). After an attack the bird often crouched facing the mirror, with its wings partly open and fanned out to the side and its tail raised, and then turned to face away from the mirror, apparently to display its raised and fluffed tail. Attacks were often repeated several times before the bird walked off into cover. The bird called frequently (Table 7.7, Calls M7-M15) during and after both attacks and aggressive displays. After a few attacks the bird often walked round behind the mirror, looking for its adversary, and then peered round from



A



B

**Plate 2**

A: male Striped Flufftail attacking its reflection in a mirror, Mt Currie, April 1991.

B: adult female Buffspotted Flufftail at a feeding station, Scotston, Underberg, October 1991.

the back to glimpse its reflection again before emerging to continue the attacks. The bird showed only brief interest in a model male Redchested Flufftail, ignoring it after a short examination.

#### 7.4.4 Breeding seasons and breeding behaviour

All published breeding information for both races of the species is summarized in Table 7.8, together with information from eggs and specimens examined during this study and including evidence from my scanning-electron-microscope (SEM) analysis of eggshell structure (P.B. Taylor, unpublished ms). Measurements and SEM studies have shown that four clutches from South Africa are referable to other flufftail species. The mean clutch size for the species is 4,17 ( $n = 6$ , see Table 7.8).

The valid South African records all fall within the period 25 September to 19 March and all are within the rainy period except the September 1992 Somerset West record, which is at the end of the winter rains. The only evidence of breeding obtained at Mt Currie was of calls indicative of sexual behaviour on 27 December 1988, a male with young chicks on 29 January 1990 (eggs laid in early January) and an agitated female near young chicks (not seen) on 13 January 1991 (eggs laid in late December). The calling patterns of territorial birds, particularly the cessation of hooting after 1-4 weeks, indicated breeding attempts from early December (November arrivals) to late January and February (January arrivals).

Breeding territories at Mt Currie were occupied immediately upon arrival, which occurred between mid-November and late January depending on the characteristics of the grassland occupied (see Section 7.4.9), and were vacated between late April and late June. The dispersal of birds after breeding is discussed in Section 7.4.10.

Little information was collected on breeding behaviour but, during experiments with models and mirrors, a male Striped Flufftail made several courtship displays to a lifelike model female. On each occasion the male walked up to the model, crouched in front of it with raised head and drooping wings, and bowed until his breast touched the ground. During the display the plumage was raised so that the body appeared swollen, and the orange-red tail was usually elevated and spread so that it was well visible. No calls were heard and after bowing the male ran off into cover, sometimes first standing briefly alongside the model with his head close to hers. The Redchested Flufftail has a very similar display (Chapter 4, Section 4.4.10.1), except that its dark tail is less obvious than the brightly-coloured tail of the male Striped Flufftail, which is also prominently raised and fluffed out during aggressive displays (Section 7.4.3).

TABLE 7.8

Published and skin/egg collection breeding information for Striped Flufftail *S. affinis* by country, with results of confirmatory investigations. Items in parentheses under "Evidence" denote material not examined by PBT. Br = British Museum (Nat. Hist.); Bu = Bulawayo; C = clutch; Conf = confirmed; Du = Durban; Imm. = immature; Meas. = egg measurements; Mus = Museum; SEM = scanning electron microscope studies; Tvl = Transvaal; V = Vienna; ? = date or locality not given.

Subspecies	Country	Date	Locality	Details	Source	Conf. species	Evidence
<i>S. a. antonii</i>	Sudan	1 May 1938	Imatong Mountains	♂♀, breeding condition, Br Mus	Cave & Macdonald (1955)	<i>S. affinis</i>	Specimens
	Kenya	5 May 1926	Trans Nzoia District	C4; ♀ collected	Mackworth-Praed & Grant (1937)	<i>S. affinis</i>	(Specimens not traced)
	"	11 Feb 1936	Mount Kenya	2♀♀, breeding condition, Br Mus	Meinertzhagen (1937)	<i>S. affinis</i>	Specimens
	Tanzania	3 March	Ugano, Matengo Highlands	Imm ♂, V Mus; eggs January?	Keith <i>et al.</i> (1970)	<i>S. affinis</i>	(Specimen)
	Malawi	14 Apr 1935	Viphya Mountains	♀, developing eggs, Br Mus	Br Mus collection	<i>S. affinis</i>	Specimen
	Zambia	7 January	Nyika Plateau	♂, breeding condition	Benson & Holliday (1964)	<i>S. affinis</i>	(Specimen)
	Zimbabwe	5 Feb 1958	Chimanimani Mountains	C5, laid January, ♂ collected	Masterson & Child (1959)	<i>S. affinis</i>	Meas; SEM
<i>S. a. affinis</i>	S Africa	19 Mar 1969	Blyde River Canyon, E Tvl	C4, identified as <i>S. elegans</i>	Porter (1970)	<i>S. affinis</i>	Meas; SEM
	"	17 Mar 1946	Mooi River, Natal	♂, breeding condition, Br Mus	Br Mus collection	<i>S. affinis</i>	Specimen
	"	6 February	Balgowan, Natal	C4 (Cottrell), Bu Mus	Keith <i>et al.</i> (1970)	<i>S. affinis</i>	Meas; SEM
	"	?	Balgowan, Natal	C1, Bu Mus (not found)	Keith <i>et al.</i> (1970)	<i>S. affinis</i>	(Meas.)
	"	27 Sep 1920	Durban, Natal	C5, Tvl Mus	T Cassidy, Tvl Mus ( <i>in litt.</i> )	<i>S. elegans</i>	Meas; SEM
	"	Dec 1909	Mid Ilovo, Natal	C1 (Bell Marley), Du Mus	Keith <i>et al.</i> (1970)	<i>S. rufa</i>	Meas; SEM
	"	?	Swellendam division, Cape	C4; ♀ collected	Stark & Sclater (1906)	<i>S. affinis</i>	(Meas.)
	"	25 Sep 1992	Somerset West, Cape	C4, hatched 10 October	Kakebeeke (1993)	<i>S. affinis</i>	Photographs
	"	1 Nov 1902	?	C4, Du Mus	Chubb (1914)	<i>S. elegans</i>	Meas; SEM
	"	29 Sep 1902	?	C3 with nest description	Chubb (1914)	<i>S. elegans</i>	Meas; SEM

#### 7.4.5 Habitat preferences at the Mt Currie Reserve study site

Chapter 2 (Table 2.5 and Fig. 2.28) gives details of the topography and vegetation of Mt Currie Reserve and shows that sourveld grassland is generally distributed throughout the reserve. Of the major habitat types distinguished within the reserve (Table 7.1) only three (sourveld with and without woody vegetation, and bracken-briar) were occupied by Striped Flufftails, the total extent of these three habitat types being 693 ha, 39.8% of the reserve area (Table 7.1).

Fig. 7.3 shows the distribution of the 59 Striped Flufftail territories which were found during the study period, while Figs 7.4-7.6 show the frequency distributions of the habitat variables measured in these territories. Forty-one territories (69%) were in pure grassland (Plate 3A) or grass with tall forbs, 17 (29%) in grassland with woody vegetation and only one in bracken-briar (Fig. 7.4A). Taking into account the differing amounts of each habitat type present (Table 7.1), and classing bracken-briar with grassland (the sample of one territory in 4 ha of habitat being too small for testing purposes), the birds' association with grassland habitat with or without trees and bushes was random ( $\chi^2_1 = 0,091; P > 0,7$ ). Of the three other vegetation types which constituted 20% or more of the ground cover in any territory (Fig. 7.4B), *Hyparrhenia* spp. occurred in 10 territories of Blocks 2 and 3 (at the base of hills and predominantly west-facing), *Tristachya leucothrix* in six territories of Blocks 5 and 6 (at similarly low altitudes, with west to south aspects), and tall forbs in five territories, facing southwest to south-southeast at medium altitudes and associated with drainage lines (Block 2) or with areas of cleared wattle plantation (Block 6). There was a significant association of vegetation type with aspect, territories with woody plants predominating on the south-southwest to southeast slopes and pure grassland territories on the west-northwest to southwest slopes ( $\chi^2_1 = 5,853; P < 0,02$ ). Of the 17 territories with woody vegetation (Fig. 7.4C), nine with *Protea* were on southwest to southeast slopes and 13 with *Leucosidea/Buddleja* faced west to southeast. The *Leucosidea/Buddleja* thickets are more extensive on the southwest to southeast slopes, their distribution (like that of *Protea*) possibly reflecting greater protection through less severe burning on these slopes in the past, and this gave rise to a significant association between the occurrence of *Protea* and the other woody plants in the territories (Fisher's Exact Test,  $P = 0,02$ ). On the western side of the mountain *Leucosidea/Buddleja* stands are more confined to drainage lines, where protection from fire is greatest. The 46 territories (78%) containing a drainage line (Fig. 7.4D) were generally distributed throughout suitable habitat and were no more frequent on south-southwest-to-southeast slopes than on west-northwest-to-southwest slopes ( $\chi^2_1 = 0,0432; P > 0,8$ ). Of the remaining 13 territories, seven had a drainage line within 50-100 m of the regularly occupied area and potentially within the home range of the pairs concerned.



A



B

**Plate 3**

A: *Themeda triandra*-dominated grassland (sourveld) on the western slopes of Mt Currie, March 1990; typical Striped Flufftail habitat.

B: the house and garden of Scotston Farm, Underberg, March 1991, showing the hedgerows, flowerbeds, bush clumps and vegetable garden which were occupied by the two breeding pairs of Buffspotted Flufftails.

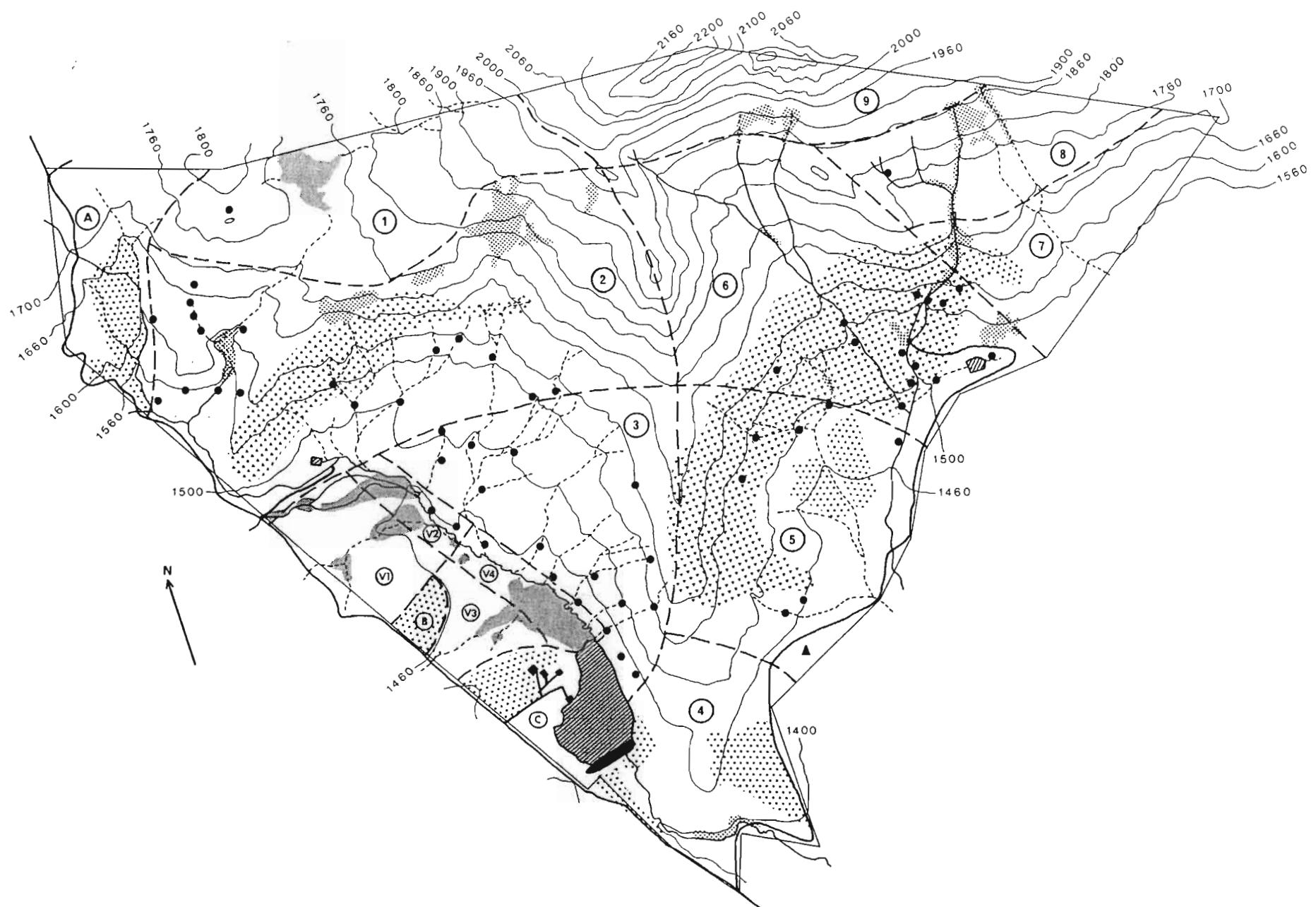
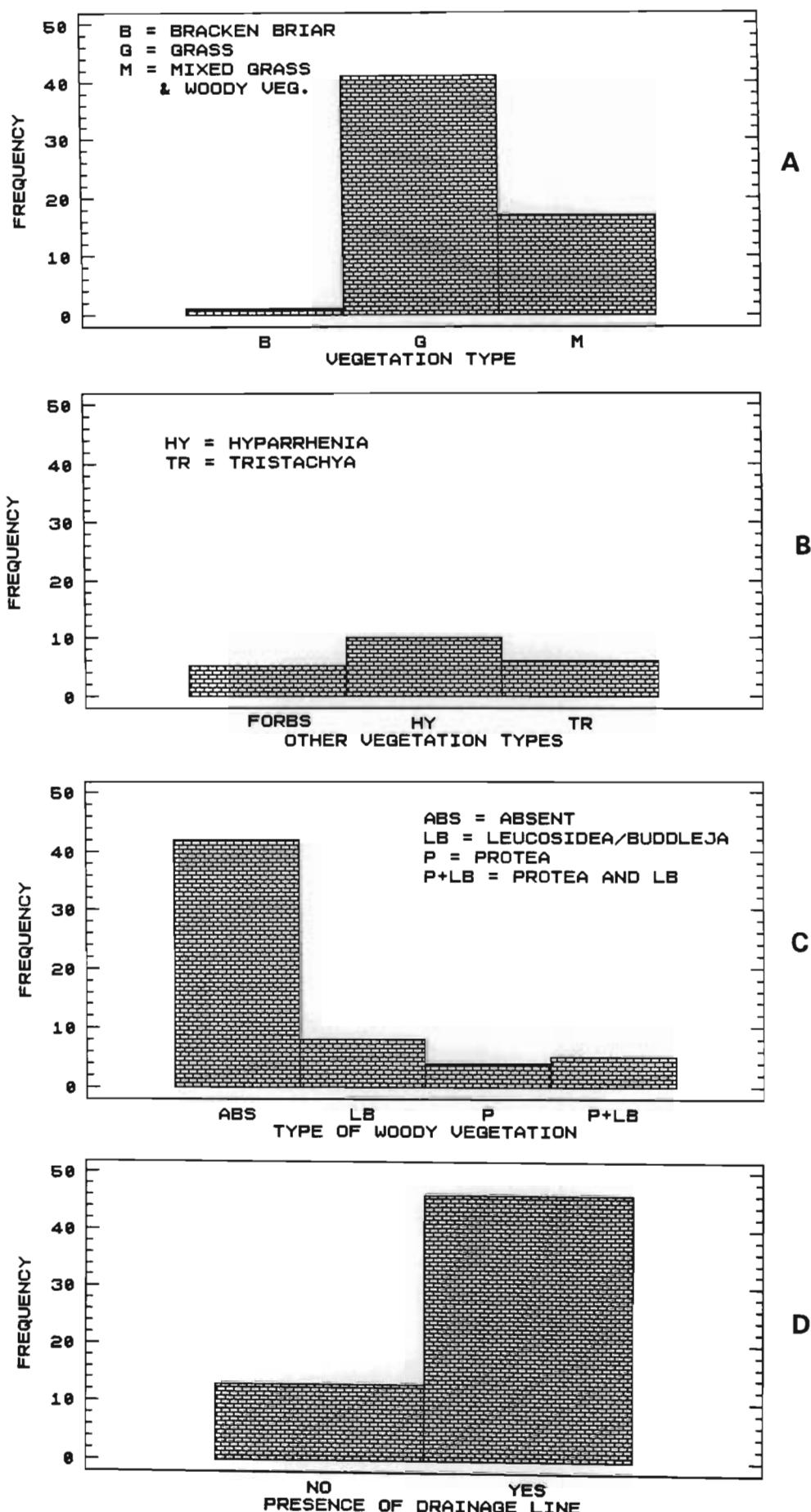
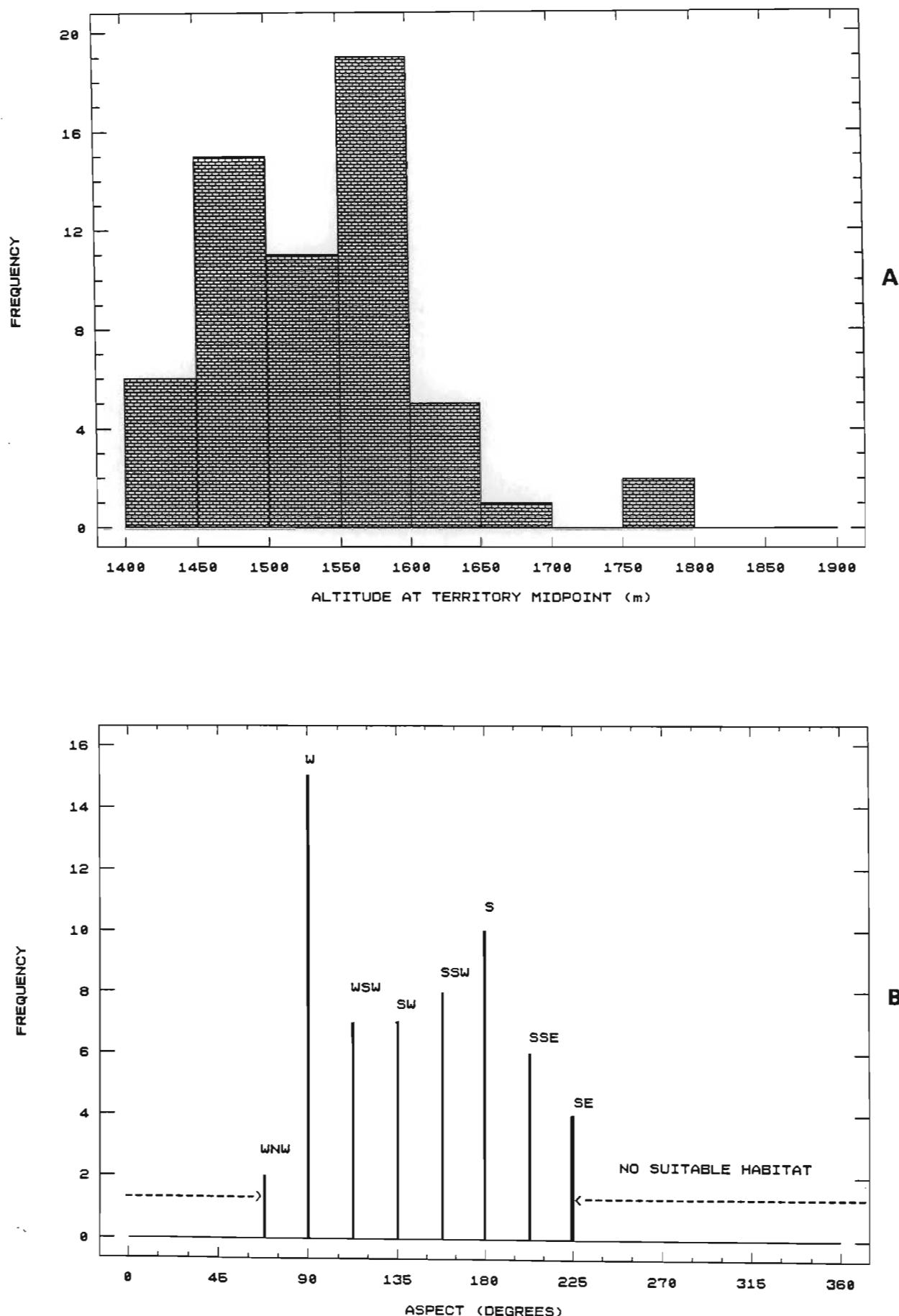


Fig. 7.3

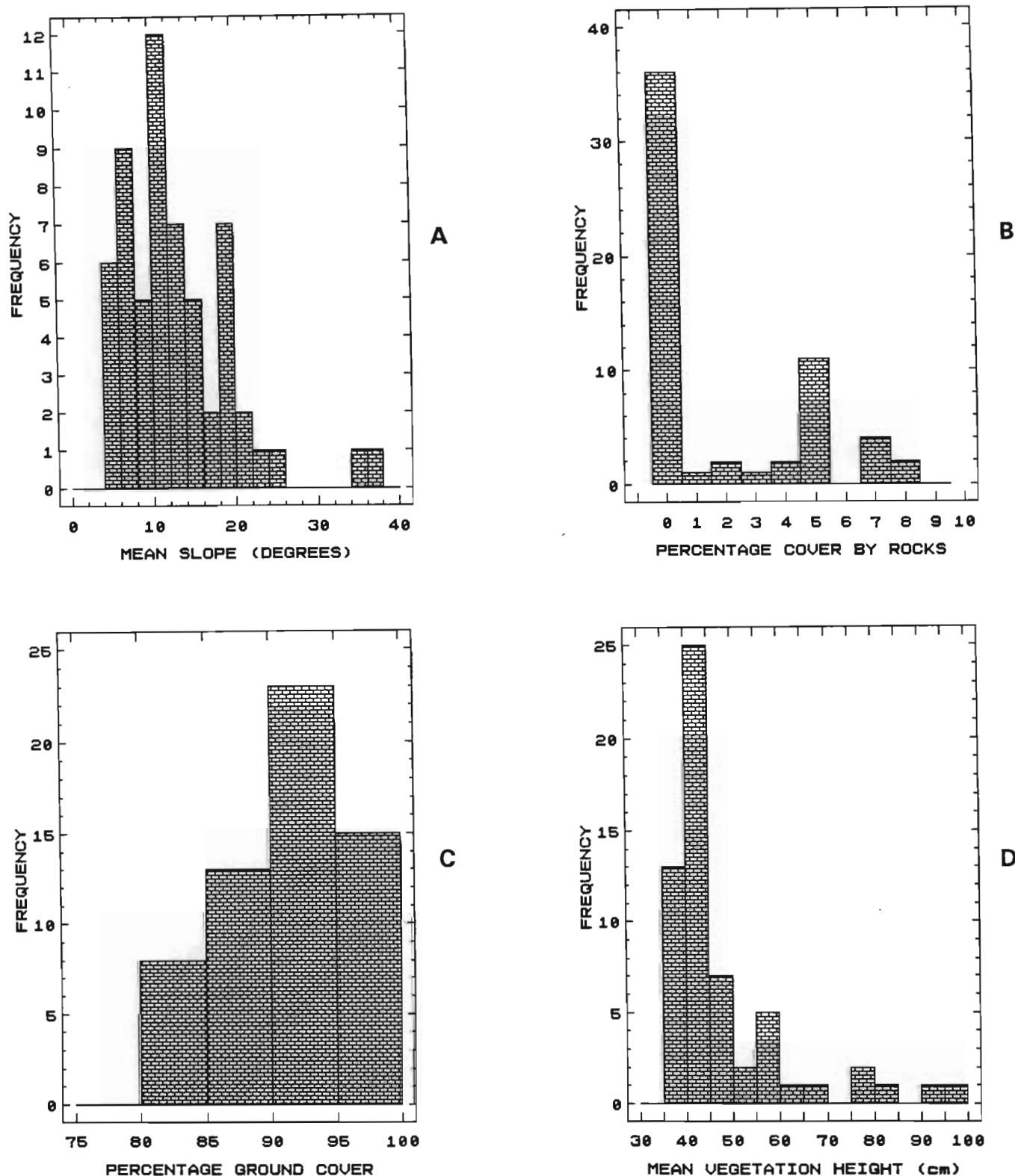
Distribution of the 59 Striped Flufftail breeding territories (large dots) recorded at the Mt Currie Reserve, Kokstad, during the study. The map key is given in Fig. 2.2.8.



**Fig. 7.4** Characteristics of Striped Flufftail territories at Mt Currie: (A) their dominant vegetation types; (B) other grasses and forbs occupying more than 20% of the territory; (C) the type of woody vegetation present; (D) presence or absence of a



**Fig. 7.5** Characteristics of Striped Flufftail territories at Mt Currie: (A) altitude at the territory midpoint; (B) aspect of the territories.



**Fig. 7.6** Characteristics of Striped Flufftail territories at Mt Currie: (A) mean slope; (B) percentage of ground covered by rocks; (C) mean percentage of vegetation cover; (D) mean vegetation height.

Most territories (51) had their midpoints at or below the 1 600-m contour (Fig. 7.5A, Table 7.9), suggesting a preference for the lower-altitude slopes. This was confirmed by determining the relative areas of habitat available above and below 1 600 m (Table 7.9), when a significant association was found between territory distribution and altitude ( $\chi^2 = 4,0767; P < 0,05$ ). Fig. 7.5B shows that the territories were distributed over all slopes of the reserve which had suitable habitat, 31 being on predominantly west-facing slopes (west-northwest to southwest) and 28 on predominantly south- to southeast-facing slopes (south-southwest to southeast). In relation to the approximately equal amount of habitat available on ground in these two sectors (333 ha and 360 ha respectively), there was no significant preference for the west-facing sector ( $\chi^2 = 0,4868; P > 0,5$ ).

With regard to the other topographical features, 57 territories (97%) were located on ground with an overall slope of 4-26° (Fig. 7.6A) and no territory had a ground cover of more than 8% of rocks (and 36 had no rocks) (Fig. 7.6B). A simple regression of altitude against slope showed a statistical relationship ( $P < 0,03$ ), higher territories having steeper slopes, and this agrees with my observations that almost all territories were on concave slopes, only two being on convex upper slopes and one on almost flat ground at the highest recorded altitude (1 780 m). Subjective observations indicated that convex slopes tended to have poorer soils, more stone or rock cover and sparser, shorter grass cover than concave slopes; obviously, they were also more exposed and lacked drainage lines. Birds avoided rocky areas at all altitudes and, although 646 ha of the 736 ha of ground with over 20% rock cover lay above 1 600 m, there was sufficient rock-free habitat above 1 600 m (Table 7.9) to accommodate some territories, albeit at a reduced density (see above). Although rocky ground was usually bare of vegetation and thus reduced the overall cover for the birds, in three territories tall overhanging vegetation effectively screened the rocks on 2-7% of the ground, so that the presence of rocks hardly affected the vegetation cover.

All territories had 80-100% of the ground obscured by vegetation (Fig. 7.6C), while the mean vegetation height ranged from 35 to 100 cm, 52 territories (88%) having a mean height of 60 cm or less (Fig. 7.6D). The seven territories with mean vegetation heights greater than 60 cm all contained large stands of herbaceous vegetation significantly taller than the normal sourveld, the five with means of 80-100 cm being those containing tall forbs, one being bracken-briar (mean height 65 cm) and one (mean height 70 cm) containing much *Hyparrhenia*. A simple regression of mean vegetation height against mean cover for 31 pure grassland territories showed no statistical relationship ( $P > 0,1$ ), observations indicating that cover was not significantly greater in the tallest vegetation. This may also be seen from the vegetation sampling results, Figs 7.11 and 7.12 showing that in early 1992 vegetation height continued to increase for 1-2 months after cover had reached its maximum.

TABLE 7.9

Total amounts of suitable habitat of all vegetation types, and total numbers of breeding territories, above and below 1 600 m a.s.l. in the blocks occupied by Striped Flufftail at Mt Currie, 1988-89 to 1991-92. For sizes and major features of blocks, see Table 2.5. Note that blocks 7, 9 and A held no territories, while blocks 4 and V1-V4 had no suitable habitat.

Block No(s)	Total habitat (ha)	Habitat below 1 600 m		Habitat 1 600 m and above	
		Area (ha)	No. Terrs.	Area (ha)	No. Terrs.
1 + 9 + A	61	0	0	61	1
2	171	135	13	36	5
3	164	164	19	0	0
5	124	122	7	2	0
6 + 7 + 8	173	103	12	70	2
<hr/>					
Totals	693	524	51	169	8

TABLE 7.10

The total numbers of Striped Flufftail breeding territories in burned and unburned vegetation at Mt. Currie, 1988-89 to 1991-92. Figures in parentheses refer to the January-February 1991 totals after the severe hailstorm of January 17 1991.

Season	Total territories		Grand total
	Burned	Unburned	
1988-89	5	25	30
1989-90	7	14	21
1990-91	8 (11)	25 (7)	33 (18)
1991-92	4	12	16

#### 7.4.6 Territories and dispersion at Mt Currie

The distribution of the 59 territories found within the reserve during the study period is shown in Fig. 7.3. Not all of these territories were used in every breeding season, the total occupied in a season varying between 16 and 33 (Table 7.10). Because of the difficulty of accurately mapping the territories of birds with no near neighbours (Chapter 3, Section 3.4 (k)), acceptably accurate maps were constructed only for 20 territories which were adjacent to other territories and/or were bordered by obviously unsuitable habitat (rocky areas, plantations, sparse or very short grass, etc.). These 20 territories were 1,05-2,3 ha in area (mean 1,64 ha; S.D. 0,357). Home range measurements (see Section 7.3.4) were also obtained for 20 pairs, 14 of which also yielded accurate territory maps, and these 20 home ranges were 2,0-3,24 ha in extent (mean 2,58 ha; S.D. 0,38). No significant relationship was found between home range and territory size.

As territories in burned grassland were so few, and the birds usually had no near neighbours, I was able to obtain only one territory area (1,7 ha) from burned ground and thus could not investigate the possible effects of burning on territory size. There was no significant relationship between territory area and (a) slope or altitude (simple regressions;  $P > 0,4$  and  $P > 0,3$  respectively), (b) vegetation type (one-way ANOVA;  $F_{1,18} = 2,06$ ,  $P > 0,1$ ), or (c) aspect sector west-northwest to southwest as opposed to south-southwest to southeast (one-way ANOVA;  $F_{1,18} = 1,725$ ,  $P > 0,2$ ). Although territories without a drainage line averaged 10% larger than those with one, the difference was not statistically significant ( $t = 0,893$ ;  $P > 0,3$ ; d.f. = 18).

The area of one pair's winter territory at Vernon Crookes was plotted from mapping done in August 1990 and was found to be 1,5 ha, close to the mean for the Mt Currie breeding territories.

#### 7.4.7 The effects of burning on vegetation structure at Mt Currie

Analysis and interpretation of variations in vegetation structure were made in relation to the habitat preferences observed in occupied territories, viz. that birds did not occur in areas with mean ground cover less than 80% and mean vegetation height less than 35 cm (Section 7.4.5).

Fig. 7.7A shows the mean percentage ground cover for the Block 2 site at Mt Currie between October 1990 and July 1992, with the periods of occupation of the site by Striped Flufftail. The site was burned on 2 September 1990 (Chapter 2, Table 2.7) and the cover had increased to 40% at the start of measurements on 23 October, eight weeks after the burn. Thereafter mean cover increased rapidly until January but attained a level of 80% only at the end of February 1991 and the site was not occupied by flufftails. The severe hailstorm of 18 January did not reduce the overall ground

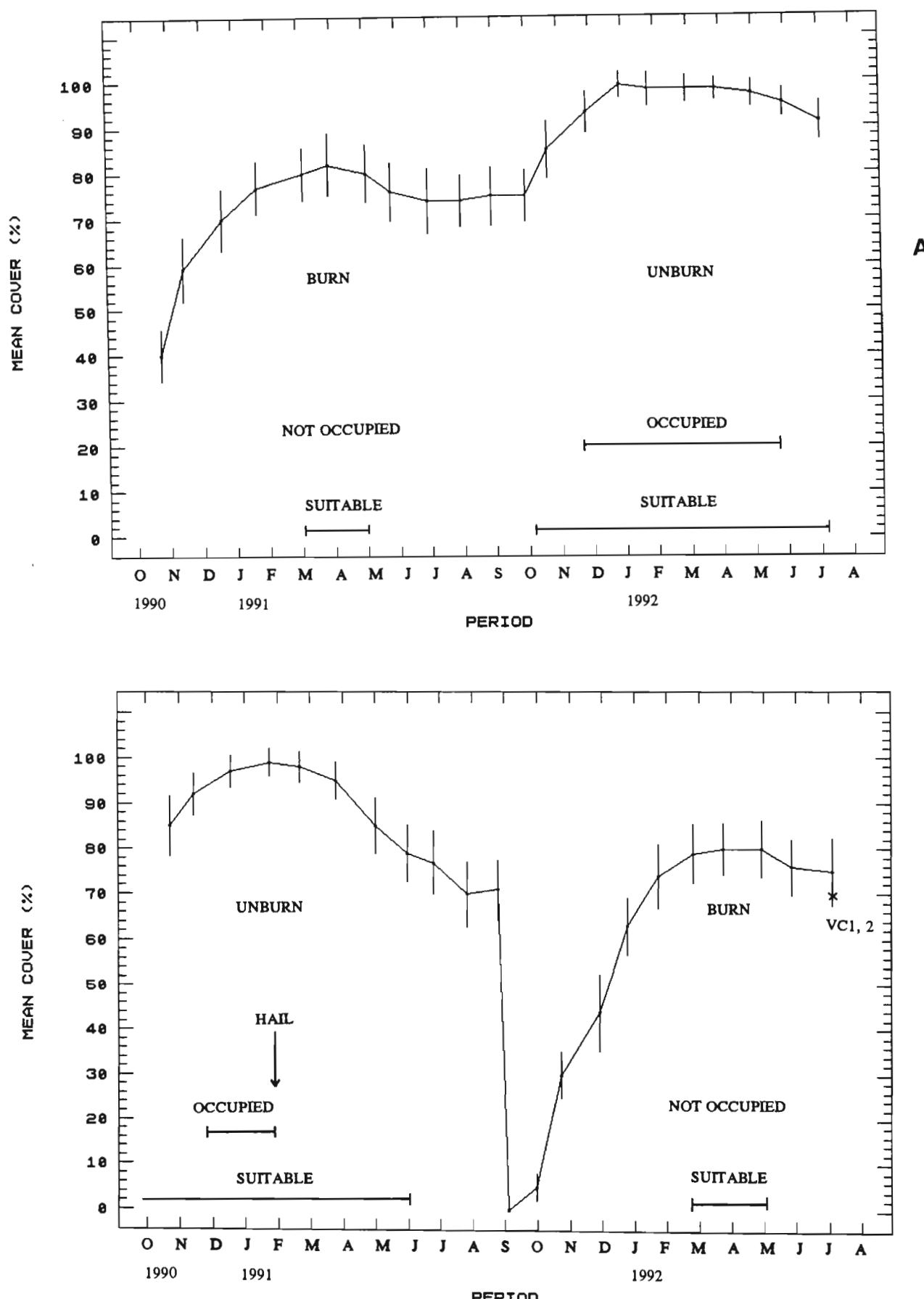
cover. In May the cover fell to just below 80% and remained at 74-76% until the end of September when growth recommenced. By late October 85% cover was present and a maximum of 99% was reached in late December, after which the level remained above 90% until the end of the sampling period in early July 1992. The site was occupied by Striped Flufftails between late November and late April, with post-breeding birds also at the same altitude in nearby grassland for a further month.

The Block 3 site was not burned in 1990 and the first sample (Fig. 7.7B), on 22 October 1990, gave a mean cover of 85%. The maximum cover of 99% was measured on 22 January 1991, four days after the hailstorm which possibly slightly increased overall cover by flattening the vegetation and which resulted in the disappearance of the Striped Flufftails which had arrived at the site in late November. Cover decreased slowly after January, fell just below 80% in late May and continued to decrease steadily to a minimum level of 70% in late July. The burn on 4 September 1991 was followed by the appearance of green shoots by the end of the month and appreciable development to 30% cover by 23 October. No birds occupied the site that summer and 75% cover was achieved only in late January 1992 and 79-80% a month later, after which there was a gradual decline to 75% in early July.

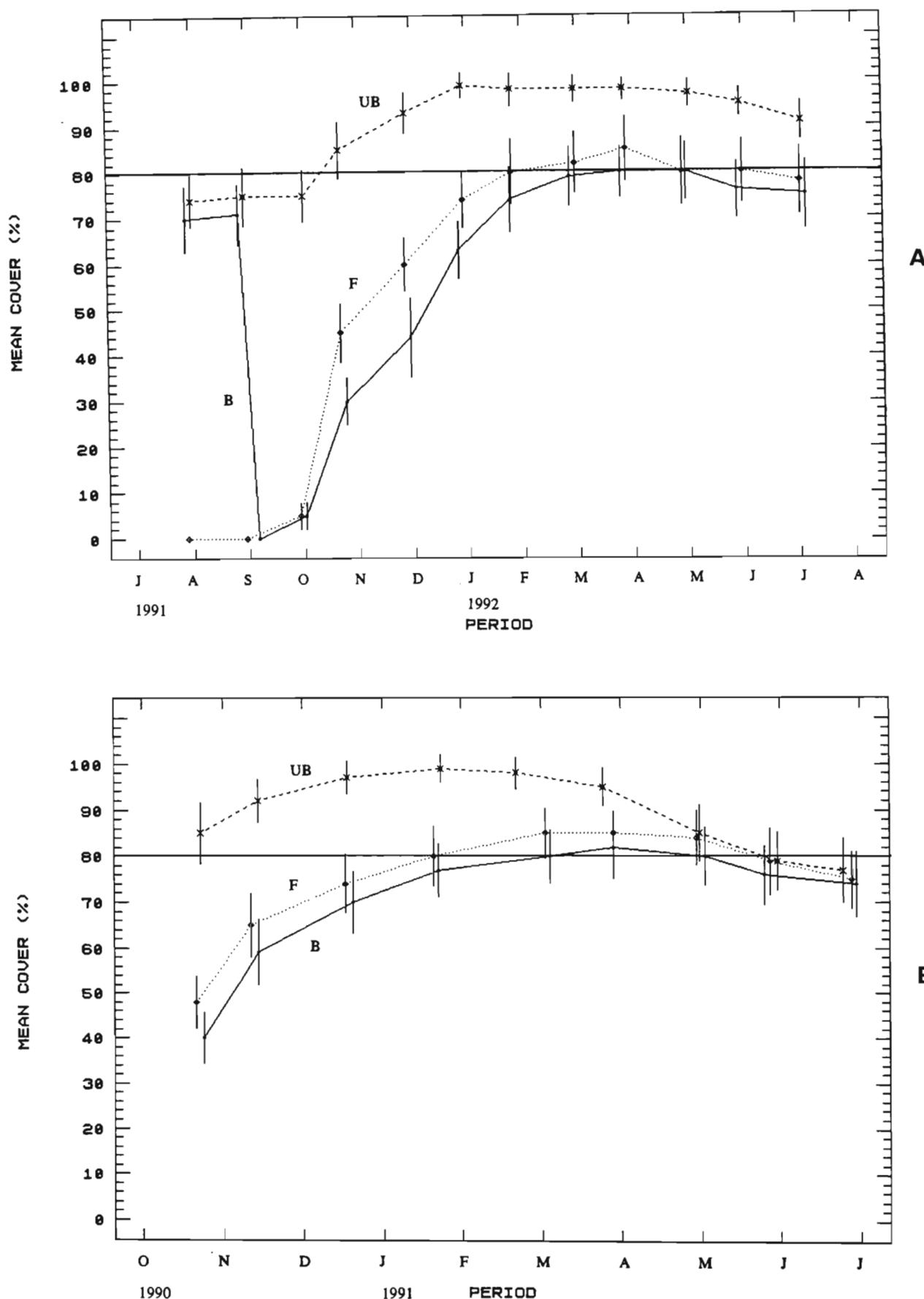
Thus at these two sites 80% ground cover was present in October when no spring burn had taken place but was not attained until late February in the summer following a burn. At both sites cover did not decrease below 70-75% in July, whether or not there had been a burn in the previous spring.

Figure 7.8A compares the mean percentage cover at burned, unburned and firebreak (burned in July) sites from July 1991 to July 1992, and Fig. 7.8B shows similar measurements for October 1990 to July 1991. It can be seen that in both periods the cover in the burned and firebreak areas remained appreciably less than the cover in the unburned area throughout the summer, and that the firebreak cover developed slightly earlier, and attained a 3-5% higher maximum, than on the burned ground. From May 1991 cover in all three vegetation areas was reduced to about 75%. In both periods the firebreak vegetation cover reached 80% in late January, about a month earlier than on spring-burned ground.

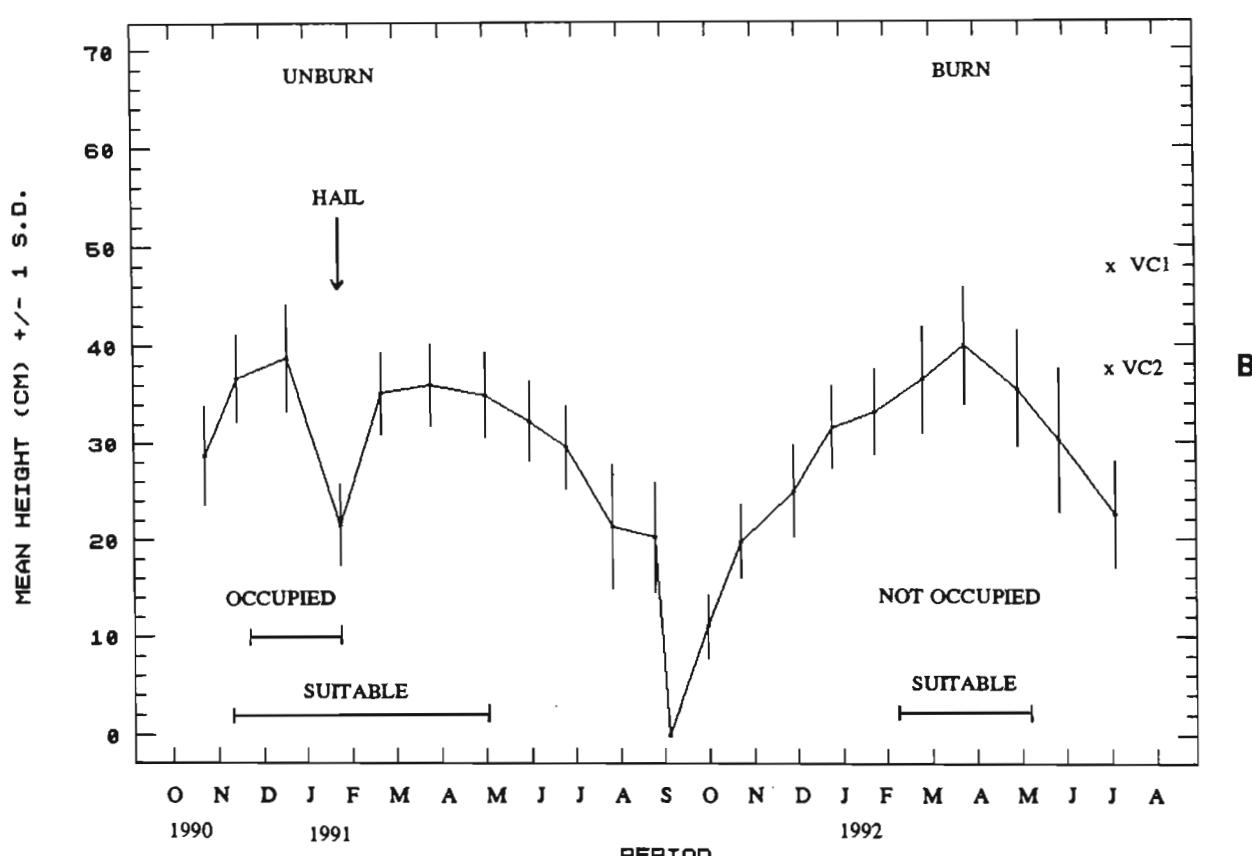
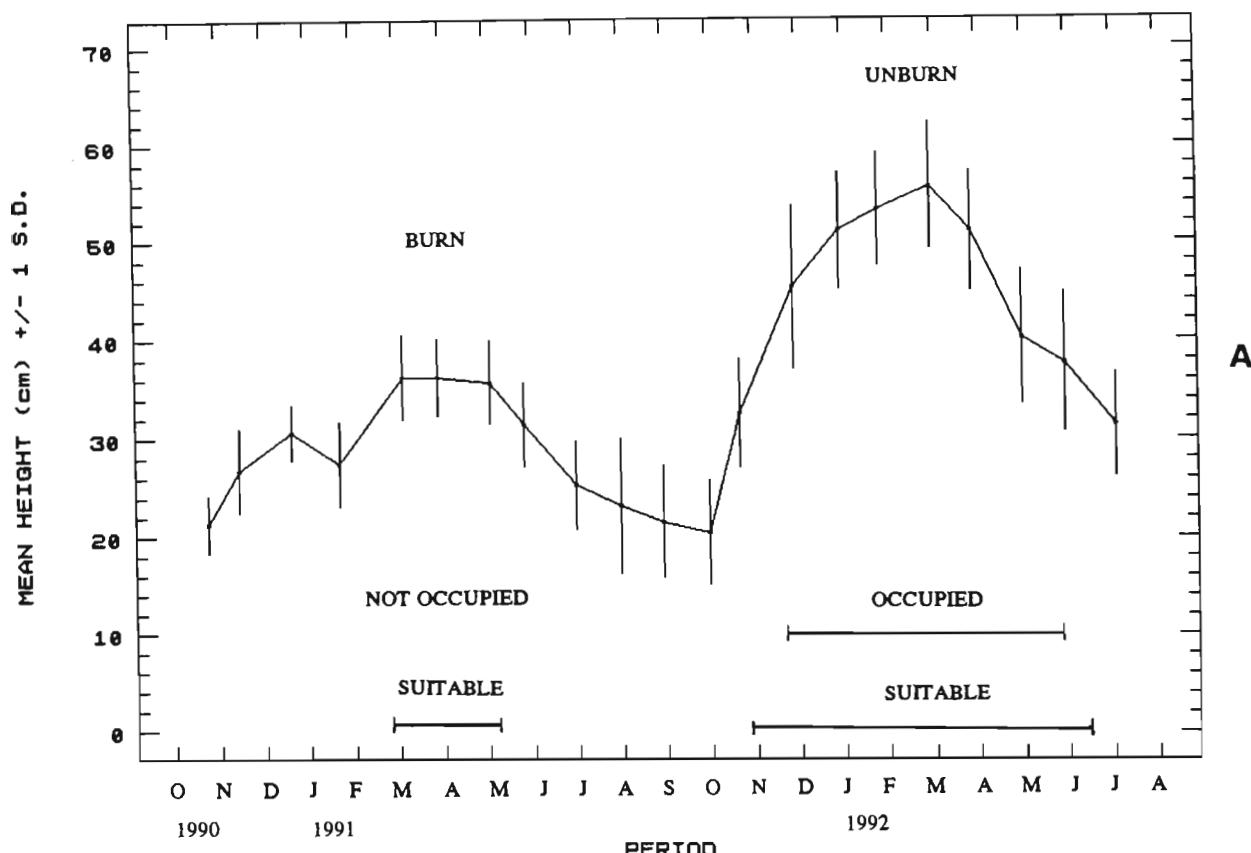
Fig. 7.9A shows the variation in mean vegetation height at the Block 2 site during the 1990-92 sampling period, with the periods of occupation by Striped Flufftail. Mean height was 21,3 cm in October 1990, eight weeks after the burn, and had reached 30,6 cm on 19 December and no birds were present. The 18 January 1991 hailstorm flattened the vegetation somewhat, reducing the mean height to 27,5 cm (measured on 21 January), and recovery occurred in February, 36,3 cm being measured in March. The mean height decreased to 31,4 cm in late May and was only 23,1 cm on 30 July. Further slight decreases occurred until growth started in late September, and a mean height of 35 cm is estimated from the graph to have been attained in late October. Birds occupied the area in



**Fig. 7.7** Mean percentage cover ( $\pm 1$  S.D.) measured at the Mt Currie Block 2 sampling site (A) and Block 3 sampling site (B), October 1990 to July 1992. Burning regime, the period theoretically suitable for occupation by Striped Flufftails (cover  $\geq 80\%$ ), and the actual periods of occupation are shown. The Vernon Crookes July 1992 cover measurements (VC1,2)



**Fig. 7.8** Mean percentage cover ( $\pm 1$  S.D.) at Mt Currie sampling sites, July 1991 to July 1992 (A) and October 1990 to July 1991 (B) for burned (B), firebreak (F) and unburned (UB) grassland. The theoretical minimum cover required for occupation



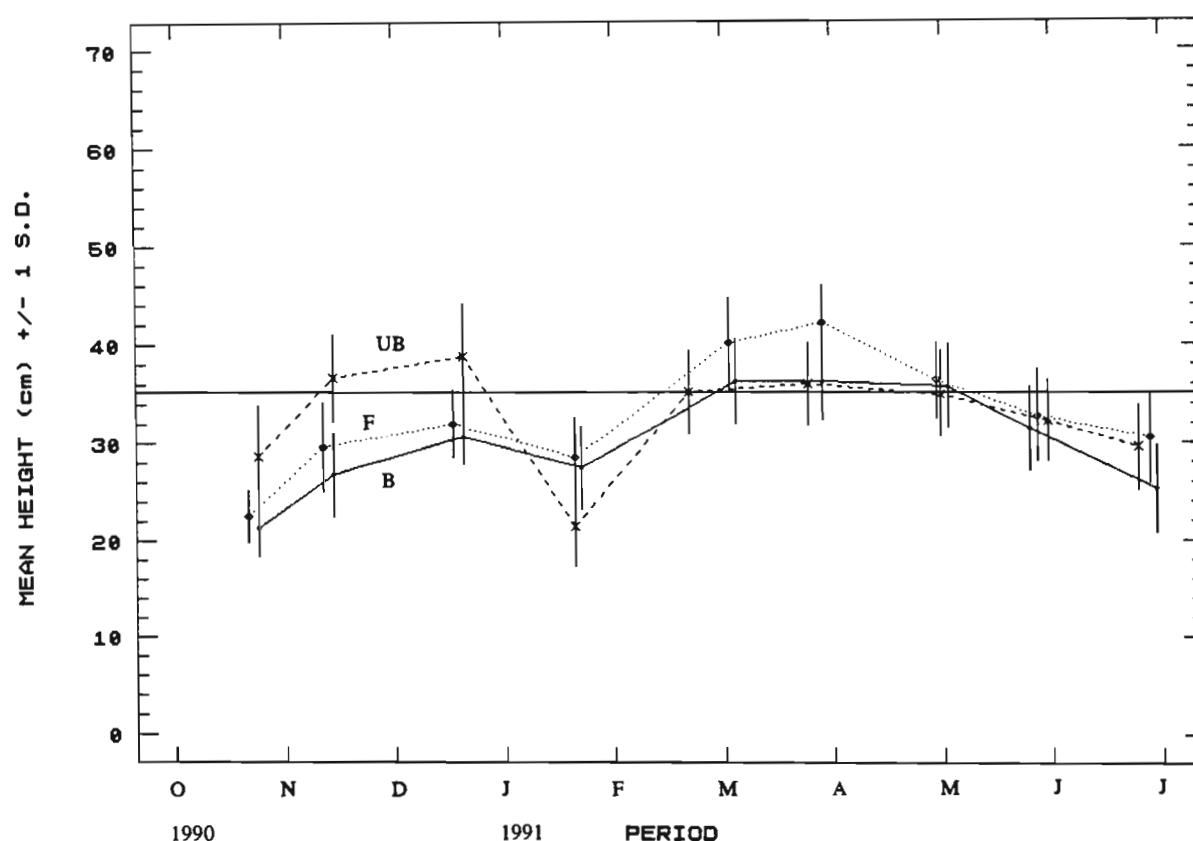
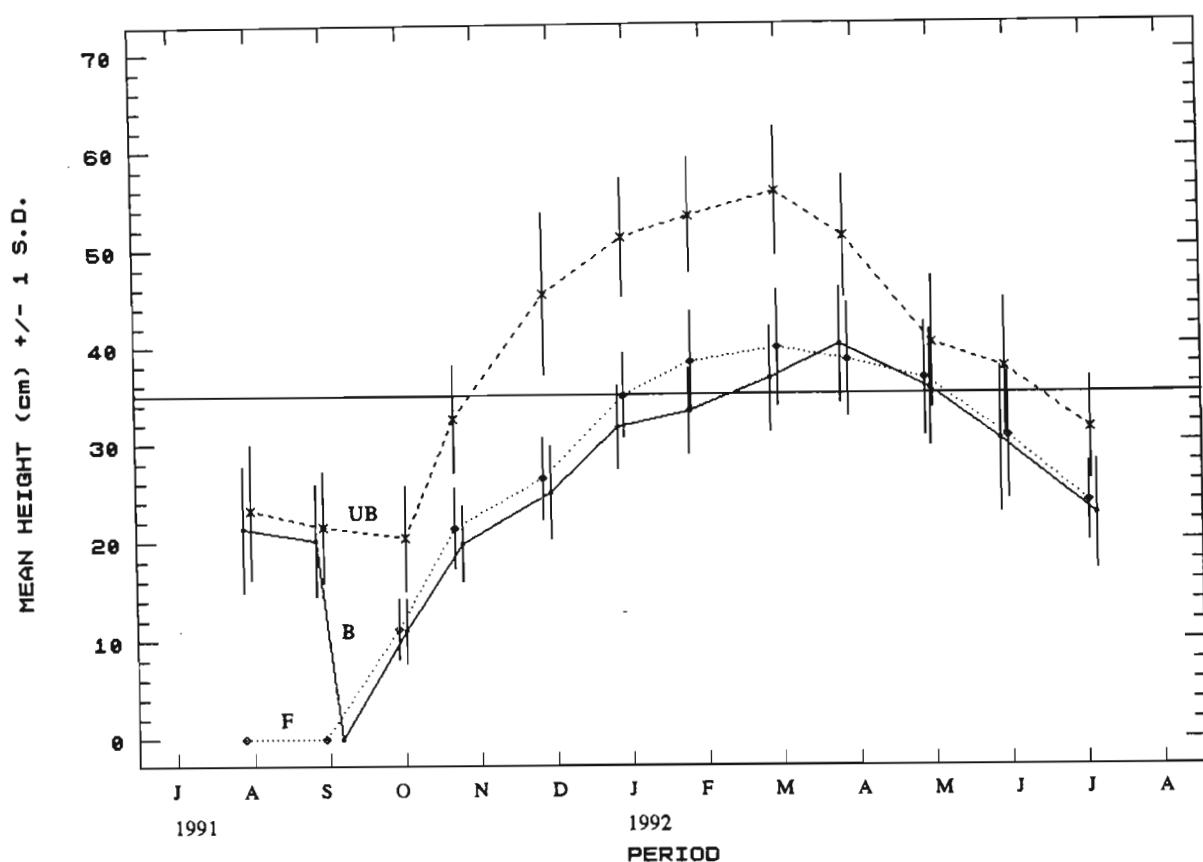
**Fig. 7.9** Mean vegetation height ( $\pm$  1 S.D.) measured at the Mt Currie Block 2 sampling site (A) and Block 3 sampling site (B), October 1990 to July 1992. Burning regime, the period theoretically suitable for occupation by Striped Flufftails (mean height  $\geq$  35 cm), and the actual periods of occupation are shown. The Vernon Crookes July 1992 mean height measurements (VC1,2) are shown (B).

late November, growth was rapid until early December, the *Themeda* coming into flower in November, and a maximum mean height of 55,7 cm was measured on 28 February. A rapid decrease then occurred down to 37,7 cm in late May, at which time the last flufftails left the area, and 31,4 cm in early July.

At the Block 3 site in the same period the unburned grassland had a mean height of 28,7 cm on 22 October 1990 and 36,7 cm on 13 November (Fig. 7.9B), when the *Themeda* was starting to flower. The 18 January 1991 hailstorm was particularly severe at Block 3 and the sampling site was hard-hit, all Striped Flufftails disappearing from the area and the mean height on 22 January being only 21,5 cm. Recovery to 35,1 cm was measured on 20 February but little further growth occurred. In May, mean height fell below 35 cm and was only 20-21 cm in July-August. After the burn on 4 September growth began quickly and a mean height of 11,0 cm was measured 26 days later. On 25 December a mean of 31,6 cm was measured and 35 cm is estimated to have been attained only in mid-February 1992; no birds occupied the area that summer. The maximum measurement of 40,0 cm on 24 March (when most grasses were seeding) was followed by a decline to 35 cm in early May and 22,5 cm in early July.

Thus when the vegetation was not burned a mean height of 35 cm was attained in late October to mid-November, while after the Block 3 burn this height was not attained until mid-February. At both sites the mean height fell below 35 cm in May to early June, somewhat earlier in burned grassland than in unburned.

Fig. 7.10A compares the mean heights in burned, unburned and firebreak (burned in July) vegetation from July 1991 to July 1992 and Fig. 7.10B shows comparative figures for October 1990 to July 1991. In 1991-92 the mean height in the burned and firebreak vegetation remained considerably lower than that in the unburned vegetation throughout the period and, while growth in the unburned area did not lead to an overall height increase until October, it was more rapid in October-November than in the burn and firebreak. The firebreak vegetation averaged slightly taller than the burn vegetation until late March, after which the heights of both were approximately equal. In 1990 the unburned vegetation, after increasing in height more slowly during November-December than in 1991, was flattened lower than the firebreak and burned vegetation (which escaped the worst of the hail) and subsequently remained lower than in the other two areas until May, after which its height was similar to that of the firebreak vegetation. November-December growth rates in burned and firebreak grassland were also lower than in 1991 and, after the hailstorm, the firebreak vegetation recovered to a greater height than the others. Overall May-July decline in vegetation heights were similar in both years.



**Fig. 7.10** Mean vegetation height ( $\pm 1$  S.D.) at Mt Currie sampling sites, July 1991 to July 1992 (A) and October 1990 to July 1991 (B) for burned (B), firebreak (F) and unburned (UB) grassland. The theoretical minimum height for occupation (35 cm) is shown.

Plots of mean vegetation height against mean ground cover for the two sites are given in Figs 7.11 and 7.12. The former shows that, at the Block 2 site, the period during which both height and cover were above the theoretical minimum was very short (February to April) in early 1991, when no birds occupied the site, but extended from October to May in 1991-92, during which season the site was occupied. At the Block 3 site (Fig. 7.12) the equivalent period was very short in both seasons, being temporarily reduced after the January 1991 hailstorm and conditions being only marginally suitable in March-April 1992; in neither season did the birds breed at the site.

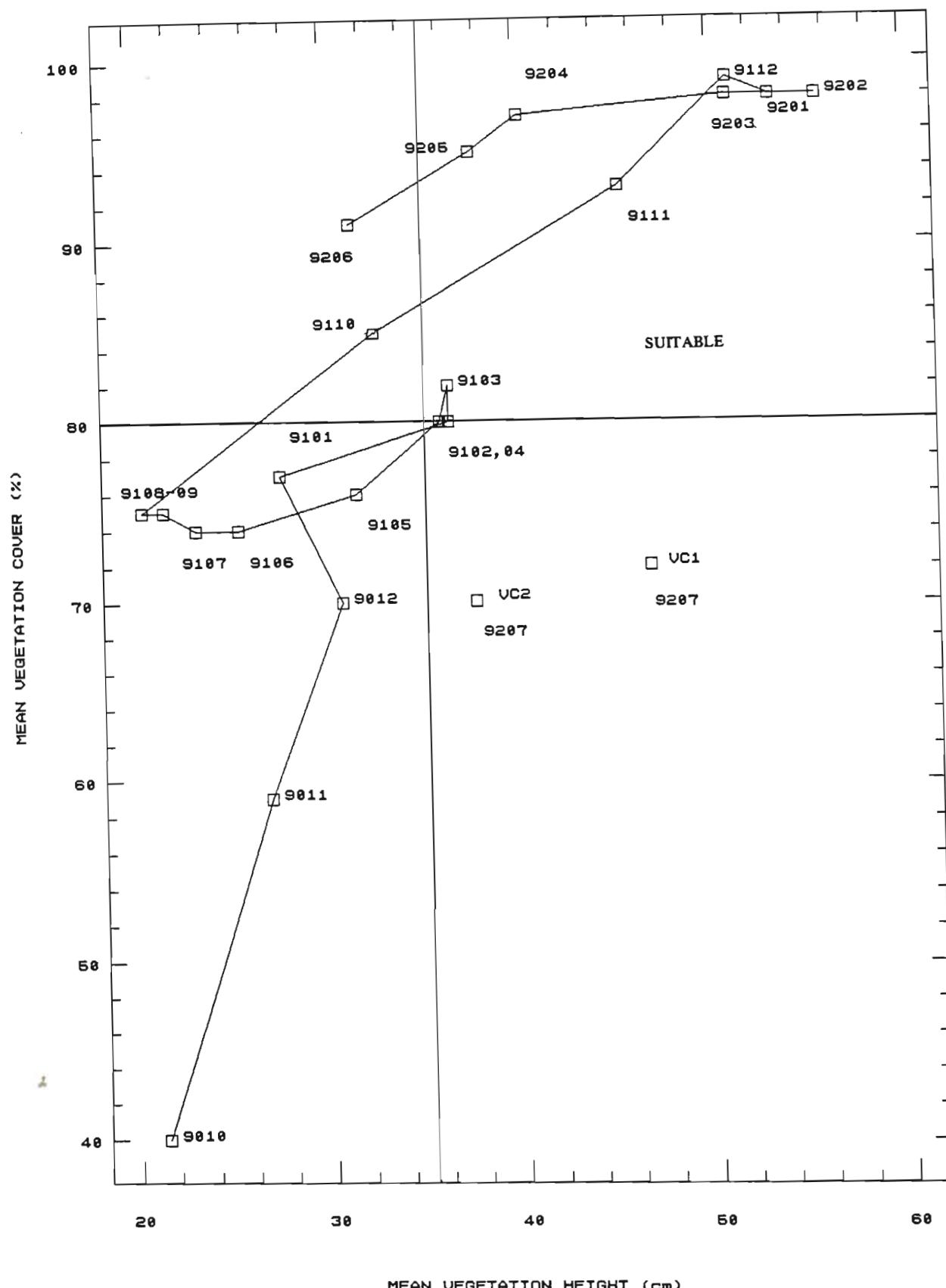
Casual observations made in other areas of habitat on the reserve provide supplementary details of vegetation development. In mid-December 1989 the bracken-briar and tall forbs in Block 6 were growing well after the spring burn but had not reached a height or density judged suitable for occupation by Striped Flufftails, this being attained in January but no birds returning to the site. Firebreaks burned in June-July showed noticeable "greening over" by early August, when the first small forbs also came into flower, but appreciable growth of grasses did not occur until September and firebreaks were extensively grazed by the reserve's large herbivores in August-September.

In late November 1991 the *Themeda* in Block 2 unburned areas was almost all in flower, and thus tall, while only 15-20% of that on the firebreaks was in flower, and very little of that in the burned areas.

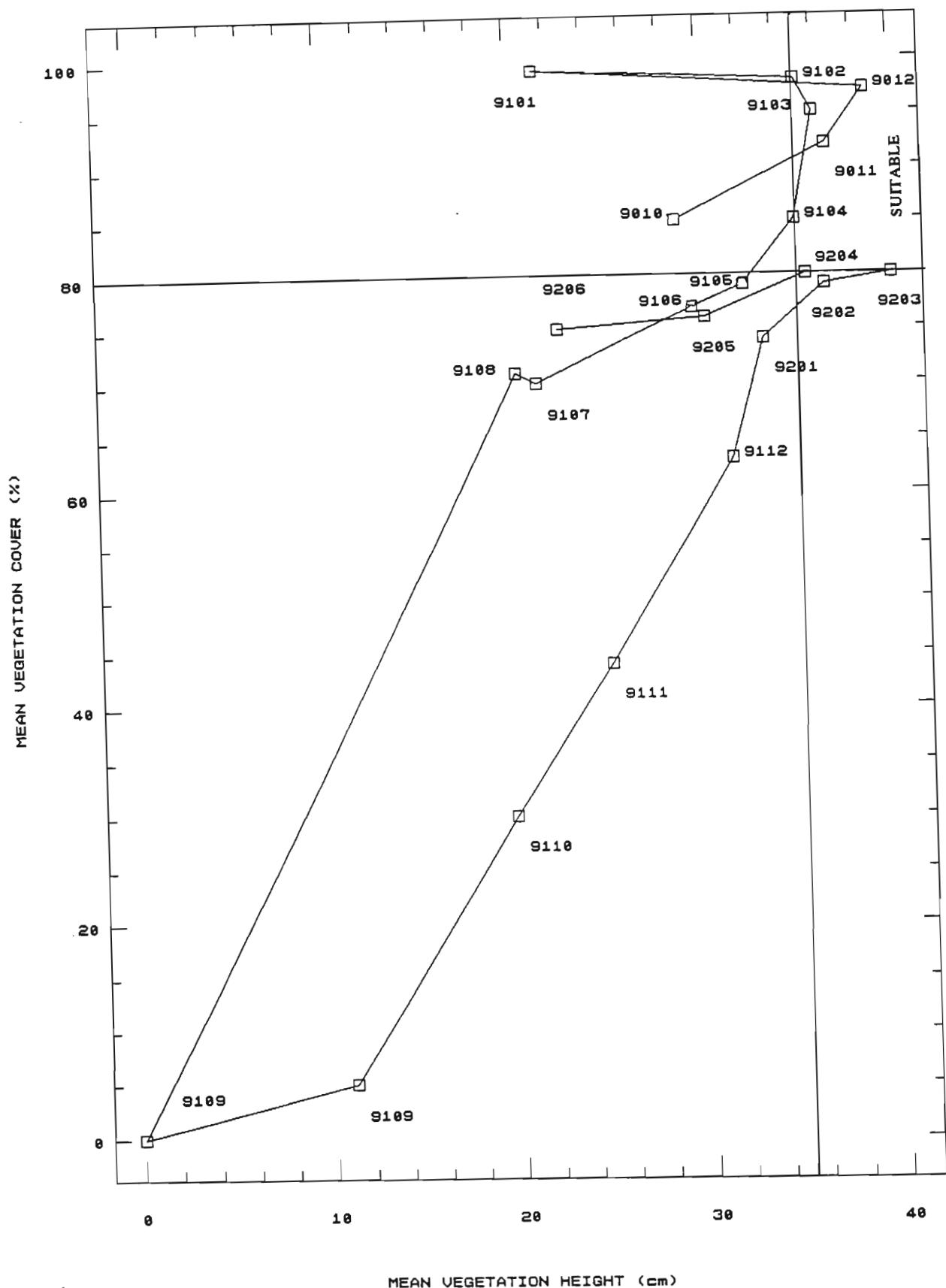
Comparative samples from occupied habitats at Vernon Crookes Reserve in July 1992 (Section 7.3.6) gave a mean ground cover of 72% and mean vegetation height of 46.7 cm in the sheltered valley mixed grasses and forbs, and cover of 70% and height of 37.6 cm on the open slope *Themeda* grassland. The cover percentages correspond to those from Mt Currie in July while the heights are considerably greater, both being above the theoretical minimum of 35 cm, and both sampling sites were occupied by Striped Flufftails. The Vernon Crookes figures are plotted on Figs 7.7B, 7.9B, 7.11 and 7.12 for comparison purposes.

#### **7.4.8      The effects of burning on invertebrate food availability**

As there is no information available to indicate the minimum density of potential prey which might render an invertebrate population economically exploitable by Striped Flufftails, my analysis of the potential effects of invertebrate abundance is based on trends and comparisons rather than on absolute numerical abundance in any vegetation type. Factors considered include the relative abundance of invertebrates in different vegetation types over a period, and the changes in invertebrate density which occurred during the periods when the birds first arrived at the reserve (November), first left breeding territories (late April) and finally left the reserve (late June).



**Fig. 7.11** Plot of mean vegetation cover against mean vegetation height at the Mt Currie Block 2 sampling site, October 1990 to July 1992, showing the periods of theoretically suitable vegetation structure (mean cover  $\geq 80\%$  and mean height  $\geq 35\text{ cm}$ ), with the Vernon Crookes July 1992 measurements (VC1,2) for comparison.



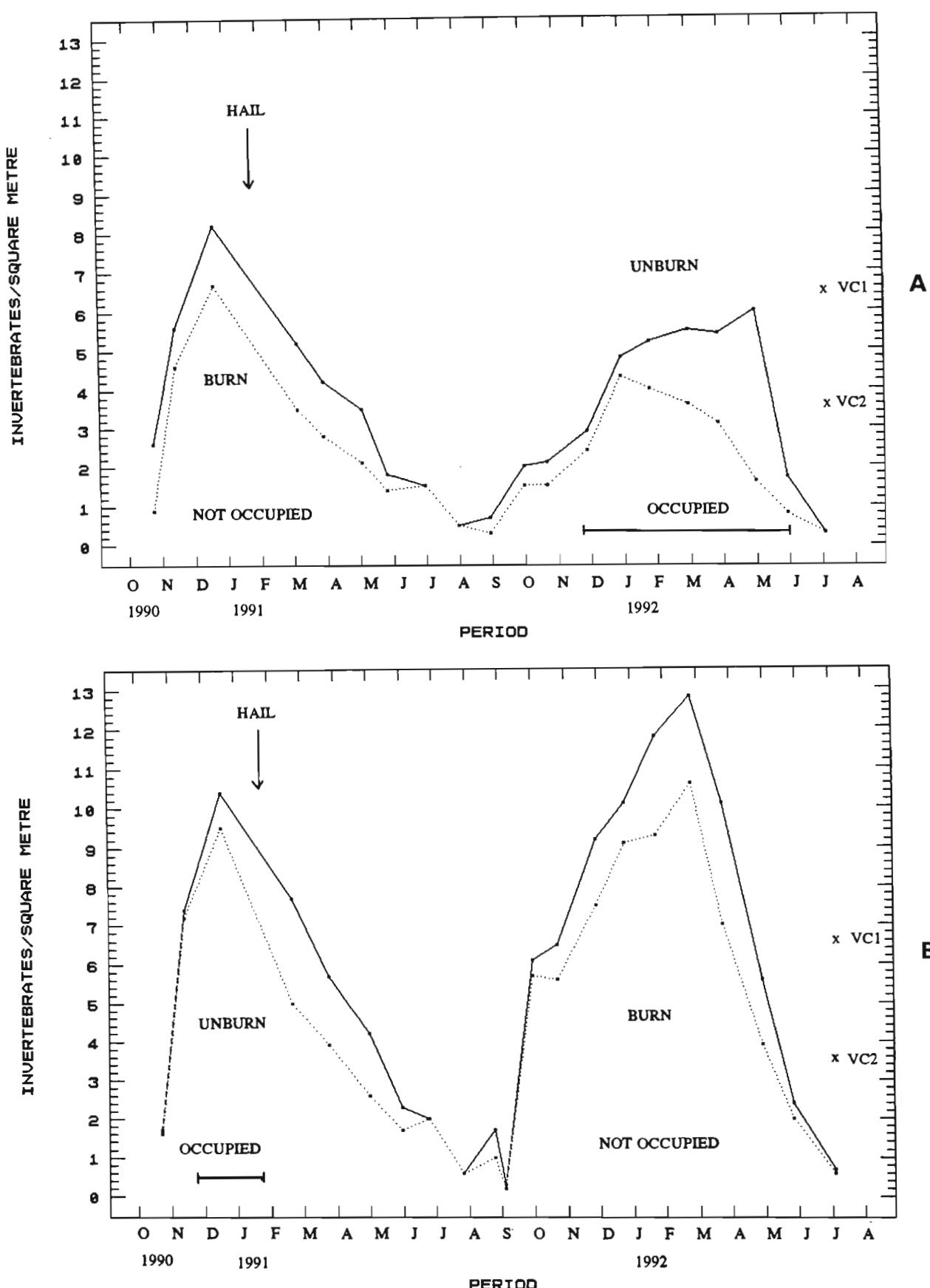
**Fig. 7.12** Plot of mean vegetation cover against mean vegetation height at the Mt Currie Block 3 sampling site, October 1990 to July 1992, showing the periods of theoretically suitable vegetation structure (mean cover  $\geq 80\%$  and mean height  $\geq 35$  cm).

The results of invertebrate sampling are shown in Figs 7.13-7.15, with the samples from Vernon Crookes also shown in Fig. 7.13. Some Mt Currie samples yielded very low numbers of invertebrates, especially in winter, and even in summer the maximum number of invertebrates recorded from any quadrat did not exceed 15 and was usually only 1-5, suggesting that Striped Flufftails may have to search extensively for food in this grassland (see Discussion). The graphs of relative abundance show both the mean number of invertebrates per square metre for each sample and the mean excluding those large actively-flying insects of the upper vegetation (e.g. large adult grasshoppers and large butterflies) which would probably not be caught by Striped Flufftails; over most of the period the two lines reflect similar variations in numbers (Fig. 7.13).

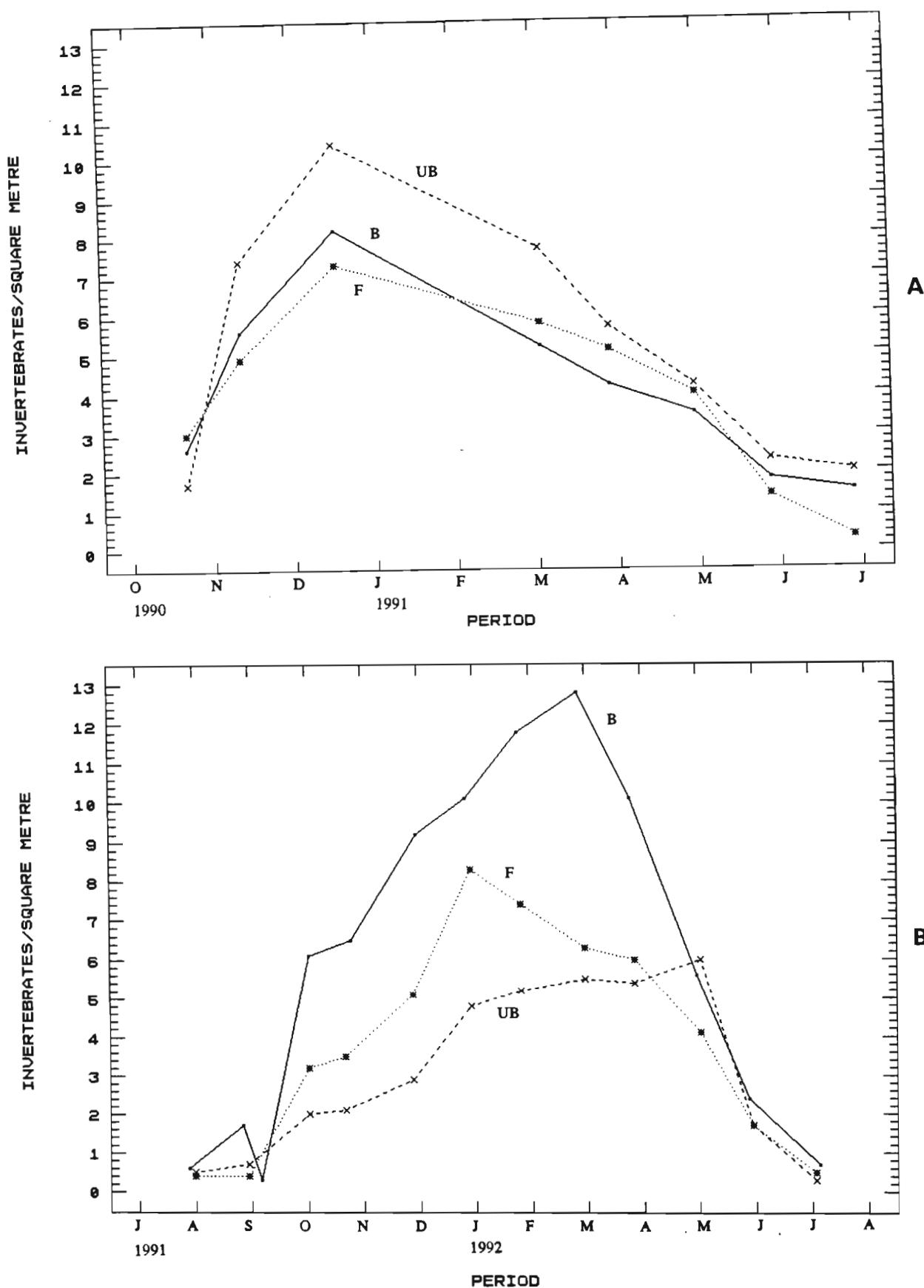
Fig. 7.13A summarizes the sampling done at the Block 2 site between October 1990 and July 1992, after a spring burn on 2 September 1990. Invertebrate numbers first rose sharply to a peak of  $8,2/m^2$  in December 1990 and were reduced, after the hailstorm of 18 January 1991, to a late-March figure of  $4,2/m^2$ , 51% of the December figure and about the same as the estimated early-November density. Decline continued rapidly (June density being equivalent to that in the previous October) to a minimum overall density of  $0,5/m^2$  in early August. By November 1991 the overall density had increased only to  $2,4/m^2$ , reaching the previous November's level only in early December, potential prey numbers declining from January, although overall numbers increased until May. This late-summer increase was due mainly to the presence of exceptional numbers of grasshoppers (see Discussion). Prey density fell in June 1992 to that recorded in November 1991. Potential prey were sparse in the very tangled vegetation at this site in early 1992.

The Block 3 samples (Fig. 7.13B) for the same period show a very rapid increase in invertebrate density in the unburned grassland, from  $1,7/m^2$  in late October to  $7,4/m^2$  in late November and reaching a peak of  $10,4/m^2$  on 17 December. Numbers were reduced after the January 1991 hailstorm, declining to the mid-November level in mid-March, while by early June 1991 they had declined to the early-November-1990 level. After a low density of  $0,6/m^2$  in July, numbers increased slightly in August but were reduced almost to zero by the burn on 4 September. A great increase took place with subsequent vegetation regrowth, to a density of  $6,1/m^2$  on 30 September while the mid-November density was about  $8,3/m^2$ . Numbers continued to increase, reaching a peak in late February when a mean density of  $12,8/m^2$  was measured. Thereafter a very sharp decline reduced the density in early April to approximately that found in the previous November, and the June density was equivalent to that in early September 1991.

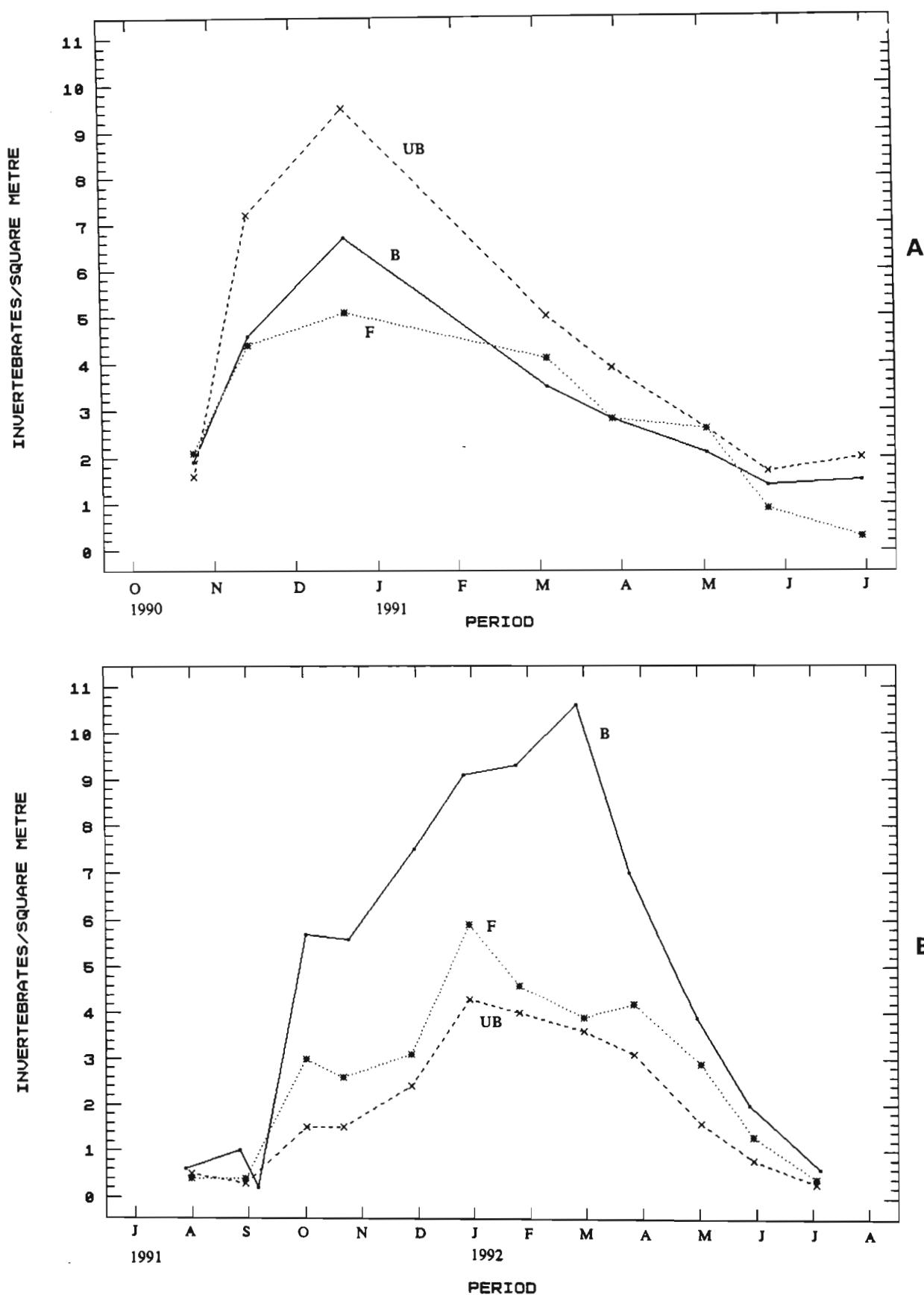
The general pattern which these figures reveal is that, in both burned and unburned vegetation, spring numbers rose very rapidly (except in the unburned vegetation of Block 3 in late 1991) and in all cases the November mean was equivalent to that measured at some time in the following March-June period, i.e. within the birds' period of occurrence. The November density was



**Fig. 7.13** Mean number of invertebrates/m<sup>2</sup> at the Mt Currie Block 2 sampling site (A) and Block 3 sampling site (B), October 1990 to July 1992, showing overall numbers (solid line) and numbers of potential prey (dotted line). Burning regime, the periods of occupation by Striped Flufftails, and the Vernon Crookes July 1992 invertebrate numbers (VC1,2) are shown.



**Fig. 7.14** Mean number of invertebrates/m<sup>2</sup> at Mt Currie sampling sites, October 1990 to July 1991 (A) and July 1991 to July 1992 (B) for burned (B), firebreak (F) and unburned (UB) grassland.



**Fig. 7.15** Mean number of potential food invertebrates/m<sup>2</sup> at Mt Currie sampling sites, October 1990 to July 1991 (A) and July 1991 to July 1992 (B) for burned (B), firebreak (F) and unburned (UB) grassland.

similar in the burn year and the unburn year at Block 3 and was greater in the burn year than in the unburn year at Block 2. Thus at the time of the first flufftail arrivals in November of both years there were no fewer invertebrates (and sometimes more) in burned vegetation than in unburned vegetation.

Fig. 7.14 compares invertebrate densities, and Fig. 7.15 potential food densities, in burned, unburned and firebreak vegetation over the periods October 1990 to July 1991 (Figs 7.14A and 7.15A) and July 1991 to July 1992 (Figs 7.14B and 7.15B). In 1990-91, both overall densities and those of potential food were greatest in unburned grassland and were slightly higher in burned grass than in firebreak grass during November-February. In 1991-92 the burned area had the highest densities, with much lower numbers in the unburned and firebreak vegetation until April.

Comparative measurements (Fig. 7.13) at Vernon Crookes Reserve in July 1992 gave a mean invertebrate density of 6,5/m<sup>2</sup> in the sheltered mixed grass and forbs, and 3,5/m<sup>2</sup> in the open *Themeda* grassland. The higher density is equivalent to that recorded at the three most productive Mt Currie sites in late November and at some time between February and April, while the lower density equates to that recorded at all Mt Currie sites at some time between October and early December and between May and June, i.e. both densities equate to those measured during the birds' occurrence period at Mt Currie.

#### 7.4.9 Relationships between occurrence patterns and (a) habitat quality, (b) the availability of cover and food, (c) burning

The results of the measurements of vegetation height and cover, and of invertebrate abundance, were compared with the observed distribution, occurrence patterns and habitat preferences of Striped Flufftails in an attempt to find relationships between (a) habitat preferences and arrival times, (b) arrival and departure times and the availability of cover and food, and (c) the relative suitability of burned and unburned vegetation for occupation. The relationships between occurrence periods and the availability of cover and food are mentioned briefly in Section 7.4.7 and 7.4.8, and are treated in detail in Section 7.5. To investigate the effects of altitude and vegetation type on the date of return I compared these variables with return dates to territories in unburned vegetation. The earliest returns in any season appeared to be randomly distributed with regard to both variables, and the analyses showed no significant correlation between return date and altitude (one-way ANOVA;  $F_{2,48} = 1,29$ ,  $P > 0,2$ ) or vegetation type ( $\chi^2_1 = 2,012$ ;  $P > 0,1$ ). The relationship between return date and aspect was analyzed with respect to burning blocks (see below).

It has already been mentioned (Section 7.4.6) that the number of occupied territories at Mt Currie varied from season to season. Table 7.10 shows that in all seasons there were more territories

in unburned habitat than in burned habitat. Furthermore, considering the situation in each burning block, the months of occupation were later during seasons following a burn than those after no burn (Table 7.11). The earliest-returning birds were always heard in unburned grassland, and in some burned blocks there was a reduction of over 50% in the number of territories compared to a season after no burn (Table 7.11). Immediately after the severe hailstorm of 18 January 1991 the number of pairs was reduced by 45% from 33 to 18, and some birds apparently moved to areas which had been less severely affected by hail (Tables 7.10, 7.11).

The recorded number of territories in Blocks 2, 3, 5 and 6 covering two biennial burning cycles (Table 7.11) were used to investigate the relationship between territory numbers and year-to-year variations, burning and variations between blocks. A Generalized Linear Model (GLM) (McCullagh & Nelder 1989) shows that there were no statistically significant year-to-year variations but that (a) Block 5 held significantly fewer birds than the other blocks, and (b) that a burned block held significantly fewer territories than an unburned block. The model is:

$$\log_e(\text{no. of territories}) = 2,444 (\pm 0,119)$$

- 1,204 (\pm 0,348) [for Block 5]
- 1,195 (\pm 0,238) [for burn]

The reduction in variance of the model ( $R^2$ ) was 83% and the goodness-of-fit was excellent ( $\chi^2_{13} = 9,551$ ;  $P = 0,655$ ). The model may be re-described in terms of a constant and two factors:

$$\begin{aligned} \text{No. of territories} &= (\text{constant}).(\text{Block 5 factor}).(\text{burn factor}) \\ &= (11,519)*(0,2999)*(0,3027) \end{aligned}$$

Thus Block 5 supports 70% fewer territories than other blocks, while burning reduces the number of territories in any block by 69,7%.

The model assumes that the areas of suitable habitat in each of the four blocks are approximately equal and this is so in Blocks 2, 3 and 6-8, which each has about 170 ha of habitat (Table 7.9). Block 5 has only 75% (124 ha) of this total, but 122 ha lie at altitudes favoured by the birds (below 1 600 m) which compares more favourably with the other blocks (Table 7.9). Block 5's smaller habitat area therefore does not adequately explain its low number (7) of territories, but habitat quality may do so. Compared with the *Themeda triandra* grassland in Blocks 2, 3, 6 and 8, some of that in Block 5 was short and sparse, giving only patchy cover, while *Tristachya leucothrix*

TABLE 7.11

The numbers of Striped Flufftail breeding territories in each occupied block at Mt Currie Reserve, 1988-89 to 1991-92, with months of occupation in each season. Figures in parentheses refer to the January-February 1991 totals after the severe hailstorm of January 17 1991. Months of occupation were not determined in the 1988-89 season.

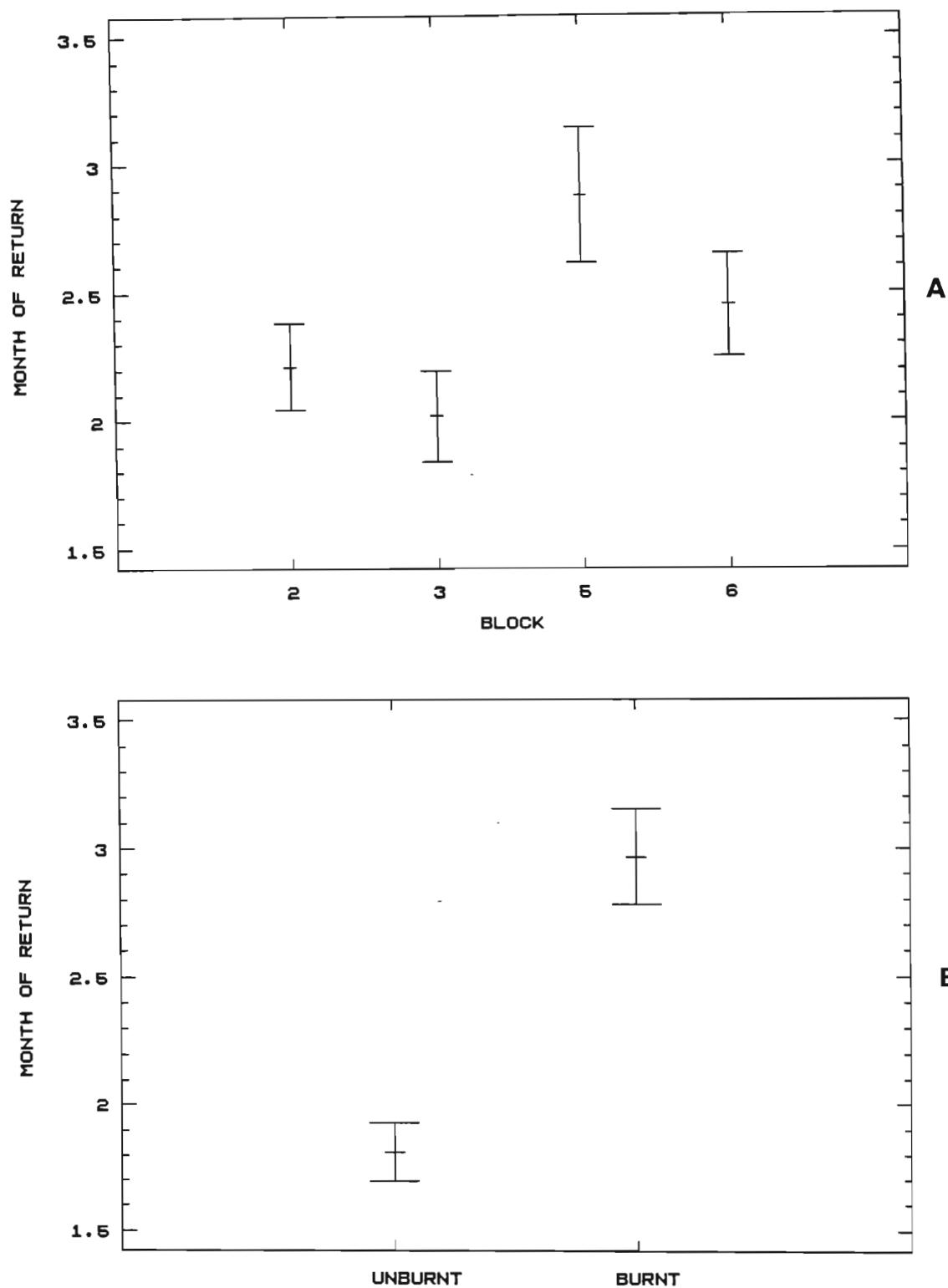
Block	Season	Burn/ Unburn	Total No. territories	Month of occupation		
				November	December	January
1	1988-89	B	0			
	1989-90	U	0			
	1990-91	B	1 (1)	0	0	1
	1991-92	U	0			
2	1988-89	B	5			
	1989-90	U	9	5	4	0
	1990-91	B	5 (9)	0	0	5
	1991-92	U	10	4	5	1
3	1988-89	U	14			
	1989-90	B	3	0	0	3
	1990-91	U	16 (4)	10	6	0
	1991-92	B	2	0	1	1
5	1988-89	B	0			
	1989-90	U	5	0	2	3
	1990-91	B	2 (1)	0	0	2
	1991-92	U	2	0	2	0
6 + 8	1988-89	U	11			
	1989-90	B	4	0	0	4
	1990-90	U	9 (3)	2	5	2
	1991-92	B	2	0	1	1

was widespread in Block 5 and was considered to be less suitable because of its more creeping habit and its tendency to close up the grassland more than does *Themeda triandra*, which produces a tussocky growth with more space for birds to move around at ground level.

A multifactor analysis of variance was done on the same data and two findings were of interest.

(a) Return was on average earlier to Blocks 2 and 3, on the western side of the mountain, than to Blocks 5 and 6 on the eastern side. The difference between the earliest return (Block 3) and the latest return (Block 5) was 0,8 months (Fig. 7.16A). The reason for this may be related to aspect and temperature. The territories in Block 3 predominantly faced west-northwest to west-southwest, those in Block 2 west to south-southwest, in Block 5 south to southeast and in Block 6 south-southwest to south-southeast. From the model developed by Schulze (1975) to predict the incoming radiant flux densities on sloping ground in South Africa, the radiation received in early summer should be most on northwest to west slopes, less on southeast and southwest slopes and least on south slopes. This pattern suggests that the Block 3 territories received the most radiation, those in Block 2 somewhat more than those in Block 6, and those in Block 5 least of all. As Everson (1985) has shown that the initiation of spring growth of *Themeda triandra* is correlated with temperature rather than rainfall, the grass on the warmer mountain slopes of Blocks 2 and 3 may provide cover earlier than that on the slopes of Blocks 5 and 6, and may also be richer in invertebrate food earlier in the summer. The burning regime at Mt Currie should also favour earlier occupation of the mountain's western slopes, since burns there are fast, whereas on the eastern side burns are slow to avoid damage to *Protea* trees (T. Snow pers. comm.). Slow burns ("back fires") burn against the wind, are hotter at ground level and significantly depress the regrowth of grass in comparison to fast burns ("head fires"), which burn with the wind, move rapidly and are cooler at ground level (Trollope 1978, 1984). Burns of the eastern slopes often occur later than those on the western side (Chapter 2, Table 2.7), the later start of regrowth possibly affecting the relatively sparse colonization of burned ground.

(b) After a burn blocks were occupied an average of 1,16 months later than after no burn, in late December to early January as opposed to late November (Fig. 7.16B). This period is less than that predicted from the development of vegetation height and cover, which may not reach theoretically suitable levels until late January or early February (Section 7.4.7), more than two months after the first November occupations in unburned areas (Table 7.11). But it must be borne in mind that some burned areas may be suitable for occupation earlier than others because of cover provided by growth of forbs or taller grass species (growth rates of these were not measured), while in January birds may have to occupy less-than-optimum habitat in order to have time to breed (see Discussion).



**Fig. 7.16** Multifactor analysis of variance means plot, with 95% confidence limits, of the variations in month of return of Striped Flufftails to Mt Currie breeding territories by block (A) and burning regime (B). See Section 7.4.8 for explanation.

#### 7.4.10 Post-breeding dispersal

Observations at Mt Currie in all years showed a similar pattern of behaviour in the period between the end of breeding activity and the time of the last birds' disappearance from the area. After the cessation of calling at the end of February, birds were still present in the breeding territories throughout March and most of April but from the end of April some territories in the pure grassland habitats were vacated and at the same time non-territorial birds began to appear low down on the west-facing hillsides of Blocks 2 and 3 which overlooked the wetland Blocks V2 and V4 (Chapter 2, Fig. 2.28). These birds called only with the alarm bark and were difficult to locate. During May and June the numbers of birds in this area increased, groups of up to four being recorded on the lowest slopes, while more territories on the mountain grassland slopes were vacated. The habitat occupied by these apparently displaced birds was initially *Themeda triandra* sourveld vegetation but, as time progressed and the weather became cooler in May and June, the birds moved lower, some entering the taller *Hyparrhenia* grass at the base of the slopes. However none was ever found across the river in the vlei Blocks V1-V4. By the end of June all these birds had gone, the latest date of occurrence recorded in this habitat being 25 June in 1989.

Not all birds left the breeding territories in May and June, however, and in three years one or two pairs were found on the low south-facing slopes of Block 6, in territories of mixed vegetation types, i.e. containing tall forbs, tall mixed grasses and some *Leucosidea* and *Buddleja* bushes. These birds sometimes remained in their territories until late June, the latest occurrence date again being 25 June in 1989. In all cases the birds continued to give *KI-KER* calls in response to taped playback throughout their period of residence, and they were therefore presumed to be territorial for the whole period. The late occurrence in either Block 6 breeding territories or Blocks 2 and 3 grassland areas occurred whether or not these areas had been burned in the spring of that breeding season.

Although no vegetation measurements were made in Block 6 vegetation, the characteristics of the late-occupied territories bore some resemblances to the mixed habitat at Vernon Crookes Reserve in which the July 1992 invertebrate density and vegetation height were greater than those in the adjacent *Themeda* grassland (see Sections 7.4.7 and 7.4.8).

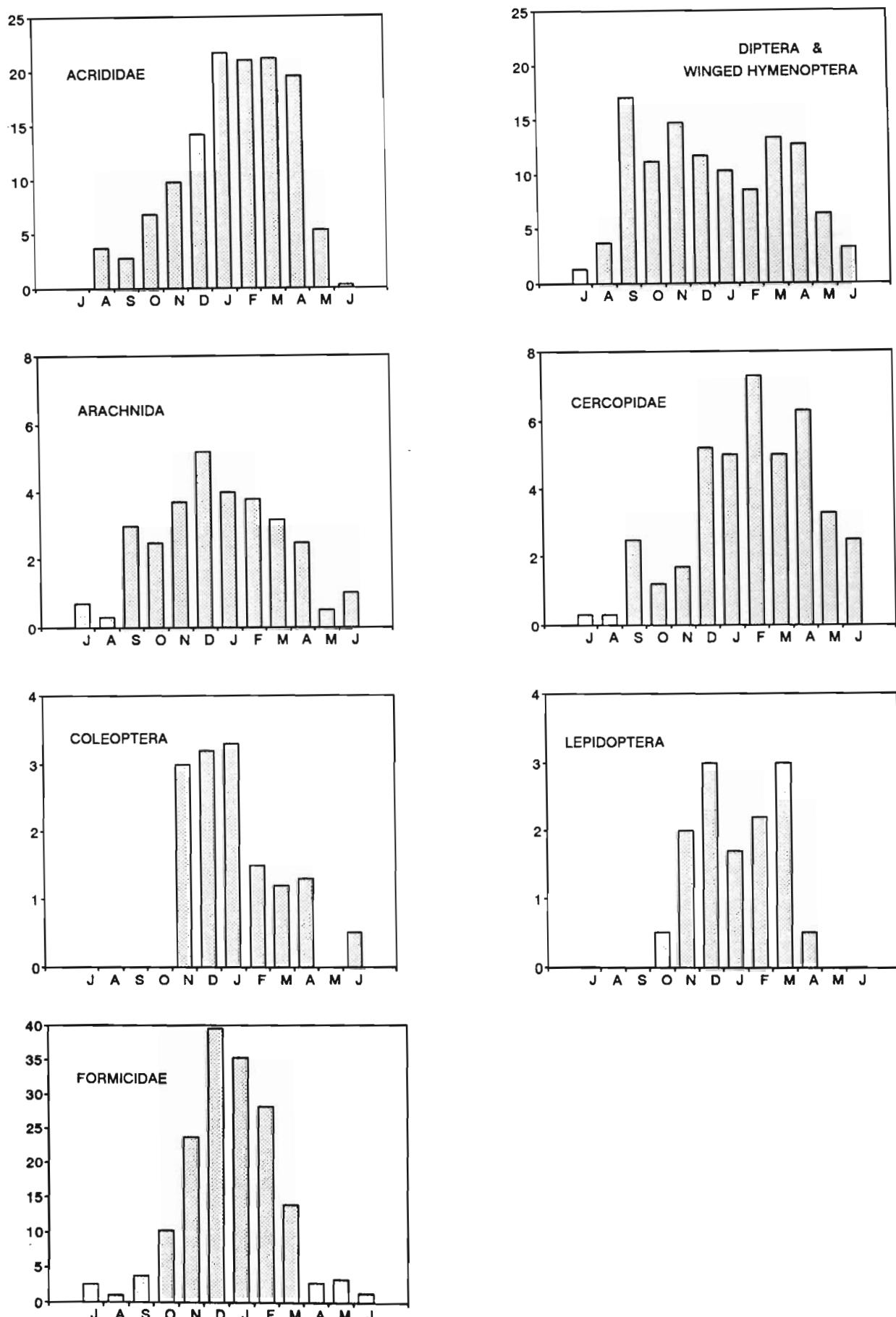
After the January 1991 hailstorm 23 of the 33 occupied breeding territories immediately fell vacant. By early February eight new territories had been occupied in grassland little affected by the hail and which had not contained territories in January, giving a February total of 18 pairs on the mountain (Tables 7.10, 7.11). No birds were heard or seen after 1 March and it was assumed that all had left the area by that date; none appeared in areas outside the territories later in the season.

#### 7.4.11 Feeding methods and food

The difficulty of observing Striped Flufftails for any length of time on the ground precluded any detailed observations of feeding, but occasional observations of foraging birds at Mt Currie indicated that this species' foraging tactics are similar to those of other flufftails. The birds take food items from the surface of the ground, move aside fallen dead plant material with the bill to search for invertebrates, search the edges of the bases of grass tussocks and other clumps of vegetation and stretch up to remove invertebrates from low-growing stems and leaves. I have not seen them feeding in water but in view of their frequent presence near small streams and moist patches on hillsides they probably regularly forage in wet areas. I have never seen them climbing in robust herbaceous or woody plants, either while foraging or in response to taped playback to obtain a better view of the observer, but they do climb into the upper parts of grass tussocks for the latter purpose (as do Redchested and Whitewinged Flufftails in wetland vegetation). They were not seen feeding among rocks or stones but occasionally a bird would use a rock as a vantage point from which to watch an observer at a lower elevation on the hillside.

My observations of feeding include birds taking invertebrates such as beetles, small lepidopteran adults (moths) and larvae, ants, grasshopper nymphs (very occasional) and possibly small spiders. They also picked up small plant food items, including grass seeds, from the ground. The gizzard of a wintering adult male from Ixopo on 6 July 1990 contained 12 partially digested grass seeds, 8 smooth hard dark seeds (unidentified) 1,2 mm long, fragments of a large beetle (Carabidae) and ten pieces of quartz grit 1-2 mm in diameter. That of a breeding adult male from Underberg on 15 December 1993 contained the remains of 30 small ants *Tetramorium* sp. and one large ant, 11 small weevils (Curculionidae) and one beetle (Carabidae), one large lepidopteran adult and 4 lepidopteran larvae, mandibles of about 20 termites, one cockroach (Blattidae) oothecum, one fly (Sciaridae), two small coleopteran larvae and 12 rounded stones 1-2 mm in diameter. This selection of invertebrates closely parallels that found in gizzards of the Buffspotted Flufftail *S. elegans* (Chapter 9). Like its congeners, the Striped Flufftail appears to be a generalist feeder on invertebrates and small seeds, possibly taking a larger proportion of seeds during the winter months.

The histograms in Fig. 7.17 show the mean numbers per sampling month of each of the seven main groups of arthropods present in the grassland samples. Of these seven groups, only the Cercopidae (spittle bugs) are not known to be taken by Striped Flufftails. Comparing the relative abundance of arthropods within and outside the November-April occurrence period of the flufftails in this grassland it may be seen that, in April-May numbers of flies, spiders, lepidopterans and grasshoppers fell below those in November, while ant numbers first fell sharply in March and were



**Fig. 7.17** Overall January-December monthly mean numbers per sample of seven different arthropod groups at the Mt Currie sampling sites ( $n = 61$  monthly samples, October)

at a very low level from April. Beetle numbers peaked in January and were halved thereafter but were reduced even more after April, while cercopid numbers fell in May but did not fall below the November mean until July. Thus most potential food species were greatly reduced in the period when the birds left this grassland.

The most abundant arthropod group was ants and these, being terrestrial and relatively slow-moving, must be among the easiest arthropods for the birds to catch. It is possible that ants form a significant part of the birds' diet during the breeding season at this site, as they may do in similar habitat elsewhere: the gizzard of the December specimen from Underberg contained the remains of 31 ants. Although relatively few African bird species are major ant predators, Fry (1992) suggests that perhaps 60% of the continent's terrestrial avifauna may prove to be myrmecophagous to some extent, while 65% of the Buffspotted Flufftail gizzards examined during my study contained ants (Chapter 9), which were sometimes the most numerous prey.

#### 7.4.12 Predation, mortality and population size

Apart from an adult male at Underberg which was killed by a cat, no instances of predation were recorded. My observations indicate that the Striped Flufftail, like all other flufftail species studied, is most at risk from terrestrial predators such as mongooses and the small cats (see Chapters 4 and 9). During behavioural observations at Vernon Crookes, the Slender Mongoose *Galerella sanguinea* was attracted both to taped playback and to wooden Striped Flufftail decoy models. Aerial predators probably do not constitute an appreciable risk to the other flufftail species studied (Chapters 4 and 9) but may present a greater risk to Striped Flufftails because of the relatively short vegetation which this species inhabits. The only recorded instance of a flufftail being killed by an avian predator is of a male Striped Flufftail taken by a Lanner (Chapter 1, Section 1.2.3.3), and at Mt Currie in July 1990 my taped playback of Striped Flufftail *KI-KER* calls attracted a Black Harrier *Circus maurus* which flew purposefully in from a considerable distance and immediately began quartering the grassland at the exact spot where I had been playing the tape one minute before. The breeding Striped Flufftails at Helderberg Nature Reserve were not alarmed by an African Goshawk *Accipiter tachiro* which circled (obviously not hunting) over the nest area (B. Kakebeeke *in litt.*) and the goshawk's normal mode of hunting, by dashing from cover to pounce on prey in flight or on the ground (Maclean 1993), should not pose a significant threat to Striped Flufftails in open grassland.

Of the other avian predators which occurred in grassland at Mt Currie, Lanner and Rock Kestrel *Falco tinnunculus* were seen occasionally throughout the summer, hunting mainly over

the higher mountain slopes, and at least four Blackshouldered Kites *Elanus caeruleus* were present throughout the study period. Both the perched and hovering hunting behaviour of the kites might pose a threat to Striped Flufftails but the kites very rarely hunted in habitats occupied by the flufftails, either by hovering over open grassland or from perches in *Protea* savanna. The kites hunted at low altitudes and usually in disturbed areas such as road verges and around cleared plantations, and over short-grassed grazing land adjacent to the reserve.

Observations made during this study indicate that significant causes of mortality may be fire and very severe weather conditions. An adult male Striped Flufftail rescued from a burn near Ixopo in July 1990 was found to have the remiges and rectrices singed off; it died in captivity shortly afterwards (J. Morford pers. comm.). Observations of Redchested Flufftails (Chapter 5, Section 5.4.6) highlight the potential danger of fire to flufftails and it is possible that very rapidly-moving intense fires could kill numbers of Striped Flufftails if refuges in unburned vegetation were not available.

In the hailstorm which occurred at Mt Currie from 20:05-20:25 on 18 January 1991 hailstones up to 3 cm in diameter fell in some areas and the hail was immediately followed by over 50 mm of torrential rain. Drifts of hailstones up to 30 cm deep remained on low-lying ground the next day and there was considerable damage to vegetation on the mountain slopes by water runoff. The following morning corpses of birds up to the size of Cape Turtle Doves *Streptopelia capicola* and Pied Starlings *Spreo bicolor* were found and the immediate reduction in Striped Flufftail numbers (Section 7.4.10) suggested that some birds had been killed; the damage to the breeding population was probably increased by the fact that the hail was heaviest in Blocks 3, 6 and 8, which had not been burned in the previous year and therefore held a high density of breeding birds (Table 7.11). Only seven out of 25 pairs remained in these blocks after the hailstorm. Some birds apparently re-established themselves in areas where hail damage had been less severe (Section 7.4.2; Table 7.11), but all calling had ceased by the end of February and no birds were found after 1 March, a departure over three months earlier than normal (Table 7.6) which suggested breeding failure throughout the reserve. Although the vegetation cover at the sampling sites was not affected by the storm (Section 7.4.7; Fig. 7.7), vegetation heights were greatly reduced and did not recover sufficiently to attain the levels which they achieved in the following year (Section 7.4.7; Fig. 7.9), while total invertebrate numbers fell immediately and continued to decline thereafter, instead of increasing during February and March as occurred in 1992 (Section 7.4.8; Fig. 7.13). It is therefore likely that conditions in the most damaged areas remained unsuitable for breeding for the rest of the season, and possible that the invertebrate density and/or vegetation height in less severely affected areas also declined to levels insufficient to support either breeding or prolonged residence into April-June.

According to local farmers this hailstorm was not as severe as some which occur in the area, while some storms in South Africa produce much larger hailstones which kill birds as large as guineafowl, ducks and herons as well as mammals such as jackals and small antelope; deaths of cattle and people as a result of being struck by hailstones are also recorded (Comrie-Greig 1985; Smuts 1985). Furthermore, hailstorms are usually very localized, as was the one at Mt Currie, and one would expect the long-term effects on the area's bird populations to be slight because only a small part of those populations would be affected. Thus no significant reduction was noted in the breeding populations of small insectivorous grassland passerines such as cisticolas, chats and longclaws in the affected blocks during the following (1991-92) summer. Although the reduced number of Striped Flufftails in 1991-92 did not constitute a statistically significant yearly variation according to the GLM (Section 7.4.9), there were 5 fewer pairs than in the 1989-90 season (Table 7.10) of equivalent burning regime (Table 2.7) and in a small population this gives some cause for concern. The numbers of birds could have been affected by factors such as the below-average January-February 1992 rainfall (Chapter 2, Fig. 2.31B) and its effects on vegetation development and invertebrate populations, but this is unlikely because the rainfall in January-February 1990 was even lower (Fig. 2.30B). It is tempting to speculate that the reduction may be a reflection of the damage done to the area's Striped Flufftail population by the previous season's assumed high mortality and breeding failure.

## 7.5 Discussion

### 7.5.1 Distribution, status and habitat

The Striped Flufftail's distribution in South Africa appears to be confined to two biomes: (1) grassland, of predominantly highland sourveld type in Natal, the Transvaal and (presumably) in the northeastern parts of the Cape, where its known distribution also coincides with the distribution of this grassland type as mapped by Acocks (1988); (2) fynbos, in grassy areas of which it occurs in the southern and southwestern Cape. Within the confines of the highland sourveld the bird's altitudinal range is wide, from 250 m to 2 100 m in Natal, and its upper limits are possibly dictated by climatic features such as low temperatures and by declining amounts of suitable tall dense grassland habitat (see Section 7.5.3). Its upper altitudinal limits in fynbos are not clear.

The results of this study indicate that the Striped Flufftail may still be relatively numerous in suitable habitat in Natal, the Transvaal and Cape Province but that suitable grassland is severely restricted, especially by grazing practices, and very few birds occur in farming areas. As the bird's known distribution is very fragmented and its grassland habitats continue to disappear, the future of the endemic nominate race is by no means secure in South Africa. In this context it is worth quoting

in detail the only comment which I have received about an observed change in the bird's status, from J. Vincent (*in litt.*) concerning his farm Firle, near Mooi River, Natal (see Table 7.2). "Striped Flufftail was very common on this farm 50 years ago, and when reaping a hay or millet crop with a mowing machine the flushing of several birds was a certainty... Now, however, my grandchildren ... do not see the birds in the same way. The drastic degradation of the habitat hereabouts, with the removal of so much red grass [*Themeda triandra*] veld which has led to the local disappearance of the cranes and bustards would seem to have had its effect on the *Sarothrurus*... The change of habitat has been very wide, and there is a great increase in human disturbance. When first we came here Striped Flufftail males were heard calling every early summer. For the last three or four years none has been heard, but this season [1988-89] one bird called in our garden each early morning throughout December, but not before or after that month." Sadly, these comments probably reflect the situation throughout Natal.

In Natal more habitat could be provided in farming areas simply by practising good veld management, including less intensive and continuous grazing, the adoption of a biennial burning schedule, and leaving some areas ungrazed for a year or two: an area as small as 2 ha adjacent to a stream would provide breeding habitat for the species. The birds occur regularly at localities such as Ixopo and Pevensey in small areas of grassland which are protected in this way.

The Striped Flufftail's future in the Natal Drakensberg Park and other Natal Parks Board reserves seems more secure but in most of these reserve areas there is at present no way of accurately estimating populations, as the total area of the potentially suitable upland grasslands has never been estimated. However, as the wintering areas of such birds probably lie at lower altitudes (Section 7.5.2) which are possibly largely outside protected regions, loss of habitat at these lower altitudes could have a considerable effect on the overall population, even if the breeding areas are protected, and could contribute significantly to a continuous decline in Natal.

The bird's coastal distribution in Natal must have been very much reduced by human pressure and the species is probably now confined to Vernon Crookes Reserve and a very few small areas of coastal hinterland grassland (although none have been found); virtually no suitable habitat appears to be left. There may be some suitable areas in the Transkei, which was not surveyed during this study.

Although there is evidence that Striped Flufftails will occupy some croplands (Chapter 1, Section 1.2.3.2), these habitats must be of a restricted and temporary nature, and there is no evidence that they are significant in terms of the bird's survival. The comments by J. Vincent (see above) on past occurrences in hay and millet fields suggest that the birds were disturbed by mowing operations, which presumably would have disrupted breeding attempts.

There is relatively little distributional information available from the Cape Province and the Transvaal. In view of the lack of recent records from ten atlas squares Striped Flufftails are probably declining in Cape Province, while their status in Transvaal is not certain, but numbers are likely to be decreasing as a result of continued habitat loss. Care must be taken when assessing the distribution and status of all flufftails on the basis of atlas maps which, because of the secretiveness of the birds and the unfamiliarity of observers with their calls, will always under-record distribution. This is obvious from a comparison of the Natal distribution maps for the Striped Flufftail produced from data provided by two atlas schemes (Fig. 7.1B) and from data collected largely during this study (Fig. 7.1A).

Although most birds in Natal have been found in sourveld grassland dominated by *Themeda triandra*, observations from both Natal and the eastern Cape show that other types of grassland are also occupied as long as the basic requirements of vegetation height, cover and structure are met. The species appears to show a definite preference for grassland with drainage lines or small marshy areas, especially in the Cape fynbos, where the birds may not occur in completely dry areas. However there is still no proper evidence that they normally inhabit marshes alongside Redchested Flufftails. The observations of Mendelsohn *et al.* (1983) from Franklin Vlei, where Striped Flufftails were present in wetland alongside both Redchested and Whitewinged Flufftails in late 1982, probably reflect an anomalous situation brought about by severe drought conditions. The farmers whose land contains the wetland recollect that during the occurrence period (October-December) the vlei contained the only moist habitat or tall grass/marsh vegetation in the area while all hillsides were very dry and overgrazed so that no Striped Flufftail habitat was available anywhere locally (P.D. Long and E.H.D. Long pers. comm.). Under such circumstances it is not surprising that Striped Flufftails should occur in the only tall dense vegetation in the area - they had nowhere else to go. I did not observe a similar occurrence at the Franklin site in the early summer of 1992-93, when drought conditions also prevailed in the region. Other observers familiar with the Striped Flufftail in Natal confirm that they do not record it alongside Redchested Flufftail. However, my own observations of flufftails occurring in supposedly atypical habitats (Chapters 4 and 9) show that flufftails are very adaptable, like other rallid species, and that one cannot be too dogmatic in defining their habitat preferences.

The wet areas to which Striped Flufftails have access in their grassland habitat are usually too small to accommodate a Redchested Flufftail territory, so that interspecific competition in such areas could conceivably occur only occasionally in winter, when habitat is at a premium, if temporarily displaced Redchested Flufftails attempted to occupy moist areas in permanent Striped Flufftail territories. Striped Flufftails appear to eat similar food to Redchested but are smaller in size, with a

much shorter tarsus and a smaller, finer bill and short toes (Keith *et al.* 1970; P.B. Taylor unpubl. ms), so they are probably less well adapted to feeding in water. This may be a major factor influencing their exclusion from larger wetland areas, but there may also be interspecific competition with Redchested Flufftails, which are permanently territorial and show intraspecific aggression throughout the year (C.C. Wintle pers. comm.; Chapter 4). However, captive Redchested Flufftails tolerate the close proximity of Streakybreasted Flufftails even in the breeding season (C.C. Wintle *in litt.*), and the only observation suggestive of interspecific territoriality between the Redchested Flufftail and another *Sarothrura* species concerns the escape reaction of a Buffspotted Flufftail to taped playback of Redchested Flufftail calls (Chapter 4, Section 4.5.3).

### 7.5.2 Migratory status

All observations and studies indicate that the Striped Flufftail is resident in areas where cover and food remain suitable all year, and makes movements only when forced to do so by decreases in food availability or cover, which are generally occasioned by low winter temperatures and the effects on vegetation of grazing or burning. Movements in Natal are probably purely altitudinal but there is no indication of the distances involved or the destinations of birds which leave upland grasslands in the Drakensberg and East Griqualand regions at the end of the summer. In late summer very local altitudinal movements in response to suggested changes in microclimate and food availability are apparent at Mt Currie (see below), and such movements presumably continue on a larger scale as winter approaches. Records of winter occurrences suggest that Natal birds may move only as far as the nearest suitable habitat below about 1 200 m, where they should be able to survive throughout the winter. A discussion of altitudinal migration in Natal populations of the Buffspotted Flufftail *S. elegans* appears in Chapter 9.

The fire-climax sourveld grasslands which the Striped Flufftail inhabits in, for example, Natal, are plagioclimaxes; they occur in areas climatically suitable for a succession from grassland to forest or savanna but this succession is prevented by burning or grazing (Acocks 1988; Tainton 1984). The intrinsically dynamic nature of such grasslands favours colonization by animals which are highly mobile and dispersive, and it is to be expected that successful colonists, by means of flexible behaviour patterns, will be able to respond adequately to rapid changes (Chambers 1992 and references reviewed therein). This is especially the case for a terrestrial bird such as Striped Flufftail, which is restricted in its distribution by a requirement for grassland of a height and density only found in areas where grazing pressure is low, and can only hope to survive by having good powers of dispersal and the ability to find and colonize new areas at any time. These capabilities are notable

characteristics of the rail family (Chapter 1), and are exploited to advantage by Buffspotted and Redchested Flufftails (Chapters 4 and 9), but their possession will not ensure the survival of Striped Flufftail in the face of continued reduction of its natural habitats and the absence of substitute habitats created as a result of human activities. Redchested and Buffspotted Flufftails, however, are able to colonize small areas of habitat created by human activities and are thus not as severely threatened as Striped Flufftail (Chapters 4 and 9).

Care is needed in assessing the Striped Flufftail's distribution during the winter months because of the infrequency of its calls during that period and the unfamiliarity of observers with its non-breeding calls (the alarm bark, for example, was unknown before this study). Thus it may remain in some breeding areas from which there are at present no records, but it is reasonable to assume that it is generally absent from high-altitude breeding sites in at least Natal and the Transvaal between July and October/November. Throughout its entire range this species may be forced by burning, grazing or desiccation to make at least local movements after breeding.

There is no evidence that any age class of the Striped Flufftail population predominates in dispersal or longer-distance movements, but in view of the findings concerning Buffspotted and Redchested Flufftails (Chapters 4 and 9) it is likely that first-year birds disperse widely from the breeding areas and may move more regularly and more extensively than adults, which should tend to occupy permanent territories wherever possible. That adults do make some movements is suggested by two documented instances of casualties at buildings (Section 7.4.1.2) which involved adult birds.

### **7.5.3      Habitat preferences at the Mt Currie Reserve study site**

When establishing breeding territories at Mt Currie, Striped Flufftails showed a preference for the lower-altitude areas of unburned grassland on concave slopes which were of slight to moderate steepness, had few or no rocks and contained a drainage line. Grass cover was dense and tussocky, of a height attained only by the more luxuriant *Themeda* growth, while the presence of woody vegetation was apparently neither an advantage nor a disadvantage. These preferences reflect the bird's requirements for dense ground cover and a good potential invertebrate food supply. At higher altitudes, and on steeper or convex slopes, grass height and cover were diminished, the proportion of stones and rocks increased, exposure was greater and temperatures were lower. Rowe-Rowe & Lowry (1982) comment on the decrease in herbage production with increasing altitude in biennially burned grassland, while it is well known that an increase in elevation is paralleled by an increasing severity of climate near the ground (Geiger 1965; Coe 1967). Killick (1961), comparing *Themeda triandra* grassland at different elevations in the Cathedral Peak area (Natal Drakensberg Park), did

not mention a decrease in height at higher altitudes but measured an increase in basal cover, from 33,8% below about 1 800 m to up to 47,45% at 1 830-2 130 m. The increased basal cover might make foraging and other activities more difficult in this vegetation. Drainage lines probably provided rich feeding sites, as well as water for drinking and bathing, while cover which was tussocky (as opposed to continuous) allowed the birds to move around and forage more freely and provided suitable nesting sites. Grass cover and height are obviously important, but the birds may sometimes feed in shorter, more open grass adjacent to dense cover. Occurrences in the relatively restricted stands of tall rank vegetation near streams, and in bracken-briar and patches of tall forbs, suggest that such vegetation was favoured - possibly because it may have provided good shelter and relatively clear conditions at ground level. However it is likely that birds in these vegetation types would require the proximity of shorter, tussocky grass for nesting sites.

It was considered possible that Striped Flufftails might make use of the runs which are known to be made by rodents (*Otomys irroratus* and *Rhabdomys pumilio*) in dense vegetation (Rautenbach 1982) but rodent runs were not common in the grassland territories, most being found in or near the vlei and associated hygrophilous grassland in Blocks V1-V4.

#### 7.5.4 Territories and dispersion at Mt Currie

The small sample size (20) of territories mapped with acceptable accuracy did not permit detailed analysis of the possible effects of habitat and topographical variables on territory size, but it is interesting that territory size was not significantly affected by altitude, vegetation type, slope or aspect. This suggests that all vegetation types provided similar levels of food, and that the range of altitudes, slopes and aspects tolerated did not significantly affect the character of the vegetation or the availability of food during the breeding months. Within any area of grassland, the birds usually appeared to select relatively sheltered sites with the best-developed growth of grass, so that the vegetation characteristics in all grassland territories were fairly similar to each other and were less variable than in unoccupied areas (where, however, habitat variables were not measured).

The available evidence suggests that Striped Flufftail breeding-season territories were multipurpose territories (Wittenberger 1981), the birds defending the resources of food, shelter and nesting sites which they contained. In birds and mammals the size of the feeding territory increases with the body size of the species, and an exponential equation may be used to express the relationship between these two variables (Peters 1983; Schoener 1966):

$$\text{Territory size} = aW^n$$

where  $a$  is the intercept of the regression line at  $W = 1$  mass unit,  $W$  is the mean body mass of the species, and  $n$  is a regression coefficient. Assuming that the Striped Flufftail is omnivorous, taking mean body mass as 28.8 g (from three available masses of males), and selecting the appropriate values of  $a$  and  $n$  (Peters 1983), theoretical values of 1.3 ha for territory and 2.25 ha for home range are obtained. These are respectively 21% and 13% less than the mean values obtained.

### 7.5.5 Burning, vegetation structure and invertebrates at Mt Currie

Comparative assessments of the regrowth of grassland under different management regimes have concentrated on the measurement of tiller production, above-ground dry matter production, crude protein yield, etc. (Everson 1985; Mentis & Tainton 1984; Tainton & Mentis 1984). Compared with my simple assessments of vegetation height and cover, such studies obviously yield more exact comparative measurements of grassland regrowth after periodic defoliation, but it is not easy directly to relate such measurements to the assumed requirements of the flufftails in terms of overall vegetation height and cover. I am aware of no published studies giving measurements of height and cover which may be compared directly with those described in this study; even Everson (1985), when measuring percentage canopy cover, did not compare the regrowth of biennial spring-burned plots' burned and unburned vegetation in the same season and confined most of his measurements to the spring and early summer. However, Everson (1985) and Tainton *et al.* (1977) showed that winter burning (corresponding to this study's July firebreak burns) stimulated regrowth earlier than did spring burning, but that the overall recovery and productivity in the summer after both treatments was similar. These observations are comparable to this study's findings.

It is not unexpected that spring and summer arthropod numbers should be at least as high in burned as in unburned grassland. In a review of the response of grassland arthropod taxa to burning, Warren *et al.* (1987) point out that, during the recovery phase after a burn, habitat modifications are frequently beneficial to arthropods as regrowth of vegetation begins, food and cover resources increase and the microclimate becomes less extreme. In comparison to adjacent unburned areas, higher soil temperatures on burned plots may stimulate earlier emergence of some arthropods, while lush post-burn regrowth may attract both phytophagous arthropods and their predators. Comparing burned and unburned grassland, these authors cite examples of greater numbers and biomass in winter-burned and spring-burned vegetation for spiders, beetles (especially ground-dwelling species), cercopid bugs, dipterans (especially those whose larvae feed on growing plants), ants, lepidopterans and grasshoppers, i.e. all the arthropod groups sampled during my study.

Regarding the timing of return to breeding territories, consideration must be given to the factors influencing the widely different arrival dates in burned and unburned grassland. The results of the vegetation and invertebrate sampling experiments indicate that, in unburned grassland at the start of the breeding season, both vegetation height and cover develop to the theoretical minimum requirement from October to early November, i.e. 2-4 weeks before the first birds return. That the birds were not seen as soon as vegetation was sufficiently developed may be explained in several ways. Unknown factors in the nonbreeding areas may have an effect on the birds' departure time, but it is not clear what factors could be involved or how they could operate. Some birds may have been present but silent and overlooked for some time before their being found, which is extremely unlikely on the basis of my knowledge both of this species and of other rallids. In the years covered by the study, spring rainfall and temperatures at Mt Currie were not significantly less than the mean, but in other years adverse climatic factors might delay the development of cover and the increase in food supply so that a slightly delayed return might be advantageous in that birds would not run the risk of finding the habitat still unsuitable. Another explanation is that food supply has not developed sufficiently until mid-November. Although the minimum level of food required is not known, before November the mean invertebrate density was less than that measured at any time during the birds' late-summer occurrence in the same grassland, suggesting that the October invertebrate density was not high enough to favour occupation.

In burned grassland, however, the situation is much clearer and arrival time was certainly dependent on the development of suitable vegetation cover and height rather than of food, as invertebrate numbers were at least as high in burned grassland as in unburned areas. Observations indicated that birds arriving in burned blocks invariably occupied the tallest, densest vegetation available in the area.

At the end of the breeding season vegetation cover and height decreased relatively slowly and, by April-June, when birds left the breeding territories, had not been reduced to levels low enough to explain the need for departure. It is therefore suggested that departure from both burned and unburned grassland was occasioned by the rapid decrease in invertebrate numbers which, in the April-June period, fell below those recorded in the arrival month of November. The increase in the number of frosty nights in May-June (Chapter 2, Table 2.6) coincided with the final departure of the birds, but it is not possible to say whether the low temperatures directly affected departure times. The invertebrate population reached its lowest level during the frosty periods and, in 1991, increased only after the end of the frosts in late August (Fig. 7.13, Table 2.6). In the adjacent valley-bottom wetlands Redcrested Flufftails tolerated frosts throughout the winter, but their invertebrate food supply was almost certainly greater than that in the hillside grassland (see Chapter 6, Section 6.5.5).

The 1992 late-summer concentration of grasshoppers in the low-altitude grassland of the Block 2 sampling site coincided with the period (May) when Striped Flufftails moved down to these lower slopes of the mountain after breeding (see Section 7.4.10). This concentration of both birds and insects may be related to altitudinal temperature differences in the grassland of the western slopes. Using the RADSLAPE computer model (Schulze & Lambson 1988), the May daily radiant flux density and mean surface temperature were calculated for the Block 2 sampling site and for three breeding territories at different altitudes on the slope above the site. The results (Table 7.12) show that in May both of these variables decrease with altitude on this hillside, the sampling site having the highest mean surface temperature and receiving almost twice as much radiation as the upper slopes. In 1992 the two highest-altitude territories, Nos. 23 and 24, (Table 7.12) were not occupied after April, while the sampling area was occupied until the end of May. It is obviously energetically advantageous for the birds to seek the warmest conditions on the lower slopes when cooler weather sets in during April-May (see Chapter 2, Fig. 2.2.9 for monthly temperature variations at Mt. Currie) and, if invertebrate numbers remain high or increase on these lower slopes when those in the higher-altitude breeding territories are decreasing, it is obviously advantageous for the birds to congregate where the food supply is greatest. Grasshoppers are known to move to sheltered areas and dense vegetation to avoid low temperatures (Stebaev 1970) and it is possible that numbers of other invertebrates may also temporarily increase on the lower slopes in May, although this was not recorded at the two sampling sites. Although the grasshoppers may be difficult to catch, they may be taken when they occur in large concentrations, especially in the late summer at times when cool temperatures render them torpid.

Further evidence for the influence of cover and food on the occurrence of Striped Flufftails is provided by the winter samples from permanent territories at Vernon Crookes Reserve. These indicate that nonbreeding birds can tolerate somewhat lower cover percentages than can breeding birds and further reinforce the argument that it is low food availability (possibly in conjunction with low temperatures) which finally forces emigration from the Mt Currie breeding habitat. The difference in departure times from territories in pure grassland and those in mixed grass, forbs and bushes (where vegetation and food probably remained suitable for longer) indicates that birds will remain in the territories as long as the resources are economically defendable.

Late winter and spring mowing of *Themeda triandra* grassland depresses the vegetation yield less than burning at the same time (Tainton *et al.* 1977; Tainton & Mentis 1984). One would therefore expect such mown grassland to be potentially more suitable than burned grassland for occupation in time for breeding during the ensuing summer. Although no studies were made in mown

TABLE 7.12

Radiation flux densities (RFD) per day (megajoules/m<sup>2</sup>) and mean surface temperature (ST) (°C) for four sites at different altitudes on an approximately west-southwest to east-northeast transect up the western slope of Mt. Currie Reserve, calculated by the RADSLOPE computer model (see Section 7.5.5 for details).

Site details	Altitude (m)	RFD	ST
Block 2 invertebrate sampling site	1470	9,81	3,4
Territory No. 20	1510	8,25	3,2
Territory No. 23	1570	5,88	0,2
Territory No. 24	1600	5,83	0,0

grassland, the birds did occur in midsummer at Ixopo in grassland which had been mown in the same spring (Section 7.4.1.2).

#### **7.5.6 Other considerations regarding occurrence patterns at Mt Currie**

The possible relationship between return time and territory aspect, in relation to the effect of aspect on incoming radiation flux densities, and consequently on plant growth and food availability, has already been discussed (Section 7.4.9). As return time to unburned grassland was apparently not affected by altitude or vegetation type, which variables might be expected to have some influence on the relative development of suitable vegetation height, cover and food availability (not measured), it is probable that returning birds were selective in their choice of habitat at various altitudes and in different vegetation types, so that the more sheltered areas with the tallest vegetation were occupied first at the higher altitudes. The late development of burned vegetation effectively made most of the burned blocks unsuitable for breeding, and the burning schedule caused considerable variation in the carrying capacity of the habitat on a biennial cycle. The failure of birds to occupy breeding territories in burned areas in late February, when vegetation became suitable, was undoubtedly a result of the very short time remaining for breeding in such areas: no indications of breeding were obtained from Mt Currie after February, although in other parts of South Africa breeding has been recorded in March.

#### **7.5.7 Responses of other birds to grassland burning**

Little work has been done on the responses of grassland bird species to burning. Mentis (1973) and Mentis & Bigalke (1979, 1981) studied the effects of fire on Greywing Francolin *Francolinus africanus* and Redwing Francolin *F. levaillantii* in the Natal Drakensberg. These species, like Striped Flufftails, are members of the fire-climax grassland community but, unlike the flufftail, are resident in highland areas and are essentially vegetarian, feeding primarily on the underground storage organs of forbs in the grassland (Mentis 1973). Thus their requirements with regard to food are not comparable with those of the flufftail. Their occurrence was, however, also related to cover and height of the grass in terms of its effects on shelter and food availability. Both species require a minimum grass cover to provide shelter from predators and adverse weather. In spring, both species prefer unburned grass to burned grass (for reasons of cover and shelter) but after 6-9 months the preference is reversed (for reasons of food availability). Although population densities recover within 1-2 years of a fire, they decline in its prolonged absence and with the accumulation

of plant material (which have adverse effects on the birds' ability to find food and to move through the vegetation).

Common Quails *Coturnix coturnix* also respond to vegetation changes following a fire, in spring occurring at higher densities in recently burned than unburned grassland (Tainton & Mentis 1984). The reasons for this preference are not given but are presumably related to the abundance of plant and animal food.

All three of these species were found at Mt Currie. The Greywing Francolin was recorded only twice (in September and December) at the highest elevations but the other two species occurred alongside Striped Flufftails throughout the reserve. The Common Quail was recorded in all months except September and October and was most numerous in burned grassland and short unburned grassland, as well as occurring commonly in grazing land and crop fields adjacent to the reserve. Redwing Francolins were resident in small numbers and occurred in denser, taller grassland than that preferred by the quail.

## CHAPTER 8

### THE BIOLOGY, ECOLOGY AND CONSERVATION OF THE WHITEWINGED FLUFFTAIL

#### 8.1 Introduction

Although the Whitewinged Flufftail's geographical range extends over about 4 700 km, from 9°N in Ethiopia to almost 33°S in South Africa (Tables 8.1, 8.2), the species is rare and is relict in its distribution, only an apparently very small population existing in South Africa and a probably much smaller one in Ethiopia, where the bird has been seen only once since 1957 (Brooke 1984; Collar & Stuart 1985; Keith 1986; Chapter 1). The very few records between these two populations, all from central-southern Africa, suggest an erratic occurrence outside the normal centres of distribution possibly brought about by periodic eruptions and long-distance dispersal (Chapter 1). The reason for the bird's virtual absence from central and East Africa has been suggested to be competitive exclusion by a congener such as the Streakybreasted Flufftail *S. boehmi* (Benson & Irwin 1971; Collar & Stuart 1985; Keith *et al.* 1970).

In recent years different authors have expressed widely differing views about the bird's population level. Brooke (1984) maintains that there is no evidence for a population decrease and Irwin (1981) even suggests a resurgence of numbers in South Africa, but other authors note with concern the continuing destruction of the bird's habitat in both Ethiopia and South Africa (Chapter 1, Section 1.2.4.2). Wolff & Milstein (1976) discount the possibility that economic development could have adversely affected the bird's population in South Africa, but nevertheless suggest that the species is possibly on the way to early extinction.

Almost nothing is known about Whitewinged Flufftail's biology and ecology. Even its calls are inadequately described (Chapter 1, Section 1.2.4.5), in contrast to other flufftail species whose principal calls are distinctive and well known (Keith 1986; Keith *et al.* 1970). During this study my principal aims were to establish whether the Whitewinged Flufftail still occurs anywhere in South Africa (no sightings had been reported since early 1983) and, if any population were found, to investigate all aspects of the bird's biology and ecology which might lend themselves to practical study given the time and resources available. In particular it was deemed important to investigate factors which might affect the continued survival of the South African population, and to establish whether the species was either resident in, or a breeding visitor to, any South African permanent wetlands which might be suitable for long-term protection as an aid to the species' survival.

TABLE 8.1

Details of all known specimens of Whitewinged Flufftail *S. ayresi* held in collections throughout the world, with relevant details and principal references. Age/sex: A = adult; I = immature (about 7 weeks old); J = juvenile (about 2 weeks old); SA = subadult (1-2 years old, not fully adult plumage); \* = specimen examined by PBT. Items in parentheses under "Co-ordinates" or "Altitude" are approximations. BMNH = British Museum (Natural History); C = Cape; CH = central highlands; HIO = Hungarian Institute of Ornithology, Budapest; HNM = Hungarian National Museum, Budapest; N = Natal; OF = Orange Free State; T = Transvaal; ? = not known.

Region	Locality	Co-ordinates (°)	Altitude (m)	Date	Numbers, age & sex	Notes	Reference	Museum
CH Ethiopia	Akaki, Sululta	(09°11'N 38°45'E)	(2 500)	27 Jul 1939	Ad*	Collected M Gajdacs	Keith <i>et al.</i> (1970)	BMNH
	Antotto, Sululta	(09°11'N 38°45'E)	(2 500)	25 Jul 1939	♂, ♀	Collected S Patrizi	Collar & Violani (1984)	Milan
				12 Jun 1942	♂	" "	Keith <i>et al.</i> (1970)	Nairobi
				"1939"	♀	" "	" "	"
	Gafersa, Sululta	09°03'N 38°40'E	2 285	11-30 Jul 1947	Ad*, 2SAd*, Aq*, SAq*		Guichard (1948)	BMNH
				17 Jul 1947	♂		" "	Tervuren
	Sululta Plain	(09°11'N 38°45'E)	(2 500)	10 Aug 1947	SAad*, Ad*		Guichard (1948)	BMNH
				1 Sep 1947	2♂		Keith <i>et al.</i> (1970)	Tervuren
				18 Jul 1948	♀		" "	HIO
				10-15 Sep 1948	Aq*, SAad*	Collected Salim Abichacar	" "	BMNH
SW Ethiopia	Charada, Kaffa	(07°45'N 36°30'E)	1 830	26 May 1905	Ad	Type of <i>Ortygops macmillani</i>	Bannerman (1911)	BMNH
	Potchefstroom (T)	(26°40'S 27°05'E)	(1 300)	4 Oct 1876	♀	Syntype of <i>Coturnicops ayresi</i>	Keith <i>et al.</i> (1970)	BMNH
				24 Nov 1876	♀	Specimen lost	" "	"
				August 1894	Ad*	Collected E Blaauw	Benson & Irwin (1971, 1974)	Leiden
	Suikerbosrand (T)	26°33'S 28°14'E	1 586	8 Aug 1975	♀	Found dead	Wolff & Milstein (1976)	?
	Bloemfontein (OF)	(29°10'S 26°12'E)	(1 400)	9 Oct 1901	SAq*	Collected S R Clarke	Keith <i>et al.</i> (1970)	BMNH
	Franklin (N)	30°17'S 29°26'E	1 520	27 Oct 1982	Iq*		Hendelsohn <i>et al.</i> (1983)	Durban
	King Williams Town (C)	(32°53'S 27°33'E)	(500)	August 1876	SAq*	Collected Lt E O Anstey	Keith <i>et al.</i> (1970)	BMNH

TABLE 8.2

Details of all known sight and sound records of Whitewing Flufftail *S. ayesi*. Altitudes and co-ordinates in parentheses are approximate. Records in square brackets are considered unsatisfactory without supporting evidence. C = Cape Province; N = Natal; SABAP = Southern African Bird Atlas Project; T = Transvaal; ? = not known.

Region	Locality	Co-ordinates	Altitude (m)	Date or period of occurrence	Maximum count	Source
CH Ethiopia	Sululta Plain	09°11'N 38°45'E	(2 500)	26 Aug 1984	1	R Massoli-Novelli ( <u>in litt.</u> )
Zambia	Solwezi District	12°30'S 27°32'E	1 350	5 Nov 1962	1	Brooke (1964)
	[near Kitwe]	(12°48'S 28°14'E)	(1 300)	13 Feb 1981	1	Collar & Stuart (1985)]
Zimbabwe	Harare	(17°50'S 31°00'E)	(1 400)	14 Jan - 2 Mar 1977 Jan - Mar 1979	1 1	Hopkinson & Masterson (1977) Hopkinson & Masterson (1984)
South Africa	Dullstroom (T)	25°33'S 30°07'E	1 870	9 Dec 1982 - 9 Jan 1983 28 Jan - 15 Feb 1990 15 Dec 1990 2-3 Feb 1991 6 Dec 1991 - 10 Jan 1992	5 8 1 1 4	Mendelsohn ( <u>et al.</u> ) 1983 J C Sinclair (pers. comm.); P B Taylor <u>et al.</u> P Cardwell & W R Tarboton (pers. comm.) SABAP (S Blane) P B Taylor <u>et al.</u>
	Rustenburg (T)	25°40'S 27°10'E	(1 150)	8 May 1955	1	Wolff & Milstein (1976)
	Wakkerstroom (T)	27°22'S 30°07'E	1 755	13-14 Feb 1992	13	P B Taylor <u>et al.</u>
	Durban (N)	29°50'S 30°55'E	?	?	?	Stark & Sclater (1906)
	Franklin (N)	30°17'S 29°26'E	1 520	25 Oct 1982 - 7 Jan 1983 10 Nov 1990 - 21 Mar 1991 23 Nov 1991 - 26 Jan 1992 5-21 Nov 1992	18 17 8 6	Mendelsohn <u>et al.</u> (1983) P B Taylor <u>et al.</u> " " " "
	Penny Park (N)	30°30'S 29°29'E	1 310	15 Feb - 9 Mar 1991 30 Jan 1992	4 4	P B Taylor <u>et al.</u> P B Taylor
	[Twee Buffels (C)]	(26°08'S 26°23'E)	?	20 Oct 1991	?	SABAP]
	Ganspan (C)	27°58'S 24°50'E	1 100	?	1	Brooke (1984)
	East London (C)	32°55'S 27°57'E	150	15 Sep 1955 5 Oct 1956	1 1	Keith <u>et al.</u> (1970) " " "
	Cambridge (C)	32°56'S 27°53'E	150	17 Sep 1956	1	" " "
	[Scheepersrus (C)]	(33°53'S 20°23'E)	?	11-14 Oct 1990	?	SABAP]

## 8.2 Survey areas and study sites

Because all records of the Whitewing Flufftail obtained during the 1980s, including the only South African instances of prolonged occurrence at any site, were from high-altitude wetlands in Natal and Transvaal (Tables 8.1, 8.2), attention was first concentrated on the larger permanent high-altitude wetlands in the designated survey area of central and southern Natal (Chapter 2, Section 2.1). As no detailed information exists on the nature of either breeding or non-breeding habitat, when initially selecting areas for monitoring I used my own judgement of the potential suitability of wetlands in terms of my knowledge of the habitat requirements of other wetland flufftails. Initial assessments were based largely on the availability of a sufficient height and density of vegetation cover, and of a suitable degree of inundation during the summer months. As Whitewinged Flufftails are known to occur alongside Redchested Flufftails *S. rufa* (Mendelsohn *et al.* 1983), any wetland holding resident pairs of the latter species was considered potentially suitable habitat for the former.

Exploratory surveys were carried out regularly over the first 17 months of the study (September 1988 to January 1990), both at the wetlands which were permanent study sites in Natal (Chapter 2), and at many other Natal wetlands of varying sizes and vegetation types. Repeated visits were made to these wetlands at different times of the year, to check for the birds' seasonal or transient occurrence. Although many small wetlands (1-5 ha) on farms and in nature reserves were regularly surveyed, it was thought relatively unlikely that Whitewinged Flufftails would have been overlooked at such small, easily accessible sites, and an attempt was made to visit regularly the larger, relatively inaccessible and little-known highland wetlands of southern Natal, in particular the following: Mvoti Vlei ( $29^{\circ}10'S$   $30^{\circ}33'E$ , at 970 m a.s.l.), Hlatikulu Vlei ( $29^{\circ}15'S$   $29^{\circ}41'E$ , at 1 580 m), Melmoth Vlei (in the Karkloof Nature Reserve) and Dartmoor Vlei, both of the Myambuvu vlei system ( $29^{\circ}17'S$   $30^{\circ}15'E$ , at 1 575 m), Stillerust Vlei in the Kamberg Nature Reserve ( $29^{\circ}23'S$   $29^{\circ}44'E$ , at 1 645 m), Mgeni Vlei ( $29^{\circ}29'S$   $29^{\circ}48'E$ , at 1 900 m), The Swamp Nature Reserve and adjacent wetlands ( $29^{\circ}47'S$   $29^{\circ}36'E$ , at 1 460 m), the few remaining fragmented wetland patches on the Cedarville Flats ( $30^{\circ}20'S$   $29^{\circ}07'E$ , at 1 440 m), and in Transkei the large and very inaccessible Ntsikeni Vlei ( $30^{\circ}07'S$   $29^{\circ}27'E$ , at 1 790 m). All of these wetlands except those on the Cedarville Flats are listed as priority Natal wetlands by Begg (1989), in which work may be found further details of their geology, hydrology, flora, use and management.

In addition to this work, surveys were made in 1990-1993 of two important wetland areas in the Transvaal, the vleis in the Belfast-Dullstroom area and the Wakkerstroom Vlei (Chapter 2), in both of which areas Whitewinged Flufftails were found during the latter part of the study. The wetland in Solwezi District, Zambia, where the 1962 sighting of Whitewinged Flufftail was made

(Table 8.1) is known to me from my period of residence in Zambia in 1974-1980, when I visited the area on several occasions without finding the species. During visits to Zimbabwe in July 1990, November 1991 and April 1992, I was able to see the wetlands at which the Zimbabwe sightings were made (Table 8.2) and to discuss with A.N.B. Masterson and G. Hopkinson the habitat in these areas at the times of the sightings. Unfortunately in 1991-1992 the prevailing drought conditions rendered these areas unsuitable for migrant crakes and thus no fieldwork was possible. Although it was hoped to visit the Ethiopian wetlands during this study, funds were not available for this purpose.

### **8.3 Methods**

In view of the unpredictability of the bird's occurrence no specific research plan was established but it was decided that, if and when the species was located, studies of its biology and ecology should take precedence over all other project work. From February 1990 to November 1992, the period during which Whitewing Flufftails were located in summer at Franklin and Penny Park in Natal, and Dullstroom and Wakkerstroom in the Transvaal (Table 8.2), work on the species concentrated on the first three sites (where the birds were found repeatedly - Table 8.2) and regular surveys were made throughout the year to establish arrival and departure times, vegetation development, the effects of burning and grazing and (in 1991-1992) the effects of the prevailing drought conditions.

The normal methods of location, observation, territorial mapping and trapping used for the other study species (Chapter 3) were uniformly ineffective for this atypical flufftail. As the birds usually responded very poorly (if at all) to taped playback and thus were probably not territorially active, normal census and mapping methods (Chapter 3) could not be used. However, during some periods at Franklin the birds called spontaneously at dawn and dusk (Section 8.4.4), allowing numbers to be estimated. During periods of occurrence when few or no calls were given the birds could be flushed quite easily and numbers could be estimated accurately from sightings made during repeated counts over 2-4 consecutive days. In periods when the birds were calling regularly at Franklin and Penny Park they were in very dense and relatively tall vegetation (Table 8.5), which made effective penetration of the habitat difficult and observation almost impossible, especially as the birds were extremely unwilling to fly at such times. Using taped playback to call the birds out to observation tracks cut in the reedbeds was not successful (Section 8.4.5). The difficulties experienced in attempting to trap the birds are discussed in Chapter 3, Section 3.8.4.

Had the birds definitely bred at any locality during the study, in vegetation which was low enough to permit access without undue disturbance, normal study methods would have been more

effective. However, at all times when conditions favoured visual observation the birds were obviously neither breeding nor in any way territorial. Thus only generalized and relatively unsystematic methods could be used. All relevant details of habitat were recorded for all occurrences, including the overall size of the wetland, the vegetation type, height and cover (i.e. the percentage of the substrate obscured by vegetation when viewed from above), the substrate type and the degree of flooding. The birds' behaviour was studied, in response both to disturbance and to taped playback of the calls of all African flufftail species and other wetland rallids. Calls were tape-recorded whenever possible, using the equipment described in Chapter 4, Section 4.3.5. Calling patterns were established and their relationship to other behaviour was investigated. The degree of spatial overlap with other rallids in the habitat was also noted.

All relevant biometric data and other information were obtained from as many museum skins as it was possible to examine. Information was requested from the very few observers who had seen the species in the field. Local farmers and landowners were approached for information but none had ever seen the birds, even at sites where occurrences had been reported by birdwatchers. The possibility of breeding in southern Africa was discussed with oologists in Zimbabwe, who have unequalled field experience of nesting *Sarothrura* species.

## **8.4 Results**

### **8.4.1 Distribution and status**

All distributional data for the species are summarized in Tables 8.1-8.3 and mapped in Fig. 8.1, including published information (reviewed in Section 1.2.4.2), records obtained during this study, unpublished observations obtained from other observers and details from the SABAP data bank. In addition to the 1981 Zambian record which I regard as unacceptable without corroboration, I have no supporting details for the two recent Cape Province occurrences obtained from SABAP (Table 8.2) and, although these records may be correct, I prefer to reserve judgement on them until further details are available. There is also one further reported occurrence, from Rwanda, where calls of birds thought to be this species were heard in January 1990 from a marsh at Kitabe, Nyungwe (Dowsett-Lemaire 1990). A recording made at the marsh has been sonographically analyzed (Section 8.4.4) and I am satisfied that the recorded calls were made by Crowned Cranes, which have a very similar call to that of Whitewinged Flufftail (Chapter 1, Section 1.2.4.5).

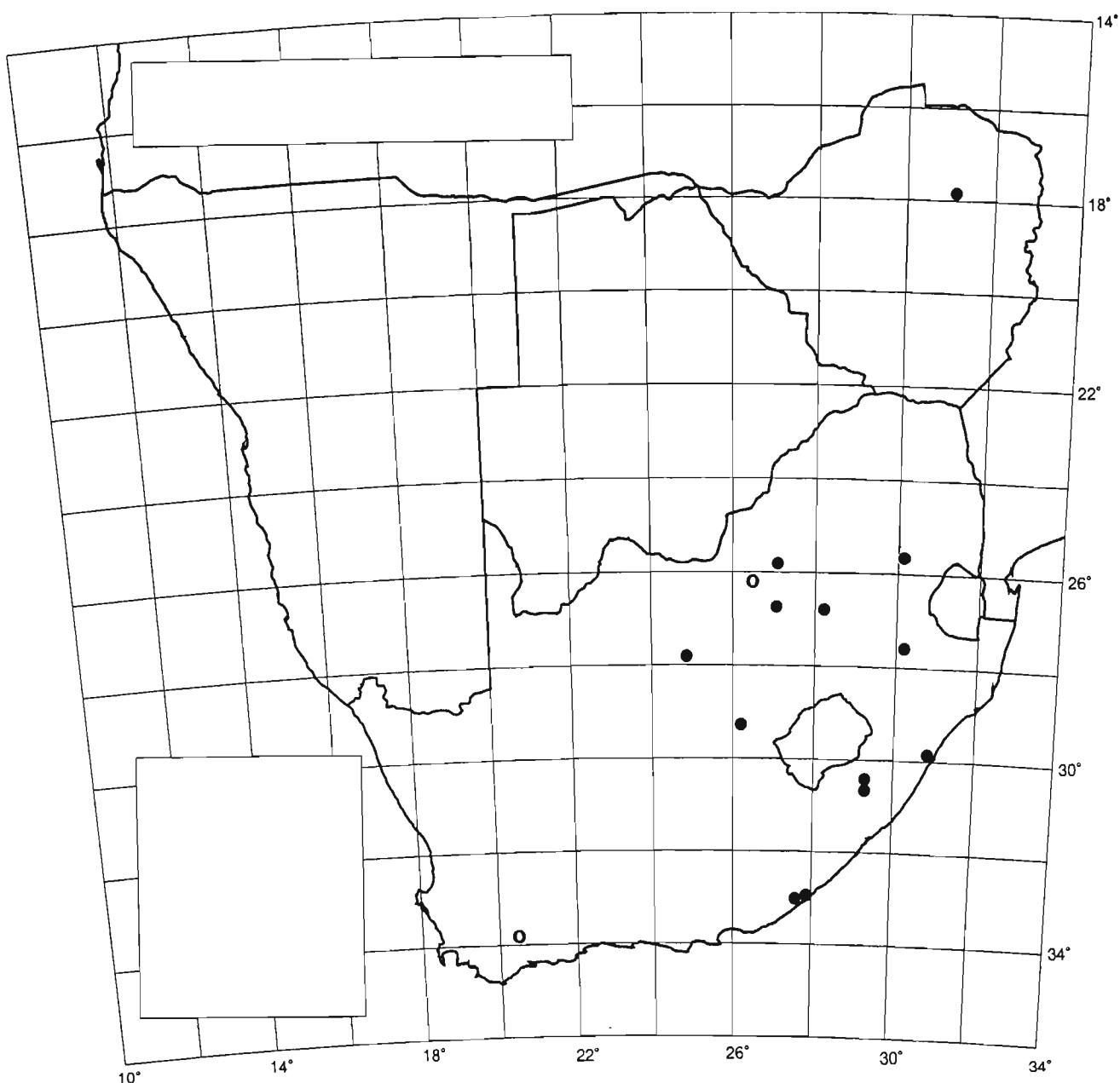
The records obtained during the period of this study (Table 8.2) have added Wakkerstroom to the known localities for the species in the Transvaal and Penny Park to those in Natal, without

TABLE 8.3

358

Monthly totals of Whitewinged Flufftails *S. ayresi* recorded throughout the bird's known range. Totals include specimens, sight and sound records and constitute a summary of the information in Table 8.1 plus monthly maxima taken from the sources specified in Table 8.2.

Country	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Ethiopia					1	1	13	5	6			
Zimbabwe/Zambia	2	2	2							1		
South Africa	35	32	8		1			3	2	18	15	33
<b>Total</b>	<b>37</b>	<b>34</b>	<b>10</b>		<b>2</b>	<b>1</b>	<b>13</b>	<b>8</b>	<b>8</b>	<b>18</b>	<b>16</b>	<b>33</b>



**Fig. 8.1** Recorded distribution of the Whitewing Flufftail in southern Africa, by quarter-degree square, showing acceptable records (filled circles) and unconfirmed records (open circles). Outline map courtesy of the Southern African Bird Atlas Project.

extending the overall range of the species. If valid, the SABAP Scheepersrus record would extend the bird's range considerably to the west, almost to the Cape Peninsula (Fig. 8.1). The repeated occurrences at the Dullstroom, Franklin and Penny Park study sites (Table 8.2) are the first instances of the bird's occurrence over two or more consecutive summers at any site in South Africa. All acceptable South African records since 1988 have been from high-altitude areas, 1 310-1 870 m a.s.l. (Table 8.2), and my extensive observations in low-altitude wetlands in southern Natal, including coastal sites, failed to provide any evidence of the bird's recent occurrence in these areas.

Recent records confirm the bird's rarity in South Africa, the maximum populations located being 17 birds at Franklin in December 1990, eight there in November 1991, eight at Dullstroom in February 1990 and 13 at Wakkerstroom in February 1992. It has already been shown that the 1982-83 counts of Mendelsohn *et al.* (1983) were probably over estimated (Chapter 1, Section 1.2.4.2), so there are no accurate figures for comparison with my recent totals. In the vlei at Franklin, although the exact calling locations of peripheral birds could be established, the more centrally located birds were difficult both to pinpoint and to approach while calling, so my estimates of dispersion were necessarily inexact and the number of calling birds may be under estimated.

The surveys of those high-altitude wetlands in southern Natal listed in Section 8.2 produced no observations of Whitewing Flufftails. In some cases this was thought to be because of a lack of suitable habitat at the vleis concerned (see Section 8.4.2.5), but at some sites habitat was thought to be potentially suitable and future surveys could possibly yield results. Surveys of wetlands in the Belfast-Dullstroom area in February 1990, December 1991 and January 1992 produced no records at any vlei except the study site itself, while surveys of wetlands around Wakkerstroom Vlei in February-March 1992 and January 1993 were similarly unproductive. The dry conditions in the 1991-1992 and 1992-1993 summers rendered many of these wetlands unsuitable for occupation (see Section 8.4.2.5), whereas in wetter years some may hold Whitewing Flufftails. Regular and frequent observations throughout the study period in wetlands at the other study sites and elsewhere in the southern Natal survey area produced no records, although small patches of potentially suitable habitat were found. For all the areas surveyed, details of the habitat types concerned are given in Section 8.4.2.

#### **8.4.2      Habitat preferences**

Tables 8.4 and 8.5 summarize the vegetation and substrate characteristics of each location where Whitewing Flufftails were either seen or heard during this study. Vegetation cover was 100% at all points where calling birds were found. Additional information on habitat at all four study sites

TABLE 8.4

Vegetation and substrate characteristics associated with all visual records of Whitewing Flufftail *S. ayresi* obtained during the study. Dom. = dominant; obs. = observations; veg. = vegetation. Vegetation types: *Ca* = *Carex* (?)*acutiformis*; *Cf* = *Cyperus fastigiatus*; HG = hygrophilous grass spp.; *Lh* = *Leersia hexandra*; *Mc* = *Mariscus congestus*; *Pa* = *Phragmites australis*; SR = Mixed sedges and rushes; *Tc* = *Typha capensis*. For details of species in categories HG and SR at each site, see Chapter 2. Vegetation heights include the range and mean of all measurements taken. Cover represents the approximate percentage of the substrate obscured by vegetation when viewed from above.

Study site	Date/period	No. of obs.	Dom. veg.	Other veg.	Veg. height (cm)	Cover (%)	Substrate moisture/flooding (cm)	Total obs.
Dullstroom	11-15 Feb 90	16	<i>Ca</i>	-	80-120 (99)	100	Moist	40
		11	<i>Ca</i>	<i>Pa</i>	100-130 (113)	100	"	
		6	<i>Ca</i>	HG	70-85 (78)	100	"	
		3	HG	-	45-55 (50)	100	Dry	
		2	<i>Pa</i>	<i>Ca</i>	110-150 (130)	95	Moist to 5 cm flooded	
		2	SR	<i>Ca</i>	80-90 (85)	90	Moist	
	6-8 Dec 91 & 6-10 Jan 92	8	<i>Ca</i>	<i>Pa</i>	80-100 (86)	100	Moist to saturated	20
		5	<i>Ca</i>	-	70-80 (77)	100	Dry to moist	
		3	SR	-	60-70 (67)	90	Moist	
		3	HG	SR	50-75 (67)	95	Dry to moist	
		1	<i>Pa</i>	-	85	90	0,5-3 cm	
Wakkerstroom	13-14 Feb 92	8	<i>Ca</i>	<i>Lh, Sc, Tc</i>	120-130 (128)	100	Dry to moist	14
		3	<i>Lh</i>	SR, <i>Tc</i>	80-90 (85)	80-100	"	
		1	<i>Pa</i>	<i>Ca, Lh, Tc</i>	170-185 (178)	100	"	
		2	<i>Tc</i>	-	150	100	Moist	
Franklin	5-7 Nov 92 & 21 Nov 92	19	<i>Ca</i>	<i>Tc</i>	70-95 (77)	65	Dry to moist	22
		3	<i>Ca</i>	-	60-80 (73)	55	Dry to moist	
Penny Park	15 Feb 91	1	<i>Lh</i>	<i>Tc, Cf, Mc</i>	110	100	30 cm	1

TABLE 8.5

Vegetation and substrate characteristics associated with all sound records of Whitewinged Flufftail *S. ayresi* obtained during the study. Dom. = dominant; obs. = observations; veg. = vegetation. Vegetation types: *Ca* = *Carex (?)acutiformis*; *Cf* = *Cyperus fastigiatus*; *Lh* = *Leersia hexandra*; *Mc* = *Mariscus congestus*; *Pa* = *Phragmites australis*; *Tc* = *Typha capensis*. For details of species in categories HG and SR at each site, see Chapter 2. Vegetation heights include the range and mean of all measurements taken. Cover (see Section 8.4.3) was 100% in all cases.

Study site	Date/period	No. of obs.	Dom. veg.	Other veg.	Veg. height (cm)	Substrate moisture/flooding (cm)	Total obs.
Dullstroom	14 Feb 90	2	<i>Ca</i>	<i>Pa, Sc, Tc</i>	130-140 (135)	Moist	2
Wakkerstroom	13-14 Feb 92	4	<i>Tc</i>	<i>Sc, Ca, Cf</i>	120-150 (130)	Moist	8
		4	<i>Lh</i>	<i>Sc, Ca, Pa</i>	80-130 (110)	Moist to saturated	
	11 Mar 92	2	<i>Ca</i>	<i>Tc</i>	110-130 (120)	Moist	2
Franklin	10 Nov 90 to 21 Mar 91	21	<i>Ca</i>	<i>Pa, Tc</i>	120-200 (175)	5-45 cm	48
		9	<i>Ca</i>	<i>Pa</i>	120-160 (145)	"	
		8	<i>Tc</i>	<i>Ca</i>	150-200 (178)	"	
		5	<i>Tc</i>	<i>Cf</i>	125-200 (170)	10-45 cm	
		5	<i>Tc</i>	<i>Ca, Pa, Cf</i>	150-230 (190)	15-45 cm	
	23 Nov 91 to 26 Jan 92	20	<i>Ca</i>	<i>Pa, Tc</i>	130-170 (145)	2-25 cm	24
		4	<i>Tc</i>	<i>Ca, Pa</i>	150-180 (165)	"	
	15 Feb to 19 Mar 91	17	<i>Tc</i>	<i>Cf, Mc</i>	160-210 (185)	20-45 cm	17
	30 Jan 92	4	<i>Tc</i>	<i>Cf, Mc</i>	140-200 (180)	5-40 cm	4

is given in Sections 8.4.2.1-4, while details of habitats at other survey areas, and information from other observers, are given in Sections 8.4.2.5 and 8.4.3.

#### 8.4.2.1 Dullstroom, Transvaal

When I first visited this site on 11-14 February 1990 the areas of wetland vegetation occupied by the Whitewing Flufftails at the time of their discovery (28 January 1990) had been very extensively disturbed by visiting birdwatchers, who had made numerous tracks through the reedbeds and had trampled large patches of vegetation. Presumably because of this the birds had moved to undisturbed parts of the vlei, which therefore may not have represented optimum habitat.

The vlei appeared to have been extensively burned, especially in the drier areas, in the spring of the 1989-90 season. Of the 40 sightings and two precisely located calling birds (Tables 8.4, 8.5), 35 (83%) were from about 40% of the wetland, in vegetation dominated by *Carex* (presumed *C. acutiformis*), the remaining seven being from the other principal vegetation types in the vlei, i.e. hygrophilous grassland and mixed sedges, rushes and reeds (see Chapter 2, Section 2.2.2 for further details of these vegetation types). These observations indicated a highly significant preference for *Carex*-dominated vegetation ( $\chi^2_1 = 30,3; P < 0,001$ ), including that intermixed with taller scattered single stems of *Phragmites* (Table 8.4). Furthermore, stands of pure *Carex* occupied only about 7% of the vlei area but accounted for 16 (38%) of all records and on 13 February all six birds flushed during one walk were concentrated in a patch of pure *Carex* about 200 m in diameter. However, this preference may have been partly an effect of the disturbance to the more species-rich vegetation which the birds apparently occupied when originally found, the first sightings having been in areas with mixed *Juncus*, *Carex* and other sedges, including some *Phragmites* (various unnamed observers pers. comm.).

All vegetation types, except the flooded *Phragmites* beds along the central drainage line, were on dry to moist ground. Thirty-five records (83%) were from vegetation averaging 85-113 cm in height, and in all cases cover was dense, being less than 100% only in mixed-species sedgebeds and some *Phragmites* (Table 8.4). The areas where the birds were originally found in January were dry to moist and had vegetation averaging 78-113 cm in height.

In December 1991 and January 1992 the birds were present after a spring burn and during a season when rainfall was well below the average (pers. obs.; no local figures are available). Of the 20 sightings in this period, 13 (65%) overall and 12 of 16 (75%) in December were in *Carex*-dominated vegetation (Table 8.4). These observations showed a somewhat less significant association with this vegetation type ( $\chi^2_1 = 4,22; P < 0,05$  and  $\chi^2_1 = 6,77; P < 0,01$  respectively). The

occupied vegetation averaged shorter than in February 1990 (Table 8.4), this obviously being partly a result of the shorter time for vegetation regrowth. In December 1991 there had been no disturbance, so the birds had all available vegetation types to choose from. However in January 1992 visitors had extensively disturbed and trampled the *Carex*-dominated vegetation types and the four observations of one bird were in moist sedges which, although some were flattened by wind to about half their former height, were not trampled and thus provided continuous 100% cover. In January the lack of rain had resulted in some drying out of the peripheral regions of the vlei, but vegetation growth had been reasonable and the very little undisturbed *Carex* habitat appeared suitable. Thus the departure of the December birds could not be explained by dryness or poor vegetation growth. Surveys failed to find any other suitable habitat in the entire Belfast-Dullstroom area during this period. During all visits the birds flew readily but they called only rarely, so I judged that breeding was not taking place.

On all three visits Redchested Flufftails (which are resident at the site) were found alongside the Whitewinged Flufftails throughout the vegetation types occupied by the latter, although Redchested Flufftails also occurred in the wettest central areas with the tallest vegetation, including *Phragmites* and *Typha*, where no Whitewinged Flufftails were found. African Rails were also present in the vlei, but were confined to the more deeply flooded areas and thickest growths of sedges, *Typha* and *Phragmites* adjacent to the dam at the southern end of the site. A Corncrake was observed on the ground next to a pool at an open patch in *Typha* at the central drainage line on 15 February 1990, and on 6 December 1991 one was flushed from dense *Carex* 1 m high on moist ground; these are unusual vegetation types in which to see this species. The Black Crake was recorded in the area only on 9 January 1992, when a duet was heard from flooded, relatively sparse *Carex/Phragmites* vegetation at 1 850 m a.s.l. in a nearby wetland; this crake is rarely recorded at high altitudes in Natal or the Transvaal (pers. obs.).

#### **8.4.2.2 Wakkerstroom, Transvaal**

In mid-February 1992 Whitewinged Flufftails were present at Wakkerstroom Vlei only in the extensive sedge beds to the south of the Volksrust-Wakkerstroom Road. This area is predominantly a mosaic of *Carex acutiformis* marsh, *Leersia hexandra* marsh and sedge/bulrush marsh, with tall *Phragmites australis* along the vlei centre (Chapter 2, Section 2.2.3; Table 2.4). The vlei had been burned in September 1991, the whole area was suffering from a prolonged drought (E. Kotze pers. comm.) and water levels were very low. Extensive areas of the peripheral hygrophilous grassland and sedge meadow were dry, and much of the marsh vegetation, which had been wet or flooded a month earlier (D. Kotze pers. comm.) was dry to moist, although significant dieback of vegetation had not

yet occurred. The birds were all located in vegetation towards the centre of the vlei, where the substrate was moister than at the edges.

Eight of 14 (57%) visual records were from vegetation in which *Carex* was either dominant or co-dominant with one other species (Table 8.4), and such vegetation occurred along 55% of the 1 400-m transect walked through this habitat (Table 2.4). In contrast to Dullstroom, there was no significant preference shown for *Carex*-dominated vegetation ( $\chi^2 = 0,026$ ;  $P > 0,8$ ). The calling birds (Table 8.5) were all located in *Typha* or *Phragmites* which, if not the dominant vegetation, was considerably taller than the surrounding growth of sedge or grass; these birds could not be flushed. As at Dullstroom, some of the *Carex* in which the birds occurred was intermixed with *Phragmites* stems but, unlike Dullstroom, the vegetation was also sometimes interspersed with stems of *Typha*. Both visual and sound records were obtained from areas of dense *Leersia hexandra* grass, which provided good cover even if growing on its own; this habitat type does not occur at the Dullstroom site.

During the four weeks which followed this visit the area received about 80 mm of rain (E. Kotze pers. comm.) and, on my next visit to the vlei in mid-March (Table 8.5), the river was flowing and some of the previously occupied areas were moister than in February. However the rain had obviously come too late in the season to stimulate any significant flush of vegetation in these areas, for dieback had continued and the overall cover had decreased. As a result of the lack of grazing in the surrounding veld, some areas of the vlei south of the road, including the previously occupied habitats, had been extensively penetrated and grazed by cattle (see Section 8.4.2.5), which had destroyed up to 50% of the cover in some patches previously suitable for Whitewing Flufftails. In particular the cattle had trampled some moist areas dominated by *Leersia*, so that the amount of this habitat available to the birds had been more reduced than had other vegetation types. I found only two Whitewing Flufftails in this southern section during the visit, and none was seen or heard thereafter.

The presence of both calling and easily flushed birds was not encountered at any other study site. Observations made at Franklin Vlei (Section 8.4.2.3), where behaviour in wet years differed markedly from that in a dry year, indicated that the habitat had been more suitable for long-term residence and effective concealment early in the summer, but that, in view of the lack of rain, the drying of the substrate and the damage by cattle, it rapidly became less suitable in February and March.

During the February visit resident Redchested Flufftails were found throughout the vlei, including those areas occupied by Whitewing Flufftails, and they were seen and heard most frequently in the wetter areas of *Typha* and species-rich sedge marsh which were not occupied by the

Whitewinged Flufftails. African Rails are also resident in the vlei but were confined to the wettest areas in the vlei centre and in flooded areas such as those along the Volksrust-Wakkerstroom Road, where Baillon's Crake has also been reported (E. Kotze pers. comm.). A single Corncrake, the first record for the area, was flushed at dusk on 13 February, in tussocky *Juncus*, *Carex* and hygrophilous grass on dry ground near the edge of the vlei.

#### 8.4.2.3 Franklin, Natal

Franklin was unique among the study sites in having a significant number of Whitewinged Flufftails continuously present for a long period (November 1990 to March 1991) and in having populations which showed totally different behaviour patterns in two different periods of occurrence. The area in which the birds were found includes that in which Mendelssohn *et al.* (1983) also located this species.

During the first two periods of occurrence, November 1990-March 1991 and November 1991-January 1992, the birds were never seen in flight, their presence being indicated only by their regular calling at dawn and dusk (Section 8.4.4). In both periods the birds were present in similar habitat: tall dense reedbeds in water 5-45 cm deep. The predominant vegetation was a mosaic of *Carex acutiformis*, *Phragmites australis* and *Typha capensis*, the *Carex* being the most abundant species and the other two commonly being intermixed (Table 8.5). All three species also grew in patches on their own, the latter two especially in the most deeply flooded regions and at pools and along channels in the marsh where clumps of *Cyperus fastigiatus* also occurred. Another tall sedge, *Schoenoplectus corymbosus*, is also widespread at Franklin (Chapter 2, Section 2.2.12) but was not significantly abundant in the areas occupied by Whitewinged Flufftails, where there are also no seasonally wet peripheral areas of sedge meadow or hygrophilous grassland.

The vegetation inhabited by the birds was tall and dense, the *Carex* commonly reaching a height of 120-150 cm, the *Phragmites* 200-250 cm and the *Typha* 200 cm, in midsummer. Although parts of the area were burned in September in both seasons, by late November the vegetation had already reached a height of 150-200 cm in some places. The main characteristics of this vegetation are its height and density, its flooded muddy substrate and its great impenetrability. Reedbuck make permanent tracks through it to the centre of the vlei, where the ground rises, vegetation height decreases and some dry grassy "islands" are present, but even these tracks are difficult to negotiate because of the depth of mud and water and the presence of numerous submerged burned reed crowns. Cattle graze the periphery in spring, but after November they do not penetrate the flooded areas. In

this region the vlei is 0,5-1 km across and the Whitewing Flufftails were found up to 300 m in from the edge, which here is bordered by short-grazed grassland and a river channel.

There is no reason to suppose that precipitation at Franklin was appreciably less than the average in these two seasons, as vegetation growth was good and flooding apparently normal. However the third period of occurrence, in November 1992, was during a period of severe drought when the wetland at Vogelvlei was almost completely dry and it was possible to walk across the vlei without encountering any saturated ground. The only water was in the river channel and associated pools, all of which were very low. The area had been spring-burned, and in early November cattle were grazing the entire vlei except for a few small wet patches, where vegetation growth was greater than elsewhere but still somewhat less than normal: the best *Carex* beds were only 60-90 cm tall, with no flowers, and ground cover was 80% or less, while the tallest *Typha* and *Phragmites* along the river reached 1,5-2 m but in the open vlei were only 90-100 cm tall with poor (40-70%) cover. In most areas, including those normally occupied by Whitewing Flufftails, the maximum height of vegetation comprising any or all of these three wetland plants was 60-80 cm, with cover of 30-70% (greatest in pure *Carex*, least in pure *Typha*). The cattle had significantly affected 70-75% of the Vogelvlei wetland vegetation by grazing and trampling, having reduced the overall vegetation height to 20-30 cm up to 100 m in from the vlei margin, with much trampling which had destroyed all continuous cover, and further into the vlei having grazed the vegetation down to 30-60 cm in some areas, where cover was only 30-40%.

In this devastated habitat all birds were scarce but the short-grazed dry sedges held the occasional Common Quail *Coturnix coturnix*, for which little suitable grassland habitat remained locally. The normally common reedbed passerines such as warblers and *Euplectes* species were few in number and were entirely confined to the ungrazed vegetation, where six Whitewing Flufftails were also present in early November, in an area of *Carex* and *Typha* where they had been found in the previous two seasons. The *Carex*-dominated vegetation was the best habitat, providing the densest cover and being the least damaged by grazing, presumably because of its relative unpalatability to cattle. The flufftails showed completely different behaviour from that noted in those seasons: they never called, they were easy to flush, and the vegetation was so sparse that sometimes they could be seen on the ground immediately before they took off. The height and cover of this vegetation were considerably less than those encountered in any other occupied locality during the study (Table 8.4). Two days after being found, both Whitewing Flufftails and Redchested Flufftails had vacated this vegetation and the Whitewing Flufftails were relocated about 200 m away in taller *Carex* and *Typha* adjacent to the river channel, in moist vegetation up to 1 m tall with 65-70% cover.

By 21 November only one Whitewing Flufftail remained, being found in the dampest remaining area of the open vlei, in mixed *Carex* and *Typha* 95 cm tall. The area continued to dry out rapidly and no more birds were observed. By early January the area was completely dry and large areas of the reedbeds were yellow with dead leaves.

The relative areas of the different vegetation types which the birds normally occupied (Table 8.5) could not be determined accurately because of the great degree of intergradation between them and the complexity of the mosaic so formed. However the *Carex*-dominated vegetation types, which covered roughly 65-70% of the occupied wetland and accounted for a similar percentage (69%) of the calling records, accounted for all the visual records. This suggested a preference for these vegetation types only during the drought year. The birds were not found in areas dominated by *Phragmites* (Table 8.5) but they did occur in *Typha*-dominated vegetation, with which they showed no significant association (31% of calling records in about 25% of the occupied wetland;  $\chi^2 = 0.908$ ;  $P > 0.3$ ).

During all three seasons Redched Flufftails were found alongside the Whitewinged Flufftails throughout the habitat occupied by the latter, although in November 1992 the Redched were more concentrated in the tallest, wettest vegetation along the river channel and around pools. In the first two seasons there were few Redched Flufftails in large deeply flooded areas with single-species stands of the tallest vegetation and most were in peripheral and less deeply flooded areas with a mosaic of several sedge and reed species.

I have never recorded Black Crakes at Franklin, but the African Rail is common in all flooded areas of dense vegetation, even penetrating flooded stands of pure *Carex*. The Baillon's Crake is sometimes locally numerous, and was especially so in November 1992 when birds were concentrated around the river channel and drying pools at Vogelvlei. Corncrakes are occasional in surrounding grassland, and on 28 January 1989 one was flushed from sedge meadows on the opposite side of Franklin Vlei.

#### 8.4.2.4 Penny Park, Natal

The wetland at Penny Park differs from all other Whitewinged Flufftail study sites in having no *Carex* beds, the vegetation in the wettest areas comprising other large sedges and *Typha* (see Chapter 2, Section 2.2.14), and having large tracts of seasonally deeply flooded *Leersia hexandra* grassland at its periphery. The small numbers of Whitewinged Flufftails at this site were confined to flooded areas dominated by *Typha*, from which they called but were never flushed, and the only sighting was from flooded *Leersia*-dominated vegetation at the edge of these *Typha* beds (Tables 8.4,

8.5). The height, density and impenetrability of the preferred vegetation resembled that of the tallest occupied reedbeds at Franklin (Table 8.5). No Whitewing Flufftails were found at Penny Park during the 1992-93 summer, when the wetland was very dry and was extensively and heavily grazed.

Resident Redchested Flufftails and African Rails were present in the Penny Park wetland, the flufftails being sparsely scattered in the less extensively flooded peripheral areas, principally those with a mosaic of *Typha*, *Cyperus*, *Mariscus*, *Juncus* and *Schoenoplectus*. Baillon's Crake was locally numerous in the summer months, being present in especially large concentrations in all vegetation types during the 1991-1992 summer, when indications of breeding were obtained. Redchested Flufftails were not found alongside the Whitewing Flufftails at this site, preferring the less deeply flooded areas.

#### **8.4.2.5 Other wetland areas surveyed in Natal and the Transvaal**

Observations in unoccupied wetland areas adjacent to those containing Whitewing Flufftails provided good indications of the characteristics which render habitats unsuitable for occupation by this bird. At the Dullstroom study site a nearby wetland of a similar size and superficially very similar habitats did not produce any records of Whitewing Flufftails during the study period. However this wetland showed the following major differences in its hydrology and vegetation: (a) its degree of flooding was much greater than that of the occupied vlei, (b) the *Phragmites* and *Typha* were confined mainly to large areas of very tall and dense monospecific growths in the deeply flooded regions, (c) the extensive *Carex* beds were confined to the central regions, where they were on a permanently flooded substrate in stagnant water, and (d) the *Carex* had a different character from that occupied elsewhere: either it was less than 1 m tall or it grew so sparsely that cover was very poor and the substrate could be seen clearly between the plants. All these features were probably unacceptable to Whitewing Flufftails: the sparse *Carex* beds were not occupied by any rallid species, while Redchested Flufftails were confined to the less deeply flooded mixed-species sedge beds, hygrophilous grassland and *Typha* beds in less permanently waterlogged areas at the periphery of this vlei.

In January 1992, surveys of other wetlands in the Belfast-Dullstroom area revealed no Whitewing Flufftails. Most of the vleis with normally moist *Carex* and other vegetation types (i.e. similar to those occupied at the study site, and thus potentially suitable) were small (< 1 ha) and almost all were very dry as a result of the drought, this probably rendering them unsuitable for occupation at that time. The largest vleis in the Lakenvleispruit system and adjacent areas were still wet but contained no suitable habitat, all their extensive *Carex* beds being either very short (50-70

cm high) or very open (cover 30-50%), and most being on flooded ground with stagnant water. These vleis held Redchested Flufftails only in dense mixed vegetation on moist to shallowly flooded ground.

At Wakkerstroom, Whitewinged Flufftails were not found in the part of the vlei north of the Volksrust-Wakkerstroom Road, which contains some potentially suitable habitat, both sedge-marsh mosaic and sedges with a predominance of *Carex acutiformis*. However some of the *Carex* beds were probably too sparse for occupation, growing in flooded central areas with stagnant water and resembling the unoccupied *Carex* at Dullstroom. In March 1992 some peripheral areas of sedge and bulrush marsh had been extensively penetrated by cattle, which had trampled the vegetation, destroyed the cover and compacted and puddled the substrate, rendering the habitats unsuitable for any flufftail species. Some mowing for fodder had also been carried out in peripheral areas, including the edges of *Carex* beds. Given sufficient rainfall and vegetation cover, some of this northern region would probably be suitable for Whitewinged Flufftails in other seasons, and the species was possibly heard calling there as early as October 1991 (W.R. Tarboton pers. comm.). Some parts of the vlei in this northern region contain areas of the vegetation type described by Kotze (1992b) as "short reed marsh", this being predominantly dense *Phragmites* (1,2-2 m tall, with thin stems) in association with *Carex acutiformis* and growing on a floating mat of roots (Kotze 1992b). This vegetation type contains very few birds of any species, even warblers and cisticolas, and no flufftails.

Smaller wetlands near Wakkerstroom Vlei were also surveyed in February-March 1992 and January 1993, and those with areas of undisturbed sedge-marsh mosaic and *Typha* patches were thought to be potentially suitable in a season of normal rainfall. Some of these wetlands contained large stands of pure *Eleocharis* sedges, a vegetation type in which Whitewinged Flufftail was not recorded elsewhere.

Parts of Franklin Vlei were not searched and it is possible that more suitable habitat for Whitewinged Flufftail exists than was discovered during this study. However, aerial and ground surveys showed that the preferred vegetation types at Vogelvlei are not present throughout the vlei. Much of the vegetation in the lower middle reaches along the river channel is dominated by *Typha* and *Phragmites* beds in deep, often flowing, water, and is unsuitable habitat, while large areas of the peripheral wetlands on the eastern and western sides of the entire vlei were deemed unsuitable either because of their management and usage or because of their vegetation. Many areas comprise seasonally flooded hygrophilous grassland and sedge meadow which lack either dense cover or sufficiently extensive stands of the sedge and reed species in which the flufftail has been found elsewhere. Regular annual burning of such areas, mentioned with concern by Begg (1989), coupled with grazing pressure, produce vegetation which either never attains sufficient height and density to support any secretive wetland bird species, or becomes habitable so late in the season as to be useless

for colonization by breeding rallids. The potentially suitable habitat at Penny Park is limited to areas of relatively undisturbed flooded *Typha* and sedge beds, and seasonally flooded hygrophilous grassland, along the course of the Manzimnyama River. This wetland is subjected to annual burning and intensive grazing which reduce the extent of such habitat away from the river. Nowhere at Penny Park do any *Carex* species occur to any significant extent, presumably because of the lack of permanently moist areas where water does not flow (see Section 8.5).

My failure to find Whitewing Flufftails in any of the other large wetlands surveyed (Sections 8.2 and 8.4.1) in some cases may be more attributable to the difficulty of locating the birds than to their complete absence from the areas concerned, several of which contain habitat possibly suitable for the species. Mvoti Vlei is peculiar in having much of its area permanently saturated and dominated by *Phragmites*, and therefore unsuitable; there is a narrow peripheral strip of mixed-species sedge marsh and seasonally wet sedges and hygrophilous grassland which holds a dense population of Redchested Flufftails and is potentially suitable for Whitewinged Flufftails, but conditions may not be suitable for long-term occupation (see Section 8.5). Hlatikulu Vlei is too disturbed, fragmented and overgrazed to contain much good habitat, while peripheral areas are rapidly succumbing to commercial afforestation. It does contain some wetland areas dominated by *Carex* but these are sometimes too sparse or grow on hummocky ground (see next paragraph). Brief observations at the Myamvubu vlei system suggested that Melmoth and Dartmoor Vleis, and the nearby much larger Scawby Vlei which was not visited (see Begg (1989) for further information), might contain some suitable habitat of *Carex* and other sedges, but that the hummocky or sparse nature of some vegetation and the lack of intermixing with other species suggest that this habitat is unsuitable (see next paragraph). The same applies to the small amounts of potentially suitable sedge beds at Stillerust Vlei.

The high-altitude Mgeni and Ntsikeni Vleis contain extensive areas of vegetation dominated by *Carex* species, as well as areas of other sedges and reeds, but large tracts of these vegetation types appear unsuitable for Whitewinged Flufftails. For example, at Mgeni the *Carex cognata* marsh tends to be quite open, while the *C. acutiformis* marsh is characterized by very stagnant conditions and few microhabitats compared with those of sedge meadow, for example; these factors appear to account for the very low plant and animal species richness of this vegetation type (Kotze 1992a). Such conditions have also been seen at other sites, in particular the stagnant *C. acutiformis* marsh near the occupied Dullstroom wetland, and it is probable that Whitewinged Flufftails would not favour such vegetation: I have never found this or any other rallid species in the typically sparsely growing vegetation on such anaerobic substrates. Furthermore, at both vleis some *Carex* marsh and much of the sedge meadow and hygrophilous grassland are on tall hummocks with water in the intervening channels. Hummock-depression morphology has been attributed to trampling by cattle (Downing

1966) but at Mgeni Vlei is thought to have resulted from site-specific factors such as the building activities of ants and earthworms (Kotze 1992a). Substrates with tall hummocks and water-filled channels appear to be avoided by flufftails: I have not found Redchested Flufftails in reedbeds on such ground and I suspect that the difficulty in moving and foraging on the ground in such areas would render them unsuitable for occupation.

In all areas where Whitewing Flufftails were found in *Carex* marsh during this study the *Carex* was either interspersed with stems of *Typha* or *Phragmites*, or with clumps of other sedges, or was growing in patches intermixed or alternating with stands of these other species. Thus the complete absence of *Typha* and *Phragmites* is another possibly significant factor concerning the high-altitude wetlands such as Mgeni, Ntsiken, Melmoth and Dartmoor Vleis, and may reflect a paucity of nutrients.

Of the other vleis surveyed, The Swamp was thought to contain little suitable habitat, while the Cedarville Flats are so fragmented and drained that only small patches of potentially suitable vegetation remain. During the study I found many small patches of dense *Carex*-dominated vegetation, intermixed with combinations of *Typha*, *Phragmites*, *Schoenoplectus*, *Leersia*, *Cyperus*, *Mariscus*, *Juncus*, etc., in many parts of the Natal survey area but none of these contained Whitewing Flufftails and none was greater than about 1,5 ha in extent. Although it is possible that such areas are too small for long-term occupation by this species, breeding birds have been reported in a marsh of 0,4 ha (Guichard 1948) and nonbreeding birds in a 0,28-ha wetland in Zimbabwe (Hopkinson & Masterson 1984).

#### **8.4.3 Seasonality and pattern of occurrence**

This study produced no evidence that Whitewing Flufftails are permanently resident at any study site and all records obtained (Table 8.2) fell in the main rainfall period at the study sites concerned: December-February at Dullstroom and Wakkerstroom (see Chapter 2, Fig. 2.5 for long-term mean monthly precipitation at these sites), November-March at Franklin (see Chapter 2, Fig. 2.27 for mean monthly precipitation) and January-March at Penny Park (see Mt. Currie long-term mean precipitation, Fig. 2.29). The very few other records obtained during the study period also fell within the November-March rainy period, with the exception of the two unconfirmed SABAP Cape Province records which were in October (Table 8.2) and from regions with a similar rainfall regime. Occurrences in South Africa overlap with those in Ethiopia in May, August and September, during which months South African records are relatively few (Table 8.3).

At the three study sites where occurrences were noted over more than one summer, regular visits were made throughout the year to establish the pattern of occurrence and the conditions of the habitat when the birds were not present. In 1989 the Dullstroom study site, as well as being spring-burned, was completely dry until the end of December (J.C. Sinclair pers. comm.) and thus presumably provided little or no suitable habitat before the birds' arrival in January 1990. No birds were present in late March (E. Forsyth pers. comm.) and July 1990; in July the substrate was still as moist as it had been in February, cover was still dense although almost all the vegetation was dead, and Redchested Flufftails were present throughout the wetland in similar numbers to those found during the previous summer. A similar situation prevailed during mid to late 1991, except that the vlei was moist in November and the birds were present from early December. By late January 1992 the vlei was drying out rapidly and most birds had left; none was found during visits in May, October and November. As the vlei was not burned in late 1992, cover in October and November was still dense although flattened and largely dead (E. Forsyth pers. comm.). It was not possible to visit the vlei after November 1992 but, in view of the prevailing drought and the moribund condition of the unburned vegetation, the birds are very unlikely to have occurred in the 1992-1993 summer (E. Forsyth pers. comm.). At Wakkerstroom the birds were not recorded during the 1992-1993 summer, when conditions were very dry (E. Kotze pers. comm.). My visit in January 1993 confirmed the unsuitability of the habitat: the vlei was almost completely dry and vegetation growth was sparse and low, with bare patches where the spring fires had burned into the peaty substrate and killed the underground parts of sedges and reeds. The *Typha* and *Carex* were dying and the sparse *Leersia* grassland was completely dry. The water table was very low, water lying about 1 m below the surface.

At Franklin in April-October 1991 and 1992 vegetation dieback was also extensive, there was some drying out of the habitat occupied during the summer, and no Whitewing Flufftails were present although Redchested Flufftails were resident throughout these years. Spring burning of the vlei in both seasons encouraged vigorous new growth which was occupied during November in both years.

The reasons for the birds' possible absence from the Franklin site in the summers of 1988-1989 and 1989-1990 are not clear, although the preferred area at Vogelvlei was first visited only in late January 1989 when the vegetation was so tall, dense and impenetrable that it was assumed (incorrectly) to be unsuitable on the basis of published accounts of preferred habitat. Regular visits during both summers produced no visual or vocal records, but coverage was not intensive enough at the times of the day when the birds normally call: at the beginning of the study it was not realized that it might not be possible to flush birds during the summer months from potentially suitable dense

sedges and reeds. In early 1990 rainfall at Franklin and elsewhere in East Griqualand was very low (E.H.D. Long pers. comm.; Fig. 2.30B) and the comparative dryness and poor vegetation growth in some areas made it unlikely that Whitewinged Flufftails would have remained, even if they had been present earlier in the season.

At Penny Park in April 1991 the wetland was drying out rapidly and much vegetation dieback had begun. In May the weather was cold and the previously occupied vegetation had been extensively penetrated and trampled by cattle, which had destroyed much cover. After a complete burn in early September 1991 and extensive spring grazing, the vegetation had developed to an apparently suitable height and density by late December and the reason for the birds' apparent absence until January is not clear.

In view of the generally accepted theory that the Whitewinged Flufftail is nomadic or migratory with periodic eruptions when populations are high (Chapter 1, Section 1.2.4.2), an attempt was made to correlate southern and central African occurrences with periods of above-average precipitation in South Africa, on the assumption that all birds in this region are derived from a South African breeding population. For each year of the period 1920-1980 Zucchini & Adamson (1987), using data from 2 500 weather stations, give the percentage area of South Africa which received rainfall below the 50%, 20% and 5% percentiles of the local annual total distribution. The acceptable records from Zambia and Zimbabwe (Table 8.2) all occurred after 7-10 consecutive years when over 50% of South Africa received rainfall above the 50% percentile and these occurrences therefore support the theory of wider dispersal after a series of good rainy seasons, when the population may be expected to have built up considerably (Hopkinson & Masterson 1977). The South African records for the period 1955-1975 (Tables 8.1, 8.2) all occurred in good rainfall years, i.e. when over 50% of South Africa received rainfall above the 50% percentile. For 1910-1976 Dyer & Tyson (1977) plot the observed annual rainfall from 62 weather stations in the northeastern half of South Africa (the area containing 11 of the 14 known Whitewinged Flufftail localities) as a percentage deviation from the 1910-1972 mean, and the 1955 and 1975 records from this region also fall during high-rainfall periods.

#### **8.4.4              Voice**

During this study six calls were ascribed to Whitewinged Flufftails, but only the escape call (Call 6) was uttered by a visible bird. The other calls were all given by birds concealed in dense cover but in view of the circumstances of the observations, the responses obtained to playback of some calls, and the studies of other species with similar calls, the identity of the calling birds was

considered reasonably certain. In all other flufftail species studied the majority of calls were first identified without the birds being seen, even though prolonged observations did result in my seeing birds making a few of the calls.

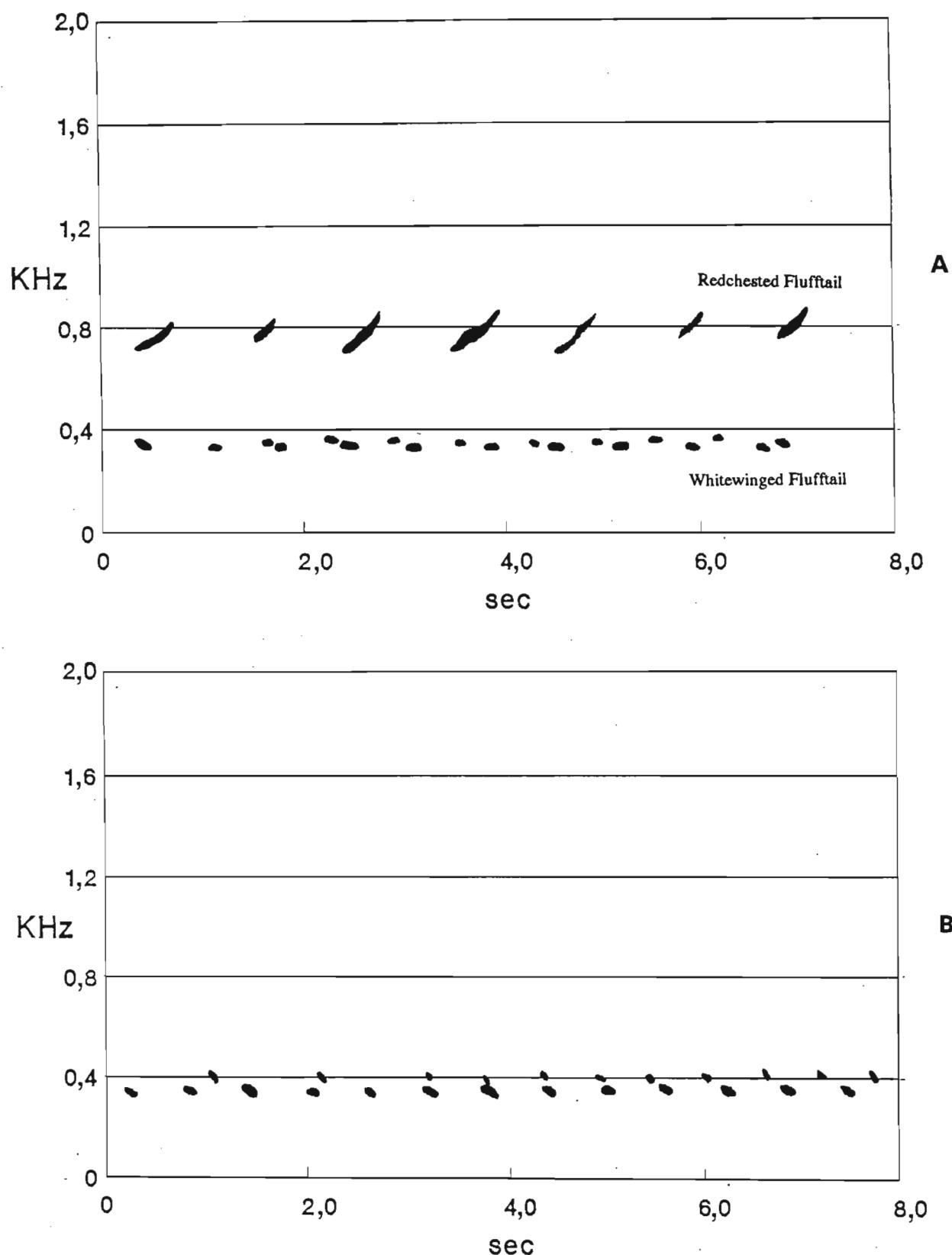
**Call 1: low-pitched *OOOOO*** (not tape-recorded). This is a deep mooing note, lower in pitch than any other call, of about 0,7 s duration and given either singly or repeated 2-3 times. It was heard in the daytime, once at Dullstroom on 14 February 1990 (during which visit this species called very infrequently) and on several occasions at Franklin in December 1990 both spontaneously and in response to playback of the duet (Call 4). At Franklin the call was given by birds at very close range and was interspersed with the normal duet (Call 4). The call may be indicative of agitation or aggression in response to disturbance or taped playback of advertising calls.

**Call 2: high-pitched *OOOOO*** (not tape-recorded). This call was heard twice at Dullstroom on 14 February 1990, coming from the tallest wettest vegetation occupied by Whitewing Flufftails (see Table 8.5). It was longer and higher-pitched note than Call 1 and my imitations of the note, recorded just after hearing the original, have a frequency of 0,3 kHz and a duration of 1-1,2 s. I have never heard a comparable note from the Redchested Flufftail and hence it is assumed that the call was made by the Whitewing Flufftail. Its function is unknown.

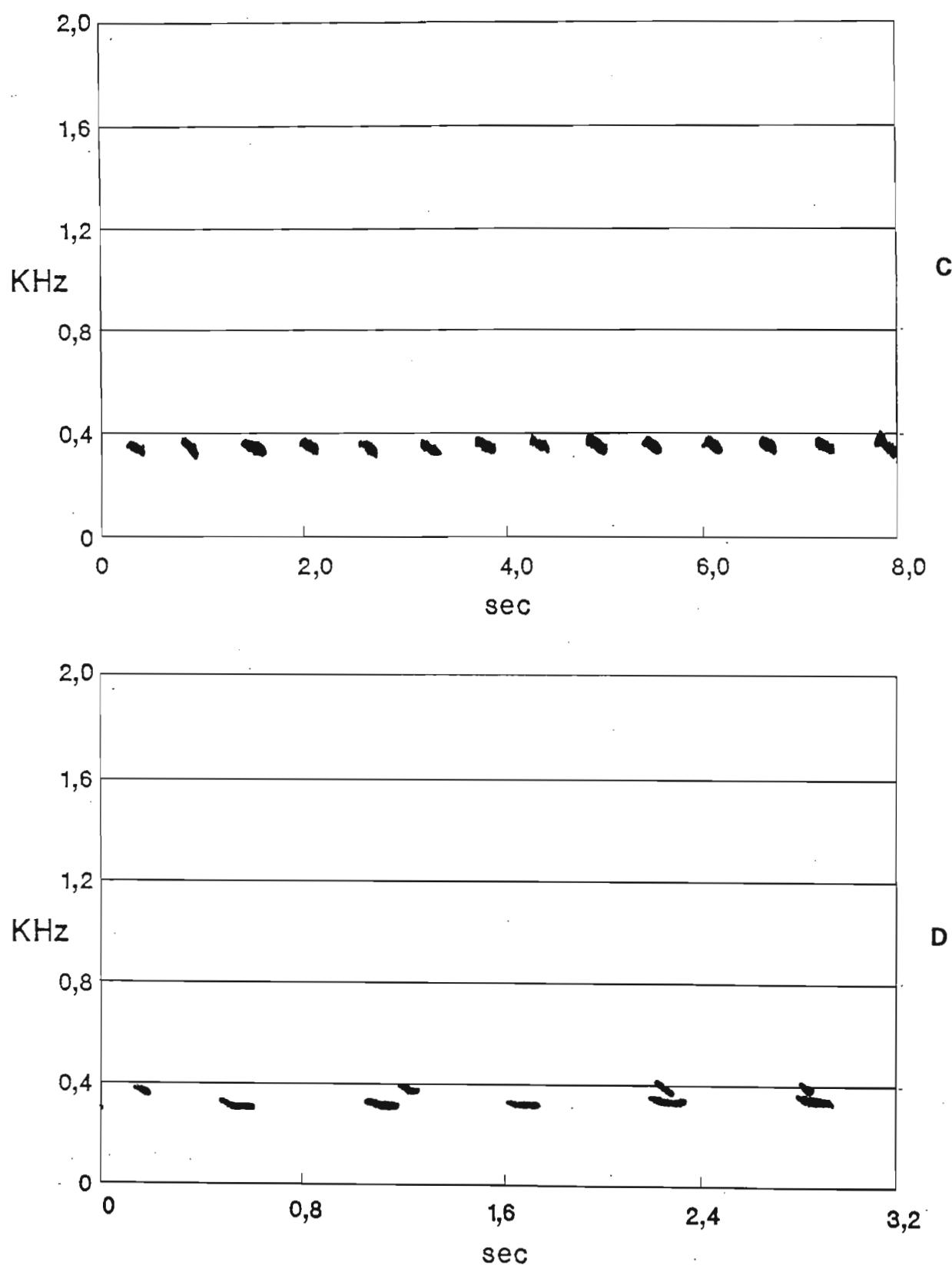
**Call 3: short hoots** (not tape-recorded). This was heard only three times at Dullstroom in February 1990 and consisted of a short *HOO* note repeated 3-5 times at about 1/s; it was assumed to come from a Whitewing Flufftail because no comparable note was recorded from Redchested Flufftails during the study. My imitation of the note has a frequency of 0,25 Khz and a duration of 0,5 s. The function of this call is unknown but a deeper, louder series of similarly short notes heard with other calls at Franklin in December 1990 possibly had a similar function to Call 1.

**Call 4: *OOP* duet** (tape-recorded: see sonograms, Fig. 8.2A-D). This was the most commonly heard call and its utterance was the chief (usually the only) indication of the birds' presence in tall dense vegetation from which they could not be flushed. It was never heard in situations where the birds were flushed readily from relatively short vegetation, such as at Dullstroom in both occurrence periods, at Franklin in late 1992 and in the shorter, drier vegetation at Wakkerstroom in February 1992. The call is a series of regularly-repeated short *OOP* notes (Fig. 8.2C) at or just below 0,4 kHz, uttered at a rate of about 2/s and continued for up to 2 min 40 s (usually for 1-1,5 min). A second bird close by usually joins in with shorter *OOP* notes, often of a slightly higher frequency, uttered asynchronously and often irregularly (Figs. 8.2A, 8.2B). Calling bouts may be repeated at intervals for up to 40 min, but most birds called for only 1-15 min.

The periods during which this call was heard at Wakkerstroom, Franklin and Penny Park are listed in Table 8.5. At the last two sites the periods of occurrence in the seasons concerned were



**Fig. 8.2** Sonograms of Whitewing Flufftail *OOP* calls (Call 4). (A) *OOP* duet, with hoots of the Redcheasted Flufftail. (B) Another *OOP* duet. (C) Calls of a single bird. (D) three seconds of the *OOP* duet from (B), for comparison with Fig. 8.7C.



**Fig. 8.2** (continued).

based on these calling records. At Franklin calling built up in November to a peak in December and then declined throughout the rest of the period, while at Penny Park it declined throughout February-March. Calling occurred twice per day: very early in the morning and at sunset. The first calls were usually heard either just before daybreak or at the very first sign of light (03:55-04:05 in November-December) and calling ceased at 04:30-05:30 (latest in late January), usually when the sun appeared over the surrounding hills. If stimulated by taped playback the birds sometimes continued calling intermittently for 10-20 min longer than normal. Evening calling usually started at or just before sunset (18:30-18:45) and continued intermittently until about 19:20, never being heard after dark. The occasional brief calling bout was heard from 17:10, usually after rain or in very dull conditions. Morning mist did not inhibit calling, but the birds did not call in strong wind or rain. This call was never heard at any time of day outside these normal calling periods. Calls were invariably given from tall dense vegetation and were usually uttered from a perch in the reeds or sedges at a height of 0.5-1.5 m above the substrate.

Although calling birds were never seen, the call was attributed to Whitewing Flufftail for the following reasons. Although not an absolutely typical flufftail call, it is of a type comparable to the hooting calls of other members of the genus but not comparable to any call of any other marsh bird with which I am familiar, except the Crowned Crane (see the following comments on the size of the calling bird). I have documented 113 different vocalizations of the Redchested Flufftail (Chapter 4), none of which is similar to this call. I was often able to pinpoint the source accurately and either to approach the bird or to encourage it closer by playback, when it would fall silent briefly and then begin again from a point a metre or two closer. Its approach was quite rapid, possibly involving descent to the ground and re-ascent at a closer position (as was noted in Redchested Flufftails), but movements were usually masked by general vegetation noise and movement due to air currents, etc. At very close quarters it was obvious that only a small bird high in the reeds could be making the call; occasionally I was able to move very slowly around the calling bird, which was sometimes only 1 m away, at which range any large or clumsy bird would have been obvious. Such calling behaviour is typical of flufftails.

The call was assumed to be territorial or advertising in function because (a) it was given at regular times, (b) calling birds appeared to be stimulated by other birds calling nearby, and (c) the birds sometimes responded to its playback. At most times the birds would not respond to taped playback of any call but in December 1990 and 1991 at Franklin the birds responded well to playback of the duet, approaching the observer closely in tall dense vegetation. After repeated tape stimulation at close quarters the birds became more agitated and the form of the duet changed into that of Call 5.

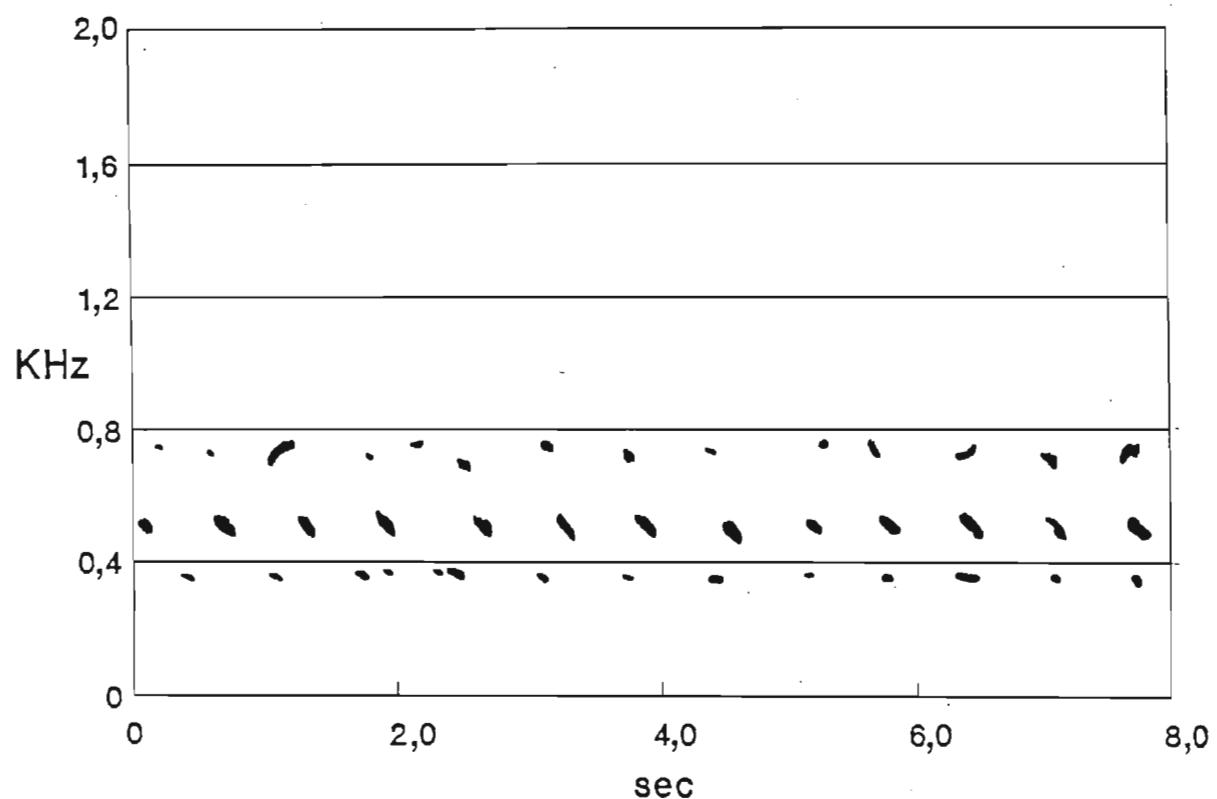
The *OOP* duet is very similar to certain calls made by the Crowned Crane, which frequently occurs alongside the flufftails, and great care is needed to distinguish the calls of these two species. The cranes give similar calls at sunrise and sunset, either singly, in duet or in chorus and, as the calling birds are often hidden in tall dense reeds and the call is difficult to pinpoint accurately, it may not be obvious that cranes are calling. With practice it is possible to distinguish the calls of the two species: the cranes' calls are louder (and therefore clearly audible from much further away), the cranes' double *OO-UP* note is possibly produced by a single bird (the components are usually synchronized), and the cranes' calls are frequently more complex than the flufftail calls, having several different components, some of a higher frequency than the flufftail calls (compare sonograms of typical crane calls, Figs. 8.3, 8.7 & 8.8, with those of the flufftail in Fig. 8.2). Furthermore, other more recognizable calls of the cranes are sometimes interspersed with their *OO-UP* calls and may be obviously synchronized with them. Cranes may also call in wind and rain, and after dark.

**Call 5: loud excited duet** (tape-recorded: see sonograms, Figs. 8.4, 8.5). This call was uttered at close range only in response to prolonged stimulation by playback of Call 4, and is obviously a derivative of that call, suggesting great agitation and presumably being both territorial and aggressive in function. The call has two distinct forms, differing from Call 4 in their greater volume and complexity, and in the increasing prominence given to the notes of the second bird. The first form, derived directly from Call 4, is shown in Fig. 8.4. The first bird's call has a U-shaped trace, often with a second higher-frequency component at its end, and is best rendered *OO-OOP*. The second bird's call, still uttered irregularly and asynchronously, is longer than that of the normal duet and is a descending *OOO*, falling from about 0,6 Khz at the start to 0,5 Khz at the end.

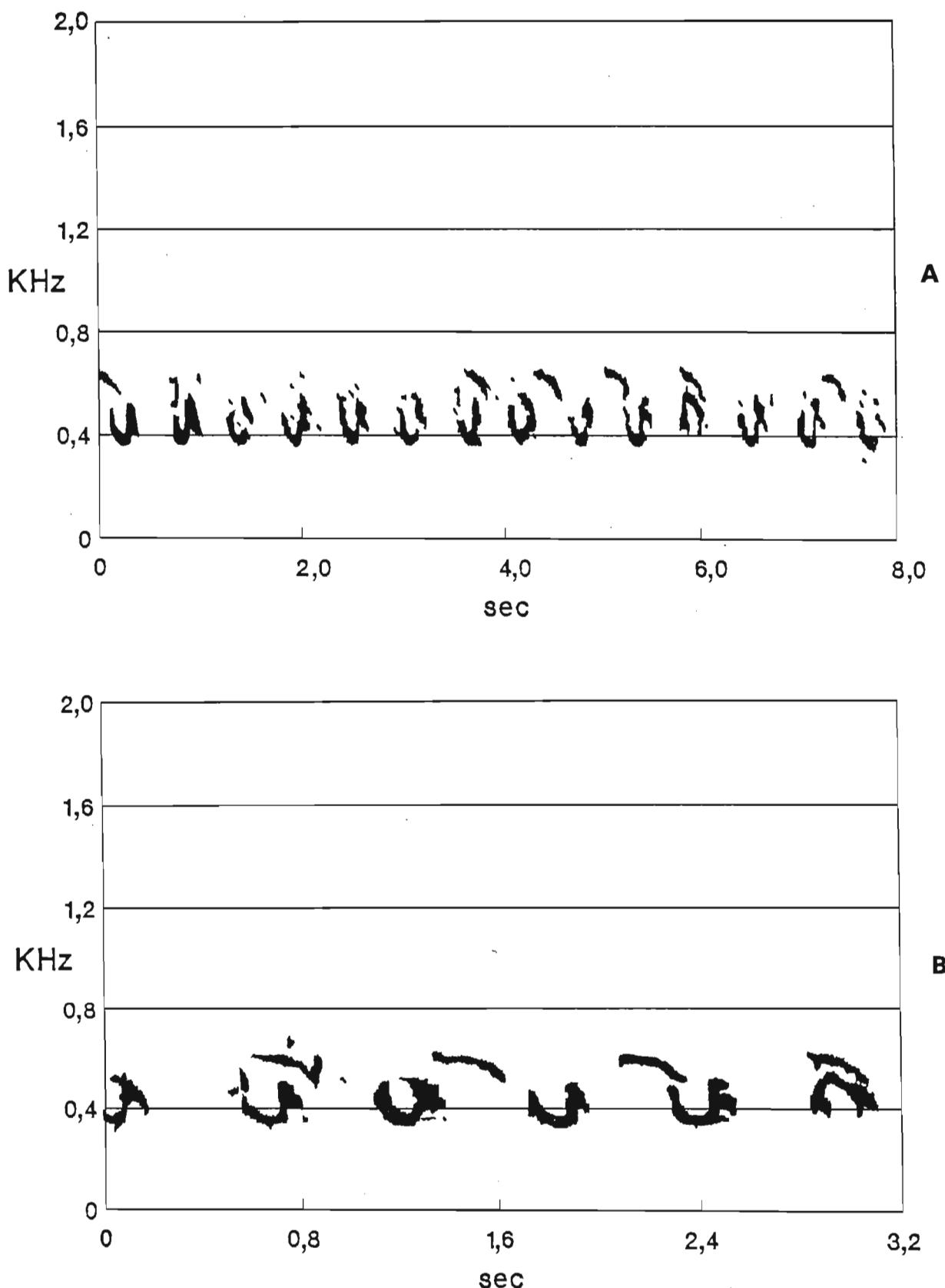
Occasionally the form of the first bird's call is inverted, starting and ending on a low frequency (Fig 8.4B). On continued tape stimulation an even more agitated duet develops, in which the first bird's notes are entirely inverted U-forms, shortened and often broken (Fig. 8.5), while the call of the second bird becomes regular, synchronised and equally prominent with that of the first (if not dominant), with higher-frequency components around 0,8 kHz.

**Call 6: escape call** (not tape-recorded). This call was heard only once, from a female surprised on the ground in sparse cover at Franklin on 5 November 1992. As it took flight the bird gave a quiet but sharp *CHICK*, which was not repeated (and would probably not have been audible over more than about 20 m).

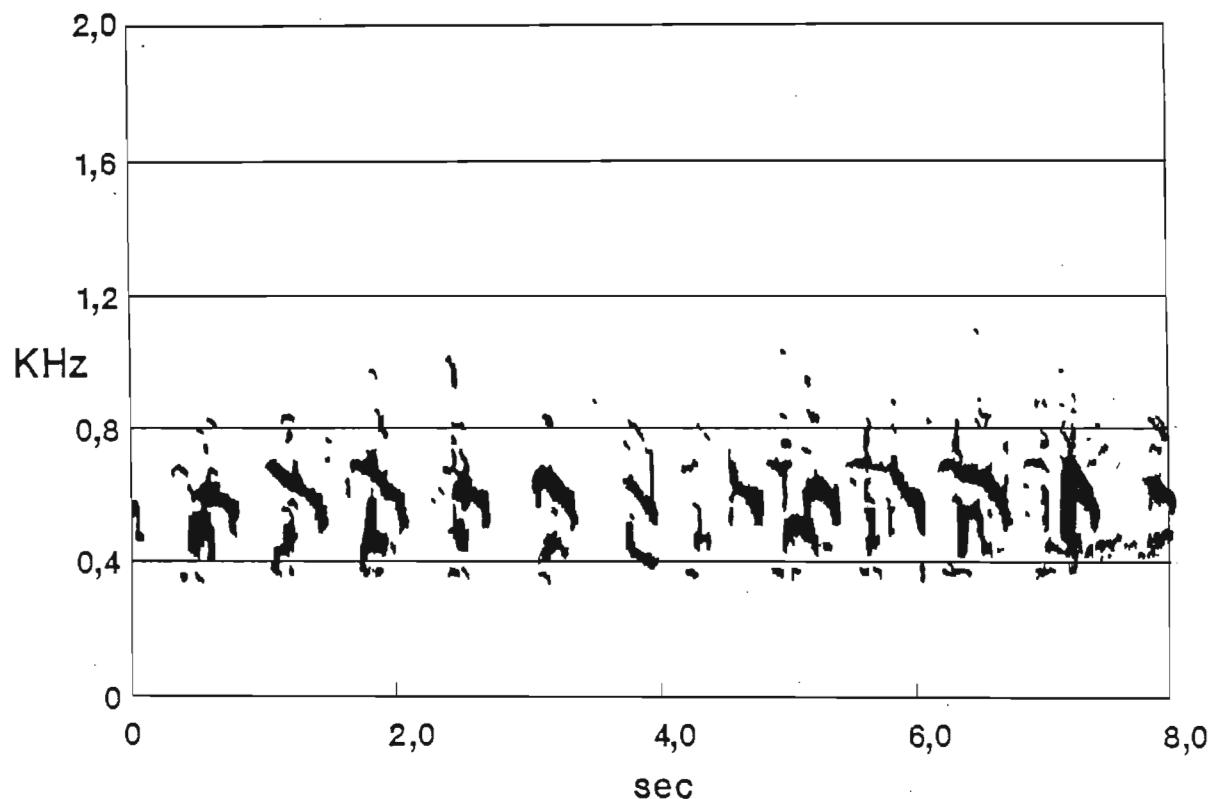
On the basis of the above findings it was possible to evaluate the only two other tape recordings of possible Whitewing Flufftail calls, copies of which were obtained from the Fitzpatrick Bird Communications Library, Transvaal Museum. The first recording was made at Franklin by J.M. Mendelsohn on 6 January 1983, during the period when Whitewing Flufftails were present



**Fig. 8.3** Typical multiple *OOP* calls of the Crowned Crane (compare with Fig. 8.2).



**Fig. 8.4** Two traces of the loud, excited duet (Call 5) of the Whitewing Flufftail, of (A) eight seconds and (B) three seconds, with one inverted note from the lower-pitched bird.

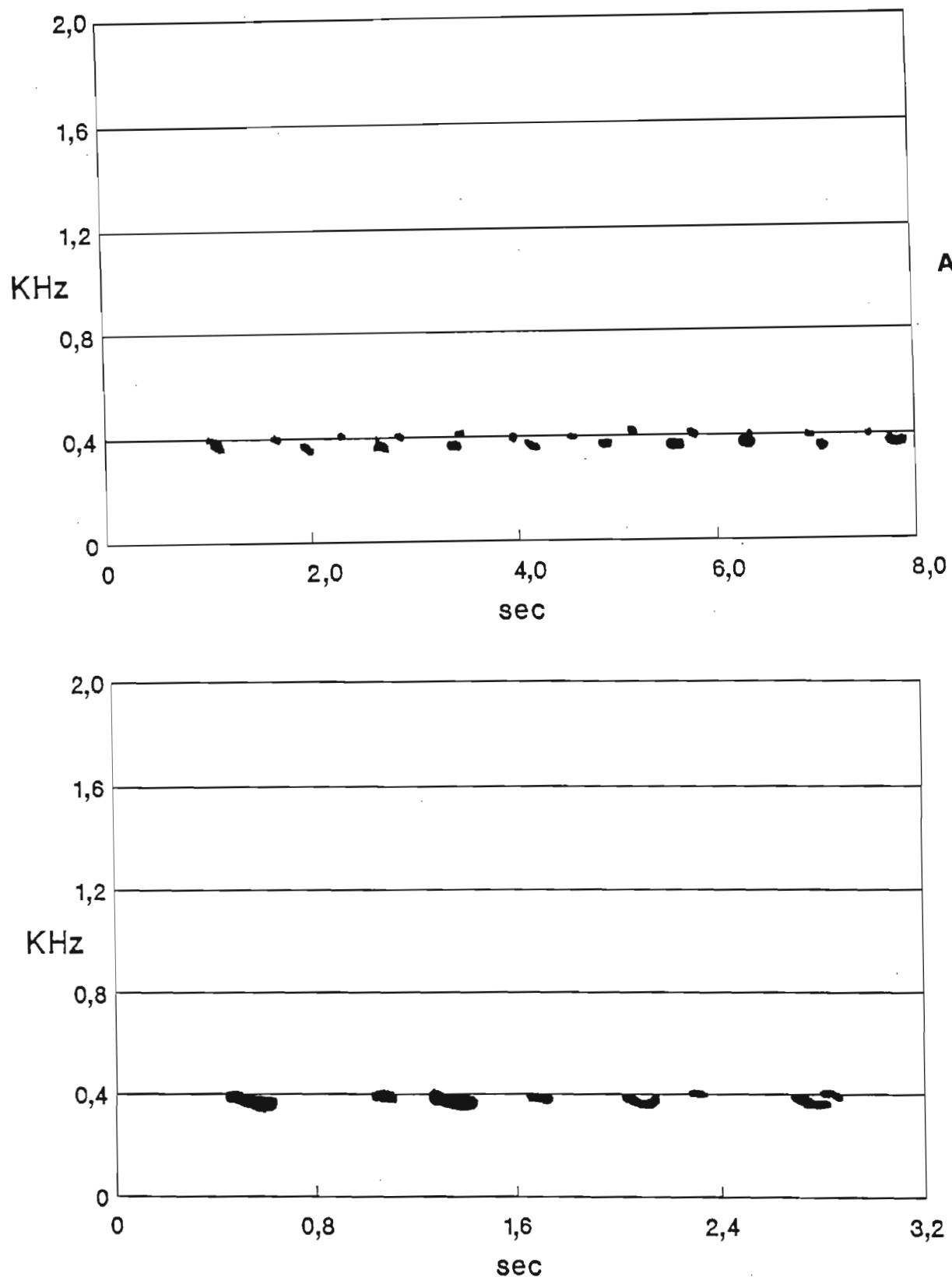


**Fig. 8.5** Loud, excited duet (Call 5) of the Whitewinged Flufftail, showing the inversion of the first bird's notes and the prominence of the second bird's calls.

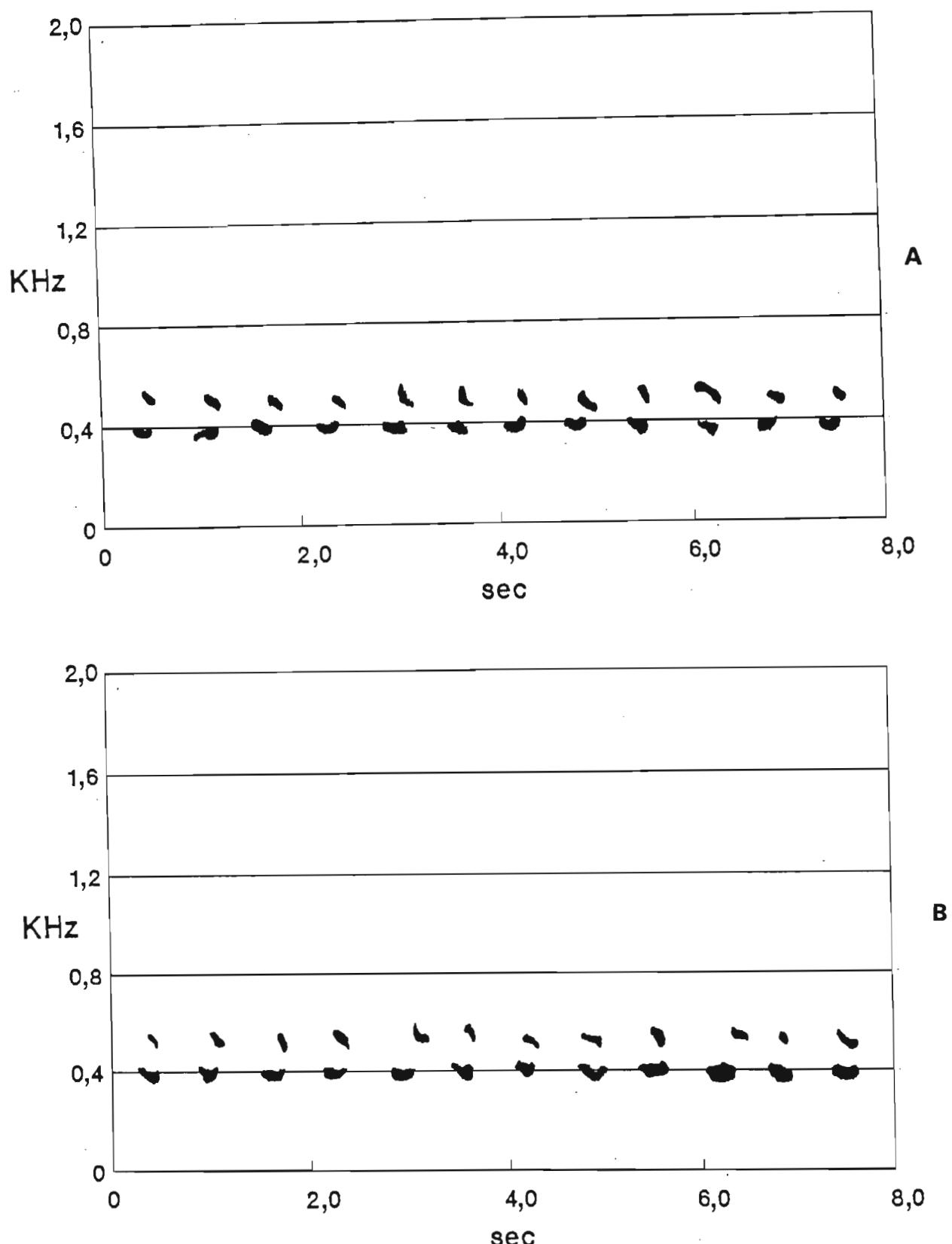
(Mendelsohn *et al.* 1983) (see Chapter 1, Section 1.2.4.5 for further details). Sonograms of some of these calls (Figs. 8.6A,B) closely resemble those of my recordings of Call 4 (e.g. Figs. 8.2A,D) and, on the basis of their structure and frequency, and the antiphonal nature of the duet recorded, I am satisfied that some of the recorded calls are of Whitewing Flufftails, although there are also many interspersed Crowned Crane calls. In his commentary J.M. Mendelsohn states that the calls were heard mostly in the early morning, between 04:30 and 06:00. The second is a series of calls recorded by Dowsett-Lemaire (1990) at Kitabe, Rwanda in January 1990 (see Section 8.4.1). Despite the very poor quality of the recording, sonographic analysis showed that the sequences were principally of one or two birds, each making synchronized double notes (e.g. Fig. 8.7A), with some more complex calls of 3-4 components, also largely synchronized (Figs. 8.7A,C). Dowsett-Lemaire (1990) errs in assuming that the common *OOP* call (Call 4 above) of the Whitewing Flufftail is normally a double note *OU-UP*; I have always found it to be a single note, second notes being produced asynchronously by another bird. All the calls on her tape may be attributed to Crowned Cranes (easily recognisable calls of which also appear on the tape) in view of their synchronization and the complexity and nature of their structure, which closely resemble those of my own sonograms of Crowned Crane calls made at Penny Park and Franklin (see comparisons, Figs. 8.7, 8.8). Three other facts (Dowsett-Lemaire 1990) also suggest that Crowned Cranes are responsible for the calls: (1) the birds were heard calling during the night, (2) the sound carried a long way, and (3) the call was "very soft at close range, somewhat ventriloquial and difficult to locate". In Natal, Whitewing Flufftails did not call after dark but Crowned Cranes did, and the calls of the cranes carried much further than those of the flufftails which, at close range, were fairly loud and enabled the birds to be located precisely. Distant Crowned Crane calls often sounded like softer calls made by closer birds, and the source was difficult to locate.

Whitewing Flufftails never made any vocal response to playback of (a) the advertising, territorial or alarm calls of the Longtoed, Streakybreasted, Striped, Buffspotted or Whitespotted Flufftails, (b) a large selection of the calls of the Redchested Flufftail (including those courtship and mating calls which sometimes elicited a response from breeding Buffspotted and Striped Flufftails), (c) various calls of other rallids such as African Rail, Black Crake and Baillon's Crake or (d) the advertising calls of the Kurrichane Buttonquail *Turnix sylvatica* and the Blackrumped Buttonquail *T. hottentotta*.

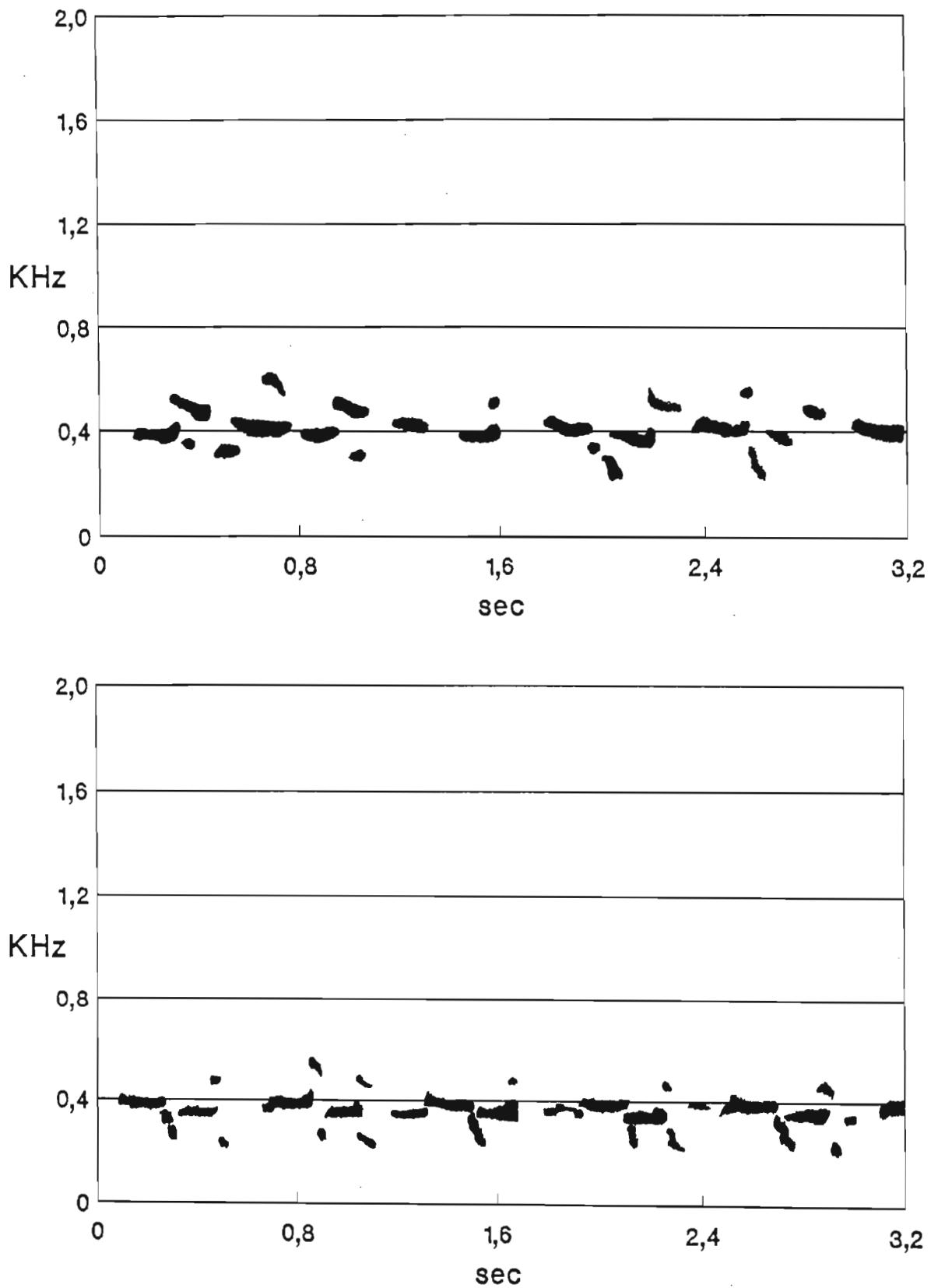
During observations at Dullstroom and Wakkerstroom in December–February (Table 8.4), when Whitewing Flufftails rarely called but could be flushed easily, breeding Redchested Flufftails called frequently from the same habitat, often with advertising hoots as well as territorial calls. I attempted to identify all hooting birds, and all those giving any calls not immediately recognizable as typical of Redchested Flufftails, in case any might be Whitewing Flufftails. In all cases other



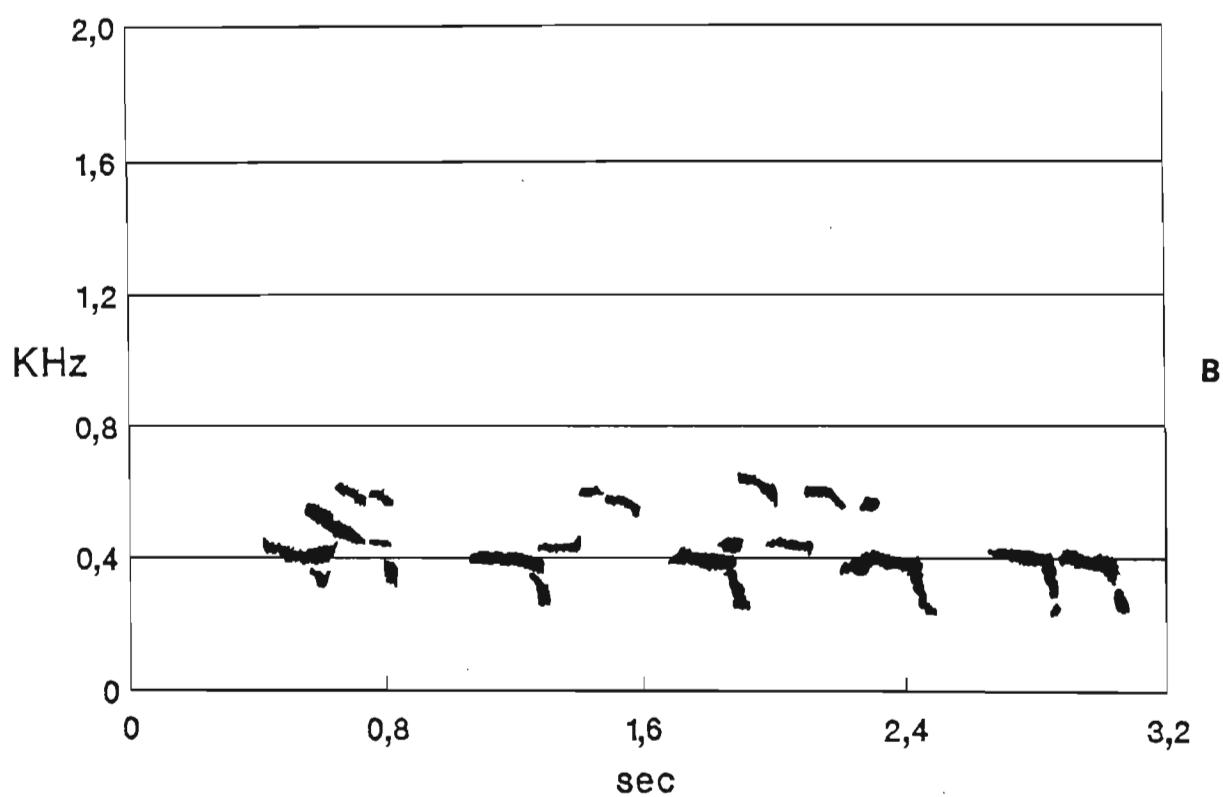
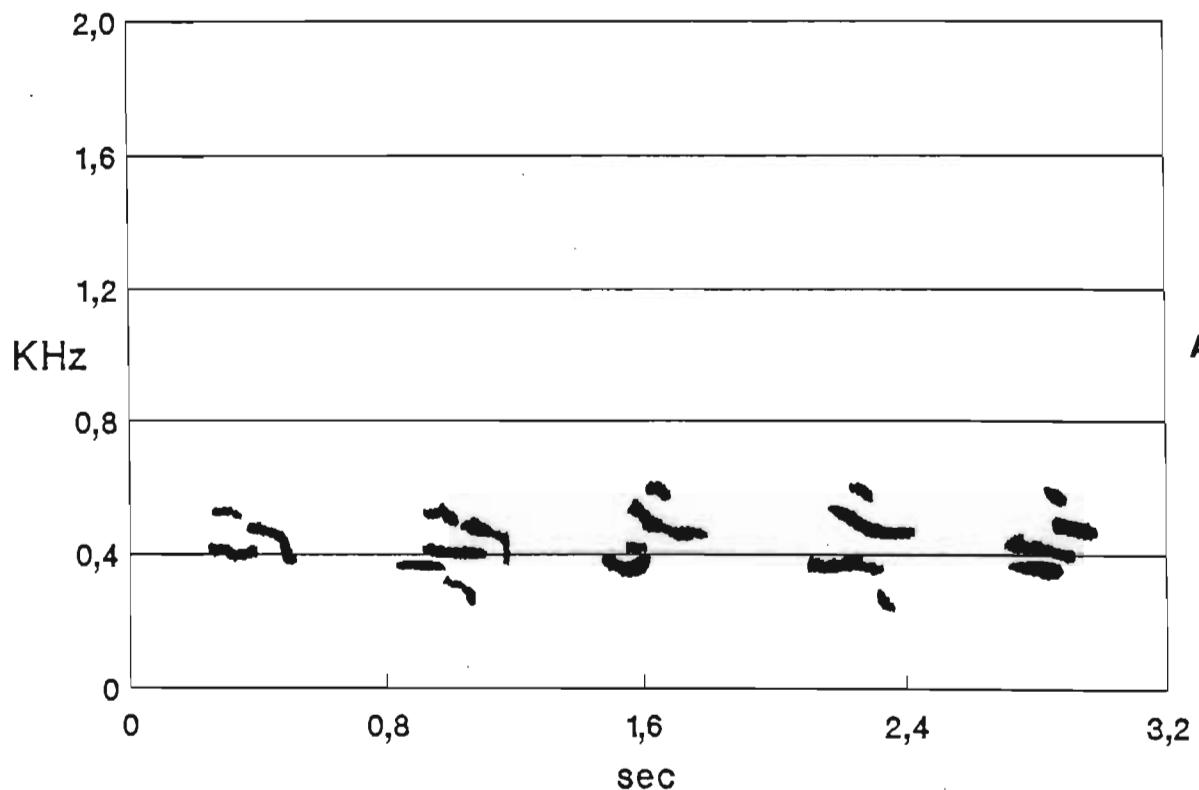
**Fig. 8.6** Duets of the Whitewinged Flufftail recorded at Franklin Vlei, January 1983, by J.M. Mendelsohn. Compare with Figs 8.2 and 8.3.



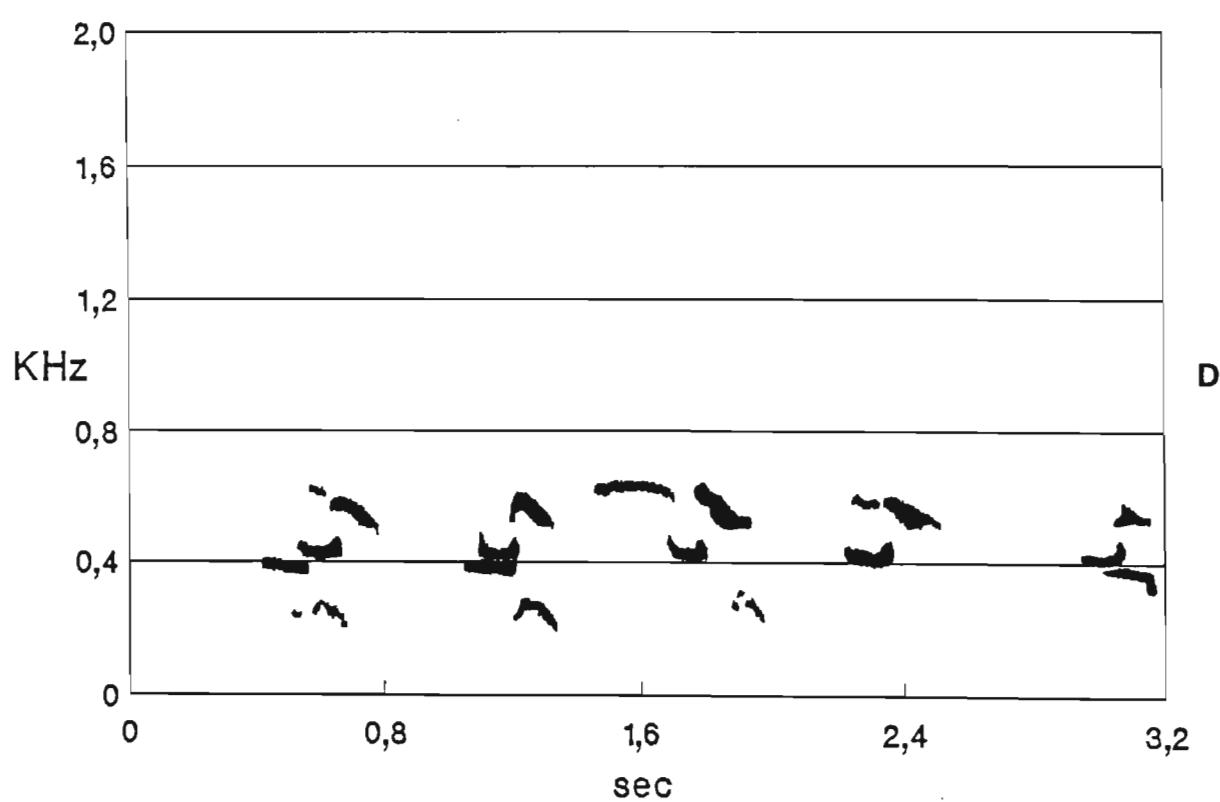
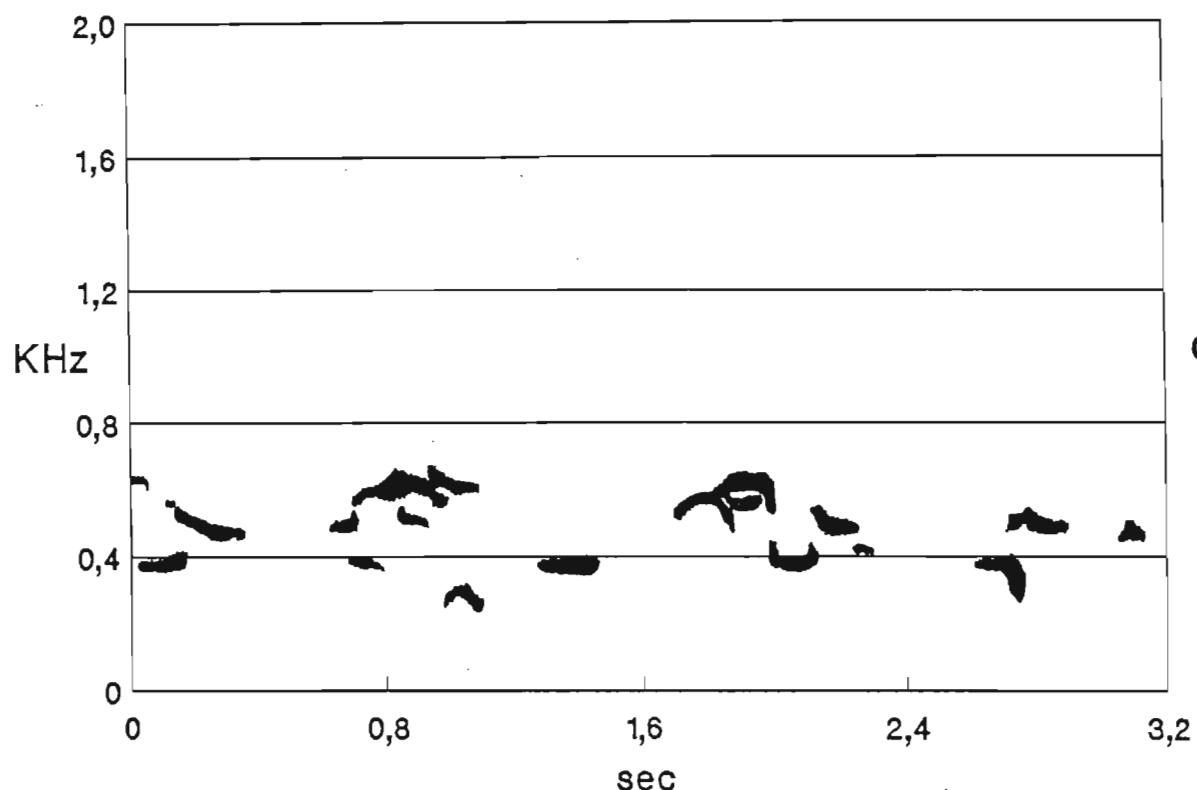
**Fig. 8.7** (A) Synchronized duet of possible Whitewing Flufftails recorded at Kitabe, Rwanda, by F. Dowsett-Lemaire. (B) calls of two or more Crowned Cranes at the Penny Park study site, Natal, showing a similar pattern. (C) Calls of possible Whitewing Flufftail, Kitabe Rwanda. (D) Calls of Crowned Crane at the Franklin



**Fig. 8.7** (continued).



**Fig. 8.8** (A) and (C) Complex calls of possible Whitewing Flufftails, Kitabe, Rwanda (F. Dowsett-Lemaire). (B) and (D) Similar calls of Crowned Cranes, Penny Park, Natal.



**Fig. 8.8** (continued).

than those described above, the calling birds were identified as Redchested Flufftails either when flushed or when responding to taped playback, but the chances of confusion with Whitewinged Flufftails are considerable if one relies only on sightings of flushed birds. On several occasions when I approached a hooting bird I flushed a Whitewinged Flufftail apparently from the exact spot where the hooting had just come, but on playback of Redchested Flufftail calls I very quickly heard typical territorial calls from a Redchested Flufftail in exactly the same spot. Similarly, Redchested-Flufftail-like hoots or other calls sometimes came from a spot where a Whitewinged Flufftail had just landed, but all such calls were readily attributed to the former species, the birds subsequently responding well to taped playback. Occasionally I flushed both species together, within 1-2 m of each other.

#### 8.4.5 General behaviour

The few observations made of Whitewinged Flufftails were almost entirely confined to the birds' flight behaviour and to their responses to taped playback of calls (described in Section 8.4.4). Whitewinged Flufftails were found to differ from other *Sarothrura* species in almost all the behaviour observed during the study.

In flight Whitewinged Flufftails differ in shape and proportions from other flufftail species, and in strong flight the differences in appearance and behaviour are very well marked. In sustained flight the bird's appearance and flight action resemble that of a small migrant crake such as the Little Crake *Porzana parva* (Taylor 1980): the wings are relatively long and pointed, the flight is fast and strong with rapid shallow wingbeats during which the inner wings appear to move through a very small arc, the legs are retracted and the body is horizontal with neck outstretched. Such flights appear even faster and more purposeful than those of the migratory Streakybreasted Flufftail *S. boehmi*, and are markedly different from the normal flight of a sedentary species like Redchested Flufftail, which flies slowly with a weak, clumsy fluttering action, the hind end of the body hanging down, the head up and the legs dangling. In very brief low flights the Whitewinged Flufftail has a similar feeble, clumsy flight action, rising just above the vegetation and dropping down after a very short distance. Long flights are often straight and fast but the bird sometimes rises high and flies less purposefully, with a turn which takes it across the observer's line of vision, as though it were at pains to observe the observer; the rather leisurely medium-distance flights have been aptly described as "bat-like" (P. Clowes pers. comm.).

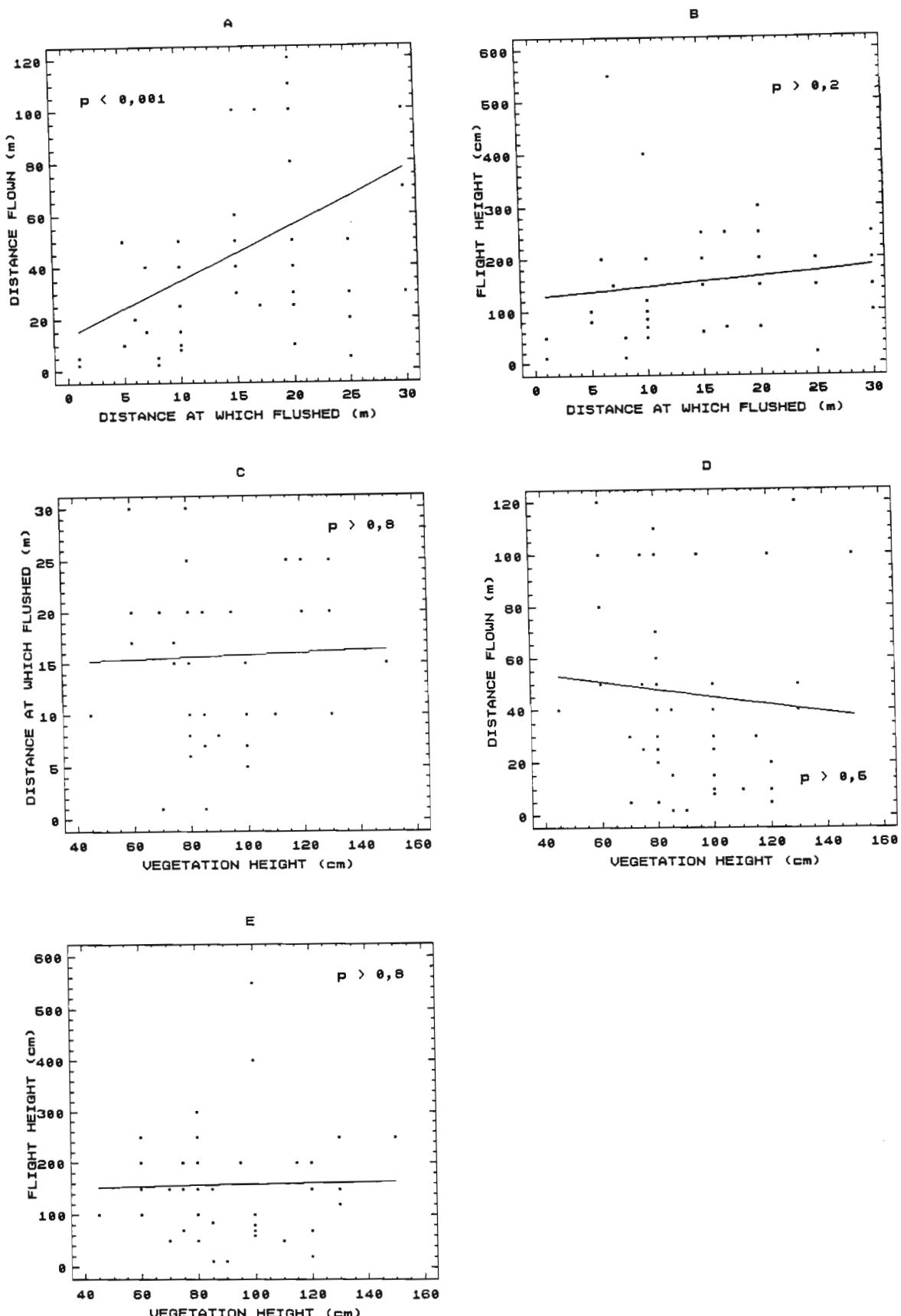
In comparison with other flufftail species, Whitewinged Flufftails normally fly further and higher. In short vegetation they flush much more readily than other flufftails, rising when the observer is still some distance away (other species usually flush only on very close approach), but I

have never succeeded in flushing them from very tall dense vegetation. Compared with other flufftails they are also easier to flush a second time, especially considering that their long flights give them more time to conceal themselves or to move away before the observer can reach the spot where they landed.

Observations of flying birds at four study sites gave some indication of the birds' normal flushing and flight behaviour. Although sexual dimorphism in plumage is relatively slight for a flufftail it was possible to sex 35 flying birds seen in good light and an attempt was made to compare the flight behaviour of males and females. Measured flights ( $n = 49$ ) covered 2-120 m ( $\bar{x} = 46,6$  m), birds rising 1-30 m from the observer ( $\bar{x} = 15,7$  m) and flying at 10-550 cm ( $\bar{x} = 158$  cm) above the vegetation. Simple regression analysis showed that the further from the observer the birds were flushed, the further they tended to fly (Fig. 8.9A;  $P < 0,001$ ), but that there was no relationship between flight height and flushing distance (Fig. 8.9B;  $P > 0,2$ ). The height of the vegetation did not appear to affect the flight behaviour of the birds, and simple regression analysis showed no significant association between the vegetation height and (a) the distance at which the birds were flushed (Fig. 8.9C;  $P > 0,8$ ), (b) the distance flown (Fig. 8.9D;  $P > 0,5$ ) and (c) the height attained (Fig. 8.9E;  $P > 0,8$ ). Comparing the behaviour of males ( $n = 21$ ) and females ( $n = 14$ ) the males tended to fly further, their flight distances ( $\bar{x} = 62,4$  m) being significantly greater ( $t = 2,416$ ;  $P = 0,02$ ; d.f. = 34) than those of females ( $\bar{x} = 31,9$  m), but both sexes tended to flush at similar distances from the observer ( $t = 0,824$ ;  $P > 0,4$ ; d.f. = 34).

When close to an observer the birds regularly climbed in the vegetation to a height presumed sufficient to allow them a good view of the observer. In very tall vegetation they often climbed to a height of about 1,5 m, from which height they called when as little as 1-2 m from the observer. In the dense shorter growth in which they did not call they climbed near the top of the vegetation, which sometimes could be seen moving. In dense short growth they always took flight from a position near the top of the vegetation but at Franklin in November 1992, when cover was very short and sparse (Section 8.4.2.3), they could be seen on the ground, from which they took flight with a jump when approached.

In December 1990 attempts were made to attract the birds into the open at an observation track cut in tall dense vegetation on wet to shallowly flooded ground at Franklin Vlei. The observers sat in a small hide at one end of the track and the birds were attracted by taped playback of Whitewing Flufftail calls at various times of the day. The birds approached close to the edge of the track but never came into the open either in response to playback of the calls of any African flufftail species, or to the visual stimulus of decoy models painted to resemble Redchested, Whitewing and Striped Flufftails.



**Fig. 8.9** Simple regression analyses of the Whitewing Flufftail's flight behaviour, showing a significant relationship only between the distance flown and the distance at which the birds were flushed (A). See Section 8.4.5 for further details.

It was thought likely that the bird's white secondaries would be well visible in flight at night and therefore that some nocturnal activity might occur. On five occasions during the birds' prolonged residence at Franklin in 1990-91 and 1991-92, all-night watches were kept to establish whether the birds were active on either moonlit or moonless nights. There was no evidence of nocturnal activity: no birds were flushed during walks in the vlei, regular sweeps with a spotlight over the vlei from adjacent higher ground produced no sightings of birds in flight, and no calls were heard outside the usual times (see Section 8.4.5), although Redchested Flufftails called at intervals throughout the night. Only once was a bird seen at night, on 6 November 1992, when I flushed one about 2 m away in 90-cm-tall sparse vegetation while playing back Whitewing Flufftail calls at 21:30. In the light of the full moon the bird's white secondaries were clearly visible and the flight was very short (about 5 m) and low. A Baillon's Crake responded with an alarm call to the Whitewing Flufftail tape during this walk, and several African Sedge Warblers *Bradypterus baboecala* were flushed.

When censusing flying birds over a period of several days, complete counts (sometimes using two observers dragging a rope) were usually made only once per day to avoid undue disturbance to the birds and the habitat. At all sites it was found that this level of disturbance did not cause the birds to move to other vegetation types (cf the effects of other observers, described in Section 8.4.2.1), but the birds were hardly ever flushed from exactly the same places on two successive days. They appeared to move constantly around the occupied area, sometimes returning to a particular small patch of vegetation only after 2-3 days, and the entire population seemed to remain in a loose association throughout these daily movements.

#### 8.4.6 Breeding

The nest and eggs of Whitewing Flufftail are still undescribed and the only existing indications of possible breeding in southern Africa are those derived (a) from the doubtfully reliable information in Mendelsohn *et al.* (1983), which suggests breeding in Natal in November, and (b) from the juvenile bird collected by those authors, which has been aged to give a possible egg-laying date of August (Chapter 1, Section 1.2.4.6). During this study I found no positive indication that the birds were breeding at any of the study sites in any season, my observations of the birds' behaviour and calling patterns, and the habitat which they occupied, suggesting that breeding was unlikely to have occurred (see Section 8.5). Furthermore one female flushed at Dullstroom on 12 February 1990 had a gap in the secondaries of the left wing which, if a result of normal remex moult, would indicate that breeding had ended some time previously: my studies of moult in the genus (P.B. Taylor unpubl. ms) indicate that post-breeding renewal of all remiges is the normal pattern.

Only one further possible indication of breeding has come to my notice, this being from Mazowe, north of Harare, Zimbabwe. The information was supplied by D. Parkes (*in litt.*), an oologist with a wide experience of the breeding habits of central African rallids, and concerns an observation made during his childhood in the 1950s. In the latter part of a good rainy season, probably in February, Parkes found two nests in seasonally flooded marshy ground on a farm near Mazowe. These nests were very similar to those of the Redchested Flufftail (with which he was familiar), being shallow grass cups with the surrounding growing vegetation pulled down to form a dome over them. They were located in emergent reedy vegetation about 75 cm tall, some 10-12 cm above water which was about 30 cm deep. Parkes (pers. comm.) describes the site as "a good area for Whitebacked Ducks" *Thalassornis leuconotus*. Each nest contained three fresh eggs, which could not be identified, and the parent birds were not seen. The eggs were collected when the nests were flooded after heavy rain, but unfortunately they were not properly labelled and subsequently became misplaced among other unlabelled and unidentified material. Following my enquiries, one egg was located and is now in my possession. It is typical of the eggs of both clutches, being ovate, white with a slight gloss, and sparsely marked all over with spots of grey-brown and olive-green, which are most numerous in a ring at the blunt end. It measures 27.2 x 20.1 mm.

The eggs of six flufftail species have been described, those of the Longtoed Flufftail *S. lugens* of central Africa and the Slenderbilled Flufftail *S. watersi* of Madagascar still being unknown. All known flufftail eggs are pure white, except those of the Streakybreasted Flufftail which sometimes have a few tiny brown spots at the blunt end (Keith *et al.* 1970; Keith 1986). Flufftails are unique among African rallids in laying pure white eggs, and the unidentified egg is very similar in size, shape and background colour to flufftail eggs. Scanning electron microscope studies of the eggshell structure of flufftails and other African ground-nesting birds, including rallids, members of the Phasianidae and Charadrii and some passerines show that the structure of the unidentified egg closely resembles only that of flufftail eggs, especially those of Redchested and Streakybreasted Flufftails (P.B. Taylor unpubl. ms).

Neither I nor the oologists in Zimbabwe are aware of any marsh-breeding (or ground-breeding) African bird - passerine or non-passerine - which lays eggs similar in colour and pattern to the unidentified egg. In view of this, and of the eggshell structure and the flufftail-like type and situation of the nest, it is thought possible that the two nests may have been of Whitewing Flufftail. As this species is an atypical flufftail in many respects (such as its lack of strongly sexually dimorphic plumage, its white secondaries, and its behaviour, flight and calls), it is possible that it may also depart from the typical flufftail pattern in egg markings. The habitat is not unlike that described for breeding areas in Ethiopia (Chapter 1; Section 1.2.4.3). Such a breeding record, at the edge of the

bird's known range in southern Africa, in a year of good rainfall and in seasonally wet habitat, would not be impossible for this undoubtedly strongly nomadic or migratory species (see Section 8.5 for a further discussion on this topic).

## **8.5 Discussion**

### **8.5.1 Distribution and status**

This study's surveys of potentially suitable habitat in Natal and the Transvaal could not be conducted sufficiently frequently, or over a long enough period of good-rainfall years, to establish the precise current distribution and status of the Whitewinged Flufftail. However, my results do confirm the bird's rarity and the very localized nature of its distribution, at least in Natal, and there is no evidence that its status is any different elsewhere in South Africa. Although it may not yet be on the verge of extinction in South Africa, its total population must be very small and it is undoubtedly very sensitive to habitat loss and disturbance. In view of the continued loss and degradation of wetland habitats (see e.g. Begg 1986, 1990; Breen & Begg 1987, 1989; Brooke 1984; Chapter 1, Section 1.2.4.2) its population is presumably decreasing. There is certainly no evidence for a population increase in recent years: although the last decade has produced more records than ever before (Table 8.2), after subtracting this study's observations the remainder appear to reflect only the recent increased interest in birdwatching (especially in seeing rarities), and the increased observer activity through atlasing work. The bird's range may now be largely restricted to high-altitude areas in Natal and the Transvaal, there being no acceptable evidence for its recent occurrence either in low-altitude areas of Natal or in the Orange Free State and Cape Province; however there are two recent questionable records from Cape Province, where perhaps it still occurs occasionally.

The records obtained during this study from sites in Natal and the Transvaal suggest that the birds occur regularly in these regions, probably returning to the same sites every year if conditions are suitable. Assumed absences from such sites, such as those recorded by Mendelsohn *et al.* (1983) at Franklin Vlei in the decade before the birds' discovery in 1982, do not take into account the extreme difficulty of locating birds in tall dense flooded vegetation.

### **8.5.2 Habitat preferences**

Analysis of the vegetation, substrate and flooding characteristics of the wetlands in which the birds were found during this study suggests that occupied habitat may be separated into two types,

principally on the basis of the height, density and growth pattern of the vegetation, and the degree of flooding.

**Habitat Type 1** (see Table 8.4). This is characterized by vegetation of medium height (range of means for all sites = 50-178 cm; overall  $\bar{x} = 96$  cm), cover of 55-100% ( $\bar{x} = 92\%$ ), and a substrate which is usually moist but is sometimes dry and rarely may be flooded up to a depth of 5 cm. The vegetation tends to grow quite evenly, the fairly regular spacing between the plant bases allowing crakes relatively free movement on the ground. However a more clumped or tussocky growth is sometimes seen, such as in mixed hygrophilous grasses and sedges, and *Carex* or *Leersia* beds interspersed with clumps of sedges and rushes. The dominant vegetation is most frequently *Carex acutiformis*, which often grows in extensive patches with no other plants but is also frequently interspersed with single stems of *Typha capensis* or *Phragmites australis*, or with clumps of sedges, rushes or grasses; under wetter conditions, some forms of Habitat Type 1 may develop into Habitat Type 2 (e.g. at Franklin). Taking into account the occasional occurrence of patches of sedge meadow and hygrophilous grassland, the plant species composition is sometimes richer than that of Habitat Type 2, although the latter tends not to have extensive areas of monospecific growth (Table 8.5). When moist to flooded, Habitat Type 1 is characteristically inhabited by Redchested Flufftails at a moderate to high density and these birds nest in the wettest areas of mixed, often tussocky, vegetation, extending into areas where flooding is deeper and Whitewing Flufftails do not occur. It is characteristically inhabited by Whitewing Flufftails for relatively short periods (up to about six weeks at Dullstroom); the birds are usually easy to flush and do not call.

**Habitat Type 2** (see Table 8.5). This is characterized by tall dense vegetation (range of mean heights for all sites = 110-190 cm; overall mean = 156 cm), with continuous 100% cover. The muddy substrate is sometimes only moist but is usually flooded up to a depth of 45 cm in patches. The vegetation structure at ground level is similar to that of Habitat Type 1 but as there is relatively little exposed mud the birds must frequently wade, swim or clamber around in the dense vegetation. The dominant vegetation is usually *Carex acutiformis* or *Typha capensis*, which is interspersed with stems of *Phragmites australis* or with clumps of tall sedges (*Cyperus*, *Mariscus* and *Schoenoplectus*). Rarely, tall *Leersia hexandra* is dominant. Habitat Type 2 occurs with Habitat Type 1 (e.g. at Wakkerstroom in February 1992) and often represents a more vigorous growth (under wetter conditions) of the more uniform Habitat 1 vegetation types, e.g. those dominated by *Carex* and *Typha*. Conversely, under unusually dry conditions it may revert to Habitat Type 1, as at Franklin in late 1992. Extensive areas of monospecific growth do not normally occur, the flooded conditions encouraging greater growth of intermixing sedge or reed species (Table 8.5). This habitat type is at best very sparsely inhabited by Redchested Flufftails and probably does not contain suitable nesting

sites for that species (Section 8.5.4). Where extensive, it is inhabited by Whitewing Flufftails for long periods (up to 4½ months at Franklin); the birds call regularly with the *OOP* duet (Section 8.4.4) and are virtually impossible to flush.

The deeply flooded *Leersia*-dominated marsh from which one sight record was obtained at Penny Park (Table 8.4) is atypical habitat which cannot be included in either habitat type and frequent visits over two seasons failed to provide any further sightings from this vegetation.

It is worth noting that all sites at which the birds were found during the study had been burned in the spring (September-October) immediately before their occupation. It is not known whether the birds would occur in similar concentrations and with similar regularity in unburned areas, but spring-burned vegetation may be preferred for at least two reasons. First, spring burning removes dead vegetation which might otherwise hamper the birds' movements at ground level in Habitat Type 1. It may have a similarly beneficial effect in Habitat Type 2, removing moribund vegetation at all levels occupied by the birds. Second, as new growth is greater in spring-burned than in unburned wetland vegetation (see Chapter 6), the flush of new growth should provide more invertebrate food, while foraging will be easier than in thicker unburned vegetation. Such considerations may be important, especially if some of the vegetation types (such as areas of monospecific growth) are less rich in potential food than other, more mixed-species vegetation (food availability was not measured).

From published details (Chapter 1, Section 1.2.4.3) it appears that, with only one exception, the habitats from which the species has previously been recorded in South Africa fall within my definition of Habitat Type 1, their main characteristics being low to moderate vegetation height, a moist to wet substrate and a wetland-vegetation species composition comparable to that in my definition. Furthermore, all records also refer to flushed birds and only one mentions calling birds. The exception in terms of both habitat type and calling behaviour is Franklin Vlei in 1982-1983, when some birds were apparently present in tall dense vegetation, probably of Habitat Type 2, and when duet calls were heard (Mendelsohn *et al.* 1983) typical of birds in Habitat Type 2. The predominantly dry 1982-1983 summer probably gave rise to vegetation transitional between Habitat Types 1 and 2, as was noted at Wakkerstroom in February 1992. The records from Zimbabwe are from habitats similar to Type 1 in vegetation characteristics and some are from typically moist substrates, but one is from more deeply flooded ground while the habitat in Zambia had vegetation typical of Type 1 and was shallowly flooded (R.K. Brooke pers. comm.). All these records also involve flying birds. Thus central African records include occurrences in more deeply flooded vegetation than is typical of Habitat Type 1 in South Africa.

The habitat described from the Ethiopian breeding areas (Chapter 1, Section 1.2.4.3), where the birds were difficult to flush, is shallowly flooded, with fairly short and possibly tussocky

vegetation of hygrophilous grasses, rushes and reeds. Flooding in some areas occurs only during the breeding season. In its combination of vegetation type and degree of flooding, it does not resemble any habitat in which the birds have been found in South Africa, seasonally flooded hygrophilous grassland, sedge meadow and sedge/rush beds being optimum breeding habitat for Redchested Flufftails at the study sites (Chapter 4). However it may bear a greater similarity to the wetter vegetation types in which the birds were found in Zambia and Zimbabwe, although it is apparently not very similar to the possible breeding habitat described at Mazowe, Zimbabwe (Section 8.4.6).

The comparisons of occupied and unoccupied South African wetlands of similar plant species composition (Section 8.4.2.5) suggest that factors contributing to the unsuitability of unoccupied areas include excessive dryness, shortness or sparseness of cover, permanent flooding with stagnant water, very deep flooding (especially with flowing water) and substrates with hummock-depression morphology (see Section 8.4.2.5). Extensive beds of tall *Phragmites* or *Typha* in deep, often flowing, water are not inhabited by any rallids which are essentially terrestrial as opposed to aquatic (such as Moorhen *Gallinula chloropus* or Redknobbed Coot *Fulica cristata*), while excessive dryness of sedge beds and a lack of cover were factors which apparently affected the timing of occupation and departure at some sites (Sections 8.4.3 and 8.5.3).

The effects of very anaerobic substrate conditions and stagnant water may be judged with reference to the different types of *Carex* vegetation found during the study. It is clear that Whitewing Flufftails occur frequently in wetland vegetation dominated by densely growing *Carex* sedge species, usually *C. acutiformis*, in the high-altitude wetlands of Natal and the Transvaal. However it is also clear that some areas of pure *Carex* are not suitable for occupation because of the short or sparse nature of the cover provided, and it is instructive to investigate the factors influencing the existence of the two very different types of *Carex* habitat in these areas. The genus *Carex* is widely distributed throughout the temperate and cold regions of the northern hemisphere and, in Africa, its species are most common at high altitudes, where they may dominate in wet habitats (Haines & Lye 1983). They occur in many of the high-altitude wetlands surveyed during this study and are dominant in some, thus being an important factor in any assessment of habitat quality for wetland rallid species. Kotze (1992a) notes that, at Mgeni Vlei, *C. acutiformis* marsh occupies central areas which are permanently to semi-permanently saturated or flooded, generally lack hummocks and open water patches and are stagnant, lacking direct streamflow input. It is hypothesised that the lack of oxygenated water and/or dissolved nutrients associated with a direct streamflow input may account for the very low plant and animal species richness of this vegetation type and may result in a much smaller invertebrate population than in richer vegetation types (Kotze 1992a and pers. comm.). Large areas of similarly sterile *C. acutiformis* marsh have been found in other wetlands and it appears that

*C. acutiformis* is better adapted than any other wetland sedge, rush or reed to the conditions which occur in the flooded interior regions of such vleis (D. Kotze pers. comm.). It has already been noted (Section 8.4.2.5) that such sparsely growing and sterile habitat may not be suitable for occupation by any rallid species.

The much richer, denser growths of *C. acutiformis* which were occupied by Whitewing Flufftails at Dullstroom, Wakkerstroom and Franklin, and which occurred in smaller patches in many parts of the survey area, occurred in two situations. Some growths were in close proximity to streamflow, either within a marsh or along inflowing streams, and thus received oxygenated and nutrient-rich water which allowed them to develop into tall, dense vegetation. The others, within marshes, were less permanently waterlogged than were areas of sparser growth, and in some cases the water table had been artificially lowered by drainage channels in the recent past, so that the substrate is now much less wet than it was when the *Carex* originally established itself. Under such less waterlogged conditions this sedge can probably persist and remain dominant for many years, even though partially invaded by other wetland plants (D. Kotze pers. comm.).

In such situations its growth pattern makes it very suitable for occupation by flufftails in that it provides tall, dense cover but is quite open at ground level, growing on flat ground with space for the birds to move and forage between the bases of the plants (see Chapter 6, Section 6.4.1.3 for relevant measurements of cover). Assuming that it provided sufficient invertebrate food, one would therefore expect it to be inhabited by flufftail species, at least during its growing season, and this was the case at all sites at which it was found. However, *Carex*-dominated vegetation normally may not be preferentially inhabited by Whitewing Flufftails, this study's results indicating a statistically highly significant association with it only when other vegetation types were disturbed at Dullstroom in February 1990 and when drought conditions prevailed at Franklin in late 1992 (Section 8.4.2).

The most important conclusions which may be drawn from this study's observation of habitat types are that: (a) in South Africa Whitewing Flufftails have not been found to occupy habitat equivalent to that in which they breed in Ethiopia, similar habitat in South Africa being occupied by breeding Redchested Flufftails, (b) their occupation of the relatively dry Habitat Type 1 vegetation overlaps that of breeding Redchested Flufftails which, however, are more numerous in wetter vegetation of similar plant species composition, and (c) the only habitat (Type 2) which was found to be occupied for long periods was one in which Redchested Flufftails were scarce and apparently did not breed. Therefore it is possible that, in South African wetlands, Whitewing Flufftails may be excluded from optimum habitat (breeding or nonbreeding) by the presence of breeding Redchested Flufftails. Further discussion on this topic appears in Section 8.5.4.

### 8.5.3 Pattern of occurrence and migratory status

During the study period Whitewinged Flufftails were recorded at the study sites and elsewhere only in November-March (Table 8.2), the period when most rain falls (see Section 8.4.3). Observations at the study sites indicated that arrival time depended on the presence of sufficiently tall dense vegetation, which develops later in dry years and after spring burns. In all cases departure took place either when premature drying out of the habitat occurred or when vegetation dieback commenced and temperatures dropped in late March-April (see Chapter 2, Figs 2.5, 2.27 and 2.29 for temperature details). Although in some cases drying out of habitat also occurred at this time, at Dullstroom the substrate remained moist throughout the winter. Vegetation cover usually did not decrease significantly during the winter in the habitats occupied by Whitewinged Flufftails in summer, and Redchested Flufftails remained in Habitat Type 1 throughout the winter.

Whitewinged Flufftails are therefore undoubtedly of seasonal occurrence in the areas studied, being absent during the colder, drier months. In the case of Buffspotted Flufftails (Chapter 9) and Striped Flufftails (Chapter 7) in the high-altitude regions of Natal, an autumn-winter reduction in food supply is thought to force emigration, while birds at lower altitudes are resident throughout the year. However there is no evidence that Whitewinged Flufftails remain anywhere in South Africa in the winter. Habitat Type 1 supports Redchested Flufftails throughout the winter, while Habitat Type 2 does not, and my observations in the survey and study areas indicate that in winter all suitable habitat is occupied by permanent Redchested Flufftail territories. Thus in winter both food and habitat availability may be limiting in Habitat Type 1, because of the presence of a permanently resident congener, while Habitat Type 2 may lack sufficient food to support any flufftail species.

The South African records earlier than this study (Tables 8.1, 8.2) include rainy-season occurrences (late October-January) at Dullstroom and Franklin but are predominantly of single birds, widely scattered throughout the eastern half of the country, all in the period August-November except for one in May. Published details suggest that the records from Suikerbosrand in August and Rustenburg in May may well refer to migrating birds (Wolff & Milstein 1976; Chapter 1, Section 1.2.4.7), but there is no relevant information available for the others and it is possible that the period of occurrence may include August-September in some regions; this must be the case if the Franklin juvenile (Chapter 1, Section 1.2.4.6), estimated to be from an egg laid in August, was from a nest in South Africa.

The relatively short overlap period of Ethiopian and South African occurrences in May and August-September (Table 8.3) might seem insufficient to rule out entirely the possibility of long-distance migrations between the two centres of distribution. However, it must be borne in mind that

from Ethiopia there are instances of egg-laying in August and flightless young in September (Chapter 1, Section 1.2.4.6), so that significant migration is unlikely to occur in these months. In South Africa the bird's occurrence pattern suggests that it has regular long-distance movements, but the extent of these is not clear. Its flight action and behaviour (Section 8.4.5) are indicative of a species which is well capable of long-distance migration and it compares favourably in these behavioural respects with Streakybreasted Flufftail, the only *Sarothrura* species known to be a regular long-distance migrant (Keith 1986).

The lack of irrefutable evidence for its breeding in southern Africa makes it impossible to dismiss the hypothesis that it is purely a non-breeding visitor to the region, although such a possibility is not considered likely (Section 8.5.4).

#### **8.5.4            Behaviour: calling, territoriality and breeding**

As there is no information available on the calling and territorial behaviour of breeding birds in Ethiopia it is not easy to relate the calling patterns and general behaviour observed in South Africa to any particular stages in the annual cycle of this enigmatic species. It is not even known whether it calls on the breeding grounds, but it is fairly safe to assume that it does, and that some calls would be similar to the territorial calls recorded in South Africa (Section 8.4.4). On the basis of my knowledge of the calling, territorial and breeding behaviour of other flufftail species, some tentative hypotheses may be constructed to explain the behaviour observed during this study and to suggest possible breeding times.

As breeding birds in Ethiopia were very difficult to flush and flew only weakly (Chapter 1, Section 1.2.4.4), although the birds seem to be relatively easy to flush and may have a strong prolonged flight in situations where they are probably not breeding (e.g. Collar & Stuart 1985; Hopkinson & Masterson 1977), a tentative working hypothesis may be established that in South Africa ease of flushing and strong flight (seen in Habitat Type 1) indicate non-breeding birds while difficulty in flushing (as noted in Habitat Type 2) possibly indicates attempted breeding. The lack of calling (or response to taped playback) in Habitat Type 1 also suggests that the birds are neither breeding nor territorial in that habitat type, while the sometimes regular calling and response to taped playback in Habitat Type 2 are indicative at least of territoriality, if not breeding.

However, before suggesting that birds may breed in Habitat Type 2, other factors must be taken into account. The birds may be unwilling to fly for reasons other than secretiveness during breeding, especially in tall dense vegetation from which flight would be difficult and where other methods of escape might be easier, either because of relatively open conditions at ground (or water-

surface) level or because of the hampering effect of the vegetation on the vision and movements of the larger terrestrial predators. Thus the impossibility of flushing birds from very tall dense vegetation does not necessarily indicate breeding. It is also unlikely that any flufftail would breed in Habitat Type 2. Both Redchested and Streakybreasted Flufftails nest in grass and sedge of short to medium height, sometimes in shallowly flooded situations, the Redchested Flufftail usually in taller, more tussocky vegetation than the Streakybreasted Flufftail (G. Hopkinson, A.N.B. Masterson, D. Parkes & C.C. Wintle *in litt.*). The Ethiopian breeding habitat of the Whitewinged Flufftail appears similar to that of Redchested Flufftail in terms of its vegetation structure and degree of flooding, but it may be more dominated by seasonally flooded grass. Thus no breeding habitat described for any of these species is similar to Habitat Type 2, or indeed to the taller, denser, more species-uniform vegetation which often constitutes Habitat Type 1.

From these comparisons it therefore seems unlikely that the Whitewinged Flufftails observed during this study bred either in Habitat Type 2 or, in view of their behaviour, in Habitat Type 1. Redchested Flufftails, however, held breeding territories in at least the wetter parts of Habitat Type 1 and nested wherever suitable sites existed in shallowly flooded mixed wetland vegetation of short to medium height (with or without tussocks) elsewhere in the open vlei or at the edge of taller reedbeds.

Therefore some explanation other than breeding needs to be found to account for the Whitewinged Flufftail's territorial behaviour in Habitat Type 2. An explanation is also needed for its apparent failure to breed in the wetter parts of Habitat Type 1 and either to breed or to occur in any other flooded areas of suitable vegetation. The only explanations which accommodate all the observed behavioural and other data gathered during this study appear to hinge upon the relationship between the Whitewinged Flufftail and its congener, the Redchested Flufftail, in South Africa, as has been partly considered in the preceding two Sections.

On the basis of the highly territorial nature of the Redchested Flufftail's behaviour (Chapter 4) it seems unlikely that Whitewinged Flufftails would be able to breed alongside them if there were any competition for resources, especially food or nesting sites. As this study has shown, some breeding Redchested Flufftails occur alongside Whitewinged Flufftails in Habitat Type 1, and therefore the two species are presumably not competing for critical resources. Food is abundant in wetlands during the summer, and may not be a critical resource in this sense: under natural conditions in captivity, breeding Redchested Flufftails tolerate the presence of breeding Streakybreasted Flufftails, which eat similar food but choose different nesting sites (C.C. Wintle pers. comm.). If the nesting sites of Whitewinged Flufftails are similar to those of Redchested Flufftails, it is possibly competition for such sites that prevents the former from breeding where the latter is established. In

Ethiopia the Redchested Flufftail is rare and has been recorded from only one locality alongside breeding Whitewinged Flufftails, where there was no indication of its breeding (Ash 1978; Keith 1986; information on British Museum specimen No. 1947.70.5 of *S. rufa elizabethae*, collected at Gafersa on 30 July 1947), so a similar situation may not occur there. Alternatively, the Whitewinged Flufftails may not be in breeding condition during this period, having bred earlier elsewhere, as is suggested by the possible age of the Franklin juvenile and the observation of remex moult in the Dullstroom adult.

Nonbreeding Whitewinged Flufftails occurring alongside breeding Redchested Flufftails probably would not show any territorial activity, as is suggested by their lack of calling, their flight behaviour, their peripatetic activity around the occupied areas, and their relatively brief periods of occurrence. On the other hand, they show markedly different behaviour in Habitat Type 2, in which Redchested Flufftails occur much less extensively and apparently do not nest. In such a situation, existing evidence suggests that Whitewinged Flufftails possibly set up nonbreeding territories for long periods during the summer months. This study has shown that at least Redchested (and possibly also Buffspotted) Flufftails set up nonbreeding territories in areas to which they move during the nonbreeding season.

The foregoing evidence all suggests that Whitewinged Flufftails do not breed in any habitats occupied by breeding Redchested Flufftails in South Africa and, given the apparent similarity in the breeding-habitat requirements of both species (leaving aside the conflicting evidence of the possible Zimbabwe breeding record), it is difficult to see how Whitewinged Flufftails could breed in this country. However, existing evidence suggests that they may breed earlier than Redchested Flufftails, possibly in August-September (but where they would find suitable breeding habitat is not clear), and/or that they may breed opportunistically, possibly in ephemeral or only occasionally seasonally wet habitats not occupied by their congener, or in areas of shorter, more grassy habitat. In this respect they would thus resemble the other strongly migratory species, the Streakybreasted Flufftail, which tends to occupy seasonally flooded short vegetation where it is not in competition with Redchested Flufftails. It is perhaps significant that competitive exclusion by the latter species has been proposed as the reason for the Whitewinged Flufftail's absence from central Africa (Chapter 1, Section 1.2.4.2).

The possible Zimbabwe breeding record of the Whitewinged Flufftail (Section 8.4.6) is from ephemeral habitat, in a seasonal marsh not occupied by Redchested Flufftails or by Streakybreasted Flufftails (in the case of the latter, presumably because of the depth of flooding), and suggests an opportunistic breeding strategy in habitat not occupied by any other flufftail species. The habitats in which Whitewinged Flufftails have been found in Zambia and Zimbabwe include wetter vegetation

(thus potentially more suitable for breeding) than in South Africa, although in all cases the birds have been easy to flush.

In conclusion, on the basis of the information collected during this study it is not possible to make any definite assessment of the Whitewing Flufftail's status as a breeding bird in South Africa, and it may be simply a nonbreeding visitor from extralimital breeding areas. However I would consider it more likely that it does breed, if only irregularly, possibly in ephemeral flooded grassy and marshy habitats where Redchested Flufftails do not nest, or before the main breeding period (November-March) of the latter species.

#### **8.6 Conclusions and recommendations for further study**

Several conclusions relevant to the conservation of the Whitewing Flufftail have emerged from this study. As it is not possible to define breeding sites for possible protection, the best that can be done until such sites are identified is to attempt to safeguard those wetlands where the species is known to occur, even if its breeding is unlikely in such wetlands. Thus it is very important to protect the few high-altitude wetlands of Natal and the Transvaal where the species has been found in recent years (i.e. the four study sites at Dullstroom, Wakkerstroom, Franklin and Penny Park). As has been shown (see the study-site accounts in Section 8.4), the bird's habitats are threatened by damage not only from excessive burning, overgrazing, and mowing for fodder, but also from the activities of birdwatchers who (especially in a small area like Dullstroom) can cause considerable disturbance and vegetation damage by attempting to flush this and other flufftail species.

As flufftails, especially this species, are very difficult to find and may often be overlooked during a superficial assessment of the avifauna of any wetland, it is also strongly advisable that any significantly large wetland which is under consideration for modification or destruction should be surveyed for the possible occurrence of Whitewing Flufftails before a final decision is made on its future. Such a survey should involve both an assessment of the extent of potentially suitable habitat and a series of visits during spring and summer (at least in October-January) to check for the bird's occurrence.

On the basis of what is known about the Whitewing Flufftail's habitat preferences it is imperative that further and more intensive searches be carried out to clarify its distribution and status in South Africa, and to search for possible breeding sites. With the knowledge now gained, such a task should not be as daunting as it was five years ago when this study commenced.

The situation in Ethiopia is almost certainly much more critical than that in South Africa, but cannot be assessed properly until an investigation has been made to establish the approximate

population of the species and the amount of habitat remaining, both in its breeding and in its non-breeding areas. A period of intensive fieldwork in Ethiopia is urgently required to establish the current distribution and status of this species, which is one of the rarest of African birds.

In view of the difficulties experienced in studying Whitewinged Flufftails in the field, the best and quickest way to establish the basic facts about the bird's biology, including its breeding seasons and breeding habitat requirements, would be to breed the birds in captivity. Great success has been achieved by C.C. Wintle in the captive breeding of wetland flufftails and other rallids (Wintle 1988; Wintle & Taylor 1993; Chapter 4). A suitable aviary has been built in Zimbabwe by C.C. Wintle for this purpose and it is hoped to establish a captive breeding programme for Whitewinged Flufftails if the necessary funding becomes available.

## CHAPTER 9

### SOME ASPECTS OF THE BIOLOGY AND ECOLOGY OF THE BUFFSPOTTED FLUFFTAIL

#### **9.1 Introduction**

Unlike the other flufftail species studied, the Buffspotted Flufftail does not normally frequent dense ground vegetation in grassland or wetland, but is essentially an inhabitant of forest and thick bush, where it appears to be equally at home in dense ground cover and on open ground with leaf litter beneath dense low woody vegetation (Chapter 1, Section 1.2.1.2). The only other flufftail species to occupy similar habitat is the Whitespotted Flufftail *S.pulchra*, but that species is typically associated with water (forest streams, swamps and pools) whereas the Buffspotted Flufftail typically occurs away from water (Keith 1986). In view of these habitat preferences, I considered that a detailed knowledge of the biology and ecology of the Buffspotted Flufftail would make an interesting and informative comparison with those of the grassland and wetland species studied during this project. Furthermore, my field experience showed that forest flufftails are less difficult to study than those in other habitats (Taylor & Taylor 1986) and, in the time available for this project, work on the Buffspotted Flufftail was likely to yield more information relevant to an understanding of the general biology and behaviour of the genus (especially with regard to breeding) than would studies on any other flufftail species of southern Africa. Although more is known about the behaviour and breeding of the Buffspotted Flufftail than about any other *Sarothrura* species, our knowledge is still very limited (Chapter 1, Section 1.2.1) and there is great scope for further detailed study.

The Buffspotted Flufftail (Frontispiece (A); Plate 2B) is widely distributed and is relatively common over much of its range, although it is rarely seen and is undoubtedly under-recorded (Chapter 1, Section 1.2.1.1). As with the Redchested Flufftail (Chapter 4), current knowledge raises interesting questions about the bird's biology and ecology, which are relevant to studies of other species. For example, although the bird is considered to be resident throughout its range there are several records (from outside South Africa) strongly indicative of long-distance movement (Chapter 1, Section 1.2.1.6), a phenomenon which one would not expect in a bird whose habitat is apparently not seasonal (Keith 1986). Unlike the Redchested Flufftail (Chapter 4) and the Whitespotted Flufftail (Taylor & Taylor 1986), the Buffspotted Flufftail calls only during the breeding season throughout most of its range, and its occurrence and behaviour during the nonbreeding season are almost unknown. Observations from South Africa and elsewhere (Chapter 1, Section 1.2.1.2) indicate that

the species is unique among flufftails in being a successful colonist of alien vegetation in gardens and cultivation close to human habitation, and the reasons for this success are not clear. Its apparent tolerance of human activities, and its ability to nest successfully in gardens, should allow studies of breeding and social behaviour which are not feasible in other species.

Studies of the seasonality of the bird's occurrence in relation to habitat quality and the availability of food are described in Chapter 10. Chapter 9 deals with aspects of the biology and ecology of the species which are essential to an understanding of the relationships between the bird and its forest or bush environment, and to an appreciation of how its life history differs from those of the other species as a result of the different constraints imposed by its unique habitat. The following topics were selected for study:

- (a) distribution, status and movements;
- (b) habitat requirements;
- (c) general behaviour and activity patterns;
- (d) the permanence of the pair bond;
- (e) territorial behaviour and the permanence of territories;
- (f) food, feeding ecology and energy requirements;
- (g) vocalizations and calling patterns, including seasonal variations, the influence of weather conditions on calling, the development of calling in young birds and the mechanisms of voice production;
- (h) breeding season, breeding biology and breeding behaviour;
- (i) relationships within the family group and the status of independent immatures;
- (j) postbreeding dispersal of adults and immatures;
- (k) breeding success, predation and mortality.

## **9.2 Study sites and survey areas**

The long-term study sites in Natal at Karkloof Forest near Howick, Ferncliffe Forest and Bisley Valley at Pietermaritzburg, Danville Park in Durban and Scotston Farm at Underberg are described in detail in Chapter 2. These sites include examples of the major habitat types and climatic conditions encountered by the species in Natal, including high-rainfall coastal forest with a mild climate (Danville), high-rainfall mid-altitude mistbelt forest (Karkloof and Ferncliffe) and relatively low-rainfall deciduous bush (Bisley Valley), all with cool winter conditions, and high-altitude artificial habitat in gardens (Underberg) with very cold winters. In addition, short-term breeding-season studies were made of birds in several gardens at Pietermaritzburg (including my own) and nearby Hilton.

No time was available for extensive surveys to establish in detail the distribution and status of the species in the southern Natal survey area. Relevant information was gathered locally during work at the long-term study sites, while information from other parts of Natal was provided by other observers (see Sections 9.3.1 and 9.3.5).

### **9.3 Methods**

#### **9.3.1 Surveys and territorial mapping**

At the long-term study sites I endeavoured to make the study known to local residents and to obtain details from them about calling birds, such information contributing to the overall picture of local distribution, status and habitat preferences. Information on the distribution of the species in Natal was obtained largely from observers who participated in the investigation of calling patterns (Section 9.3.5), people who provided specimens of birds found dead (Section 9.3.2), and Natal Parks Board field staff. I attempted to visit all sites where the birds were heard or seen in the southern Natal survey area (Chapter 2, Section 2.1) and I also visited most sites where dead birds were found, to obtain first-hand information on the availability of suitable habitat and the status of the species in the areas concerned. All distributional information was plotted by month on summary maps of Natal, as described in Chapter 4, Section 4.3.1.

Shortage of time prevented any attempts to map territories, either by taped playback experiments or by other means, the only information obtained being from the breeding birds in the garden at Scotston Farm, Underberg.

#### **9.3.2 Periods of occurrence and movements**

Information on these topics was obtained from two sources:

- (a) observations of colour-ringed birds at Danville, Bisley Valley, Ferncliffe and Underberg;
- (b) visual and vocal records from (i) the long-term study sites, (ii) other observers, principally those obtained during the survey of calling patterns and occurrence (Section 9.3.5) but also isolated sightings of birds in unusual habitat, and (iii) casualties obtained in southern Natal.

Casualties comprised birds found dead near buildings or in gardens, where they had been either caught by cats or inadvertently killed in some other way. From these birds biometric data were obtained, age was estimated from plumage characters, fat deposits and gizzard contents were examined, and breeding condition was assessed by examination of the gonads.

### 9.3.3 Behaviour and breeding

Territorial behaviour was monitored at many sites by observation of wild birds under natural conditions, and also by using taped playback (see Chapter 3, Sections 3.1 and 3.4) and by observing the reactions of individuals to models and mirrors (see Chapter 4, Section 4.3.2 for further details). The Buffspotted Flufftail models used (adult males and females and an 11-day-old chick) were made from skins of casualties received during the study. All models had realistic glass eyes. Models of juveniles and immatures were not necessary, direct observations of birds at Underberg providing ample information regarding behaviour related to birds in these age groups. Life-sized wooden models of Redchested Flufftails, with glass eyes, were also used in some experiments.

Two permanent hides were built at Scotston, Underberg for continuous observation of the two resident pairs throughout the breeding season, but most observations at other sites were made with the observer concealed by natural vegetation or a temporary screen, or with the observer not concealed in any way. Males were rarely disturbed by a visible observer and would perform many activities in full view, whereas females and most young were much more retiring. The reactions of nesting birds, and of pairs with dependent young, to an exposed observer were relevant to the study, but in most cases observations were made from a concealed position to eliminate any effect a visible observer might have on the birds' behaviour. At Scotston the birds were always fully aware of the presence of an observer in a hide, but this apparently did not affect their behaviour adversely (see Section 9.4.4.5). To allow detailed observation it was never necessary to clear more than very small amounts of vegetation at any site. At Scotston the birds were encouraged to remain in the vicinity of the hides by the provision of mealworms (see Section 9.3.4) and of fresh water for drinking and bathing.

Birds were trapped, weighed, measured and colour-ringed (see Chapter 3, Section 3.8.1 and 3.9) at all long-term study sites except Karkloof Forest, and observations of colour-ringed individuals were made for periods of up to 2 years. At Scotston young birds were periodically retrapped, weighed and measured throughout their development and after independence, until they left the area. Territorial and agonistic behaviour, all normal daily activities, and the plumage development of young birds, were recorded on video film. The entire breeding cycle, with the exception of egg-laying, incubation and hatching, was also recorded on video film; about 35 hours of film were taken of this species during the study, most at Scotston.

#### **9.3.4 Food, feeding ecology and energy requirements**

Direct observations of food and foraging behaviour were made at all long-term study sites and at many other localities, and foraging behaviour was filmed. Additional information on prey was obtained from the gizzard contents of all casualties obtained during the study, and the proportions of prey items of different invertebrate types were compared with those found in samples of leaf-litter taken monthly at four sites for one year (see Chapter 3, Section 3.7.3 for the methods used). Identification of invertebrate fragments in gizzards was often facilitated by comparison with the material collected from leaf-litter.

At Scotston mealworms were provided for the breeding birds and their offspring at feeding stations close to both hides at frequent intervals throughout each day, from January to April 1991 and throughout the second study season (October 1991 to March 1992). As the garden held two breeding pairs during the second season, when up to 15 birds (adults, independent immatures, dependent young and temporary immigrants) were present at times, the consumption of mealworms was often about 500 per day (sometimes up to 1 000), and an intensive breeding programme for these insects had to be maintained throughout the study period.

Although it was not possible to undertake controlled feeding experiments to establish daily energy intake, at Scotston it was sometimes possible to observe adults continuously for periods of one hour or more at all times of the day and thus to note the number of mealworms eaten in periods when no other types of food were eaten. Taking overall mean numbers eaten during each hour during the day, and estimating the mass of the mealworms eaten (only one size of mealworm was used in such experiments), very rough estimates were obtained of the total daily intake and of feeding activity throughout the day. The energy value of the mealworms and the field metabolic rate for the species were obtained as described in Chapter 4, Section 4.3.4.

The gizzard contents of 52 of the 53 casualties from Natal were examined (one bird was too decomposed for detailed study). All invertebrate prey was identified to class or order and, if possible and relevant, to family, genus or species.

#### **9.3.5 Vocalizations**

Throughout the study detailed notes were kept of all vocalizations made by all birds encountered, and of the timing and duration of all advertising calls heard throughout the survey area. Calls were tape-recorded whenever possible, using the equipment described in Chapter 4, Section 4.3.5. To obtain information on the seasonality of calling and on the times of day and the weather conditions during which the birds call, an appeal was made in early 1989 for observers in Natal

willing to record the birds' occurrences and calling patterns. A good response was obtained and 32 people participated in the survey, 23 of them submitting regular returns from localities in coastal, mid- and high-altitude areas during the period September 1989 to March 1992. Most observers could only record weather conditions on occasions when the birds called, but eight people (myself included) provided daily weather records, during at least one breeding season, whether the birds called or not. From these daily records, collected at Pietermaritzburg, Richmond, Ixopo, Balgowan and Underberg, it was possible to investigate the effect of time of day and weather on calling. From the first to the last date on which the birds called during a breeding season a daily record was kept of calling and weather as follows (definitions of weather conditions were necessarily simple and subjective):

- a) times of day (local time) and duration of calling (male advertising hoots only);
- b) temperature (cold or warm);
- c) cloud cover (clear to partial cloud, or predominantly cloudy);
- d) precipitation (mist, drizzle or rain).

For all analyses, weather conditions and calling occurrences were summarized on a half-day basis: am (midnight to midday; almost all observations were made between 05:00 and 12:00), and pm (midday to midnight). For general analysis, half-days on which precipitation occurred were included in the "cloudy" category but were also analyzed separately to investigate the effects of different precipitation types on calling.

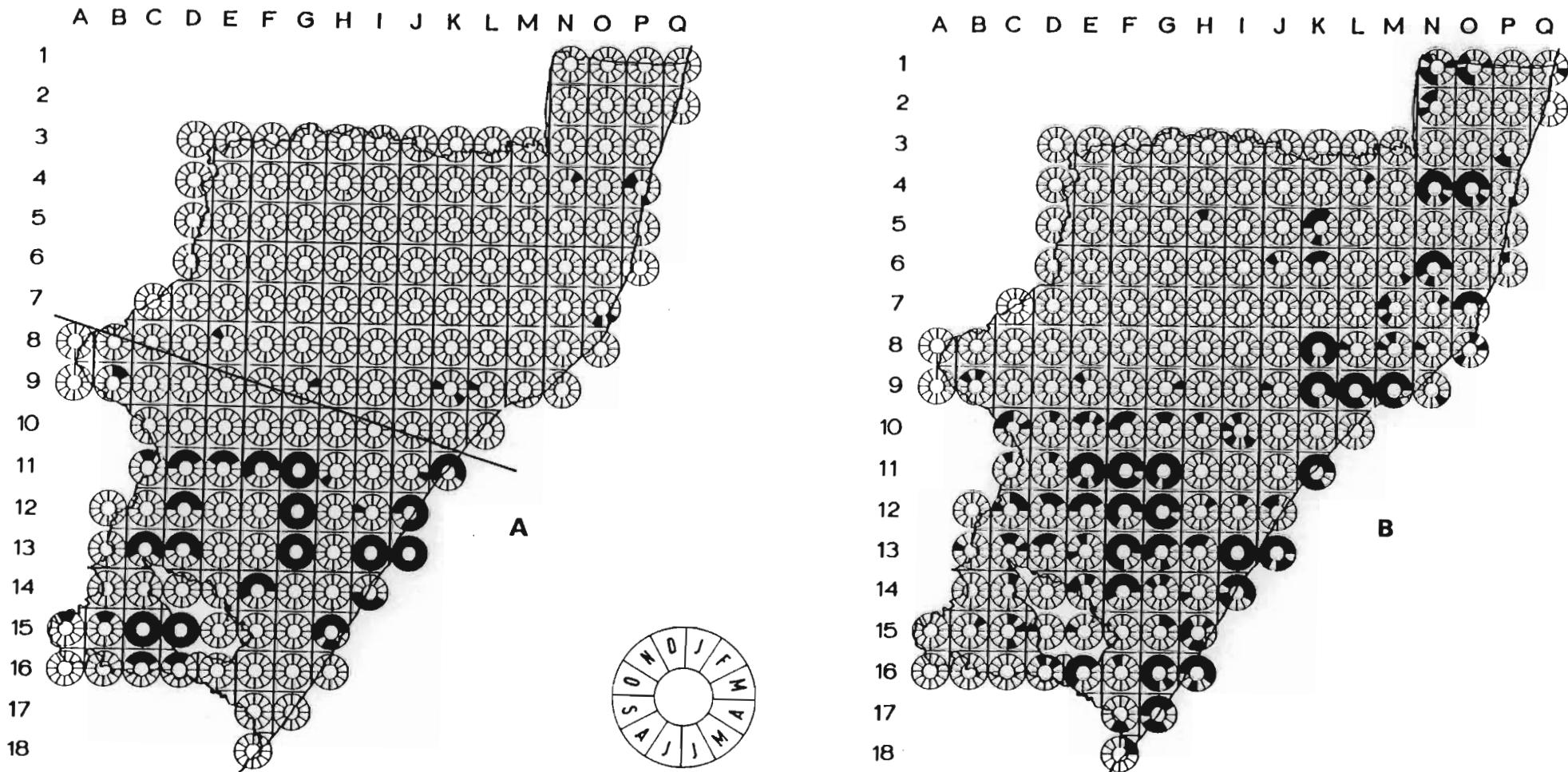
### **9.3.6      Moult and plumage development**

The plumage development of young birds, and moult of all age groups, were investigated by field observations (including of trapped birds) and by the examination of museum skins (Chapter 3, Section 3.11) and the dead birds received during the study. Study skins were prepared from some casualties and a series of wings of juveniles and immatures was collected to show the sequence of moult and the age-related variation in plumage pattern on the upperwings.

## **9.4      Results**

### **9.4.1      Distribution and status**

Figure 9.1A shows the monthly distribution of occurrences recorded in Natal during the study, while Fig. 9.1B summarizes all other Natal distributional data, combining records from Cyrus



. 9.1

Monthly distributional data for the Buffspotted Flufftail in Natal, by quarter-degree square. A: data collected from January 1989 to December 1993 (the transverse line marks the northern limit of the southern Natal survey area). B: combined data from Cyrus & Robson (1980) and the Southern African Bird Atlas Project. Data presentation follows the mapping system used by Cyrus & Robson (1980), described in Chapter 4, Section 4.3.1. Inset: monthly information (January to December), recorded clockwise within each quarter-degree-square symbol.

& Robson (1980) and the Southern African Bird Atlas Project (SABAP) databank. The patchiness of the bird's southern-Natal distribution shown in Fig. 9.1A is not real and reflects the absence of general distributional survey work and the inclusion of records from observers who (a) monitored occurrences only at single sites such as gardens and farms or (b) found casualties, usually in their gardens. Combining all records from 1970 to 1993 suggests that the Buffspotted Flufftail, having been recorded from 57 quarter-degree squares in the southern-Natal survey area (Fig. 9.1), may be somewhat more widely distributed in this region than is the Redchested Flufftail, which is recorded from 51 squares (Chapter 4, Fig. 4.1). However it must be borne in mind that the Buffspotted Flufftail, because of its occurrence close to human habitation and its very distinctive advertising call, is often more likely to be recorded than is its wetland counterpart.

This distribution pattern confirms my subjective impression that the Buffspotted Flufftail is likely to occur in suitable habitat (Section 9.4.2) anywhere in Natal. Its ability to occupy deciduous thickets, either seasonally or permanently (Section 9.4.2; Chapter 1, Section 1.2.1.2) may enable it to extend significantly into areas of thornveld in the north of the Province. Although most records have come from low- to mid-altitude sites, I have recorded the species at 1 900 m a.s.l. at Mt Currie Reserve, East Griqualand, and its upper altitude limits are presumably dictated by the availability of suitable dense bushed or forested habitat.

This study has produced relatively little information from northern Natal, but in the mid-1970s the species was regular at Sodwana Bay (A. Jacobs pers. comm.), where it has recently been recorded in good numbers, apparently on passage (W. W. Howells pers. comm.; see Section 9.4.3.2).

Some observers have suggested that the Buffspotted Flufftail has appeared in new localities or increased in numbers locally in recent years. For example, B. Stuckenberg (pers. comm.) judged the species uncommon and locally distributed in Pietermaritzburg when he arrived there in 1953 but noted that the bird apparently became more common and widespread in the 1960s and 1970s, when many specimens were brought to the Natal Museum. At Underberg, P. Clowes (pers. comm.) suggests that the birds have become more widespread since the mid-1970s, although they have been recorded in at least one local garden for the last 30 years (D. Wilson pers. comm.). Other observers also suggest that the birds have been more widely reported in gardens in recent years, but this may be partly explained by increased observer awareness. However it is very probable that, in the recent past, the species has been able to extend its local range in the relatively treeless upland areas of southern Natal, where some forest patches are unsuitable for occupation (Section 9.4.2), as a result of the creation of suitable habitat in gardens and associated cultivation on farms.

#### 9.4.2      Habitat

In Natal the Buffspotted Flufftail occurs in a wide range of vegetation types associated with forest, thick bush and other dense woody cover. Generalized observations show that the species occurs as frequently in predominantly exotic vegetation as in natural bush or forest. Of 33 breeding-season territories seen in Natal, nine (27,3%) were in natural forest or dense bush, 14 (42,4%) in mixed indigenous and exotic vegetation and ten (30,3%) in purely exotic vegetation.

Good examples of typical, predominantly natural, habitats are those at Karkloof Forest, Howick, Ferncliffe Forest and Bisley Valley, Pietermaritzburg, and Danville Park, Durban, described in Chapter 2, Sections 2.2.4, 2.2.6, 2.2.8 and 2.2.9 respectively. At Ferncliffe the birds were present only in natural forest, avoiding predominantly rocky ground (where foraging sites were few) and not occurring in stands of exotic conifers and wattles, vegetation from which they are generally absent throughout southern Natal, presumably because of the lack of dense low cover, soft ground and moist leaf-litter. At two sites in Natal calling from wattle clumps was noted, these clumps being small and surrounded by suitable dense habitat. Observations in the Underberg area and at Mt Currie Reserve suggest that much of the mistbelt forest at higher altitudes in Natal may be unsuitable for occupation, consisting of fairly tall trees growing on steep rocky ground and lacking adequate low cover and leaf-litter foraging areas. At Mt Currie the birds were only present in one patch of hillside vegetation dominated by dense *Leucosidea sericea* bushes on soft soil, with additional dense low cover of herbs and brambles.

At Pietermaritzburg, Buffspotted Flufftails occur at Darvill Sewage Works in old exotic poplar plantations on patchily moist ground where the poplar trees are large and well spaced, some are dead, and there is dense low cover of bugweed *Solanum mauritianum* and mulberry *Morus nigra* bushes, with patches of grass and herbs and a dense growths of balloon vine *Cardiospermum grandiflorum* at the plantation edge. The soil is soft, open ground exists under dense cover and leaf-litter is plentiful. In the Pietermaritzburg area the birds also occur in exotic *Lantana* thickets, often at their edges where there is a mixture of brambles, other bushes, herbs and grasses.

The birds tolerate a very wide range of exotic vegetation types in gardens and on farms. A typical example is that of the Scotston Farm garden at Underberg (Chapter 2, Section 2.2.10; Plate 3B), where the cover is largely seasonal (Chapter 10). Here they also occur in an old poplar plantation on soft soil, with some bushes and an almost continuous dense ground cover of periwinkle *Vinca*. Elsewhere in the area they are present during the summer in gardens where the predominant dense cover includes privet *Ligustrum lucidum* bushes and hedges, *Hydrangea*, *Canna*, *Agapanthus*, *Rosa*, *Rhododendron* (azaleas), *Lonicera*, *Bougainvillea*, *Rubus* etc. At Scotston they foraged in the

vegetable garden (Chapter 2, Section 2.2.10), and in many gardens they forage in flowerbeds, herbaceous borders, at the edges of lawns and in drainage channels.

An unusual habitat recorded during the study was a field of tall sugar cane at New Hanover, in which a bird was caught on an unspecified date (P. Coulon pers. comm.). In the absence of further details it is not clear whether the area might have been suitable for prolonged occupation or whether, as is more likely, the bird might have occurred temporarily while moving.

Only at Scotston were accurate measurements made of territory sizes and the extent of different types of vegetation. However, rough estimates at the 33 breeding-season territories observed in Natal indicated that the following features were common to all territories:

- (a) at least 10% of the ground covered by low trees, bushes or woody herbs, usually 1,5-3 m tall, which provided closed canopy cover from a height of 50 cm or more and also provided calling perches;
- (b) areas of open ground with leaf litter for foraging, usually within this closed cover;
- (c) in addition to (b) - or partly replacing it - open ground with soft soil for foraging, usually beneath and around dense clumps of herbaceous plants such as are found in garden flowerbeds and herbaceous borders;
- (d) an area of dense ground vegetation (spreading erect herbs, creepers, or grass) near woody cover, or an area of very low-growing bush cover, in which the nest is situated;
- (e) good foliage cover on the woody and tall herbaceous vegetation.

The proportion of the ground suitable for foraging need not be large. Two territories mapped at Scotston in the 1990-1991 breeding season contained about 1 175 m<sup>2</sup> (35% of the total territory area) and about 1 210 m<sup>2</sup> (24% of the territory area) of foraging substrate.

Water is not an essential requirement, but birds in forested habitat often had a stream within their territory and, in some areas, permanent residence was thought to depend on the presence of streams or of permanently watered ground (see Sections 9.4.3.1 and 9.4.3.2). At Scotston the birds readily took food from water (Section 9.4.6) and foraged in mud and shallow water at a small stream overhung by a dense ground cover of *Vinca*. Some forested habitat associated with streams closely resembled that occupied by the Whitespotted Flufftail in western Kenya (Taylor & Taylor 1986), where both species have identical foraging habits in leaf litter and low vegetation but are ecologically segregated in most places by the Whitespotted Flufftail's association with forest streams, which are its main feeding areas. The Buffspotted Flufftail's ability to increase its foraging options in South Africa by exploiting shallow water appears to constitute an example of niche expansion in the absence of a congeneric competitor (Cody 1974). The ability to exploit wet habitat is also useful in the winter, when normal foraging areas become dry and food supplies diminish, an example of this being the

observation made at Danville Park, Durban, on 14 May 1991, when a male Buffspotted Flufftail foraged around the observation hide in the middle of the wetland, at least 50 m from its normal forested habitat (Section 9.4.6).

The Buffspotted Flufftail's habitats in Natal are not occupied by any other rallid species, although its terrestrial foraging niche in natural vegetation is also exploited by several passerine species, full details of which appear in Section 9.4.6. However, no other bird species appears fully to exploit its terrestrial niche in the exotic vegetation of gardens, etc. (Section 9.4.6).

#### **9.4.3 Occurrence patterns and movements**

Information on the dispersal of juveniles during the breeding season is given in Section 9.4.11.

##### **9.4.3.1 Long-term study sites**

Considerable differences in periods of occurrence and migratory status were observed at the different study sites and possible reasons for these differences are discussed in Chapter 10. When observations began at Karkloof Forest, near Howick, on 16 October 1988, a territorial pair occupied the study site, another pair was resident nearby and other calling birds were heard in the area. No birds were ringed, but frequent observations throughout the 1988-1989 summer showed that the two resident pairs remained until May 1989, the study-site birds last being seen on 21 May. Regular searches and taped playback revealed no flufftails in the area for the next three months, but a silent male was seen on 31 August 1989 and calling began again on 29 September, after which a pair was resident at the study site until observations were discontinued in late November. In 1990, occurrences were recorded from early September (P. Burdon pers. comm.). The relatively short period of absence from this site suggested that the birds had not migrated from the area but had moved locally, perhaps to moister ground near streams at slightly lower altitudes. This theory is supported by the evidence of O. Wirminghaus (pers. comm.), who heard the species calling occasionally elsewhere in the forest in July and August 1988 and June 1989.

At Ferncliffe Forest, Pietermaritzburg, observations were made at least once a month at one site from September 1990 to December 1991 and irregularly elsewhere until June 1992. At the regularly watched site birds were recorded on each visit from 8 September 1990 to 15 March 1991 and were then not present for 6 months, return being noted on 10 September 1991. Thereafter birds were seen there until 22 December 1991, after which disturbance (tree felling) caused them to move away. Birds were recorded nearby in the forest until 15 April but were not found in May or June and

regular observations ceased at the end of June. Both males and females were recorded throughout the two occurrence periods. A newly arrived territorial adult male colour-ringed at the observation site on 23 September 1991 was not seen in October, when the site was occupied by another territorial adult male which was colour-ringed on 15 October and remained in residence until 22 December 1991.

At Bisley Valley, Pietermaritzburg, birds were first recorded in mid-April and May 1991 by H. Adie (pers. comm.). Thereafter I made observations at this site at least once a month from June 1991 to June 1992. The male of a resident territorial pair was colour-ringed on 22 June and proved to be a first-year bird; it was present until late August, when both it and its accompanying female showed much less intensive territorial behaviour. On 24 September the site was occupied by a new territorial male, which was colour-ringed and proved to be an adult; no female was seen. On 18 October the site was occupied by a territorial pair which gave various breeding calls; the male was unringed, thus being at least the third male to occupy the site in five months. An unringed pair was present here until 24 February 1992 but no birds were found from March to June, when drought conditions had caused a significant deterioration in cover and food availability (Chapter 10).

At Danville Park, Durban, where the forest held at least three breeding pairs, birds were recorded in every month of the year. A colour-ringed territorial male was observed in exactly the same spot each month for 11 months (March 1991 to January 1992 inclusive), after which regular observations were discontinued. During this period an unringed female was observed with the male in all months except July, while other females (none was colour-ringed) were observed elsewhere in all months except June and July; females were probably present throughout the winter, when their retiring habits and low level of territorial activity (Section 9.4.5) made observation very difficult. During the drought in 1992 (Chapter 2, Section 2.2.9), when cover deteriorated significantly, occasional observations suggested that the resident birds left the forest after April, but a male was seen at the edge of the marsh in May (E. P. Smith pers. comm.); Section 9.4.2 gives further evidence of seasonal occurrence in wet habitat at this site.

At Scotston in early 1990 resident birds were seen regularly until 2 March, after which a single male called every night from 10 to 20 March and roosted until 23 March, when it disappeared. From September 1990 to March 1992 daily observations enabled precise details to be obtained of occurrences and movements. Details of breeding-season activities are given in Section 9.4.10 and are summarized, with occurrence periods, in Fig. 9.13. Advertising calls were first heard on 12 October 1990 and two pairs were resident in the garden until mid-January 1991, but only one (Pair 1, Fig. 9.13) remained to the end of the season. The other pair is not shown in Fig. 9.13: the female disappeared on 11 January and her mate then gave advertising calls for a few days, presumably to attract another mate, but on 20 January Pair 1 moved into the area occupied by the unmated male,

which was not seen subsequently (see Section 9.4.5.1). Pair 1 bred once in the new area and then left, the female departing on 9 March and the male on 13 March. The five young from the last brood remained until April, departing on 6, 9, 13, 17 and 23 April respectively. Elsewhere in Underberg an adult female seen with 10-day-old young on 2 April (N. Treleaven pers. comm.) would probably have left in the last week of April, while an immature female was seen on 24 April (R. A. Taylor, pers. comm.).

In the 1991-1992 season Pair 1 returned to the Scotston garden on 4-5 October and several calling birds were first heard in Underberg on 10 October, including a non-territorial male at Scotston, which called until 18 October, when it was killed by a dog. Another male arrived in the Scotston garden on 7 November, disappearing after 11 November, when yet another male appeared and established a territory. This male succeeded in attracting a female and these birds (Pair 2, Fig. 9.13) remained for the rest of the season. Both pairs were still present when observations were discontinued on 8 March 1992. No birds returned to Scotston in the drought season of 1992-1993, when very few were recorded from the Underberg area and the first call was not heard until 25 October (Table 9.1). Conditions improved in late 1993 but no birds were found at Scotston, although calls were heard in the Underberg area as early as 10 September.

#### **9.4.3.2 Other visual and sound records**

Table 9.1 summarizes details from areas where observers recorded calling periods for the survey described in Section 9.3.5, and Fig. 9.1A summarizes monthly distributional data collected by observers in Natal who assisted with the study. These results show that the species is present throughout the year at some localities, at altitudes ranging from sea level to 1 570 m. However the birds were found only seasonally at other localities within this altitudinal range, principally in mid-to high-altitude areas of the Natal Midlands such as Ixopo, Hilton, Balgowan, Underberg and Himeville, where they were recorded from September/October to February/March. At Richmond, although the birds are seen throughout the year at low altitudes (about 670 m a.s.l.), they have been recorded only during the summer (September to March) at higher altitudes (B. Porter pers. comm.), and at Pietermaritzburg there are records for all months at some sites, but only for the period September to April at Ferncliffe Forest (Section 9.4.3.1) and in my own garden. The results of the wider coverage provided by the two atlas projects (Fig. 9.1B) agree with the pattern of occurrence for southern Natal shown in Fig. 9.1A and show that the species is probably also present throughout the year in the lower-altitude regions of northern Natal.

With only one exception, records from this study from all localities above 950 m a.s.l. fall in the period September to April, suggesting at least local movements in these areas (see Chapter 10).

TABLE 9.1

First and last dates of Buffspotted Flufftail advertising calls heard by observers in Natal during the study, with additional information on residence periods. Localities are listed in order of increasing altitude. Observers supplying information were: W. Addison, S. Alexander, S.M. Auchincloss, J. Baxter, P.D.A. Burdon, P. Butlin, P. Clowes, E. Forsyth, R.F. Horner, M. Keep, J.M. Keightley, R.J. Lund, D.L. Mackenzie, M. Maréchal, S.C. Mathieson, J.S. Morford, J. Morrison, B. Porter, P. Reid, M. Smith, E.P. Smith, A. Southwood, D. Spencer, L. Streatfield, C.A. Taylor, P.B. Taylor, R.A. Taylor, P. Thomson, N.L. Thurston, R. Topman, D.J. van den Heever, A. Walker, G. Wilton.

Locality	Altitude (m a.s.l.)	General information	Season	First Date(s)	Last Date(s)
Durban area	15-200	Permanently resident at some sites	1989-90	24 Aug	27 Feb
			1990-91	16 Sep	-
			1991-92	3 Sep	-
Richmond	670	Present all year at this altitude	1989-90	-	7 Feb
			1990-91	9 Oct	15 Feb
Pietermaritzburg	710-950	Present all year at some sites	1988-89	30 Aug	-
			1989-90	6 Oct	11 Feb-20 Mar
			1990-91	21 Aug-17 Sep	
			1991-92	4-19 Sep	16 Feb-7 Mar
Ixopo	1000	No records outside calling periods	1989-90	22 Oct	6 Feb
			1990-91	8 Oct	16 Feb
			1991-92	15 Sep	-
Hilton	1100	No records outside calling period	1989-90	10 Oct	6 Feb
Balgowan	1380	Recorded between 9 Sep and 14 Mar	1989-90	29 Oct	20 Feb
			1990-91	9-14 Sep	4 Feb
			1991-92	25 Sep	-
Dargle	1400	No other details available	1990-91	13 Sep	-
Underberg	1500	No adults seen outside these periods	1989-90	-	20 Mar
			1990-91	4-11 Oct	-
			1991-92	1-5 Oct	-
			1992-93	25 Oct	-
			1993-94	10 Sep	-
Himeville	1520	Recorded between 9 Oct and 12 Mar	1989-90	15 Nov	12 Jan
			1990-91	9 Oct	-
Franklin	1570	Present all year at this site	1992-93	7 Oct	-

The exception is at Franklin, East Griqualand, where birds have been recorded throughout the year on a farm at 1 570 m a.s.l. (G. Wilton pers. comm.). Although in a cold area with regular winter frosts, the farm garden provides excellent permanent habitat, having some dense cover of woody evergreen plants and a permanent stream with good ground cover. In addition, the whole garden is watered and sprinkled throughout the year, resulting in permanently damp ground and leaf litter. These factors, discussed in Chapter 10, presumably result in sufficient food and cover being available all the year at this site.

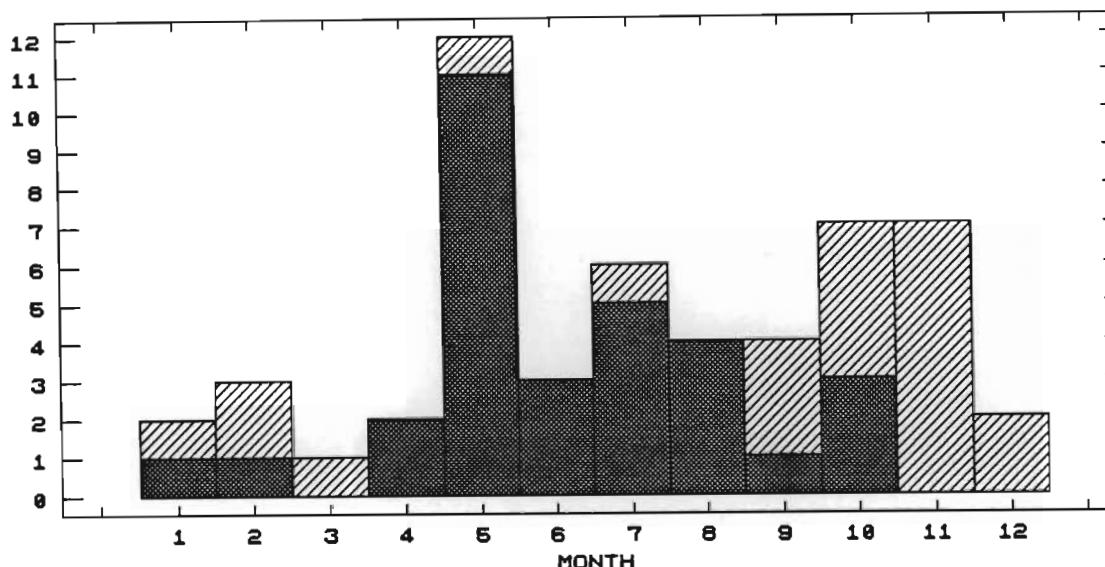
Other records indicative of movements were confined to those summarized in Section 9.4.3.3, plus the following four observations.

- a) One early morning in mid-May 1989 R. Davidson (pers.comm.) saw a male Buffspotted Flufftail running around in a clump of small canna lilies on the central island of a dual carriageway in Durban, away from suitable cover.
- b) In the early morning of 11 December 1989 a male was found on the doorstep of an office in Pietermaritzburg's central business district. It was kept for a few hours and released in a local garden.
- c) At Richmond a male was caught in the bedroom of a house on high ground on 21 April 1992. It was kept overnight in an aviary and repeatedly tried to fly out, so it was released the next day (J.H. Hawkins pers. comm.).
- d) At the Natal Parks Board's Sodwana Bay Reserve in northern Natal, many birds appear just before the rains each year (usually in October), some flying into walls and windows (W. Howells pers. comm.). Calls are heard for a short time and the birds then disappear; there is no evidence of return movements at the end of the rains.

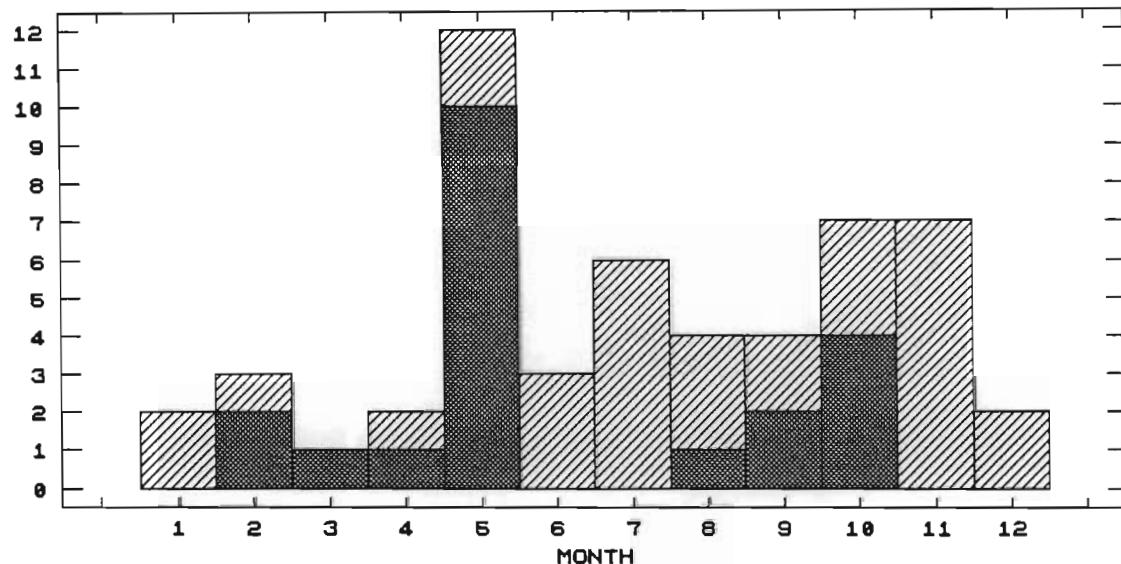
#### 9.4.3.3      Casualties

During the study 53 fresh or frozen specimens were obtained, 22 from inland localities (including 17 from Pietermaritzburg) and 31 from coastal localities (including 22 from the Durban area). The monthly distribution of the records (Fig. 9.2A) shows a preponderance of coastal specimens in the period April to August and of inland specimens from September to December. Each bird was classed as either resident or moving, the following criteria being used to evaluate its status. **Resident ( $n = 32$ ; 60%).** Birds killed or found dead in gardens with suitable habitat, where the birds are known to be regularly resident in the seasons when casualties were found. These birds had no appreciable fat deposits and 29 of them (91%) had the gizzard at least half full of food. All birds in breeding condition fell into this category.

NO. OF SPECIMENS

**A**

NO. OF SPECIMENS

**B****Fig. 9.2**

(A) Monthly distribution (January to December) of Buffspotted Flufftail specimens ( $n = 53$ ) obtained during the study, from inland (hatched;  $n = 22$ ) and coastal (shaded;  $n = 31$ ) localities. (B) Monthly distribution of Buffspotted Flufftail specimens ( $n = 53$ ) designated resident (hatched;  $n = 32$ ) or moving (shaded;  $n = 21$ ). See Section 9.4.3.3 for further details.

**Moving ( $n = 21$ ; 40%).** Birds killed or found dead (a) in places where they had never been heard or seen previously, despite long residence by the finders, and/or (b) where no suitable habitat exists in the vicinity, or (c) where they had obviously flown into a wall or window at night. Of these birds, 20 had large fat deposits, especially subcutaneously in the thoracic region and around the neck, abdomen and thighs, and often also internally around the viscera. Such deposits are typical of those laid down by birds before migration (P.R. Evans *in* Campbell & Lack 1985). The only bird without appreciable fat deposits was an immature female from Durban on 25 May 1991, which was possibly undergoing normal juvenile dispersal (see Section 9.4.11). In contrast to the resident birds, only four (19%) of the moving birds had an appreciable amount of food in the gizzard.

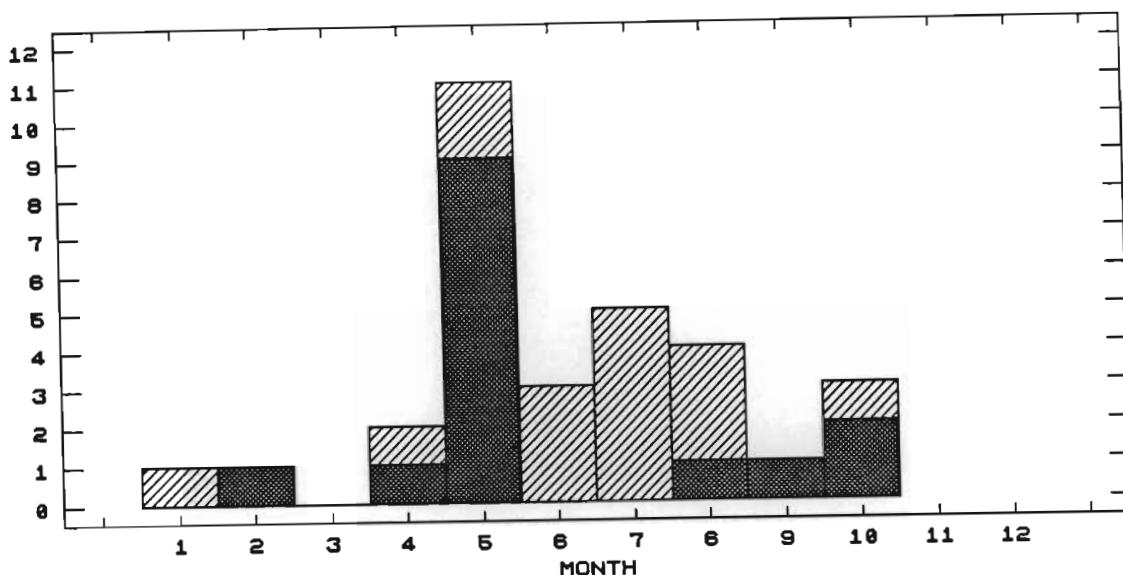
Figure 9.2B shows that the 21 moving birds were obtained only in the periods February-May and August-October, of which ten (48%) were in May. Most ( $n = 15$ ; 71%) were from coastal localities, which accounted for nine of the ten May records, other records being scattered throughout both movement periods (Fig. 9.3A). Fewer ( $n = 6$ ; 29%) moving birds were obtained at inland localities, where records were scattered throughout the movement periods (Fig. 9.3.B). Most ( $n = 16$ ; 76%) of the moving birds were immatures, the five adults being from the months of May and October (Fig. 9.4).

#### 9.4.4 General behaviour

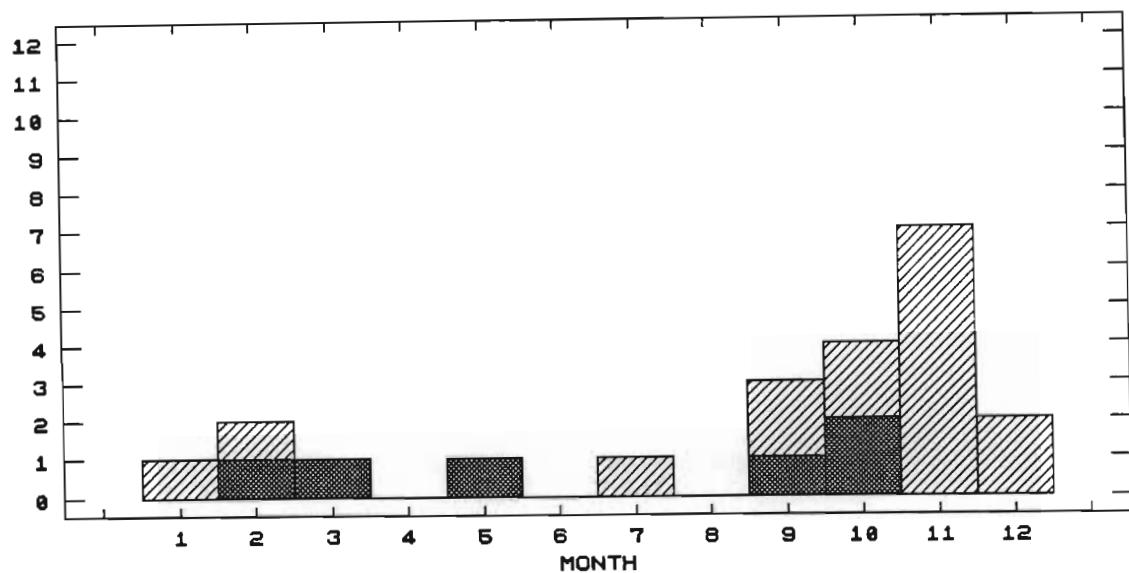
##### 9.4.4.1 Activity patterns and characteristic behaviour

Like the Redchested Flufftail, the Buffspotted Flufftail is normally entirely diurnal and crepuscular in its activities, birds appearing at, or just after, first light and going to roost at dusk. The only nocturnal activities encountered during the study involved movements, evidence for which came from birds which hit walls and windows at night (Section 9.4.3.3), and calling. Males made nocturnal advertising calls periodically throughout the breeding season and, in some areas, also in other months (Section 9.4.8). At peak calling periods males called throughout the night, with some breaks, and sometimes called almost continuously for 12 hours or more. Such calling birds normally showed no reaction to taped playback of advertising calls at close range, falling silent only when the observer approached too close or searched the bushes using a torch. When thus disturbed, a bird might move along the branches, or down to the ground and up into a nearby bush from which it would call later, but usually the bird remained still in its original position. Newly arrived birds which hooted feebly (Section 9.4.8) usually fell silent when taped playback was used, and more often retreated a little way from the stimulus.

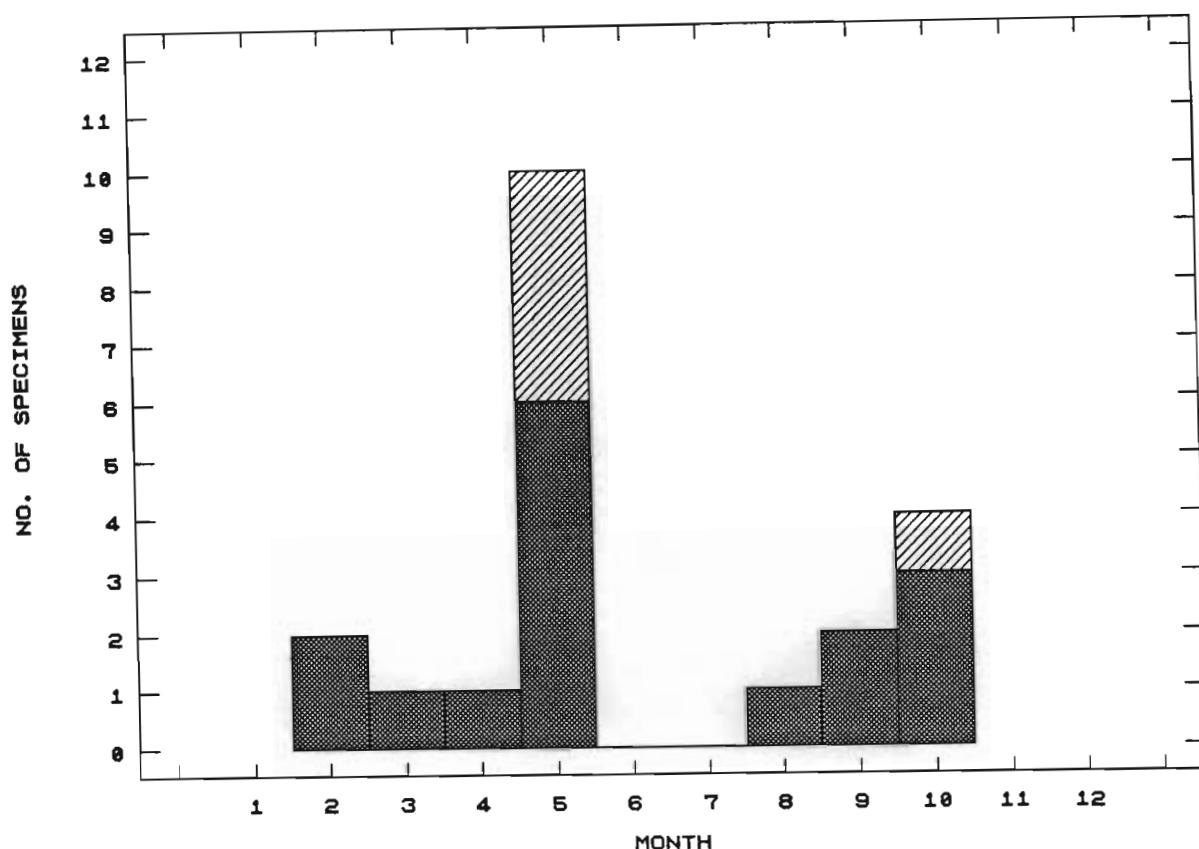
NO. OF SPECIMENS

**A**

NO. OF SPECIMENS

**B****Fig. 9.3**

(A) Monthly distribution (January to December) of Buffspotted Flufftail specimens ( $n = 31$ ) designated resident (hatched;  $n = 16$ ) and moving (shaded;  $n = 15$ ), at coastal sites. (B) Monthly distribution of Buffspotted Flufftail specimens ( $n = 22$ ) designated resident (hatched;  $n = 16$ ) and moving (shaded;  $n = 6$ ), at inland sites.

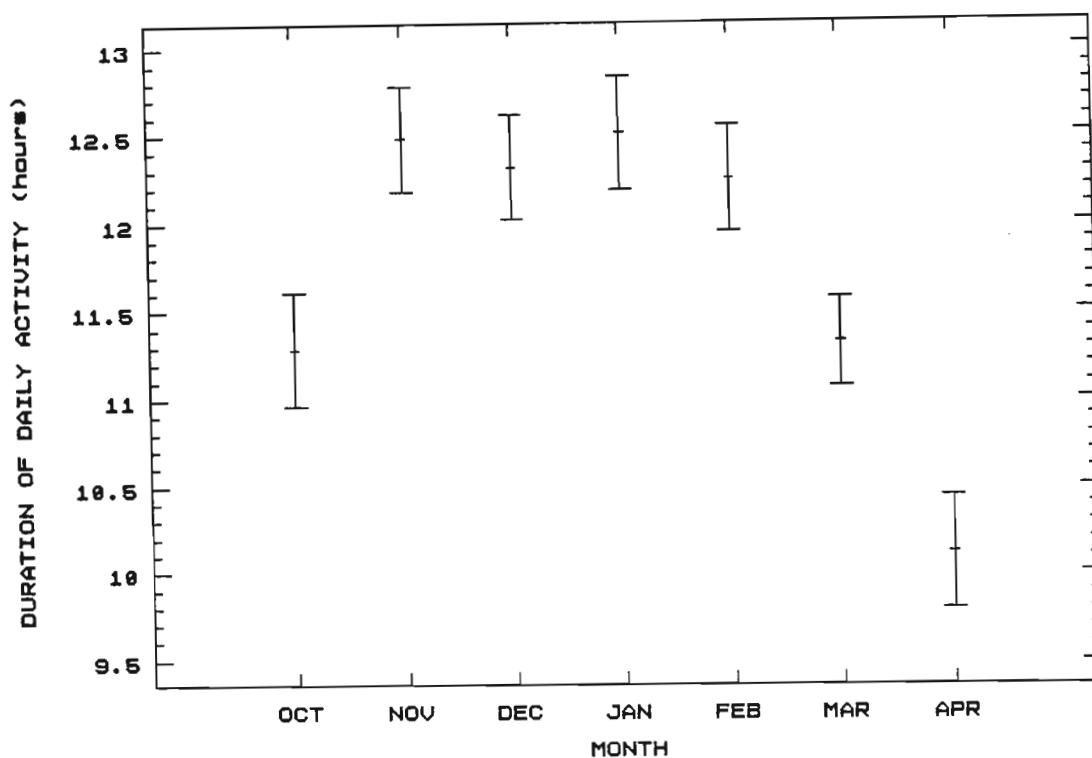


**Fig. 9.4** Monthly distribution (January to December) of Buffspotted Flufftail specimens ( $n = 21$ ) designated moving, split into adults (hatched,  $n = 5$ ) and immatures (shaded;  $n = 16$ ). Immatures are birds less than one year old.

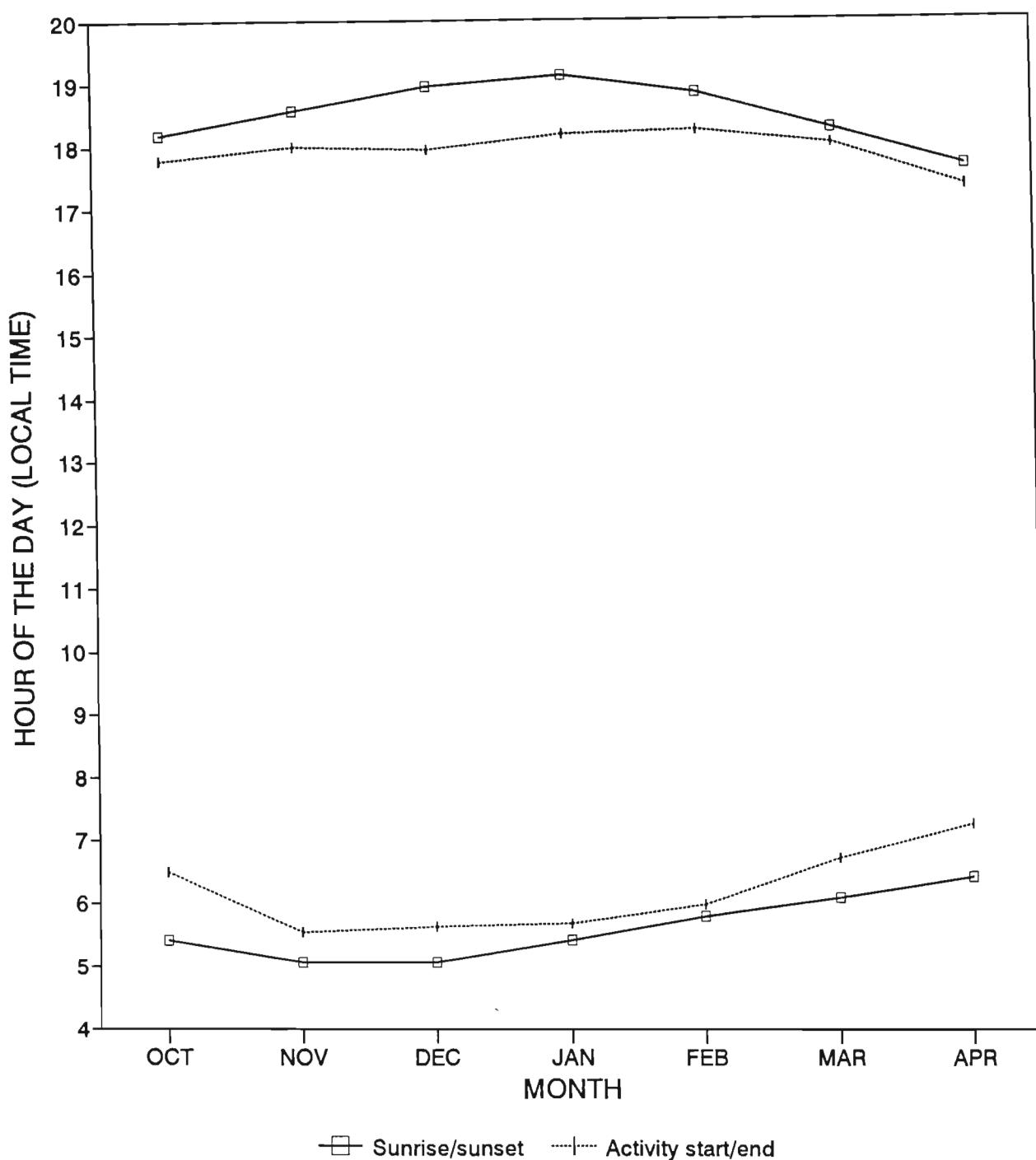
Daily activity patterns were recorded at Scotston during two breeding seasons, when the duration of daily activity was accurately measured on 49 days during the October-April periods of occurrence, 6-10 full days of activity being monitored in each month. A one-way analysis of variance on these data showed that variances were equal ( $P > 0.05$ ) and that the data fell into three homogeneous and significantly different groups ( $P < 0.001$ ) (Fig. 9.5): the longest activity periods occurring in the four months from November to February, when the birds had dependent young and were often active for 12-13 h/day, shorter activity periods occurring in October and March, when birds were normally active for 11-12 h/day, and the shortest activity periods (approximately 10 h/day) being recorded in April (1991 only), when only immatures remained at the site (Section 9.4.11).

As well as the probable effect of dependent young on the duration of daily activity (by increasing the time required for foraging), at these latitudes variations in day length must also have an effect on the birds' activity periods. A comparison between the mean monthly times of sunrise and sunset (local time) and the mean monthly times of the start and end of daily activity (Fig. 9.6) shows that the activity curves roughly follow the sunrise and sunset curves, but that there is some variation. The birds became active earliest in relation to sunrise during the four months (November-February) when they had dependent young and when mild temperatures allowed successful foraging at all times of the day. However, they also roosted earlier (in relation to sunset) during these months than at other times, a fact which appears to be at variance with their apparently needing longer activity periods to feed the chicks. I suggest that this anomaly may be explained by the increased risk of predation as the light fails rapidly in dense cover towards sunset and the dark-coloured chicks and juveniles become increasingly difficult to locate. Despite the intensive use of contact calling (Section 9.4.8) it would be relatively easy to lose chicks at dusk, and lost young at night would be at great risk of succumbing to predators, low temperatures or heavy rain (Section 9.4.10.4.6). If temporarily lost early in the morning, at least they can be located more easily as the light grows. In the other months the relatively late start of the day's activities may be a result of the colder conditions in the early morning, which might affect the activity of some terrestrial invertebrates. In these months activity continued nearer to sunset, possibly to give extra foraging time not available in the early morning.

Buffspotted Flufftails have relatively larger eyes than any of the other African *Sarothrura* species, presumably an adaptation to living and foraging in the permanently dim light beneath dense cover in forest habitat. Ground doves of the forest interior also have proportionately larger eyes than closely related species in more open habitats (Fry 1984). Subjective observations indicate that more light is probably available at ground level in most of the wetland and grassland vegetation occupied by the other species, and that the other forest species, the Whitespotted Flufftail, spends much of its time foraging in relatively light conditions at forest streams (Taylor & Taylor 1986). The Redchested



**Fig. 9.5** Monthly variation in the duration of Buffspotted Flufftail daily activity over the occurrence period (October to April) at Scotston during the study (one-way ANOVA; means and 95% confidence limits). Activity periods are consistently high during the months when birds have dependent young (see text).



**Fig. 9.6** Comparison between the times of sunrise and sunset (local time) and the start and end of daily activity in the Buffspotted Flufftails at Underberg during the study. All values are expressed as monthly means; 6-10 full days' activity were monitored in each month.

Flufftail is active from daybreak to dusk (Chapter 4, Section 4.4.4.1) but the Buffspotted Flufftail is not, probably because adequate light penetrates dense thickets later, and disappears earlier, than in more open conditions.

Like Redchested Flufftails (Chapter 4, Section 4.4.4.1), Buffspotted Flufftails quickly become distressed if exposed to strong sunlight, and they are not normally seen in full sunlight, keeping to shade under cover, where their spotted plumage provides excellent camouflage in patches of dappled light and the bright orange-rufous on the male assumes a dead-leaf colour. They are normally totally silent in their movements, causing no rustling of dead leaves and no movement of vegetation, and they take advantage of every scrap of cover, even small fallen twigs, especially when walking close to a visible observer. When confident, however, they may make some noise, especially when throwing dead leaves around while foraging. They often take little notice of a visible observer who remains still and quiet, but they may approach to less than 1 m in cover to investigate; when confident they usually ignore quiet talking. When conducting taped playback experiments with models from an exposed position, I have often had males come into the open to attack a model less than 1 m from my feet, a degree of confidence exceeded only by that of Whitespotted Flufftails, which sometimes foraged with their young around my feet (Taylor & Taylor 1986). During this study several observers reported instances of foraging Buffspotted Flufftails walking into courtyards and houses through open doors and, if undisturbed, sometimes walking quietly out again after a few minutes.

When first introducing the Scotston adults to mealworms I sometimes observed locomotory behaviour which I termed the "chameleon walk". This occurred when a bird was encouraged to emerge from cover to feed at a dish of mealworms but was nervous about doing so because of the presence of an unconcealed observer less than 2 m away. In this situation, obviously in the grip of conflicting urges to emerge and to flee, the bird would walk to the food dish extremely slowly, placing one foot forwards very hesitantly and sometimes drawing it back again, pausing, and rocking the body slowly backwards and forwards before taking another step. The whole process was very like the slow, hesitant progress of a chameleon along a branch.

Buffspotted Flufftails are adept at climbing around in low trees and bushes, usually flying up into the lowest branches and walking or jumping to get higher, and they perch readily, crosswise on small twigs and often lengthways on larger branches. Unlike wetland flufftail species, they normally examine an observer from ground level, not from a perch in the vegetation, but they are fond of using rocks as preening and observation posts. They normally flush only when surprised outside cover, when they usually fly at a height of 1.5 m or less for a short distance and land either on the ground or in a bush. When running to escape, their speed, manoeuvrability and silence on the ground are remarkable. Before running into cover they usually pause briefly, presumably to scan for possible danger. Their reactions to movement are quicker than those of any other bird species which I have

observed near them, and they are often uncomfortable in windy weather, when the constant noise and movement of leaves and branches must interfere with their perception of possible danger.

Breeding-season observations showed that adults with dependent young often roosted in flimsy roosting nests (descriptions of two such nests are given in Section 9.4.10.2). Nonbreeding pairs, independent young and other single birds usually roosted in the low branches of a dense bush, presumably to avoid ground predators such as rats and snakes.

#### **9.4.4.2      The pair bond**

The pair bond was maintained throughout the breeding season and the male and female shared the duties of incubation and caring for dependent young. No definite evidence was obtained for the permanence of the pair bond outside the breeding season because all colour-ringed females belonged to pairs which disappeared after breeding, while nonbreeding females in other areas were usually very unobtrusive and difficult to observe, showing much less territorial activity than the males. However an unringed female was seen with the colour-ringed male at Danville (Section 9.4.3.1) on several occasions during the nonbreeding season, while at Bisley Valley pairs were seen together in June and August, the June female showing territorial behaviour as strong as that of the male, so it is possible that the pair bond is sometimes permanent in birds which are resident at a site throughout the year.

At Scotston in 1991 the colour-ringed female left the garden on 9 March, four days before her mate, which suggests that the birds may not have moved off together. On the evening of his return (4 October 1991) this male courted and fed an unringed female, but on the following morning the ringed female appeared and the pair remained together throughout this second breeding season.

The relationship between pair members in the Scotston breeding birds was apparently different from that in the captive and wild Redchested Flufftails observed during the study (Chapter 4, Section 4.4.4.2). For example, paired Buffspotted Flufftails were never observed to allopreen or to rest for long periods together, and the female was continually wary of her mate, whose persistent courtship behaviour was often unacceptable to her (see Section 9.4.10.1).

#### **9.4.4.3      Comfort activities**

Unlike Redchested Flufftails (Chapter 4, Section 4.4.4.3), Buffspotted Flufftails were never seen to sunbathe, although at the long-term observation sites there were a few small sunlit patches within cover where they could have done so in safety. It is possible that the birds could have sunbathed on the ground out of sight, or by climbing into bushes to catch the first or last of the day's

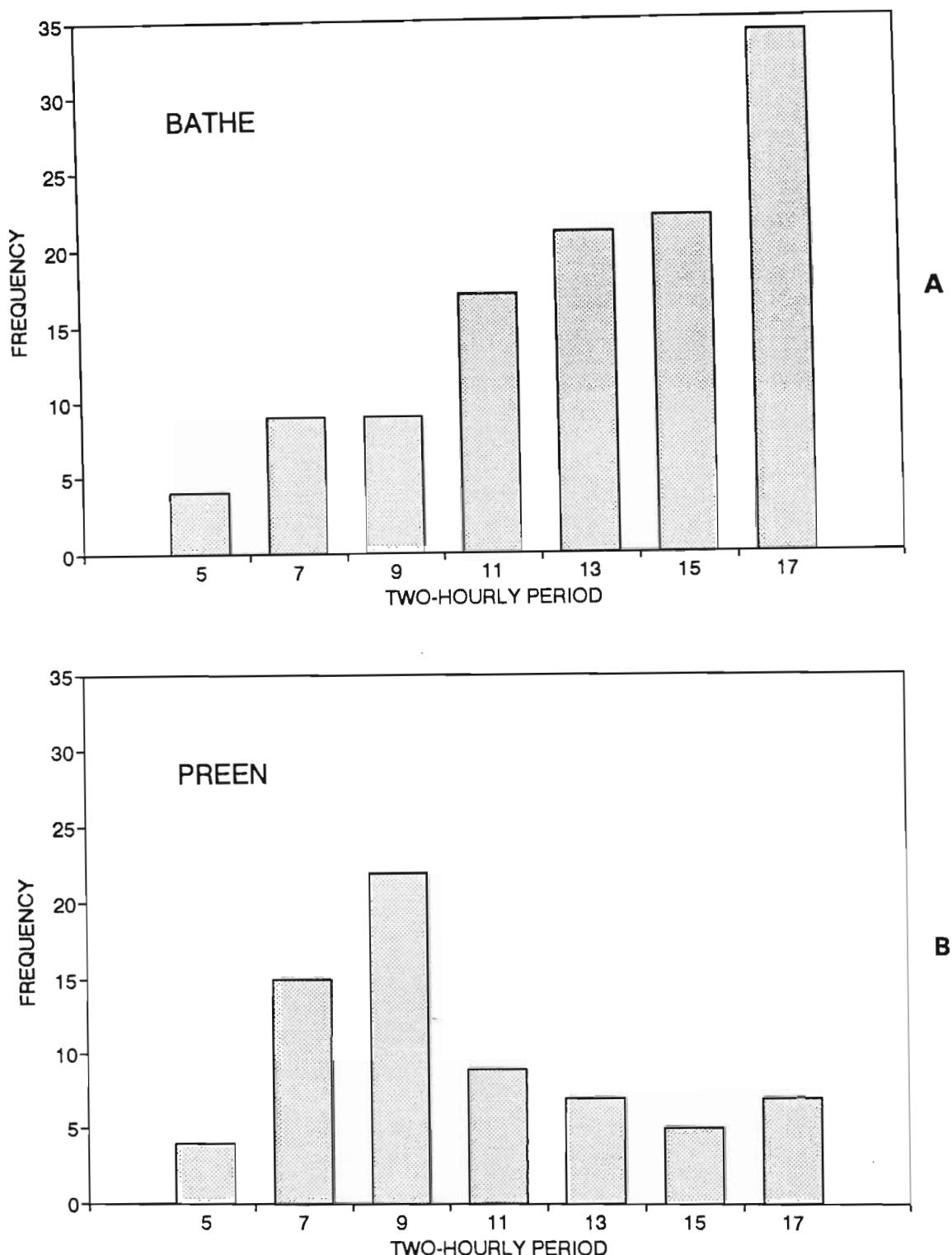
sunlight, as calling birds were observed to do by Packenham (1943). If it does occur, sunbathing is unlikely to be as frequent an activity as it is for the Redchested Flufftail.

Bathing, however, was a daily activity of all adults and young birds during the breeding season at Scotston, where at each hide fresh water was always available in a plough-disc. Chicks bathed from the age of 10-11 days, when the body had become well feathered (Section 9.4.10.4.2). At Scotston, bathing was recorded in every hour of the daily activity period and an analysis of 116 recorded bathing sessions by two-hourly time period (Fig. 9.7A) shows that the frequency of bathing increased during the day, being greatest in the 1-2 hours before the birds roosted; there is a highly significant association between activity frequency and time period ( $\chi^2 = 37,761; P < 0,001$ ). The duration of bathes ranged from a few seconds (usually when the bird was disturbed) to 6 min 30 s, the longest bathes being taken by adults which had just finished an incubating session (Section 9.4.10.3) and by birds in hot weather. During and after thorough bathing the birds invariably preened for several minutes, and during bathing they frequently made jaw-stretching movements. Adults always bathed alone but dependent young would occasionally bathe together.

Preening was a very frequent daily activity, especially in the mornings and after bathing, and its occurrences were infrequently recorded in detail. An analysis of 69 recorded preening bouts not associated with bathing showed that preening activity was greatest in the four hours between 07:01 and 11:00 (Fig. 9.7B), and there is a highly significant association between activity frequency and time period ( $\chi^2 = 25,257; P < 0,001$ ). The duration of preening sessions varied from 10-15 s to 28 min, long sessions consisting of preening bouts interspersed with short rest periods. Preening was often accompanied by upward both-wing stretching and co-ordinated wing-leg stretching. The birds often preened for long periods after bathing, but the longest sessions were practised by the female of Pair 1 during incubation periods, when she was off the nest throughout the day (Section 9.4.10.3) and did little except feed, bathe, preen and rest. The adults and young of this pair often preened and rested on a moss-covered rock 6 m from the hide, from which vantage point they had a clear view of the feeding and bathing station, and of the hide. Allopreening was never observed in this species.

#### **9.4.4.4 Flight**

Buffspotted Flufftails normally fly very little, usually only to escape from potential predators and aggressive conspecific individuals. Like Redchested Flufftails (Chapter 4, Section 4.4.4.5), the Buffspotted Flufftails at Scotston sometimes flew up into bushes to attain elevated observation posts from which they could look into the hide. Young birds made their first flights up into the low branches of bushes (Section 9.4.10.4).



**Fig. 9.7** Frequency distribution of bathing (A;  $n = 116$ ) and preening bouts (B;  $n = 69$ ) of Buffspotted Flufftails by two-hourly period of the day (local time). X-axis periods: 5 = 05:01-07:00; 7 = 07:01-09:00 etc. to 17 = 17:01-19:00.

#### **9.4.4.5 Play and inquisitiveness**

The Buffspotted Flufftails at Scotston were never seen to indulge in social play activities, unlike both captive and wild Redchested Flufftails, which did so frequently (Chapter 4, Section 4.4.4.5). However, one example of object play (M. Bekoff *in Campbell & Lack 1985*) was observed, involving the female of Pair 1 at Scotston. When bathing, this bird would sometimes pause and look intently at one of the floating dead leaves which had fallen into the water from the overhanging Japanese Quince *Chaenomeles lagenaria* bushes. She would then push the leaf under the surface with her bill, watch it bob up and then push it under again. This action was repeated a number of times and the bird sometimes pushed the leaf around so that it rose to the surface in a different place, or picked it up and dropped it in a different place before pushing it under again. No examples of object play were recorded for the Redchested Flufftail.

During studies of the breeding birds at Scotston, observers in the hide were sometimes watched for several minutes by birds which were standing on nearby rocks and on several occasions a single adult or immature walked to the door flap and looked in at the hide's occupant. Once an immature female walked into the hide while the observer was present, walked around for a short time and then walked out again.

#### **9.4.5 Territoriality and aggressive behaviour**

##### **9.4.5.1 Territory size**

Two territories mapped at Scotston in December 1990 occupied approximately 3 400 m<sup>2</sup> and 5 000 m<sup>2</sup> respectively, the smaller including the vegetable garden and adjacent flowerbeds and hedgerows and the larger encompassing the flowerbeds, shrubberies, hedgerows and lawns around the house (Fig. 2.21). In January 1991 the pair occupying the smaller territory disappeared (Section 9.4.3.1) and the other pair (Pair 1) moved into the vacant area, in which they nested and raised their third brood. They thus increased their home range to about 8 400 m<sup>2</sup> but did not defend or use all of this ground: almost all their activities were confined to the new area and the original area was used infrequently. In the 1991-1992 breeding season the territories occupied by the two breeding pairs approximated to those occupied in December 1990, Pair 1 returning to reoccupy the smaller territory and a new pair (Pair 2) occupying the larger area. These observations suggest that the smaller area was more favoured, presumably because it contained a large continuous area of suitable foraging and nesting habitat, comprising the vegetable garden and adjacent hedgerows.

#### 9.4.5.2 Territorial behaviour

Experiments with models and taped playback, field observations at long-term study sites, and studies of calling patterns, all indicate that Buffspotted Flufftails are monogamous, form a strong pair bond which persists at least throughout the breeding season, and are strongly territorial, at least during the breeding season. The situation in the nonbreeding season is less clear, but observations at the long-term study sites (Section 9.4.3.1) indicated that some winter residents, such as those at Danville Park and Bisley Valley, were paired during the nonbreeding season. Males at the long-term sites remained territorial throughout this period and all could be induced, by taped playback, to attack a model male Buffspotted Flufftail in any month of the year, although the intensity of the attack and the rapidity of response to the stimulation declined during the nonbreeding season, and they normally ignored model females during this period. It is probable that males, even if unpaired, will defend an individual winter territory, either at a suitable breeding site where they are permanently resident or in a wintering area. During the breeding season, territorial males were usually very aggressive to all other conspecific individuals older than about three weeks (the age at which juveniles were rejected by their parents), although they sometimes attempted to court and mate with immigrant females, model females and independent female offspring (Section 9.4.10.1).

Observations at Bisley Valley suggest that those females which remain paired during the nonbreeding season also show some territorial activity at this time, although they were often very retiring and difficult to observe, and were only occasionally induced to attack a model female Buffspotted Flufftail, usually preferring to remain in cover and give occasional territorial or aggressive calls. Although the male always played the major part in territory defence at all times of the year, during the breeding season females were very aggressive to live and model females, and to immature birds of both sexes, although they were never seen to attack a model male. Both males and females consistently ignored a model 11-day-old chick at all times of the year.

The Buffspotted Flufftail does not have a loud, far-carrying and frequently-used territorial call equivalent to the Redchested Flufftail's *DUEH* (Table 4.1, Calls M10 and F3), the Striped Flufftail's *KI-KER* (Table 7.7, Calls M4 and F1), and the Whitespotted Flufftail's *GOONG*, which are given by these species throughout the year (Chapters 4 and 7; Taylor & Taylor 1986). Most of its calls (Tables 9.2 and 9.3) are of low frequency and are audible only at close range. Its repertoire contains a higher proportion of close-range aggressive calls than is found in the Redchested Flufftail (Table 4.3) and long-range communication is restricted to the advertising hoot and its variants (Table 9.2). Thus seasonal variations in territorial behaviour cannot easily be assessed by calling patterns, except that the birds which utter strong advertising calls at any time of the year may be presumed to be territorial

TABLE 9.2

Buffspotted Flufftail vocalizations described during the study. All calls are repeated as a sequence unless otherwise specified. D = days (age of young); F/Y, M/Y, M/F = equivalent calls of female, male or young; see relevant sections of table for details. Contexts: A = advertising; C = courtship; E = encouraging young to feed; G = aggression; M = mating; S = soliciting food (young); T = territorial; X = warning/alarm; Z = contact. Secondary or possible contexts are placed in parentheses.

## ADULT MALE

No.	Description & phonetic rendering	Context	F/Y
M1	Long hoot: 00000000; loud (established territory holder) or soft, sometimes wavering, (bird not yet established)	A	
M2	Shorter hoot with "voice-break" to higher-pitched note	A(T)	
M3	Long, plaintive, moaning hoot, falling in pitch	A(T)	F3
M4	Very low-pitched MOO-WOOOO, much more resonant than M49	A(T)	
M5	Quiet moo and descending feeble hoot of intruding male in an established pair's territory: MOO-00000	A(T)	
M6	Long, quiet, very low-pitched moaning, wavering hoot	T(G)	
M7	Long, low-pitched, quiet hoot-grunt: 000000-GRH, sometimes preceded by call M70	T	
M8	Quiet hoot, rising in pitch, of non-established bird	T(A)	
M9	Faint low groaning hoot, irregular and descending in pitch: GROOOO, of territorial male in nonbreeding season	T	F4
M10	Short, very low-pitched hoot, preceded by grunt: GRUG-OO	T(G)	
M11	Gulps: GUG-GUG; GUG-A-DUG; UG-UG to taped playback	T	F5
M12	Grunts: GRUH or GRG; also given by birds in the hand	T(G)	F6
M13	Quiet, rapid, higher-pitched version of call M19: NI-NI, usually given only from cover	T(G)	F7
M14	Throaty, buzzing, low-pitched GZZZZZZZ, to taped playback	T(G)	
M15	Quiet growls: GRRR, in hand and after chasing immature	G	F10
M16	Quiet growl-squeak: GRRR-EEK	G	
M17	Guttural GUH after chasing rat with calls M25	G	
M18	Long GRRREK-GRRREK to model male and taped playback	G	
M19	Common aggressive call used in most attacks: nasal NÉ-NÉ	G(T)	F14
M20	Loud NAA-NAA, standing close to model male after attack	G	
M21	Very annoyed high-pitched NERK-NERK to male decoy, observer and playback of call M48	G	F15
M22	Slow CHÉ-CHÉ given by territorial male in winter before attacking model male	G	
M23	Low-pitched rapid CHÉ-CHÉ; low-intensity aggressive call to immature female	G	

/continued

TABLE 9.2 (continued)

## ADULT MALE (continued)

No.	Description & phonetic rendering	Context	F/Y
M24	Very angry, loud, low-pitched <i>CHER-CHER</i> to model male	G	
M25	Loud <i>CHEK-CHEK</i> in defence of nest and when attacking rats	G	F16
M26	Quiet <i>CHIK-CHIK</i> at approach of rat, before call M25	G	
M27	Annoyed, loud, rapid <i>CHKY-CHKY</i> when aggressive to immature	G	F17
M28	Quiet rapid <i>KEKEKE</i> when seeing rat at some distance	G	
M29	Sharp <i>ZEK-ZEK</i> on attacking model male Redchested Flufftail	G	
M30	Short hard <i>TK-TK</i> to visible observer	G	
M31	Rapid sharp <i>KEK-KEK</i> to playback of call M65 at dusk	G	
M32	Grating <i>KER-KER-KER-KRE-KRE-KRE</i> to playback of call M48	G	
M33	Harsh, grating <i>KRE-KRE</i> when attacking model male	G	
M34	Nasal, grating, low-pitched <i>CHÉÉÉÉ</i> in hand	G	F18
M35	Buzzing <i>ZEE-ZEE</i> to observer and to model female	G	
M36	Buzzing hum: <i>MMMM-MMMM</i> to visible observer	G	
M37	Snake-like hiss at nest to human intruder	G	
M38	High-pitched rattle: <i>TRRRRR</i> , after attack on model male	G	
M39	Plaintive descending <i>NEEEEAA</i> in hand	X(G)	
M40	Sharp <i>NEK</i> to model female	X(G)	
M41	Loud <i>DIK-DIK</i> when running after chick released from trap	X	
M42	Quiet <i>ZUK</i> or <i>TZUK</i> to family when going to roost	X(Z)	F21
M43	Warning to young of unseen danger: <i>KO-KO-KO-ZUK-ZUK-ZUK</i>	X	
M44	Very low-pitched mooing hoot: <i>MOOOOO</i> , after call M52	C(A)	
M45	Long, low-pitched, quiet hoot, sometimes falling in pitch	C	
M46	Low-pitched hoot with voice-break in middle: <i>OOO-EEE-OOO</i>	C(A)	
M47	Very quiet wheezy hoot, to attract female	C	
M48	Common courtship call: <i>MOO-EEE</i>	C	
M49	Loud moo-hoot: <i>MOO-WOOO</i>	C	
M50	Complex call sequences: <i>MOO-OO-SCRR-WEE</i> ; <i>OO-OO-WAA</i> ; <i>MOO-SQUEE-EE</i> ; <i>MOO-MOO-WEE</i> ; <i>MOO-SCHH-WEE</i> , with calls M53	C	
M51	Moo-whine: <i>MOO-ÉÉÉÉÉ</i> , after call M54	C	
M52	Quiet <i>MOO-OOP</i> (combining elements of calls M48 & M68)	C	
M53	Very rapid SLHs (call M65) with call M48	C	F24
M54	Very long, quiet SLHs (call M65) to playback of call M48	C	
M55	6-8 short quiet hoots, slower at the end: <i>O-O-O-OO-OO-OO</i>	C	F25

/continued

TABLE 9.2 (continued)

## ADULT MALE (continued)

No.	Description & phonetic rendering	Context	F/Y
M56	Double WEE-WEE or WAA-WAA, like second part of call M48	C(T)	
M57	Short gulping hoot: GOOP, infrequently after call M70	C(M)	
M58	Quiet GUGUGU-GROO, calling female to nest	C	
M59	GROO-EEE and GROO, after failing to attract female to nest	C	
M60	Rapid G-G-G-G-G, becoming GUG-GUG-GUG, with call M61	C	F27
M61	Quiet wavering growls: GRR-RR-RR, with call M60	C	
M62	Short GZZZ, before call M63	C	
M63	Quiet G-G-G-GRR-GRR	M(C)	
M64	Rapid GRUK-GRUK or GRKGRK, sometimes with call M68	M(C)	F28
M65	2-5 short low-pitched hoots (SLH): OO	Z	F31
M66	Soft rapid series of 3-4 short hoots, to chicks: OO-OO-OO	Z	F32
M67	Short quiet GOO, after call M70	Z(C)	F33
M68	Intermittent quiet OOP notes; usually preceding birds' appearance at food	Z(C,M)	F34
M69	Little quiet BOOP or BUP notes to chicks	Z	F35
M70	Low quiet GRUK, sometimes repeated; may follow calls M57 & M67	Z(C, M, T)	F36
M71	Conversational quiet GRUG-GRUG-GRUG-OO-OO to female at food	Z	
M72	Conversational quiet DUK notes to mate or young, also to observer in hide whenever food ran out	Z	F37
M73	Inquisitive quiet CHERP-CHERP to visible observer and to playback of call M48	Z(C)	
M74	Faint CHUK-CHUK; CHUK-A-CHUK-CHUKKI-CHUK; CHKI-CHKI etc.	E	F38
M75	Faint squeaking TEEKY or TIKKI notes	E(Z)	

/continued

TABLE 9.2 (continued)

## ADULT FEMALE

No.	Description & phonetic rendering	Context	M/Y
F1	High-pitched hoot, rising in pitch: OOOOOO	A	
F2	Rapid high-pitched hoots, rather like call F1 of the Redchested Flufftail	A	
F3	Long, plaintive, moaning hoot, falling in pitch	T	M3
F4	Quiet moaning hoot: GROOOO, falling in pitch	T	M9
F5	Gulps: GUG-GUG; GUG-A-DUG; UG-UG to taped playback	T	M11
F6	Grunts: GRUH or GRG; also given by birds in the hand	T(G)	M12
F7	Quiet, rapid, higher-pitched version of call F14: NI-NI	T(G)	M13
F8	Rapid buzzing grunt: GZZUNNG or GUUNNG	G	
F9	Very low-pitched buzz: GZUU-GZUU, to immature female	G	
F10	Quiet growls in hand: GRRR	G	M15
F11	Very loud prolonged growls in hand: GRRRRRR	G	
F12	Low-pitched GRRK in aggressive display to unseen animal	G	
F13	Quiet dry CRK-CRK from cover to observers	G(X)	
F14	Common aggressive call used in attacks: nasal NÉ-NÉ	G(T)	M19
F15	Sharp NERK when attacking model female	G	M21
F16	Loud CHEK-CHEK to observer near chicks	G	M25
F17	Loud CHK-CHK-CHK-TKY-TKY-TKY, chasing immature female	G	M27
F18	Harsh nasal CHÉÉÉÉ in hand	G	M34
F19	Harsh CHEEEK after call F14	G	
F20	High-pitched whine: ÉÉÉÉÉÉ (2 seconds long) to tape hoots	G(T)	
F21	Agitated ZUK when approaching chicks in box	X	M42
F22	Clicking TIK-TIK as male displays to model male	X(G)	
F23	Loud BUP-BUP with call F14, to alarm calls of chicks	X	
F24	Very rapid series of call F31 (SLH)	C(M)	M53
F25	6-8 short quiet hoots, slower at the end: O-O-O-OO-OO-OO	C(M,Z)	M55
F26	Short É É in response to male's call M58	C	
F27	Rapid G-G-G-G or GUG-GUG	C	M60
F28	Rapid quiet GRUK-GRUK	M(C)	M64
F29	Quiet GZEK-GZEK, ZEK-ZEK or ZEKKI-ZEKKI	M	
F30	Faint, sharp, high-pitced KE-KE	M	

/continued

TABLE 9.2 (continued)

## ADULT FEMALE (continued)

No.	Description & phonetic rendering	Context	M/Y
F31	2-5 short low-pitched hoots (SLH): OO	Z	M65
F32	Soft rapid series of 3-4 short hoots to chicks: OO-OO-OO	Z	M66
F33	Short quiet GOO, after call F36	Z(C)	M67
F34	Intermittent quiet OOP notes; usually preceding birds' appearance at food	Z(C,M)	M68
F35	Little quiet BOOP or BUP notes to chicks	Z	M69
F36	Low quiet GRUK, sometimes repeated	Z	M70
F37	Quiet, conversational DUK notes to mate or young	Z	M72
F38	Faint CHUK-CHUK or CHUK-A-CHUK	E	M74

/continued

TABLE 9.2 (continued)

## YOUNG BIRDS: 1-70 DAYS OF AGE

The figures for days (D) represent the period over which the call was heard.

No.	Description & phonetic rendering	Context	M/F
(a) DOWNTY CHICK (1-7 DAYS)			
Y1	Short ZI, possibly a precursor of call Y2; 2D	Z	
Y2	Loud cheeping ZEEK, given as soon as chicks are active out of nest; very common 3-7D, less to 20D, rare to 28D	Z(S)	
Y3	Shrill WEE or WEEP, descending in pitch; distress call; 3D	X	
Y4	Piercing loud squeal in hand: SQUEEE, SQUEEA or scratchy SCHREE; distress call; 3-31D	X	
(b) FIRST PLUMAGE TO INDEPENDENCE (8-20 DAYS)			
Y5	Trill: PREEE, replacing call Y2 as the predominant contact call; precursors heard from 6-7D; predominates from 10-11D to 20D; occasional to 28D; once at 69D	Z(S)	
Y6	Plaintive ÉÉÉ, intermediate between calls Y5 & Y2; 11-17D	Z	
Y7	Sibilant SI preceding early trills (call Y5); 10-11D	Z	
Y8	Sharp ZIK (possibly a derivative of call Y1); 14D	Z	
Y9	TEEE, harsher TÉÉÉ or shorter TI-TI, intermediate between calls Y5 and Y23; 17-25D	Z	
Y10	Squeaky high-pitched trill; 17D	X	
Y11	Tiny squeaks in hand or to aggressive adult; 19-34D	X	
Y12	Tiny squeak when close to parent, soliciting food; 11D	S	
Y13	Tiny musical TIK-TIK or PIP-PIP when with parent; 9-20D	S(Z)	
Y14	Plaintive PEE, DEE or DI-DI when parent not close; 10-28D	S	
Y15	Plaintive SEEE to approaching adult; 17D	S	
Y16	Soft PEEP when close to feeding parent; 17-28D	S	
Y17	Soft CHKI-CHKI, TKY-TKY, CHK-CHK, with parents; 17-20D	S(Z)	M74
Y18	Soft conversational TEE-CHRE-CHRE-CHRE-CHRE when fed; 19D	S(Z)	

/continued

TABLE 9.2 (continued)

No.	Description & phonetic rendering	Context	M/F
<b>(c) INDEPENDENCE TO END OF POSTJUVENILE MOULT (21-70 DAYS)</b>			
Y19	Pure high-pitched note: <i>EEEEEE</i> or <i>WEEE</i> , derived from call Y9; from 27D	Z	
Y20	High-pitched short hoots; develop earliest (from 33D) in the absence of adults, later (to 69D) if adults present	Z	M65
Y21	Plaintive <i>KEE-KEE</i> of male in trap; 25D	X	
Y22	High-pitched <i>KLEE-A</i> of female in hand; 20D	X	
Y23	Descending <i>EEE</i> , alone or with trill, of bird in trap; 21D	X	
Y24	Explosive <i>DUK</i> of female in trap; 31D	X	F21
Y25	Sharp <i>CHK-CHK</i> of female approached by adult male; 55D	X	
Y26	Loud <i>CHUCK</i> of male approached by adult male; 58D	X	
Y27	Loud sharp <i>JEEP</i> of female when courted by adult male; 49D	X	
Y28	Sharp quiet <i>CHIKKI</i> or <i>SQUIKKI</i> ; 28D	X(G)	
Y29	Rapid <i>CHIP-CHIP</i> followed by <i>PEE-PEE</i> ; 21D	S	
Y30	Grunts: <i>GRUG</i> or <i>GRG</i> , in hand; 27-70D	G	M12
Y31	Short growl: <i>GRRK</i> in hand; 33D	G	M15
Y32	Short <i>CHI-CHI</i> in hand; 35D	G	M23
Y33	High-pitched <i>CHEK-CHEK</i> in hand; from 38D	G	M25
Y34	Squeaky <i>EEE-CHEEE</i> ; precursor of call Y35; 24D	G	
Y35	Loud <i>CHEEE</i> , <i>CHAAA</i> or <i>CHWEEE</i> in hand and on release; 30-70D	G	M34
Y36	Quiet <i>E</i> or <i>E-E</i> with calls Y35, in hand; 35D	G	
Y37	Cricket-like <i>CREE-CREE</i> from male; 69D	G	

TABLE 9.3

Different vocalizations of Buffspotted Flufftails described during the study.  
 Abbreviations: A = adult; C = chick (1-7 days old); F = adult female; I = immature (21-70 days old); J = juvenile (8-20 days old); M = adult male; Y = young (i.e. C, I and J).

Vocalization function	Total calls	Total given by:					Total shared by:	
		M	F	I	J	C	M&F	A&Y
Advertising	6	5	2				1	
Territorial	10	9	5				4	
Aggressive	34	24	13	8			6	5
Alarm	18	5	3	10	3	2	1	1
Contact	17	9	7	5	6	2	7	1
Courtship	20	19	4				3	
Mating	4	2	3				1	
Encouraging to feed	2	2	1				1	
Soliciting food	8			3	7			
<hr/>								
Grand totals :	119	75	38	26	16	4	24	7

(Section 9.4.8). Advertising calling has been recorded, albeit at a greatly reduced level, throughout the nonbreeding season in some areas of Natal (Section 9.4.8), suggesting that at least some winter residents in these areas are territorial.

Observations indicated that the level of territorial activity varied during the breeding cycle. The information collected is too great to allow detailed analysis to be made for this thesis, but it is clear that breeding males show the strongest aggressive behaviour at the beginning of the breeding season before the first clutch is laid, while strong aggressive reactions are also given between broods at times when mating, egg-laying and incubation are in progress (see Section 9.4.10). However during hatching and for 16 days afterwards males showed less aggression, none attacking a model male in this period. In contrast, the males attacked conspecific females only during this period, while at all other times during the breeding cycle they often courted or attempted to mate with live or model females.

#### 9.4.5.3 Aggressive behaviour

Observations were made throughout the year of the reactions of male and female Buffspotted Flufftails to models, but observations of the reactions of the birds to their images in mirrors were made only during the breeding season. Many aggressive displays and attacks by both sexes were filmed. On most occasions the birds were first attracted by taped playback of territorial, advertising or courtship calls, which were continued during the birds' displays and attacks.

Threat displays from the male were given to model males and females, and also to mirrors. When first investigating a stimulus object the male usually approached as close as possible in cover and, if not confident (e.g. when the bird had not yet established a territory, or when the observer was unconcealed), crept around cautiously with body, head and tail stretched out in a horizontal line, all plumage compressed and with sinuous movements of the head and neck. Four types of threat display were recognized, all being given in the open near the stimulus object.

1) **Swollen creep.** This is the most common display. It indicates strong aggression and is usually given before and between strong attacks. The bird crouches and creeps slowly up to the model or mirror, with the head, body and tail held horizontally, the neck retracted, the tail spread so that the orange and blackish bars are well visible, the head and body plumage raised and the wings often drooped so that the tips touch the ground. The approach is often accompanied by aggressive *NÉ-NÉ* or other calls (Table 9.2, Calls M19, M21, M22 and M24). The male either pauses near the object and crouches lower, or walks slowly round it, often still calling, before attacking or moving away.

**2) Droop-winged run.** This display appears to indicate a lower level of aggression and was given in situations where a conflicting urge was probably present, such as that to flee when the male approached a stimulus object inside a trap, or that to court when an unmated male first approached a strange female (see Section 9.4.10.1). The bird runs round the model, drooping either one or both wings and sometimes giving *NÉ-NÉ* calls.

**3) Bow.** This display was rarely seen and was given immediately before attacks on a model male. The attacker crept out of cover with raised plumage and flexed legs, approached the side of the model, bowed forwards with head raised and breast touching the ground, opened, shuffled and closed the wings and then attacked the model.

**4) Strut.** This display was given only once to the mirror and consisted of a strutting walk around the mirror, the bird having the body plumage raised, the head stretched up and the head feathers raised; no calls were made. The bird's mate was close by, and this display appeared to be closely allied to the courtship strut (Section 9.4.10.1).

The type of attack varied with the intensity of the bird's aggression, and it was always observed that a model male in a normal stance with the head raised (i.e. in a non-aggressive pose) was attacked more violently than one in a crouched, aggressive stance. Three types of attack were recognized.

**1) Glancing attack.** This was the least intensive attack and was sometimes given by males when first presented with a model male, or when wary of a visible observer, as well as by paired males to a model female. The bird approached silently in cover to a position alongside or behind the model, crouched and ran out, delivered a glancing peck to the model's head, veered off without pausing and ran back into cover.

**2) Lunge and retreat.** In this the male approached the side of the model in cover, crouched and then ran out to deliver from one to five hard lunging pecks at the model's head or body before running back into cover, from which it then gave *NÉ-NÉ* calls. This attack was less intense than type 3 and was usually given by males in the presence of an exposed observer; it was usually made to model males, occasionally to model females. During the attack one or both wings were sometimes flicked, opened or drooped.

**3) Fluttering jump.** This was the most violent attack and was made from a position in the open, close to the model or mirror, often after the performance of Threat Display 1. The male, usually with open or drooped wings, rushed at the object, approaching a model from any angle (usually from the side). It jumped and fluttered up and down, pecking violently at the head and neck region and sometimes also striking with the feet. Attacks were often brief, involving only a few pecks, but more aggressive birds made longer attacks, sometimes circling a model, pecking at other parts of the body and pulling

feathers. All pecks were delivered horizontally or upwards, some being strong enough to rock the model on its wooden base. Buffspotted Flufftails were never seen to stretch up next to a model and peck downwards at its head and neck, the common form of attack made by the Whitespotted Flufftail (Taylor & Taylor 1986). In the most violent attacks, given to models in the head-up, non-aggressive position, the male jumped on to the model's back or head, sometimes knocking it over; if the model remained upright the male stood on its back for long periods, pulling feathers out of it and pecking violently at its head and neck. Occasionally a wing was broken loose, or the model was scalped and the attacker then pulled the cotton-wool stuffing out of it. Such attacks were accompanied by much aggressive calling. Males often examined the edges and back of the mirror, looking for their adversary and, like the other two species studied, progressively lost interest in both the mirror and the model, eventually ignoring them.

Breeding-season attacks on independent young from previous broods, and on temporarily resident unknown immatures, were much less violent, usually involving the male running silently at the young bird, which immediately ran or fluttered off. If very aggressive, the male gave *NÉ-NÉ* or other calls (Table 9.2), and sometimes ran or flew after the intruder for several metres, even chasing it up into overhanging low branches.

The reactions of territorial female Buffspotted Flufftails to model females were similar to those of males, the birds performing Threat Display 1 and Attacks 2 or 3 but never actually dismembering a model. Females were particularly prone to making a slow, creeping, menacing walk to within 5 cm of the model, and pausing for several seconds to stare fixedly at it before suddenly unleashing a violent attack. They were rarely induced to react to mirrors; only threat displays (Type 1) were seen and after the initial display the female would investigate the side and rear of the mirror. Their aggressive reactions to independent young and strange immatures were identical in form and intensity to those of males.

As in the Redchested Flufftail (Chapter 4, Section 4.4.5.2), vocal stimuli are often important for the release of attack behaviour, and attacks were stimulated, intensified and prolonged by taped playback. Experiments on males using models of different colours and patterns showed that visual stimuli are also important, the birds normally showing great interest in, but no aggression towards, models having an atypical colour or pattern such as body stripes instead of spots, a plain black or red tail instead of bars, a black head and neck, and white (instead of buff) spots on the upperparts. However at Danville Park, a breeding male in a forest territory adjacent to a wetland Redchested Flufftail territory was once induced to make one very mild lunging attack on a model male Redchested Flufftail, after 30 min stimulation with taped playback of Buffspotted Flufftail calls from a loudspeaker concealed near the model.

At Scotston, adults and fully grown young of both sexes were aggressive to Olive Thrushes *Turdus olivaceus* and Cape Robins *Cossypha caffra*, which frequently attempted to take mealworms at the feeding stations. The flufftails were dominant to these birds, which were the only species making extensive use of the same feeding habitat in the garden (Section 9.4.6), and they ignored birds such as sparrows and weavers, which drank and bathed at the water dish, and species such as the Dusky Flycatcher *Muscicapa adusta*, which very occasionally took mealworms. Displays were usually silent (or occasionally preceded or followed by quiet *NÉ-NÉ* calls) and involved the bird crouching forwards facing the intruder, raising its plumage and spreading its wings to the side before raising them over its back to present their expanded upper surfaces to the intruder. If this display did not cause the other bird fly off, the flufftail then ran at it, when it always retreated. Other types of attack behaviour, directed against potential predators, are described in Section 9.4.10.4.5.

#### 9.4.6 Feeding methods, food and energy requirements

During field observations the birds were recorded eating many types of insect, including small ants, termite workers and alates, flies, adult Hemiptera, adult and larval Coleoptera, small moths, and lepidopterous larvae, as well as earthworms up to about 10 cm long, small gastropods, minute Collembola only 1.5-2 mm long, woodlice (Isopoda) and small spiders. They were not seen to eat seeds, which were not usually available at the observation sites. At Scotston, adult and young birds readily ate mealworm larvae (rarely pupae) but rejected the adult beetles, and occasionally ate crushed oat grains from the mealworm dishes. Discussions with local aviculturalists who have kept the species in aviaries revealed that captive birds took frog spawn (J. Taylor pers. comm.) and readily ate grass seeds such as "manna" *Pennisetum typhoides* and "teff" *Eragrostis tef* (R. Davidson pers. comm.).

Although some birds fed in shallow water (see below) almost all foraging took place on the ground, most frequently in leaf litter but also on soil among plants in flower beds, on moss-covered rocks, at the edges of tracks, in mown or very sparse grass, under low spreading cover on the forest floor or in vegetable beds (e.g. among potato and marrow plants), and even among tall maize plants in gardens. The birds either walk slowly along, searching the ground as they go, or move in short rapid runs with pauses for intensive searching. When moving slowly and searching the ground intently they regularly look up and stand motionless for a few seconds before continuing foraging. The bill is used to turn over, push or throw aside dead leaves and to move aside moss and low plants, while the feet are occasionally used to scratch among dead leaves. The birds probe beneath the edges of stones and rocks, and into leaf mould, soft earth and mud, to find earthworms and larvae, and into decomposing wood on the forest floor. Very short mown grass is occasionally searched in the same

manner as open ground. Leaves (especially their undersides and those with holes) of low-growing plants are scrutinized in passing for caterpillars, moths, flies, beetles, bugs, etc. Birds will run rapidly to catch small creeping or low-flying invertebrates. They pick up lumps of earth, which they shake and drop, obviously trying to break them or dislodge small invertebrates, and they perform similar actions with curled-up dead leaves, looking into the end of the leaf-tube after each attempt. Very large prey items are often passed sideways through the bill several times before they are swallowed.

When taking food from the ground the birds often peck vertically downwards but sometimes crouch and give an almost horizontal peck with the head tilted to one side. As in the Redchested Flufftail (Chapter 4, Section 4.4.6), the tail is often wagged or vibrated rapidly from side to side when feeding intensively, especially at rich food sources such as the mealworm dishes. They avoid feeding in rain, when the constant movements of leaves and the drip of water on the leaf litter disturb them.

Foraging individuals and groups were sometimes observed for long periods, when it was noted that they often confined their activities to a relatively small area, returning regularly to research the same ground; one bird revisited the same spot three times in 30 minutes, but more usually a return was made every 15-30 minutes. At Scotston families with chicks often foraged in one part of the garden for 2-4 days before moving to another part of the territory for a similar period. About half to one-third of the territory was utilized in each period, rough estimates of 1 700 and 1 900 m<sup>2</sup> being obtained for the two garden territories. Similar behaviour was noted in the Whitespotted Flufftail at Kakamega Forest, Kenya, where a pair with young changed their foraging area every 2-5 days, each area covering about 1 400 m<sup>2</sup> (20%) of the territory (Taylor & Taylor 1986).

At Scotston the birds were less dependent on the mealworm supply after rain, when natural food was more plentiful and easier to obtain on the damp substrate. Similarly, whenever possible the birds foraged on ground which had been wetted by garden sprinklers. In areas where the birds' occurrence is normally seasonal, residence may be prolonged by sprinkling and irrigating the inhabited areas throughout the year, as is the case at the Franklin site (Section 9.4.3.2). The birds' association with water has already been discussed (Section 9.4.2) and they readily take prey from shallow water: the Scotston birds very quickly became adept at taking mealworms from the water in their bathing dish, immersing their heads fully to do so, and the chicks learned to perform this feeding action (albeit less efficiently) before they were fully grown (Section 9.4.10.4.4). In contrast, Olive Thrushes and Cape Robins never learned to take mealworms from the water, although Brown Rats *Rattus norvegicus* quickly did so. The male Buffspotted Flufftail which foraged in the marsh at Danville Park (Section 9.4.2) behaved exactly like a Redchested Flufftail, feeding in mud and shallow water, among *Phragmites* and *Typha* clumps, and searching the sheaths of dead leaves on low stems.

In Natal several other species of small bird widely exploit the terrestrial foraging niche occupied by the Buffspotted Flufftail in indigenous forest and dense bush, feeding on similar prey in soil and leaf litter. These species include the Terrestrial Bulbul *Phyllastrephus terrestris*, Spotted Thrush *Turdus fischeri*, Kurrichane Thrush *T. libonyana* and Olive Thrush, Cape Robin, Natal Robin *Cossypha natalensis*, Whitethroated Robin *C. humeralis*, Starred Robin *Pogonocichla stellata* and Brown Robin *Erythropygia signata*. Of these species, only the Olive Thrush and the Cape Robin have been seen to exploit the flufftail's terrestrial feeding niche in the interior of exotic vegetation in the gardens under observation, but they also forage extensively away from cover on lawns and open areas, where the flufftails rarely venture. In situations where all feed together the flufftail appears to be dominant, and it is clear that, in Natal, only the flufftail makes extensive use of the rich foraging substrates associated with dense exotic cover in gardens, etc. The fact that it can do so has undoubtedly contributed to its continued success and its present widespread distribution (Section 9.5).

The gizzard contents of 52 casualties obtained in Natal are summarized in Tables 9.4 and 9.5. The numbers of prey eaten were estimated as accurately as possible from all remains, including hard parts such as mandibles, legs, wings and fragments of elytra. The tables show that this flufftail takes a wide range of invertebrate prey but most food items ( $n = 1020$ ; 77.2%) were ants and termites, while almost 10% were beetles whose remains were found in 65% of the gizzards. Counts of this type may not accurately reflect the relative importance of all invertebrate groups in the bird's diet: small hard items like ant mandibles must survive in the gizzard for longer than other fragments, while soft, rapidly digested prey such as earthworms leave few traces. Thus, field observations indicated that earthworms are taken frequently and are sometimes an important part of the diet, a fact which is not clear from the small number of earthworms found in the gizzards. Relative sizes of prey are also important: two gizzards were filled by single large cockroaches (Blattidae), three by single grasshoppers (Acrididae), and one by three very large amphipod crustaceans, while another was packed with 183 small termite workers. Such observations suggest that very large prey sometimes make a significant contribution to the diet.

Table 9.5 shows that some invertebrate types, such as cockroaches, grasshoppers and bugs (Hemiptera) were found only in gizzards from coastal sites, while weevils (Curculionidae) were most numerous in gizzards from inland localities. Such findings suggest a variation in the availability of prey types by altitude, a factor discussed in more detail below and in Chapter 10. Insufficient gizzard samples were available to investigate seasonal variations in diet.

Many gizzards also contained seeds (Table 9.4). Grass seeds, present in six samples in the February-September period, were often fragmented, obviously being food items, but most hard seeds were entire. Of these, seeds of two very common forest-edge trees were abundant in samples from

TABLE 9.4

Summary of an analysis of the gizzard contents of 52 Buffspotted Flufftails obtained as casualties in Natal during the study. Invertebrate food items are each listed in decreasing order of abundance (column 2). No. of items (column 3) is the total number of individuals of each food type recorded in the gizzards (see text). Full details of the invertebrate prey identified in gizzard contents are given in Table 9.5.

Invertebrate food type	Total in sample	% of sample	Gizzards in which found	
			Total	%
Isoptera	518	39,2	18	34,6
Formicidae	502	38,0	34	65,4
Coleoptera	127	9,6	34	65,4
Diptera	53	4,0	7	13,5
Amphipoda	33	2,5	17	32,7
Isopoda	21	1,6	7	13,5
Diplopoda	15	1,1	10	19,2
Mollusca	13	1,0	11	21,2
Blattodea	9	0,7	6	11,5
Orthoptera	6	0,5	6	11,5
Lepidoptera	5	0,4	4	7,7
Hemiptera	5	0,4	4	7,7
Chilopoda	3	0,2	3	5,8
Oligochaeta	2	0,15	2	3,8
Nematoda	2	0,15	2	3,8
Collembola	2	0,15	1	1,9
Ixodidae	2	0,15	2	3,8
Other invertebrates	3	0,2	3	5,8
<hr/>				
Total	1321	100	from 50 gizzards (96,2%)	

(continued)

TABLE 9.4 (continued)

Summary of an analysis of the gizzard contents of 52 Buffspotted Flufftails obtained as casualties in Natal during the study (continued): seeds and other items. Seeds are listed in decreasing order of abundance (column 2). Full details of the seeds identified in gizzard contents are given in Appendix 1. Abbreviations: *S. mauritianum* = *Solanum mauritianum* (Bugweed); *T. orientalis* = *Trema orientalis* (Pigeonwood). species identified were: *Panicum aequinerve*, *Setaria megaphylla* and *Oplismenus hirtellus*.

Type of item	Total in sample	% of sample	Gizzards in which found	
			Total	%
Grass seeds*	69	100	6	11,5
Hard seeds: <i>S. mauritianum</i>	481	48,0	23	44,2
<i>T. orientalis</i>	389	38,8	21	40,4
unidentified	133	13,2	15	28,8
Total	1003	100	from 40 gizzards (76,9%)	
Stones, diam.: < 0,5 mm	2135	89,9	10	19,2
0,5-2 mm	108	4,6	23	44,2
2,1-4 mm	130	5,5	33	63,5
Total	2373	100	from 50 gizzards (96,2%)	

TABLE 9.5

Detailed description of invertebrate food items found in the gizzards of 52 Buffspotted Flufftails obtained as casualties in Natal during the study. Sequencing of items follows that in Table 9.4. Abbreviations: Butts/mths = butterflies or moths; Inl. = inland.

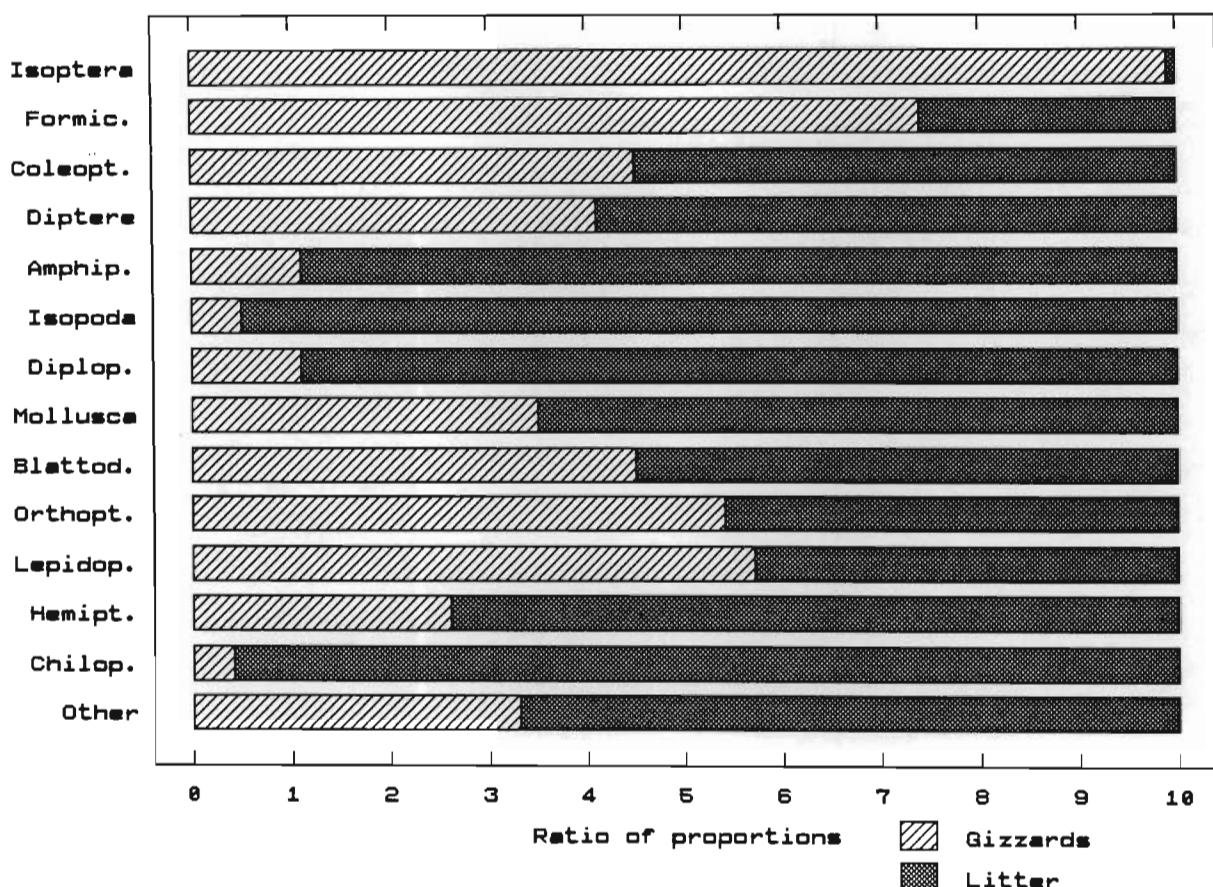
Type	Order/ Class	Family	Representatives found	No. of gizzards		
				Coast	Inl.	Total
Termites	Isoptera	Termitidae	Workers of undifferentiated species	10	8	18
Ants	Hymenoptera	Formicidae	1-5 mm long: <i>Pheidole megacephala</i> , <i>Tetramorium avium</i> , <i>T. grassii</i> Over 5 mm long: <i>Tetramorium spp.</i> , <i>Dorylus helvolus</i> , <i>Pachycondyla spp.</i>	10 9 1 2 2 2	8 12 2 2 2 3	18 21 3 4 4 5
Beetles	Coleoptera	Carabidae Scarabaeidae Lampiridae Tenebrionidae Chrysomelidae Circulionidae	Unidentified adults " " " " " " " " " " (weevils) & larvae	3 3 0 5 0 4	7 5 1 7 2 15	10 8 1 12 2 19
Flies	Diptera	Mycetophilidae Calliphoridae	Unidentified larvae " adults	1 1	2 3	3 4
Amphipods	Amphipoda	-	Unidentified	9	8	17
Woodlice	Isopoda	-	Unidentified	5	2	7
Millipedes	Diplopoda	-	Unidentified	7	3	10
Molluscs	Euthyneura	Streptaxidae Endodontidae Urocyclidae	<i>Gulella obovata</i> (gastropod) <i>Trachycystis sp.</i> (gastropod) <i>?Urocyclus sp.</i> (slug)	3 1 1	4 2 0	7 3 1
Cockroaches	Blattodea	Blattidae	Unidentified; includes discrete oothecae	6	0	6
Grasshoppers	Orthoptera	Acrididae -	Unidentified Unidentified	3 2	0 1	3 3
Butts/mths	Lepidoptera	-	Unidentified larvae	1	3	4
Bugs	Hemiptera	Lygaeidae	Unidentified	4	0	4
Centipedes	Chilopoda	-	Unidentified	2	1	3
Earthworms	Oligochaeta	-	Unidentified	1	1	2
Nematodes	Nematoda	-	Unidentified	0	2	2
Springtails	Collembola	Entomobryidae	Unidentified	0	1	1
Arachnids	Araneida Acaria "	Ixodidae Orbatiformes	Unidentified (spider) " (ticks) " (mite)	1 1 0	0 1 1	1 2 1
Flatworms	Tricladida	-	Unidentified	1	0	1

all months of the year: the exotic Bugweed *Solanum mauritianum* predominated in gizzards from inland localities, occurring in 13 (68,5%) of 19 gizzards from mid-altitude sites but only ten (32%) of 31 from coastal sites, while the indigenous Pigeonwood *Trema orientalis* predominated in gizzards from coastal localities, occurring in 18 (58%) of the 31 gizzards but in only three (16%) of the 19 from mid-altitude sites. Many birds eat the fruits of these trees (Oatley 1984; Johnson & Johnson 1993) and it is possible that flufftails at inland sites supplement their diet with Bugweed fruit, especially in the winter when invertebrate food is less abundant, although the birds were never seen to eat these fruits. Pigeonwood fruits may be eaten for the same reason, but most fruiting of this tree occurs during the summer, when invertebrate food is plentiful.

The hard, rough seeds of these two trees are similar in size to the larger stone fragments used for grinding food in the gizzards (Table 9.4), having a diameter of 1,5-2,5 mm. It is possible that these (and other) hard seeds serve this function, and that the flufftails pick them up specifically for this purpose in places where grit is not readily available (e.g. on leaf-litter-covered ground at forest edges).

Figure 9.8 shows the ratio of the proportions of invertebrate groups in the 52 gizzard samples to those of in the leaf litter samples, combining data for all sites and all months. Although such a comparison is of limited value, principally because (a) few of the gizzard samples came from sites where leaf litter was sampled, and (b) leaf litter samples at Underberg include four winter months (May-August) when Buffspotted Flufftails were absent, it does show that termites (Isoptera) and ants (Formicidae) were of much more frequent occurrence in gizzard samples than in litter samples. This may be explained by the relatively clumped distribution of these two types of insect and the failure of most random litter samples to fall in the vicinity of a nest of either insect. The predominance of these food items in the gizzards suggests that the flufftails actively search for ant and termite colonies and eat large numbers of workers when they are found. Other preferred food items appear to be grasshoppers (Orthoptera), and lepidopterous adults and larvae. Invertebrates such as amphipod crustaceans, woodlice (Isopoda), millipedes (Diplopoda) and centipedes (Chilopoda) were present in much greater proportions in the environment than in the gizzards, suggesting that these animals are not preferred food items but, as they are predominantly large prey, the above-mentioned caveat concerning the relative size of food items should be borne in mind.

An analysis of the relative abundance of the major invertebrate-prey groups at the three altitudinally distinct sampling areas of Durban, Pietermaritzburg (Bisley and Ferncliffe) and Underberg showed (Fig. 9.9) that the most numerous invertebrate group varied with altitude, Isopoda being the most abundant at Durban, Amphipoda at Pietermaritzburg and Diplopoda at Underberg. Several other groups usually formed 5-15% of the invertebrate counts in all areas and it is clear that

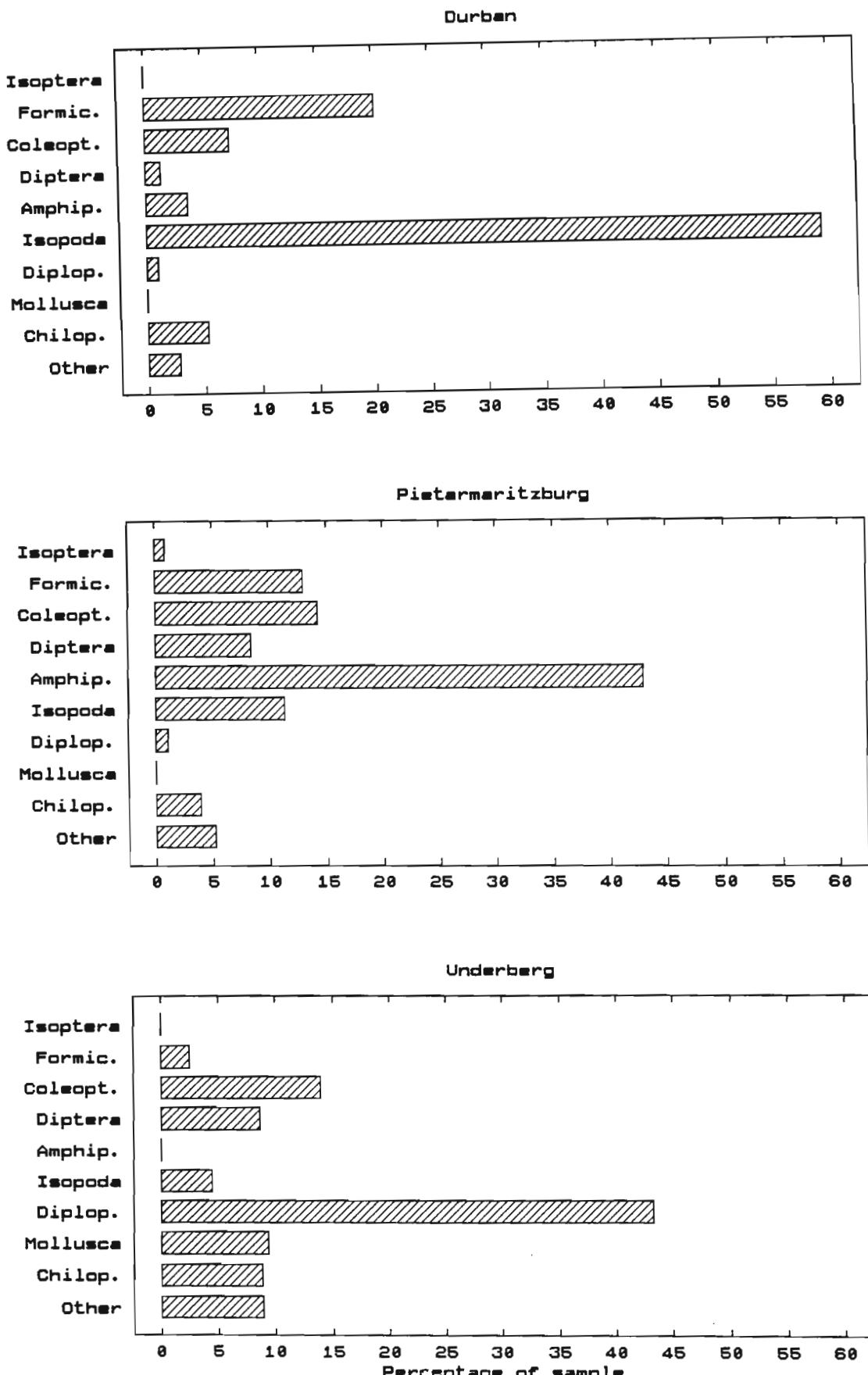


**Fig. 9.8** Ratio of the proportion of invertebrates (by group) in 52 Buffspotted Flufftail gizzards ( $n = 1\ 321$  food items) to those in leaf-litter samples ( $n = 4\ 356$  potential food items). Data from the four sampling sites, at Durban, Pietermaritzburg (2) and Underberg, for the sampling period (1 year) are combined. Abbreviations: Amphip. = Amphipoda; Blattod. = Blattodea; Chilop. = Chilopoda; Coleopt. = Coleoptera; Diplop. = Diplopoda; Formic. = Formicidae; Hemipt. = Hemiptera; Orthopt. = Orthoptera.

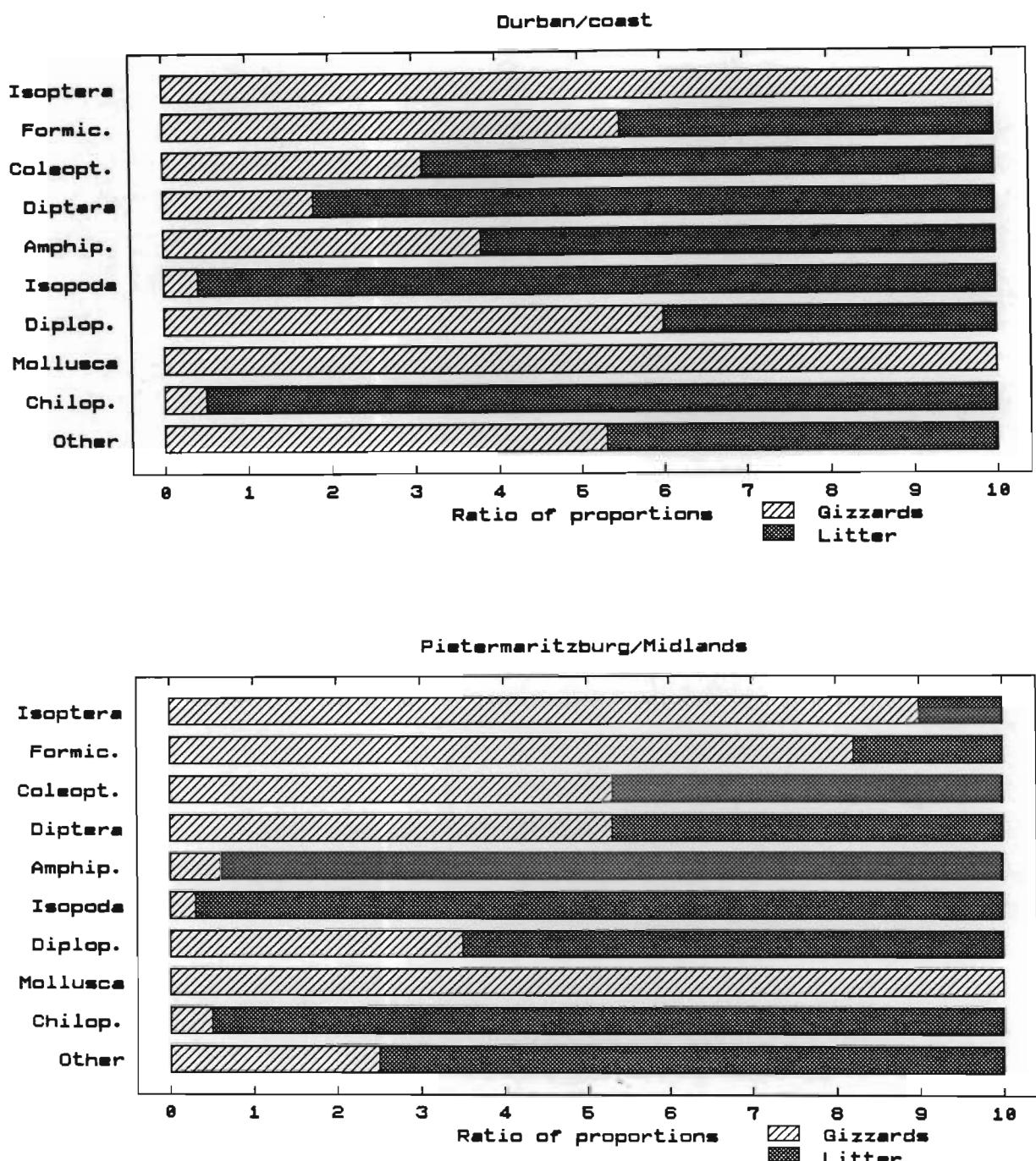
gastropod molluscs and Diplopoda were numerous only at Underberg, where Amphipoda were absent and ants were infrequently sampled. Comparing the ratio of the proportions of invertebrate groups in gizzard samples from coastal sites to those in Durban leaf litter samples, and those in mid-altitude gizzard samples to those in leaf litter from Pietermaritzburg (Fig. 9.10) gives a somewhat different picture from that obtained from the overall comparison shown in Fig. 9.8. While again highlighting the preference for ants and termites, the comparisons also suggest that small gastropod molluscs were preferentially taken in both areas, as were Diplopoda at the coast. Data from Underberg were excluded from this comparison because the small number (two) of gizzard samples does not allow a valid comparison; however in both those gizzards weevils were numerous, while field observations suggested that small gastropod molluscs were taken whenever encountered.

The great diversity of invertebrate prey taken by Buffspotted Flufftails is further emphasized by the fact that only three invertebrate groups which were widespread in leaf litter samples (i.e. present at more than two sampling sites) were not represented in gizzards and are thus possibly not eaten by the birds. They comprise earwigs (Dermaptera), aphids (Aphididae) and harvestman arachnids (Opiliones).

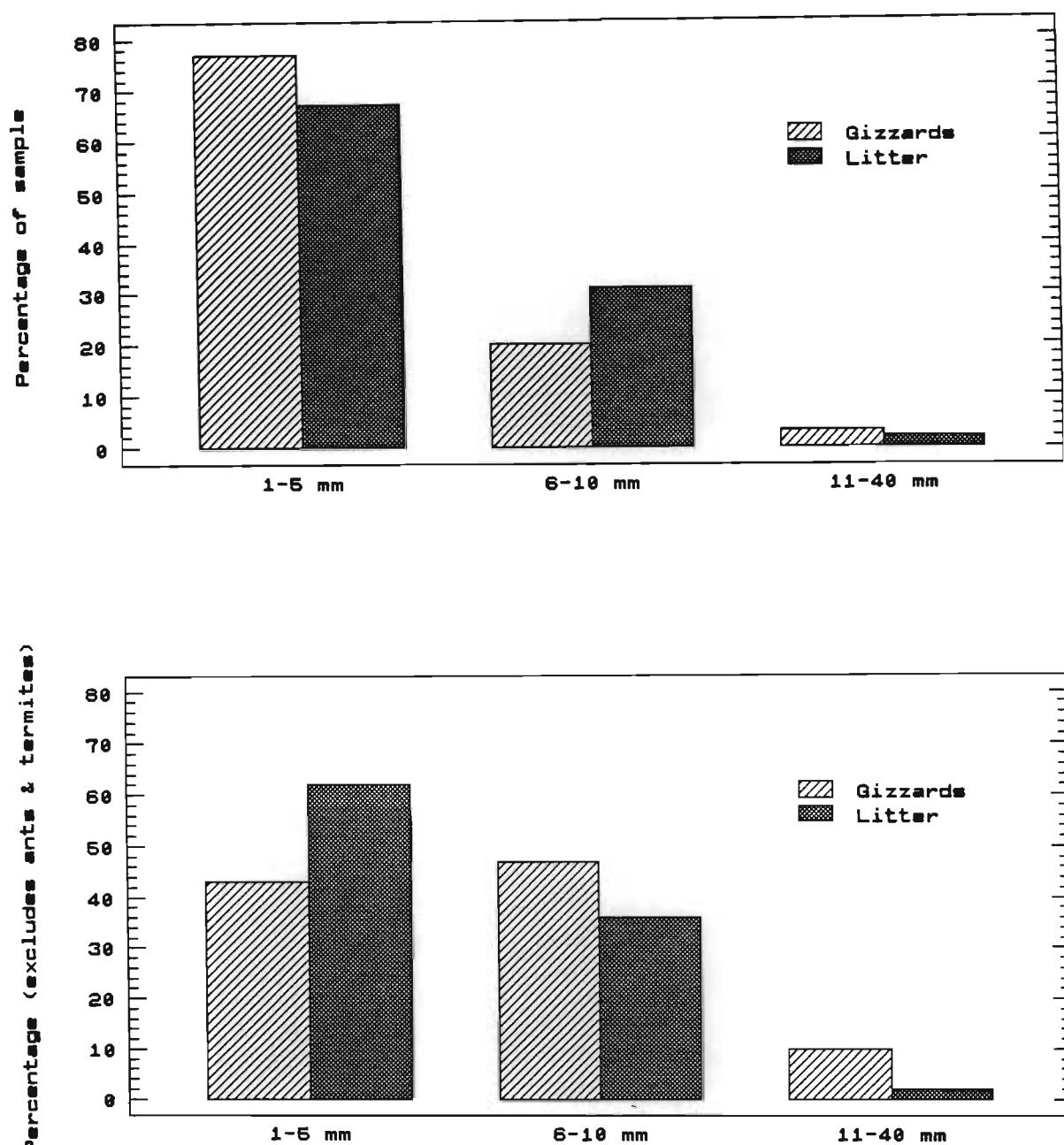
Both gizzard samples and field observations showed clearly that invertebrate food items varied greatly in size. Very small items were recorded infrequently, the smallest (1-2 mm long) being Collembola, ticks (Ixodidae) and minute beetles, while the largest earthworms measured 100 mm, one centipede 17 mm, one millipede 32 mm, a lepidopterous larva 28 mm, grasshoppers and cockroaches up to 15 mm, and amphipods up to 10 mm. Dividing invertebrate prey into three classes according to length (1-5 mm, 6-10 mm and 11-40 mm), a comparison was made between the proportions of items of different classes in gizzards and leaf litter samples, excluding the data from Underberg because of the small number of gizzard samples for that locality. Results are shown graphically in Fig. 9.11. When ants and termites are included in the analysis (Fig. 9.11A) there is a highly significant association between sample size and prey-size class ( $\chi^2 = 57,57$ ;  $P < 0,001$ ), birds selecting for the smallest and largest prey sizes and against the intermediate size. However this analysis may not be satisfactory because ants and termites do not figure significantly in the leaf litter samples, and because it is not known what sizes of these prey types are commonly available in the environment. An analysis excluding these prey types also indicates a highly significant association between sample size and prey-size class ( $\chi^2 = 82,25$ ;  $P < 0,001$ ), but this time the birds are seen to select for the two largest prey-size classes and against the smallest size (Fig. 9.11B). In view of the energetic advantages of consuming fewer and larger prey, this may reflect the birds' true preferences (given a good selection of prey types and sizes) and it agrees with subjective observations

**Fig. 9.9**

Percentages of potential food items for the Buffspotted Flufftail in leaf-litter samples collected during the study. At each site 12 monthly samples were taken, from July 1991 to June 1992, each comprising 5 l of leaf-litter collected at random from Buffspotted Flufftail feeding areas on open ground below dense woody cover. Durban:  $n = 1\,647$  potential food items collected at Danville Park. Pietermaritzburg:  $n = 1\,925$  items, from Bisley



**Fig. 9.10** Ratio of the proportion of invertebrates (by group) in 48 Buffspotted Flufftail gizzards ( $n = 1\ 292$  food items) to those in leaf-litter samples ( $n = 3\ 506$  potential food items) at coastal and inland localities in Natal. Leaf-litter sampling sites were at Danville Park, Durban, and at Bisley Valley and Ferncliffe, Pietermaritzburg. Data from Underberg are not shown because the small number (two) of gizzards obtained do not provide enough food items for comparison. Abbreviations as for Fig. 9.2



**Fig. 9.11** Percentages of invertebrate food items (by size class) in 48 Buffspotted Flufftail gizzards, and of potential invertebrate food items in 12 monthly leaf-litter samples, from all sites except Underberg (see text). A: samples including ants and termites ( $n = 1\ 117$  gizzard items and  $3\ 572$  litter items). B: samples excluding ants and termites ( $n = 298$  gizzard items and  $2\ 972$  litter items).

that fully grown birds, when presented with a dish of mixed small and large mealworms, usually ate the large ones first.

Calculations of daily energy intake (DEI) were made using a mean body mass of 47,32 g ( $n = 55$ ; adults of both sexes) calculated from live masses obtained during this study plus masses obtained from fresh casualties, literature sources, museum collections and the South African Bird Ringing Unit. The calculations gave a Field Metabolic Rate (FMR) of 128,66 kJ/day and a DEI of 171,55 kJ/day. Totalling the overall mean numbers of large mealworms consumed by adults during each hour of the day ( $n = 54$  hours of observation over two breeding seasons at Scotston) gave a mean daily consumption of 157 mealworms, each of which provides approximately 1 130 J of energy (calculated by bomb calorimetry experiments), and a DEI of 177,41 kJ, very close to the theoretical value obtained.

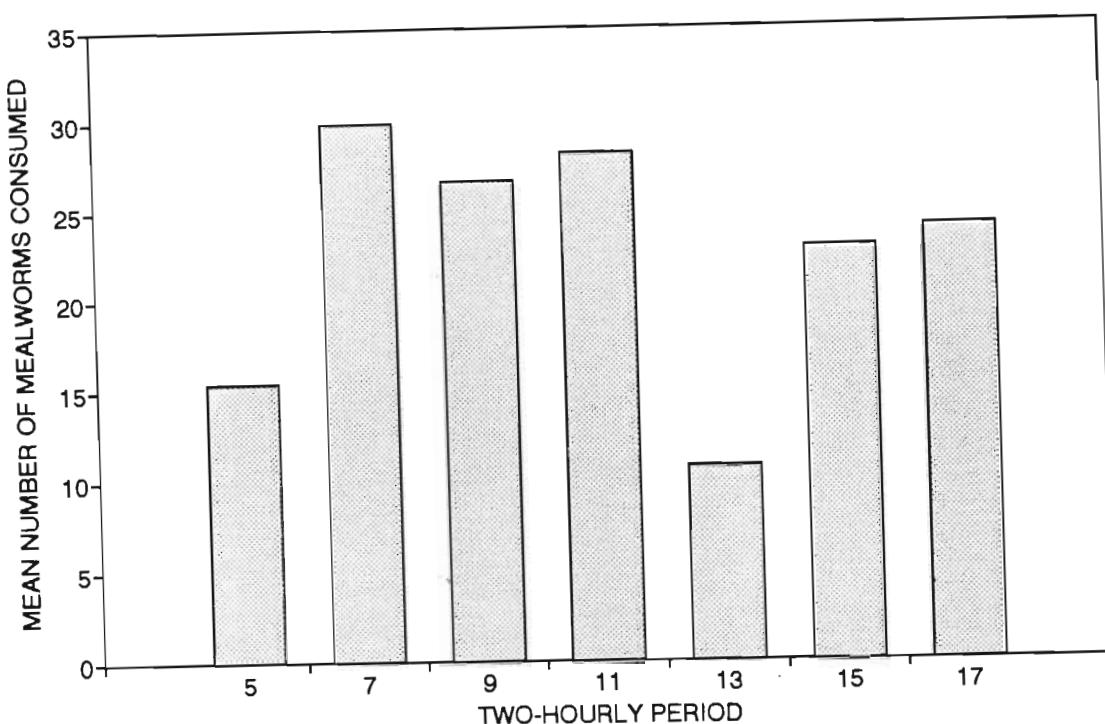
The Scotston birds were seen to feed throughout the day, whether or not they had dependent young, but appeared to forage most actively during the morning and least actively during the hottest period in the middle of the day. The 54 hours' observations of mealworm consumption by adults were used to calculate the mean number of mealworms consumed per two-hour period of the day and the results are plotted in Fig. 9.12. There is a significant association between the numbers consumed and the time period ( $\chi^2 = 12,995$ ;  $P < 0,05$ ), the results suggesting that the birds forage least in the middle of the day, taking most of their food from 07:00-13:00 and from 15:00 until they go to roost. The low early-morning consumption could be explained by the birds' frequently observed habit of foraging for natural prey for some time before first coming to the mealworm dishes.

#### **9.4.7 Other feeding-related behaviour**

The Scotston birds drank daily, often several times per day. Although water was always available at feeding stations, the birds very rarely washed food items.

#### **9.4.8 Vocalizations and calling patterns**

The vocal repertoire of the Buffspotted Flufftail is very extensive and during this study I identified 119 recognizably different vocalizations (Table 9.2), which may be separated into eight groups on the basis of their primary functions (Table 9.3). The number of vocalizations is slightly higher than that recorded for the Redchested Flufftail (Chapter 4, Section 4.4.8; Tables 4.1 and 4.3) and, as in that species, many of the calls are variants of a smaller number of basic call types, such as the advertising hoot (Table 9.2, Call M1), the low-frequency mooing note (Call M44), the short



**Fig. 9.12** Mean number of mealworms eaten by adult Buffspotted Flufftails at Underberg per two-hourly period throughout the day during the months November to February inclusive. Observations from both breeding seasons (1990-1991 and 1991-1992) are pooled. X-axis periods: 5 = 05:01-07:00; 7 = 07:01-09:00 etc., to 17 = 17:01-19:00,

low hoot (Call M65) and the aggressive nasal *NÉ-NÉ* (Call M19). As in the Redchested Flufftail, derivatives of some call types are used in several different contexts, for example quiet *OOP* notes are used in contact, courtship and mating vocalizations, and low-frequency *MOO* notes are given in advertising, territorial and courtship calls.

Buffspotted Flufftails are very vocal during the breeding season but are relatively silent for the rest of the year, a calling pattern similar to that of the Striped Flufftail and quite different from that of the Redchested Flufftail, which frequently makes loud territorial calls throughout the year (Chapter 4, Section 4.4.8). In this connection it has already been noted (Section 9.4.5.2) that the Buffspotted Flufftail does not have a loud territorial call similar to that of the Redchested Flufftail, and that most of its calls are of low frequency and are audible only at close range. The proportions of calls ascribed to different functions differ from those of the Redchested Flufftail (compare Tables 4.3 and 9.3), which has many more territorial calls and fewer aggressive and alarm calls. In the Buffspotted Flufftail the greater recorded variety of courtship calls, of vocalizations associated with feeding dependent young, and of the calls of immatures, must be at least partly the result of the much greater amount of close and intensive study of wild birds during the breeding season.

The four most characteristic calls of this species, which are heard frequently and by which the presence of the birds may easily be established, are the advertising hoot, the ubiquitous short low hoot (SLH) contact call, and the courtship call *MOO-EEE* (Call M48) and the aggressive call *NÉ-NÉ*, which are both frequently heard during the breeding season (and the *NÉ-NÉ* also outside it), especially in response to playback of territorial and courtship calls. Throughout the year the quiet SLH is the best indication of the birds' close proximity to an observer, and in the nonbreeding season it is usually the first indication of the birds' presence. They often give this call from close range in cover when approaching to investigate an intruder, especially if the observer vocally imitates this or any other common call.

The Buffspotted Flufftail's advertising hoot differs markedly from the advertising calls of other *Sarothrura* species in its very low frequency and its intensity, resonance and duration. The maximum distance at which I have heard the call is 2,8 km: this occurred at Mt Currie, where a bird calling on a still night from an isolated forest patch on the mountain was well audible from the lower slopes across the intervening grassland, even though both Redchested and Striped Flufftails were also making their advertising calls at much closer range. The call is often audible from up to 1 km away in wooded country and at Kakamega, Kenya, I found that the call was well audible at night at a distance of 0,5 km through dense equatorial forest and I was able to trace birds calling at this distance, to locate them precisely and to approach them very closely. The call has been described as ventriloquial (Chapter 1, Section 1.2.1.4) but it is not always so, and my numerous observations of

calling birds (by night and day) have shown that the ventriloquial effect is produced when the bird slowly turns its head from one side to the other as it calls; this gives a listener the impression that the call either increases or decreases greatly in volume and makes the source difficult to pinpoint. Both I and other observers in Natal have heard birds call almost continuously throughout the night, sometimes for more than 12 hours, and most calling takes place at night and in the first and last two hours of daylight. Calling in the middle of the day is infrequent, but during the study was occasionally recorded during the breeding season in both clear and overcast conditions; in Pietermaritzburg one bird even called almost continuously from 14:00 to at least midnight on two successive days in January 1990 (S. Auchincloss pers. comm.).

At very close quarters the call often seems relatively quiet but its intensity and resonance at greater distances are remarkable. Almost all strongly calling birds which I have seen have been calling from an elevated perch in a bush or low tree, usually at a height of 1-1,5 m above the ground, often well within the bush but occasionally among the leaves at its edge (when the bird's head is relatively easy to see). The birds usually call from the same place each day. The strong, continuous nocturnal calling of such birds is normally completely unaffected by taped playback of any Buffspotted Flufftail call and, although the birds often briefly fall silent when first illuminated by a torch or when observers first approach, they soon resume their calling. In March 1990 a bird calling continuously at night in the Scotston garden was photographed with a camera set up 1,5 m away; it was unaffected by the camera flash, the prolonged use of a torch for observation of its calling, and the quiet movements and talking of several observers 2-3 m away.

This bird's calling behaviour was typical of that seen in other individuals. It crouched on a small branch, with neck retracted and body plumage roused, and when about to call it pointed its bill downwards, rose slightly from its crouch, assumed a fixed, intent expression looking downwards, inflated the entire neck and the breast, and began the call, keeping its bill closed. As the call continued the bird swelled even more, when the call increased in volume. At the end of the call the bird deflated its neck and breast, crouched down again and raised its head to a horizontal position, sometimes turning its head to look at the observers.

Using fresh casualties I found, as did Chapin (1948), that blowing air into the oesophagus of males causes great inflation of the neck and breast, to an extent which I had observed in calling birds, i.e. including all the areas of rufous plumage and extending slightly into the spotted area below the rufous on the breast. On dissecting a fresh male casualty which had been calling strongly before being killed, I found that the oesophagus was enormously distensible for the first 3,5 cm of its length, to a point just above the location of the syrinx at the base of the trachea. When partially inflated it formed a double sac, constricted in the middle, but when fully inflated it was almost spherical, having a diameter of over 3 cm and pushing the trachea to one side; when inflated in life it is more likely

to extend around, or even engulf, the trachea. In such a situation it forms a resonating chamber of a type which could increase the broadcast efficiency of the low-frequency advertising call (Wiley & Richards 1982). All the skin of the neck was very loose and was covered on its inner surface with a gelatinous substance which formed a layer 2-3 mm thick and extended to the base of the neck. It is not clear whether this layer has any effect on the production of the call, or whether it serves a lubricating or protective function when the neck region is greatly inflated. The upper oesophagus also functions as a crop; in two other dissected males it was considerably distended with recently eaten termites and woodlice for which there was no room in the packed gizzard.

The acoustic properties of the advertising hoot, and the behaviour of calling birds, are well suited for maximizing transmission through dense forest vegetation. Thus the low frequency of the note (about 0.5 kHz) ensures very effective transmission through forest habitats, where trunks and leaves cause significant attenuation of sounds (by absorption and scattering) at frequencies above 1-2 kHz (Wiley & Richards 1982). Signal attenuation from atmospheric turbulence is least at night (Wiley & Richards 1982) and singing from a position 1 m or more above the ground ensures the most effective transmission of the low-frequency sound (Marten & Marler 1977), especially since some studies have shown that calls of very low frequencies (less than 1 kHz) may suffer increased attenuation if given at ground level (Marten & Marler 1977; Wiley & Richards 1978). Forest bird sounds tend to be purer in tone and relatively constant in frequency when compared with bird sounds from other habitats (Morton 1975) and the Buffspotted Flufftail provides an excellent example of the great distances over which a pure-toned low-frequency call may be propagated.

Differences in the territorial and paired status of males were found to be reflected in the nature and frequency of advertising hoots produced. Thus, newly arrived unpaired males which were seeking to establish a territory gave an intermittent, feeble, high-frequency version of the advertising hoot both day and night, from various locations and often from the ground. The calling posture was often crouched but sometimes upright, the neck was less inflated than for the strong hoot and the breast region sometimes was not inflated; the throat often moved in and out before the call commenced. These males were easily intimidated by the stronger calls of established males or by taped playback, quickly falling silent, usually moving away from the source of the strong call, and sometimes leaving the area completely. Once a territory was established, unpaired males gave typical strong, loud calls almost continuously from evening to early morning, obviously to attract a mate and possibly also to deter potentially intruding males. During the breeding season, paired males did not call unless strongly stimulated by the calls of an intruder or by prolonged taped playback; the male of Pair 1 at Scotston, on returning for the second season, was paired to his original female from the day after his return (Sections 9.4.3.1 and 9.4.4.2) and never uttered any advertising calls during that breeding season. However, if a male lost his mate he immediately began calling again, and continued

until a female was attracted; if unsuccessful he would eventually either leave the area or be driven off by an adjacent territory holder, as possibly happened at Scotston in January 1991 (Section 9.4.3.1).

Observations of captive birds made by R. Davidson (pers. comm.) support these findings. Captive paired males did not give advertising hoots but a male which lost its mate immediately began to call continuously and eventually had to be released because a female could not be obtained for it.

Unlike the Striped and Redchested Flufftails, the Buffspotted Flufftail occasionally gives its advertising hoot outside the normal breeding season. During the study observers in the Pietermaritzburg area recorded occasional instances of hooting in the four months from April to July, i.e. outside the normal calling period shown in Table 9.1, and calling was also recorded throughout the year at the Franklin site (see Section 9.4.3.2). It has already been suggested (Section 9.4.5.2) that such calling is indicative of winter territorial activity but it must be borne in mind that the permanently territorial Redchested Flufftail did not give its advertising hoot during the winter in the Natal survey area (Chapter 4). In view of the calling behaviour already described, it is possible that unseasonal hooting in the Buffspotted Flufftail may be indicative of two things other than simple territoriality: either the loss of a mate or a readiness to breed outside the normal season.

The raw data obtained on the seasonality and pattern of advertising calling are summarized in Tables 9.6-9.8. To investigate the influence of time of day, temperature and cloud conditions on calling, a Generalized Linear Model (McCullagh & Nelder 1989) was built using the GENSTAT computer package (Anon 1988) to give the expected proportions (and hence numbers) of birds calling in the eight possible combinations of time period and weather conditions (see Table 9.6). A  $\chi^2$  test showed that there was no significant difference between any of the observed and expected calling numbers ( $P > 0.05$  in all cases; Table 9.6), while the model fits the observed data excellently ( $\chi^2_4 = 6.85$ ;  $P > 0.05$ ). Results indicate that the birds call more frequently (a) in the evenings than the mornings, (b) in cloudy rather than clear weather, and (c) in cool rather than warm weather. The ranking of the eight possible sets of conditions by decreasing proportions of calling is shown (Table 9.6) on the basis of predicted proportions, these figures taking into account the relatively small sample sizes in some categories. Of the 16 occasions when the start of a season's calling was accurately dated by observers (i.e. when daily observations had been made for at least a month prior to the first call being heard), 15 (94%) were in the evening and in cool, cloudy conditions, eight of these being in mist and five in drizzle.

The relative frequency of calling during different types of precipitation is shown in Table 9.7. The results show that there is a highly significant association between the type of precipitation and

TABLE 9.6

The influence of time of day and weather on the breeding-season calling of the Buffspotted Flufftail in Natal. See text for details of the survey period and areas covered. A season's recording began on the day the birds were first heard and ended on the day they were last heard. Half-day: am = midnight to midday, pm = midday to midnight; no. of  $\frac{1}{2}$ -days = number of half-days on which the specified weather conditions were recorded; incidence of calling = number of half-days on which calling was heard (observed) or estimated (predicted) from the Generalised Linear Model (see text). Conditions are listed in reverse order of predicted frequency of calling (last column). Each individual  $\chi^2$  value shows that there is no significant difference between observed and predicted calling numbers (d.f. = 1;  $P > 0,05$ ), while the overall  $\chi^2$  value shows that the model fits the observed data excellently (d.f. = 4;  $P > 0,05$ ).

Half -day	Weather conditions	No. of $\frac{1}{2}$ -days	Incidence of calling		$\chi^2$	% occurrence of calls	
			Observed	Predicted		Observed	Predicted
pm	cold, cloud	397	217	231,91	0,958	54,6	58,4
pm	warm, cloud	106	58	53,42	0,392	54,72	56,38
pm	cold, clear	63	39	31,13	1,989	61,9	49,41
pm	warm, clear	296	125	122,54	0,049	42,23	41,39
am	cold, cloud	368	137	131,34	0,243	37,23	35,68
am	warm, cloud	57	21	16,33	1,335	36,84	28,63
am	cold, clear	92	27	25,62	0,074	29,35	27,84
am	warm, clear	347	64	75,71	1,811	18,44	21,82
TOTALS:		1726	688	688,0	6,851		

TABLE 9.7

The influence of precipitation type on breeding-season calling frequency in the Buffspotted Flufftail in Natal. See text for details of the survey period and areas covered. No.  $\frac{1}{2}$ -days = number of half-days on which precipitation occurred; no. calls = number of these half-days on which calling was heard; prop.  $\frac{1}{2}$ -days = proportion of half-days on which calling occurred.

	Mist	Drizzle	Rain	Total
No. of $\frac{1}{2}$ -days	116	139	155	410
No. of calls	61	79	38	178
Prop. $\frac{1}{2}$ -days	0,53	0,57	0,25	

TABLE 9.8

Variation in calling frequency during the Natal breeding season in the Buffspotted Flufftail. See text for details of the survey period and areas covered. No. days = number of days on which records were kept during the month (a season's recording began on the day the birds were first heard and ended on the day they were last heard); no. calls = number of days on which calling was heard; prop. days = proportion of days on which calling was heard.

	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Total
No. of days	24	108	201	199	215	113	22	882
No. of calls	18	70	134	113	126	47	4	512
Prop. days	0,75	0,65	0,67	0,57	0,59	0,42	0,18	

the incidence of calling ( $\chi^2 = 36,689; P < 0,001$ ). Both drizzle and mist appear to stimulate calling while rain has the opposite effect.

The monthly calling figures (Table 9.8) show that the frequency of calling also varied during the normal breeding season (September to March). Although in some years the first calls were heard in August (Table 9.1), these were isolated records and no detailed observations were available for that month. There was a highly significant association between calling frequency and month ( $\chi^2 = 38,081; P < 0,001$ ), birds calling most frequently early in the season (September-November) and relatively infrequently towards the end of the season (February and March), while calling in December and January (the height of the breeding period) was at an intermediate level.

#### 9.4.9 Breeding season

The intensive study over two breeding seasons at Scotston enabled accurate information to be collected on the timing and duration of breeding of the two pairs under observation in each season, while at other localities breeding records were obtained by observing adults with chicks and juveniles which could be aged accurately. These records, plus those obtained in Natal by other observers during the study period, total 45 and are summarized by month in Table 9.9, which also summarizes ten other Natal records obtained from the SAOS Nest Record Card Scheme, museum specimens and egg collections. In Natal the breeding season extended from September to March, birds from coastal and mid-altitude regions apparently beginning to breed 1-2 months earlier than those at high altitudes. The peak laying month was November.

Only one breeding record fell outside this September-March period, this involving an immature which was found dead in a garden at Amanzimtoti, south of Durban, in mid-August 1991. The bird was estimated to be 10 weeks old, i.e. hatched from an egg laid in mid-May. Although there is no evidence that the bird was hatched locally, such a late clutch is more likely to have come from a coastal locality, where in May food availability is greater than at higher altitudes, cover is still good (Chapter 10) and many birds are present throughout the year. This record is interesting in that it suggests that this species may breed well outside the normal season when conditions are favourable.

Comparing the distribution of breeding records with the recorded periods of advertising calling (Tables 9.1 and 9.8), it appears that calling may begin up to a month before egg-laying normally commences and that calling ceases in February and March, the last months in which eggs are laid. Observations at Scotston in two breeding seasons showed (Fig. 9.13) that the breeding birds arrived in the garden between 16 and 29 days before laying commenced, and it is obvious that a 2-4-week period is required for establishing a territory, finding a mate, selecting a nest site and building

TABLE 9.9

Buffspotted Flufftail breeding records obtained in Natal during the study, plus (in parentheses) those obtained from the SAOS Nest Record Card Scheme, museum specimens and egg collections (see Chapter 3, Section 3.11, for a list of sources). The months are those in which the eggs were laid. Records include those of chicks and juveniles which could be aged accurately. Areas: Coast = Durban north to Stanger; PMB = Pietermaritzburg; UBG & EGq = Underberg (including Coleford) and East Griqualand (Franklin).

Area	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Total
Coast	2(1)	(2)	1(2)			1	(1)		1	5(6)
PMB area	2(1)	2	5	1(1)	1(1)	1(1)	1			13(4)
UBG & EGq		1	8	7	7	3	1			27
Totals	6	5	16	9	9	6	3	0	1	55

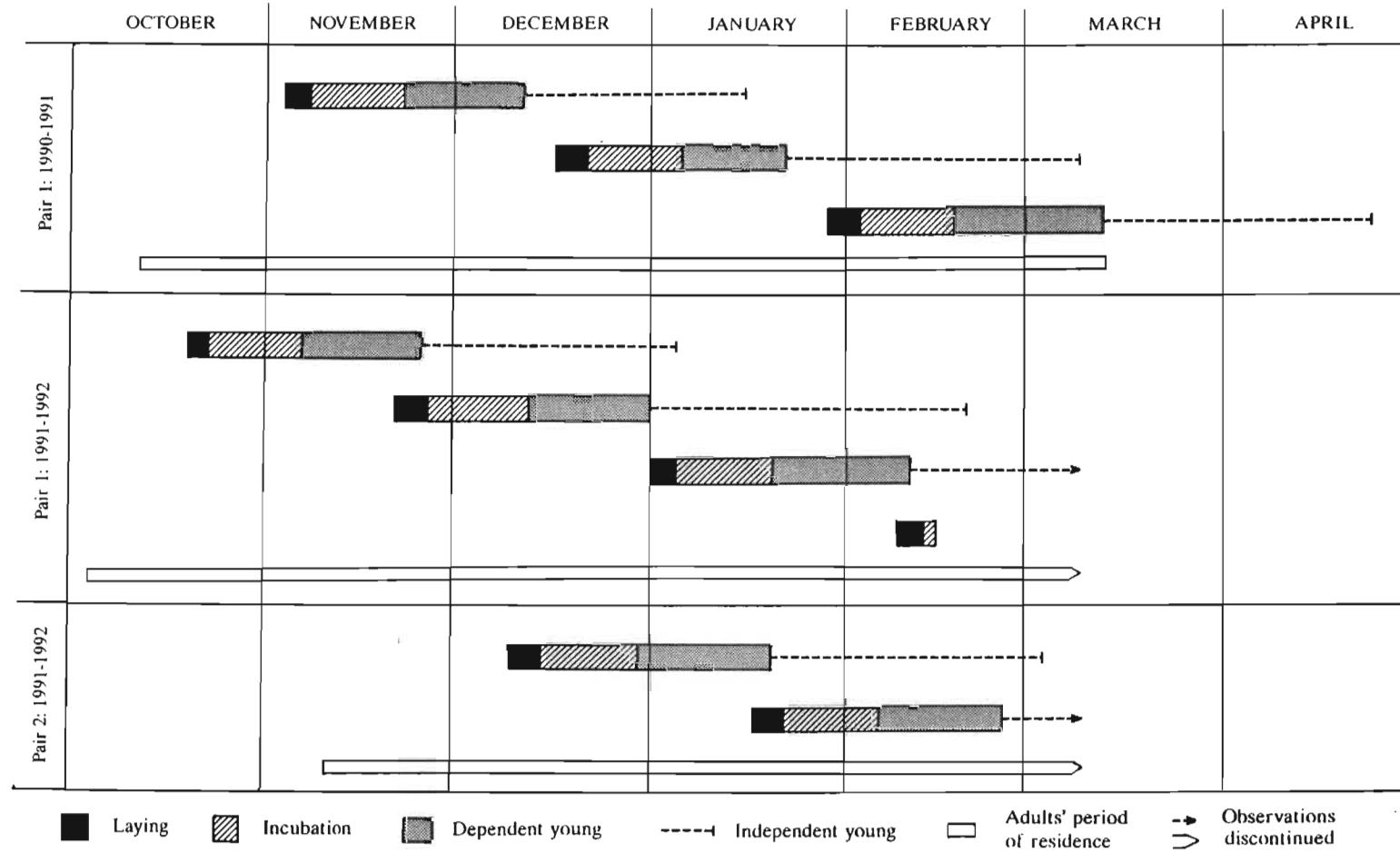


Fig. 9.13

Occurrence and breeding activity of two pairs of Buffspotted Flufftails at Scotston Farm, Underberg, in the 1990-1991 and 1991-1992 breeding seasons. In the latter season observations were discontinued on 7 March, when adults and young of both pairs were still present.

the nest. In October 1991, Pair 1 at Scotston were together on the day after the male's arrival, settled immediately into the territory without any advertising calling, showed strong courtship and mating behaviour from the second day and began the first clutch 15 days after the female's arrival.

#### **9.4.10 Breeding**

##### **9.4.10.1 Courtship and mating**

Although courtship has never been described, the male exhibits courtship behaviour very frequently throughout the breeding season and I observed it on many occasions, sometimes to model females but usually to the bird's mate. In the full display the male assumes a very upright posture, standing tall with the body raised about 70° above the horizontal at the front end and the neck stretched up as far as possible. The closed tail is held in line with the body and is often vibrated rapidly from side to side but is sometimes wagged more slowly. The body plumage may be raised, but the neck and head plumage is always markedly raised, the feathers standing straight up on the nape and the crown. In this pose the male either struts or runs towards the female; she may ignore him (when he often stops displaying) but often walks or runs away, either in a normal or a crouched pose. If the female is aroused she may first walk off with her head raised, or she may immediately crouch, inviting mating. The display often develops into a courtship chase, the male upright and the female crouched, and if the female is willing to copulate she stops and crouches to the ground.

During the courtship strut or chase the male may be silent, but he sometimes makes quiet gulping, grunting or growling calls (e.g. Calls M57, M60, M61 and M70), some of which are also given during copulation (Table 9.4). However, much calling often precedes or follows courtship displays, the male commonly uttering the *MOO-EEE* (M48), the quiet hoots of Call M55 and the rapid SLH (M53), but also Calls M44-M52, M54, M56 and M62. These calls are given from either a normal or a crouched pose. At the start of the breeding season the *MOO-EEE* and M55 calls may be given periodically all day, the former sometimes continuously for half an hour or more and apparently being used to attract the female. After sunset on the day of his return in 1991, the Scotston Pair 1 male, not yet reunited with his mate (she appeared the next day), flew up into a bush and crouched, silhouetted against the fading light, on a horizontal branch 1 m up to give loud and continuous *MOO-EEEs* and SLHs for 8 min, until it was almost dark. He was possibly stimulated by another male outside the garden, giving a similar and just audible performance at the same time. At the appropriate stages of the breeding cycle (see below), playback of almost any advertising or courtship call was sufficient to stimulate strong courtship behaviour in the male.

The female makes relatively few courtship calls (Table 9.4) and three (F24, F25 and F27) are equivalent to male calls, being given in response to those calls.

Two other courtship displays were seen. The first was a muted version of the normal upright display, when the male walked slowly up to a model female, wagging his tail and drooping his wingtips so that the primaries were visible, and pecked gently at the model's head, pausing from time to time as though waiting for some response. Eventually he lost interest and walked away. Another male stood in a similar droop-winged upright pose, facing his mate in cover, and making Call M55, but his tail was slightly raised and spread, and his undertail coverts were fluffed out. The second display was completely different and was seen once at Kakamega, Kenya, where a male in the normal upright courtship pose approached a model female and walked repeatedly around it with a dancing motion, alternately stretching up and lowering his body, and sometimes jumping up and down. His tail was immobile during the display.

In January 1991 a Scotston male performed an intriguing display when stimulated by playback of Redchested Flufftail courtship/mating calls (Table 4.1, Calls A6-A9) and in the absence of a model: he ran around in the open with rapidly flapping wings, sometimes fluttering up and down, and then ran off into cover. This display could have contained elements of both the courtship dance and the Fluttering Jump attack (Section 9.4.5.3).

Copulation was much more difficult to observe than was courtship, usually taking place out of sight or in very poor light at dusk or dawn, but it was seen well on six occasions. The male mounted the crouching female from the side or rear, wagging his tail from side to side, pecked gently at her crown and face, and copulated for 5-45 s, sometimes making treading movements with his feet. The female usually crouched flat on the ground with her tail to one side and her neck either retracted or stretched out to the front. Both sexes often made quiet calls (Table 9.4) while copulating.

After copulation the pair resumed normal activities, either separating immediately or standing close together for a short time. A post-copulatory display was seen twice, when the male faced the female, raised his wings above his back and drooped the primaries, pecked gently at the female's head and then resumed a normal pose. The female then stood up and the birds briefly stood side by side before walking off.

The Scotston males showed strong courtship and copulatory behaviour throughout the breeding season. Such behaviour was most prolonged and intensive at the start of the season (before the first clutch was laid), was noted infrequently during incubation and the first nine days of the life of each brood, and was frequent again from the tenth day after hatching to the time when the next clutch was laid. In both seasons, males continued courtship displays after the last brood of the season was ten days old, when it was obvious that the females were no longer receptive and, after the failed fourth breeding attempt of Pair 1 in 1992, the male showed very strong courtship, even though the female

actively avoided him. Throughout the breeding season paired males courted and attempted to mate with strange females and occasionally even with their own female offspring which had completed postjuvenile moult into adult-type plumage. The noticeably chase-and-avoid relationship between male and female during the breeding season was markedly different from that between Redchested Flufftail pair members, which coexisted more amicably, apparently with a much less dominant courtship/copulation urge on the part of the male. Buffspotted Flufftail females were wary of their mates throughout the season, usually taking care to avoid close contact even when growing chicks were present, as the male was likely to begin unwelcome courtship approaches at any time. Thus the pair were rarely together when resting or feeding at the mealworm dishes. However, courtship feeding was seen several times, the male either assuming a typical upright courtship stance or a more normal stance and taking mealworms to the female, who crouched and took them from his bill.

It is very difficult to observe the courtship behaviour of newly established males which are trying to attract a mate, primarily because almost all males were already paired when first encountered during the breeding season. However in late October 1991 I was able to conduct experiments with models on a newly arrived male in a Hilton garden. The bird was easy to observe (he provided me with my only video film of a male making the advertising call in daylight) and, when first encountered on 23 October, was making the characteristic high-frequency daytime hoots of an unmated male in the process of establishing a territory. He avoided a model male but showed a strong interest in the playback of female SLH calls, searching for the source of these sounds. Two days later, on 25 October, he was much more aggressive, the presentation of a head-down model male eliciting Threat Display 1 and Attack Types 2 and 3 (Section 9.4.5.3), and he called with a lower-frequency, more resonant hoot in response to playback of high-frequency male hoots. When presented with a head-down model female he was at first very wary, examining the model from cover, but when female SLH calls were played he came out and first attacked the model with typical Type 3 attacks. These soon ceased and the male then performed Threat Display 2 (Section 9.4.5.3), circling the model with one wing drooped to the ground. He then approached the model, pecked at her head and then mounted her several times, standing on her back and at first pecking her upperparts indiscriminately but later pecking her head in an attempt to encourage copulation. During all this behaviour the male's head feathers were raised, but at no time was the neck stretched up in a typical courtship attitude.

This performance combined aspects of typical aggressive, courtship and mating behaviour, and suggests that a newly established male's first reaction to a potential mate involves a conflict between territorial/agonistic and courtship/mating drives.

#### 9.4.10.2 Nest and nest building

Details of eight nests from gardens in the Underberg district were obtained during the study: one from Coleford, six from Underberg (five of these from Scotston), and one from Pevensey. All but the Pevensey nest were examined and measured (Tables 9.10 and 9.11), while the site of another nest at Scotston was known but was not disturbed. Two nests from Scotston were apparently roosting nests (see below) but all the others were breeding nests. All nests were built on the ground and all those from Underberg were domed, the only undomed nest being from the Pevensey garden, where it was built under a very low bush which formed an effective roof (A. Rennie pers. comm.).

Of the five breeding nests examined (Nests A-E, Tables 9.10 and 9.11) three were built in dense ground cover of creepers and two in sparser ground cover. One roosting nest (F) was also built in dense creepers but the other (G) was on the ground below a pile of twigs and bramble clippings and a similar site was used by Pair A in the 1991-1992 breeding season for their breeding nest, which was under a large flattened pile of hedge clippings and pampas grass cuttings between the vegetable garden and the hedgerow where Hide 2 was situated (Fig. 2.21). Such a situation had obvious protective advantages, and effectively prevented direct observation of Pair 1's laying, incubation and hatching, although it did not prevent the fourth clutch from apparently being destroyed by a predator (Section 9.4.10.4.6).

Three nests, all on soft soil and in easily moved ground vegetation, were sited in a shallow depression in the ground which was excavated by the bird. At Danville at 05:55 on 14 November 1989 a male was seen making such a depression in loose sandy soil under tall *Oplismenus hirtellus* herbs 1 m from a forest track. He crouched down, spread his wings, and scraped and shuffled around, rotating his body to create a circular depression. During this process a female, with roused body plumage, walked around nearby.

All nine nests were built on ground shaded by tall trees, or within clumps of bushes, or adjacent to bushes and hedgerows. Breeding nests in dense cover were approached by a tunnel or track through the vegetation, this being quite indistinct and being formed merely by the frequent passage of the adults. In nests A-D, a small cleared space in front of the entrance provided room for the male to stand and observe his surroundings, and where he made threat displays to human intruders.

The overall proportions of the five domed nests (A-D and G) were similar (Table 9.10), the nests being almost circular, but in two the roof was slightly shorter than the floor. Nests E and F resembled a heelless slipper in shape, being longer than broad and having a relatively short roof. The size of the internal cavity of all the nests was similar and all nests except G had thick walls and a

TABLE 9.10

The location, situation and dimensions of seven Buffspotted Flufftail nests located in the Underberg district during the study. Full details of materials used in the construction of all nests are given in Table 9.11. All dimensions are given in centimetres. Abbreviations: Br = breeding nest; D = depth; H = height; L = length; LB = length of base; LT = length of top; Ro = roosting nest; W = width. Depression = shallow depression in ground, excavated by bird, in which the nest rested.

Nest	Type	Locality	Vegetation	Situation	Approach
A	Br	Scotston	Lamium ground creeper, 30-40 cm tall, under oak trees.	5,2 m from hedge and 1,5 m from opposite side of patch.	Tunnel through creepers to hedge.
B	Br	Scotston	Lamium ground creeper, 20-25 cm tall, in flowerbed with bushes and tall herbs.	1 m from house, 40 cm from narrow path on opposite side of creeper patch.	Tunnel through creepers to path.
C	Br	Coleford	Sparse grass and Vinca under azalea bushes with trailing honeysuckle.	75 cm into azalea bushes, which began 75 cm from lawn.	Short approach run under azalea bush.
D	Br	Scotston	Lamium ground creeper and oak saplings, 30-60 cm tall.	3 m from hedge and 50 cm from grass clump.	Tunnel through creepers to hedge.
E	Br	Underberg	Leaf-litter below large cypress trees; 20% cover of ground herbs.	2 m from cypress trunk and 2,5 m from low-growing rose bush.	Faint track into rose bush.
F	Ro	Scotston	Vinca ground creeper, 20-30 cm tall, adjacent to grass and vegetable beds.	50 cm from edge of vegetable beds and at edge of dense Chaenomeles hedge.	No noticeable track.
G	Ro	Scotston	Pile of bramble, hedge and grass clippings, 1,7 x 1,2 m and 50 cm deep, under trees on sloping ground.	On ground under pile, 95 cm from downhill edge which was 50 cm from adjacent hedge.	Tunnel to edge of pile and track to adjacent hedge.

TABLE 9.10 (continued)

Nest	Clear space in front?	Depression			Entrance		External measurements				Internal cavity		
		L	W	D	H	W	LB	LT	W	H	L	W	H
A	Yes	8	8	2,5	6	7	16	14	20	10	8,5	8,5	7,5
B	Yes	8	8	1	6,5	6	19	19	19,5	10,5	10,5	8,5	7
C	Yes	7,5	7,5	1	7	7	18	17	19	9,5	8	8	6
D	Yes	None			7	7,5	18	18	19	10	8	8	7
E	No	None			6	7	18	13	13	9	8	8	7
F	No	None			7	6	17	11	12	8,5	8	6	7
G	No	None			5	5,5	9	9	9	9	8	7,5	6

TABLE 9.11

Materials used in the construction of seven Buffspotted Flufftail nests (A-G; see Table 9.10 for full details), all from the Underberg district, which were examined during the study. All plant materials were living unless otherwise stated. Abbreviations: (N) = nest; (L) = lining; vol. = volume.

Nest	Material	Length (cm)	% by vol.	Comments
A (N)	Dead oak leaves	5-10	87	Largest leaves round outside of nest.
	Sloughed plane tree bark	2-3	12	
	Grass stems & blades	3,5-7	1	
(L)	Dead oak leaf fragments	0,5-1,5	9	
	Grass blades; leaf petioles	1-3	90	
	Root fibres	1-4	1	
B (N)	Dead oak leaves	5-11,5	22	
	Moss	1-7	35	
	Grass stems & blades	2-8	28	
(L)	Dead <u>Pinus patula</u> leaves	4-16	15	Some weaving of grass and <u>Pinus</u> leaves.
	Dead oak leaf fragments	0,5-2	-	Very few.
	Moss	1-4	15	
C (N)	Dead <u>Pinus patula</u> leaves	3,5-16,5	54	<u>n</u> = 306 leaves. Nest materials interwoven.
	Dead azalea & privet leaves	1,5-6	35	
	Large green leaves	7-12,5	1	
(L)	Grass, roots & small twigs	1-8	8	
	Moss	1-5	2	
	Grass fragments	0,5-1,5	80	
D (N)	<u>Pinus</u> leaf fragments	0,5-1,5	10	
	Dead hydrangea flowers	1-2	10	
	Grass fragments	1-3	2	These comprised a scanty nest lining.
E (N)	Dead oak leaves	4-11	98	
	Grass fragments	1-3	2	
	Grass stems and blades	3-14	92	Nest materials interwoven. No nest lining.
	Dead twigs	4-9	5	
F (N)	Rootlets	4-8	2	
	Grass stems and blades	3-6	1	
	Pad of grass fragments	2-12,5	76	Materials interwoven. No lining. Roosting nest, with basal pad of grass fragments.
G (N)	Dead twigs	1-4	15	
	Dead leaves	3-12	6	
	Dead hydrangea flowers	1-5	1	
	Clumps of roots	1-2	1	
	Grass and dead twigs	2-3	1	
G (N)	Dead oak leaves	4-11	95	Roosting nest. A piece of cellophane,
	Grass and dead twigs	2-12	5	70 x 50 mm, was incorporated into the roof.

substantial roof. All nests were probably built up from an initial thick pad or cup of material on the ground but the walls and roof of nest G were only 3–4 leaves thick: a robust structure was not needed in this nest, which was built under a pile of dead twigs.

Nests were largely built of whatever material happened to be most readily available, usually either dead leaves or grass, and sometimes moss (Table 9.11), and the birds often used material from exotic plants, such as the leaves of *Pinus patula* which at two sites were plentiful, having been spread as a mulch around plants in adjacent flowerbeds. Any lining was usually predominantly grass fragments.

Males were seen carrying nesting material on many occasions but females never were, these and other observations indicating that the male chose the nest site and built the nest unassisted by the female. Males occasionally carried nesting material during the incubation and rearing periods, presumably to repair or improve the breeding nest. The nest (B) next to the house at Scotston was built entirely by the male in about three days, building starting on 12 December 1990 and being completed early on 15th. From 13 December the male was observed and filmed regularly and the following activities were noted.

**13 December.** Building occurred for long periods (up to 1 h 30 min continuously) until 14:05, the male giving occasional SLHs (Table 9.2, Call M65). At first visits were as frequent as every 30 s but later the male remained in the nest for several minutes on each visit, presumably while shaping the structure. From 14:05 to 14:35 the male called continuously with Call M58 (*GUGUGU-GROO*), at first while walking around in front of the nest, later from within the nest. The female appeared at 14:29, listened, and walked off at 14:35, giving a rapid SLH call (Call F24); the male emerged and followed her. Observations ceased at 15:00.

**14 December.** The male built for long periods throughout the day, starting at 04:59 and continuing until at least 16:00. In one continuous morning session of 2 h 38 min he made 73 visits (all filmed), averaging one per 2 min 10 s, bringing materials as follows: dead oak leaves (on 36 visits), *Pinus patula* needles (34 visits), moss (16 visits) and grass (15 visits). Two types of material were often brought together. From 10:55 onwards he frequently made Call M58 and also Call 48 (*MOO-EEE*) to attract the female, without success.

**15 December.** Building activity ceased during the morning. The male remained at the nest, giving Calls M48, M58 and M65 all day until the female appeared at 15:00. In response to Calls M48 and M59 the female gave Call F26 for 1 min before walking off, followed by the male. Heavy rain fell for the rest of the afternoon. The female was not seen at the nest again, and had obviously rejected it, perhaps because it was so close to the house.

**16 December.** At 09:00 the male was encouraged to approach the nest by playback of various courtship calls, but he did not remain in the vicinity.

**17 December.** The female began laying her second clutch in another nest which, considering the short time elapsed since the rejected nest was completed on 15th, may already have been in existence and was possibly the nest in which the first brood had been hatched.

The detailed observations of this male's building showed that all nesting material was collected on the ground, usually within 20 m of the nest, and that the male always walked to and from the nest. Dead leaves were collected under nearby herbs and shrubs, where oak and *Pinus* leaves had been placed as a mulch, while dead and living grass was vigorously pulled from creeping clumps near the nest and moss was collected from nearby rocks. The male completely ignored observers watching and filming through the open window immediately overlooking the nest, and ignored domestic chickens foraging nearby. He ignored most bird calls but, at a chicken's alarm call, he immediately retreated to cover, where he stayed looking out for some time before emerging.

At the beginning of the 1991-1992 season, the same male began building actively on 11 October, eight days after his arrival. He called the female to the nest with typical *GUGUGU-GROO* calls on the second day and continued building actively all the third day (13 October), after which building apparently ceased. The first egg was laid a week later, on 20 October.

Although disturbance may encourage a male to build a new nest for each clutch, the same nest may be used repeatedly if the site remains undisturbed. Thus Pair 1 at Scotston used the same nest throughout the 1991-1992 breeding season, whereas in the previous season a different nest was used for each brood.

#### 9.4.10.3 Laying, incubation and hatching

During the study details of five full clutches were obtained, four of five eggs and one of four. To avoid undue disturbance to the birds and the habitat at Scotston no prolonged efforts were made to locate nests which were in use, and most nests were located after they had been vacated. In the second season the breeding nest of Pair 1 was known to be under a pile of dead vegetation, in which situation it could not be observed directly. Thus at Scotston no direct observations were made of clutch size, laying interval or incubation period, but continuous observation of the two breeding pairs made it easy to determine the incubation period and hatching date of each clutch. Before and during laying, both adults were seen throughout the day but as soon as incubation commenced a regular routine was established by both pairs, the male incubating during the day and the female at night. Thus the male was seen frequently in the early morning but he disappeared between 08:00 and 10:00,

the female always appearing 10-30 min later and remaining near the food and water at the hide all day until 16:30-17:30, when she disappeared and the male then reappeared to feed and bathe before going to roost. This unvarying routine continued until the chicks hatched, when both adults were seen, showing agitated behaviour and each making brief visits to the food and water while the other parent remained at the nest. Thereafter, both adults regularly carried food to the chicks, which remained in cover in or near the nest for 1-2 days, usually being first heard or seen on the second or third day after hatching.

Such detailed observations made it possible to calculate the incubation period and hatching date for each clutch of Pair 1 at Scotston in both breeding seasons, and for Pair 2 in the 1991-1992 season, and the results are shown in Fig. 9.13. Incubation periods were either 15 days ( $n = 6$ ) or 16 days ( $n = 2$ ). As no nest was later found to contain unhatched eggs, clutch sizes were taken to equal the number of young chicks seen, being 3 ( $n = 1$  clutch, the first of the season for Pair 1 in October 1991), 4 ( $n = 2$ ) and 5 ( $n = 5$ ). Laying periods were calculated on the assumption that one egg was laid daily, as is known to occur (Chapter 1, Section 1.2.1.5). The only clutch for which details could not be calculated was Pair 1's fourth clutch, laid in February 1992, which was apparently destroyed by a predator (Section 9.4.10.4.6).

Observations at Scotston in the 1991-1992 season (Fig. 9.13) showed that on three occasions a female began to lay a new clutch before the current brood of young had reached independence and had been rejected by the parents, this occurring in November and February (Pair 1) and January (Pair 2). It has already been noted (Section 9.4.10.1) that courtship and mating often began again when a brood was 10 days old, the observed interval between the resumption of mating and subsequent laying on three occasions being 5, 8 and 12 days; mating was also first observed 11 days before Pair 1's first clutch was started in the 1991-1992 season.

The Scotston birds easily managed to produce two or three broods of young per season. In 1990-1991 the Pair 1 female laid three clutches between November and February, while in 1991-1992, the same bird laid four clutches between October and February (Fig. 9.13); had the last clutch not been destroyed, the fourth brood would have been independent by about 19 March, until when food and cover would have remained adequate (Chapter 10), especially with the food supply supplemented by artificial feeding. In the latter season the late-arriving Pair 2 managed two clutches, in December and January. From these observations it appears that three broods are possible in a full season's residence, while four are possible in a season when food is plentiful and no catastrophes occur. Other observations from the Underberg area (Table 9.9) indicate that laying can occur as late as March in some years, while it begins in September in warmer, lower-altitude areas, where the extra month should make four broods possible, at least in good seasons. The possibility of winter

breeding in coastal areas (Section 9.4.9) further increases the period during which breeding may be attempted.

#### **9.4.10.4 Development and care of the young**

##### **9.4.10.4.1 Introduction**

All data on development and care of the young were collected over the two breeding seasons at Scotston, when eight broods of chicks were observed from the day of their first appearance (usually two days after hatching) until the fully grown and independent immatures left the parental territory. The adults of both pairs were colour-ringed, as were all young ( $n = 22$ ) of all broods in the second season, while in the first season Pair 1's third brood ( $n = 5$ ) and one young of the second brood were also colour-ringed. Thus 28 young bred in the Scotston garden were colour-ringed during the two seasons, and 26 of these birds were retrapped 1-5 times to obtain data on growth and plumage development. Catching both adults and young was easy: all the birds were encouraged to feed in walk-in traps close to the two observation hides (Chapter 3, Section 3.8.1) and were caught by the observer in the hide closing the trap door by means of a fine thread. After being processed, the birds were usually feeding in the trap again within 10-30 min of their release.

Young birds could not usually be caught in traps until they were 11 days of age, when they were too large to squeeze through the mesh. Most were ringed as soon as possible after they were 16-17 days old, at which age the tarsus had developed sufficiently to be unaffected by the ring. Before this age the tarsus was considered too soft to risk fitting even a very loose plastic colour-ring: the tarsus of a chick colour-ringed at seven days of age swelled and caused the bird great discomfort, interfering with its movements and feeding, with the result that its growth was retarded. The ring was removed and the bird recovered fully, to grow normally and leave the territory after the brood became independent.

##### **9.4.10.4.2 Growth and plumage development**

Natal down is black and is replaced by a largely plain, grey-brown juvenile plumage. From about the age of independence juveniles may sometimes be sexed on the pattern of the scapulars, mantle and remiges. Sexing on plumage is straightforward after postjuvenile moult has begun. The principal stages in the growth and plumage development of the young may be summarized as follows.

**1 day.** Newly hatched chicks are covered with black down, the bare parts are black, the bill is very small, with a small white egg tooth and pink (occasionally yellowish) gape flanges, and the eyes are dark brown with white eyelids. The toes are short.

**2-3 days.** The egg tooth is lost.

**4-5 days.** The toes look longer, the remiges appear in pin, and the increased size of the chicks makes the bare skin on the ear-coverts and around the eye more obvious.

**6 days.** The remiges are more obvious, but usually still in sheath, and the first few plain grey-brown body feathers appear.

**7-8 days.** The remiges are out of sheath ("paintbrush"), upperwing coverts appear in pin, and more body feathers appear (Plate 4A). The birds look about one-third grown.

**9 days.** Growing feathers now make the body look more grey than black, but the head is black, with bare skin around the eye and ear-coverts, and a black line of down extends prominently down the centre of the breast. The tips of the growing remiges are well visible in the folded wing.

**10-11 days.** The colour change to grey-brown is now well apparent, much of the body being feathered. A grey stripe is visible down the centre of the crown but the rest of the head, and the neck, are black and downy, except for the bare lores and ear coverts. The growing tertials may appear longer than the other remiges in the folded wing. The upperparts are slightly darker than the wings, flanks and underparts. The upperwing coverts are "paintbrush"; medians are just emerging. The tail is still downy and there is much down on the rump and tail coverts. The toes, about as long as in the adult, appear disproportionately large from now until at least day 23.

**12-13 days.** More feathers have grown on the neck, mantle, scapulars, back, sides of the breast and the flanks. Down is still present on the head and neck, belly, undertail coverts and tail (which is beginning to grow), and the central breast streak of down is still visible. The first orange-brown bars are visible on the remiges, and the primaries are c. 5 mm out of sheath. On the upperwing there is down on the lesser-coverts area but the medians and greater are respectively 5-7 mm and 8-10 mm out of sheath. The legs and feet begin to grow paler, dark grey-black, often with a pinkish tinge.

**14 days.** Down is still visible on the rump, belly and all tail coverts, while feathers are growing on the head and thighs. The head looks very patchy, having a broad black streak along the side of the crown extending down the side of the neck to join a black downy half-collar from the shoulder (where it is a large patch) to the nape (where it is often incomplete), and black on the chin and throat. The central breast streak has almost disappeared. The first spots appear on the tertials (well visible) and other remiges, and the outer primaries are c. 2 cm long, 1.2 cm of which is sheath. The rectrices may be 6 mm long, with downy tips. The tarsus is still soft and not fully grown and the eyes begin to fade to dull, dark grey-brown. The young look half grown.



A



B

**Plate 4**

A: eight-day-old Buffspotted Flufftail chick at a feeding station, Scotston, Underberg, November 1991.

B: independent 22-day-old immature Buffspotted Flufftail at a feeding station, Scotston, Underberg, November 1991.

**15-16 days.** The plumage now looks almost complete except for the downy patches on head, neck and tail. The mantle is darker and browner than the breast and flanks, which appear grey, palest on the lower breast. The body plumage is entirely plain except for the scapulars, where a few spots are appearing, as on the remiges. The rectrices may be 11-13 mm long.

**17-18 days.** There is still a variable amount of down on the head and neck, usually confined to a streak over the eye, patches (from the collar) at the side of the neck and on the nape, and on the chin and throat. Brown bars are visible on the upperwing coverts and the rectrices, and the lesser upperwing coverts are starting to grow. More spots appear on the scapulars, mantle and remiges, and males tend to have larger, brighter spots than females, especially on the tertials, so that it is sometimes possible to sex the young tentatively, especially when siblings are seen together (female chicks are also shyer than males). The wings are often long enough to project beyond the tip of the small tail. The birds appear about 80% grown and the bill begins to look disproportionately long, remaining so until about day 30, when the body looks fully grown.

**19-21 days.** The amount of down on head, neck and tail regions is further reduced, some birds (especially females) having lost almost all down at this age. The scapulars are well spotted and the remiges have clearly visible bars and spots. On the upperwing, the alula and lesser coverts also show more spotting but the greater and median coverts, although sometimes showing small spots at close range, are predominantly barred with dull orange-brown and form a large plain central panel in the closed wing. The bill begins to fade to dark grey-black and to develop a paler (pink or horn) cutting edge; occasionally the entire lower mandible may become pale with a dark tip. The gape flanges begin to fade to grey.

Males often have more down on the head and have brighter spots on the scapulars (often appearing as a prominent double line), lesser coverts, alula and remiges (whitish on the outer webs), contrasting more with the plain central wing panel. The barring on the remiges is also brighter. The most advanced birds may have a few rufous feathers growing at the sides of the breast.

Females have fewer, smaller, less distinct spots on the wings and scapulars, and duller barring. In poor light the young, especially females, often look all dark with a barred posterior end (remiges and tail).

**22-24 days.** See Plate 4B. The tail, still with downy tips, begins to project beyond the wingtips as it grows. Some birds are virtually fully feathered, other still have patches of down on the collar, chin, and eyebrow. Some females begin to grow feathers on the ear coverts.

**25-26 days.** The spotting on the upperparts increases as the feathers grow out, but the underparts are still plain. The underwing coverts begin to appear in some birds. The tail looks well grown.

Males. Most still have no trace of rufous feathering. The larger, brighter markings on the upperparts and ends of the wings contrast more with those of the duller females.

Females. Most have only a few dull buff spots on the scapulars and mantle.

**27-29 days.** The lesser upperwing coverts are growing well and appear well spotted; thigh feathers are still growing. Some birds have lost all traces of down. The back and centre of the mantle are still plain in most birds.

Males. Large adult-type spots are appearing on the scapulars and mantle, often with black around them. Some show some vague barring on the flanks.

Females. Some begin to show patches of adult-type barring on the flanks.

**30-32 days.** The tail is almost fully grown. Many still have traces of down on the head and neck.

Males. Some show rufous feathers on the crown, lores and sides of the breast, and the first spots and bars on the lower breast and flanks. The upperparts are well spotted.

Females. The ear coverts may appear orange-brown, a common female character at this age. Ventral barring begins to show in most birds.

**33-36 days.** The back begins to show spots, brighter in males than females. The lesser upperwing coverts are well spotted and the underwing coverts are growing. The eye colour tends to be brighter and browner in males than females at this age and the colour now stabilizes.

Males. Some are very rufous on the face, the sides of the crown and the sides of the breast, others show much less colour (none on the breast). Spotting increases or appears on the lower breast and belly.

Females. In some the lores and face begin to appear mottled. The grey-brown of the neck and breast is noticeably darker than that of the belly, while the upperparts are darker still. Some birds begin to show small golden spots on the neck and scapulars, and more barring and mottling on the underparts.

**37-39 days.** All down has disappeared. The underwing coverts are growing well.

Males. Most are predominantly rufous on the face and have two good lines of rufous down the neck and sides of the breast. The upperparts may have adult-type spots over 25% of their area and the underparts vary from almost unpatterned to about 20% spotted.

Females. Most have the head fully feathered, some with many small spots and others almost plain. The upperparts are usually well spotted and the underparts often almost plain. Some have the first barred feathers showing on the throat. The upper tail coverts and rump now appear spotted.

**40-42 days.** Birds are fully grown.

Males. Most have much rufous on the head (with a darker centre crown), neck and breast, the two breast lines almost meeting in the middle so that only the very edges of the breast are grey. The amount of adult-type body spotting is variable, some having 40-50% of the upperparts and underparts

well spotted, others less. Many of the spots are surrounded by black and the upperparts spots are much larger than those of the female. The tertials are much blacker, with brighter buff spots, than those of the female.

Females. Most are well marked with small spots all over the upperparts and bolder buff spots on the tertials. The underparts may be predominantly plain but some have extensive barring on the throat and breast.

**48-49 days.** A slight gape flange is still apparent. Adult leg colour is attained.

Males. Many have the breast almost all rufous and up to 80% of the head rufous, with a browner centre to the crown. About 80% of the upperparts are often marked with adult-type spots but as little as 50% was also recorded. The centre of the back and mantle may still be plain. About 40-60% of the underparts are spotted, mostly on the lower breast and flanks. The tail is well barred.

Females. The head is becoming more spotted. Most of the upperparts are spotted, adult-type spots appearing everywhere among the smaller, duller markings. The centre of the mantle and back are often plain. Small spots and bars are appearing at the sides of the neck, and the centre of the neck and breast are well barred.

**54-56 days.** Males. Almost all the head and breast are rufous (the centre of the crown and the ear coverts are often still brown), but some birds may still have grey feathers intermixed with the rufous. The upperparts often have only scattered juvenile feathers, but may be no more than 70% moulted. Over 60% of the underparts are spotted.

Females. Most look almost adult, now being spotted on the crown, face and nape, and having adult-type double spots on the upperparts. The underparts are well barred and spotted except for the thighs, the lower flanks and belly.

**60-62 days.** Males. Moult is almost complete on the head and breast. The crown feathers have brown tips, rendering the rufous duller than in the adult. The large spotted scapular feathers extend further over the plain wing coverts panel, making it appear smaller. The remiges look rather faded and brown compared with the fresh upperparts feathers, and have duller spots. The lesser coverts are brightly spotted, having grown late. The underparts are 80% spotted.

Females. The face has more spots and the upperwing coverts form the only plain patch on the upperparts, somewhat reduced in area by overlying scapulars. The underparts are very well barred.

**65-70 days.** Moult is more or less complete and birds resemble adults except for the plain wing panel.

Two males did not conform to this plumage development pattern with regard to their head region. They both retained all the head down until day 20 and then began growing rufous feathers on the head without first developing grey-brown feathers on the crown. Thus these birds showed the first rufous head feathers about ten days earlier than those following the more usual pattern.

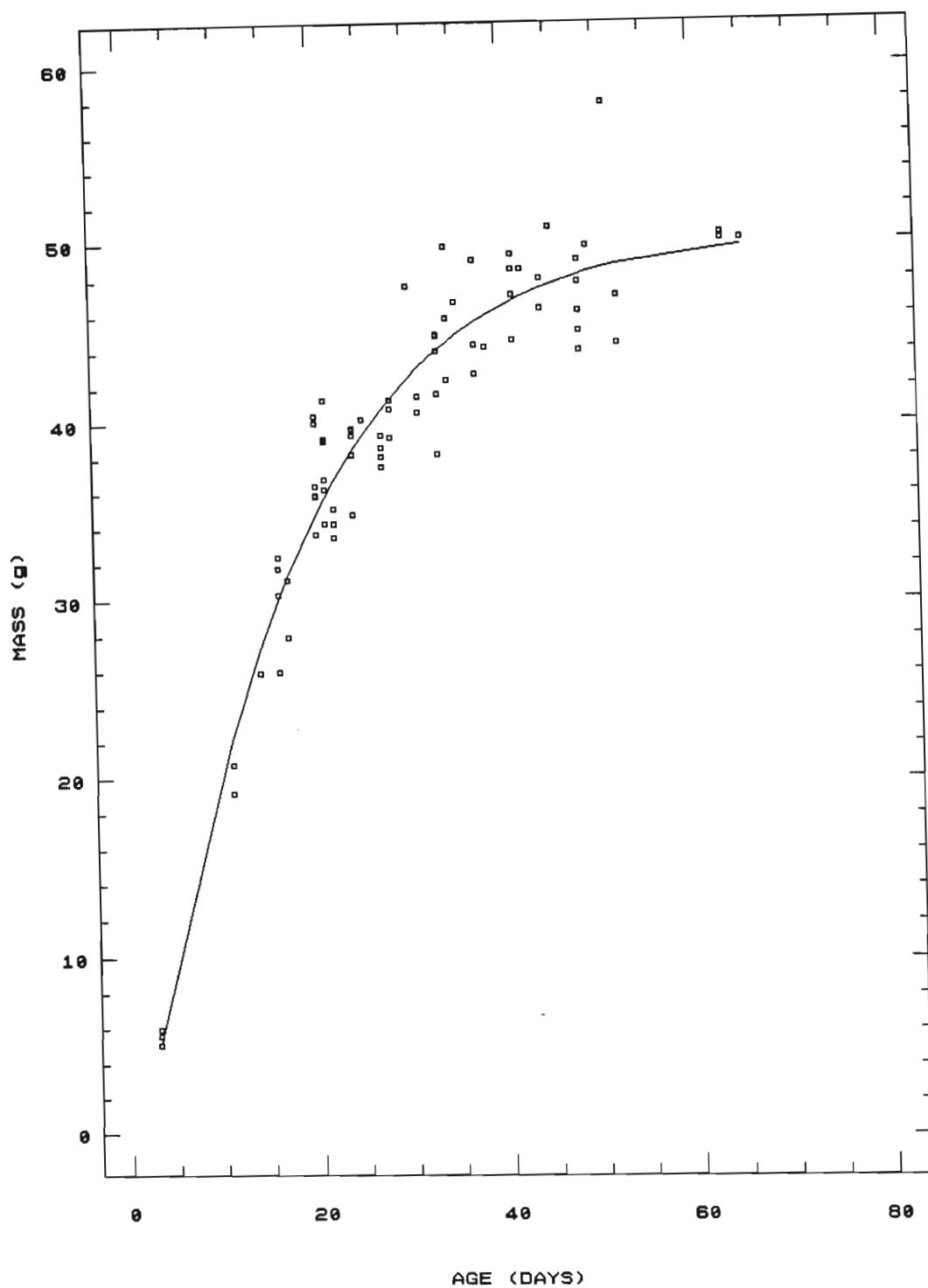
Using the data collected by trapping the Scotston young over the two seasons, fitted growth curves were constructed for body mass and for the length of the bill, wing, tail and tarsus, using the non-linear regression module of GENSTAT (Anon 1988). Figs 9.14-9.23 show the fitted curve for each dataset and plots of the growth curves of the 5-7 individuals for which three or more measurements were obtained. It may be seen that individual growth curves generally agree well with the fitted curves.

The fitted curve for mass (Fig. 9.14) shows that the mean adult mass of 47.3 g (Section 9.4.6) is attained at about 45 days of age, after which the mass continues to increase slowly. It is interesting that, of the 25 young which disappeared after becoming independent, only five (20%) of the birds left before they were 45 days old (see Section 9.4.11). Of the body parts measured, the bill and tarsus (Figs 9.16 and 9.22) are 95% grown by day 21 and fully grown by about day 35, the tail reaches its full length between days 40 and 60 (Figs 9.20 and 9.21) and the wing (Figs 9.18 and 9.19) between days 40 and 50. When the young first fly at 19 days the curve shows the wing to average 70 mm, 79% of the mean adult wing length (89 mm;  $n = 104$ ) for the nominate race, while the mass is about 35 g, 74% of the mean adult mass.

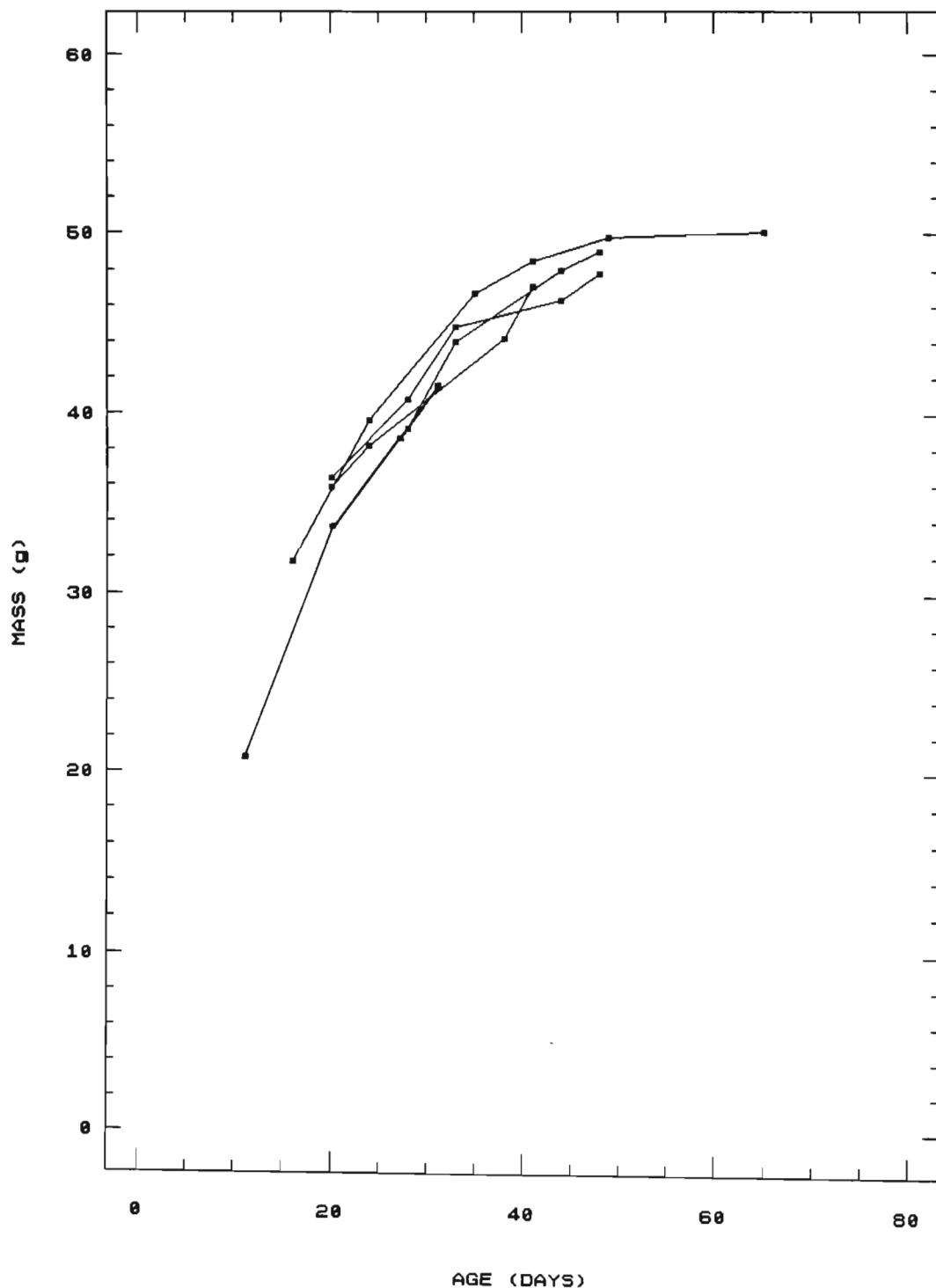
When considering how far these assessments of growth and plumage development may be typical of the whole flufftail population it must be borne in mind that the experimental subjects, although unconfined, were reared in an environment in which there was a continuous abundance of food. Thus these birds may have developed more rapidly than they would have done under more normal conditions, when food supplies probably would have been more fluctuating and less plentiful. These results may thus represent the optimum rate of growth and development for the chicks of this species (see also Section 9.4.10.4.6 for comments on breeding success).

#### **9.4.10.4.3 Development of vocalizations**

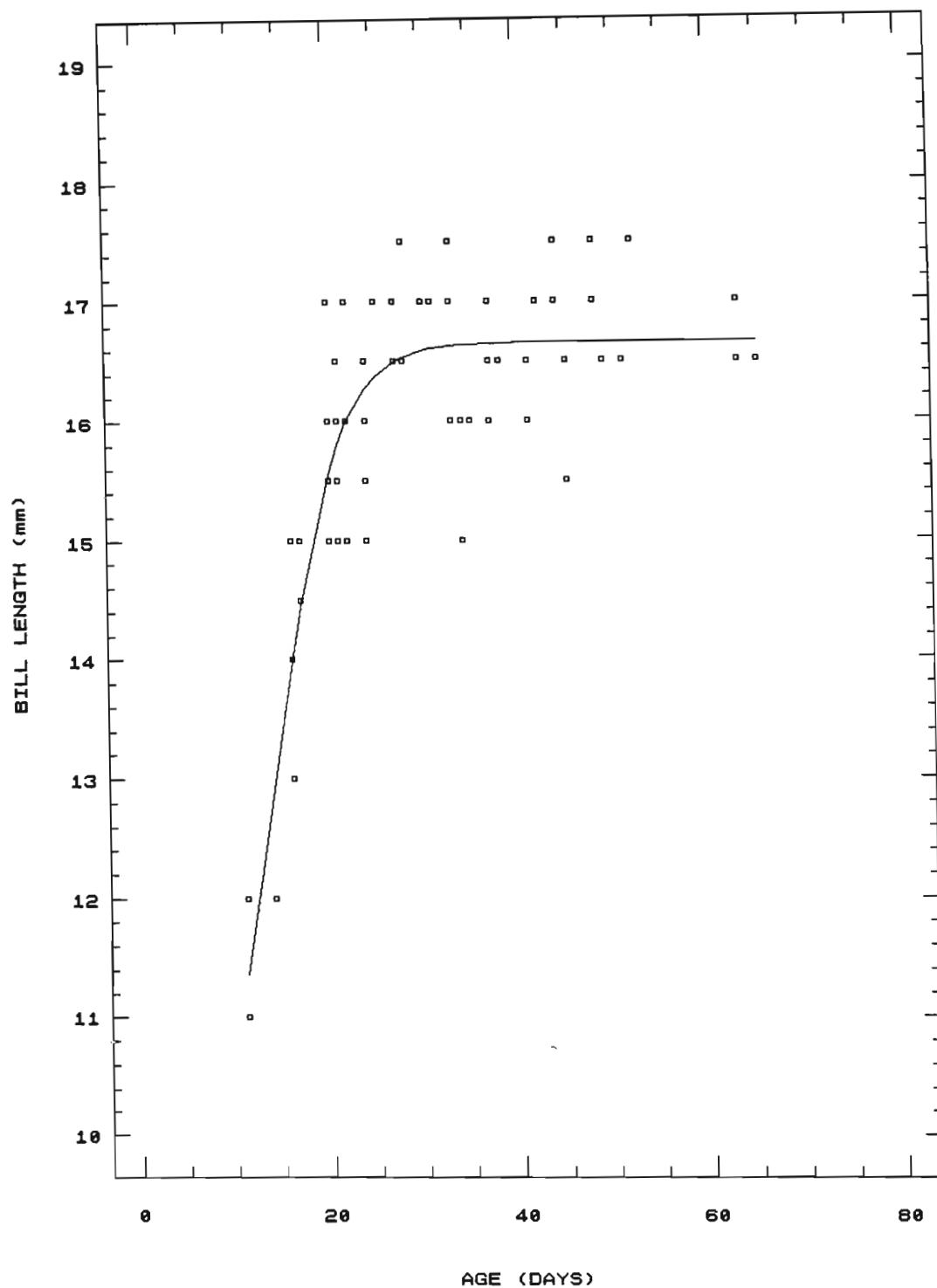
Intensive observations at Scotston enabled the development of vocalizations to be recorded in detail for most of the broods studied. Results are summarized in the final section of Table 9.2 (Young birds: 1-70 days of age). Downy chicks up to one week old made only four calls (Y1-Y4), two of contact and two of distress, the common *ZEEK* (Call Y2) contact call also being used when soliciting food from the parents. This and the distress squeal (Call Y4) remained part of the birds' vocabulary until 28-31 days, well after independence. From the start of the second week until independence (12-13 days later) the *PREEE* trill (Call Y5) replaced the *ZEEK* as the common contact/soliciting call; it was derived from the *ZEEK*, and intermediates were often heard. During this period 13 other calls were also developed, seven of them having a primarily food-soliciting function,



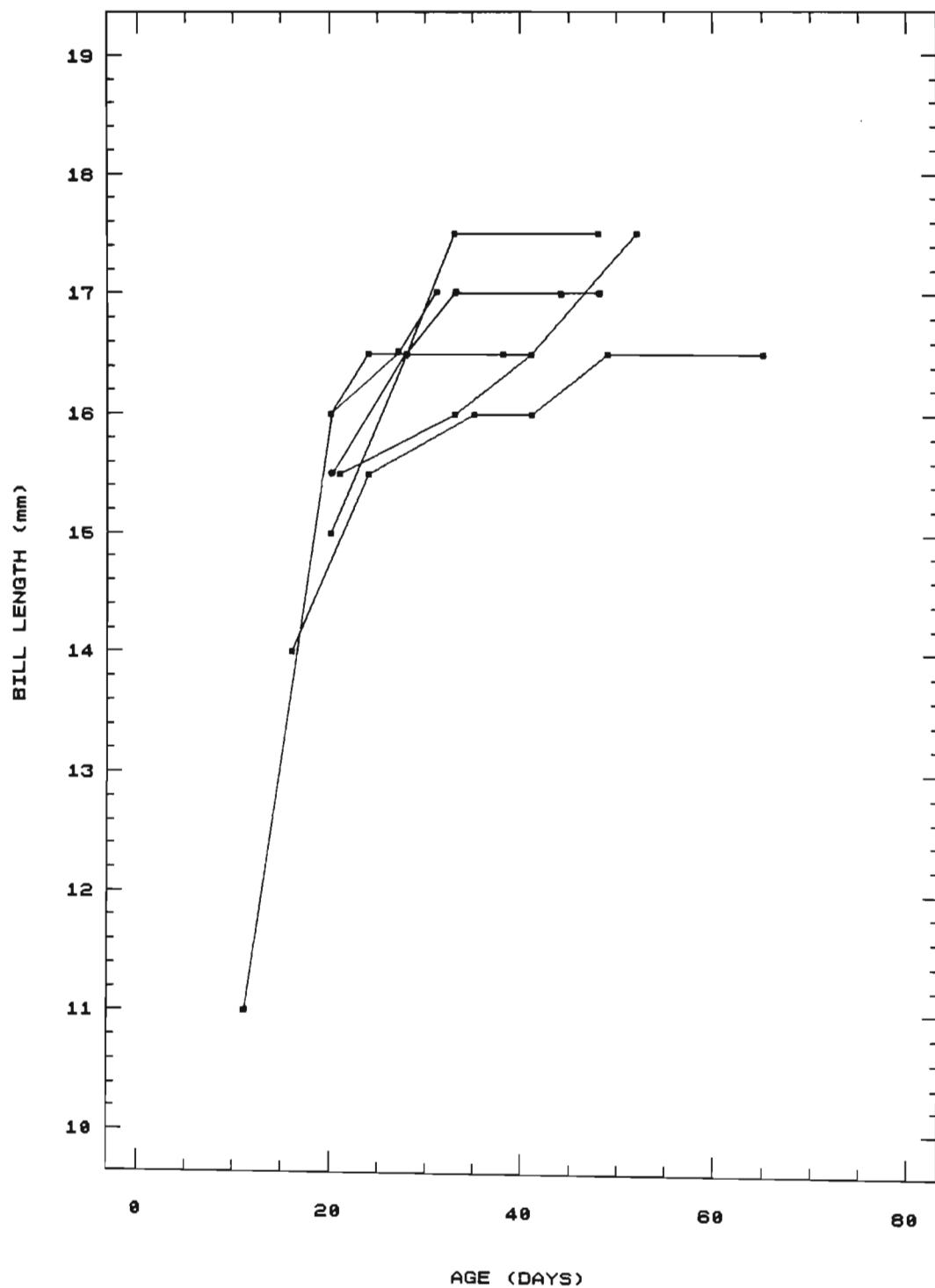
**Fig. 9.14** Postnatal growth of the Buffspotted Flufftail (mass against age;  $n = 76$  measurements), with a fitted growth curve.



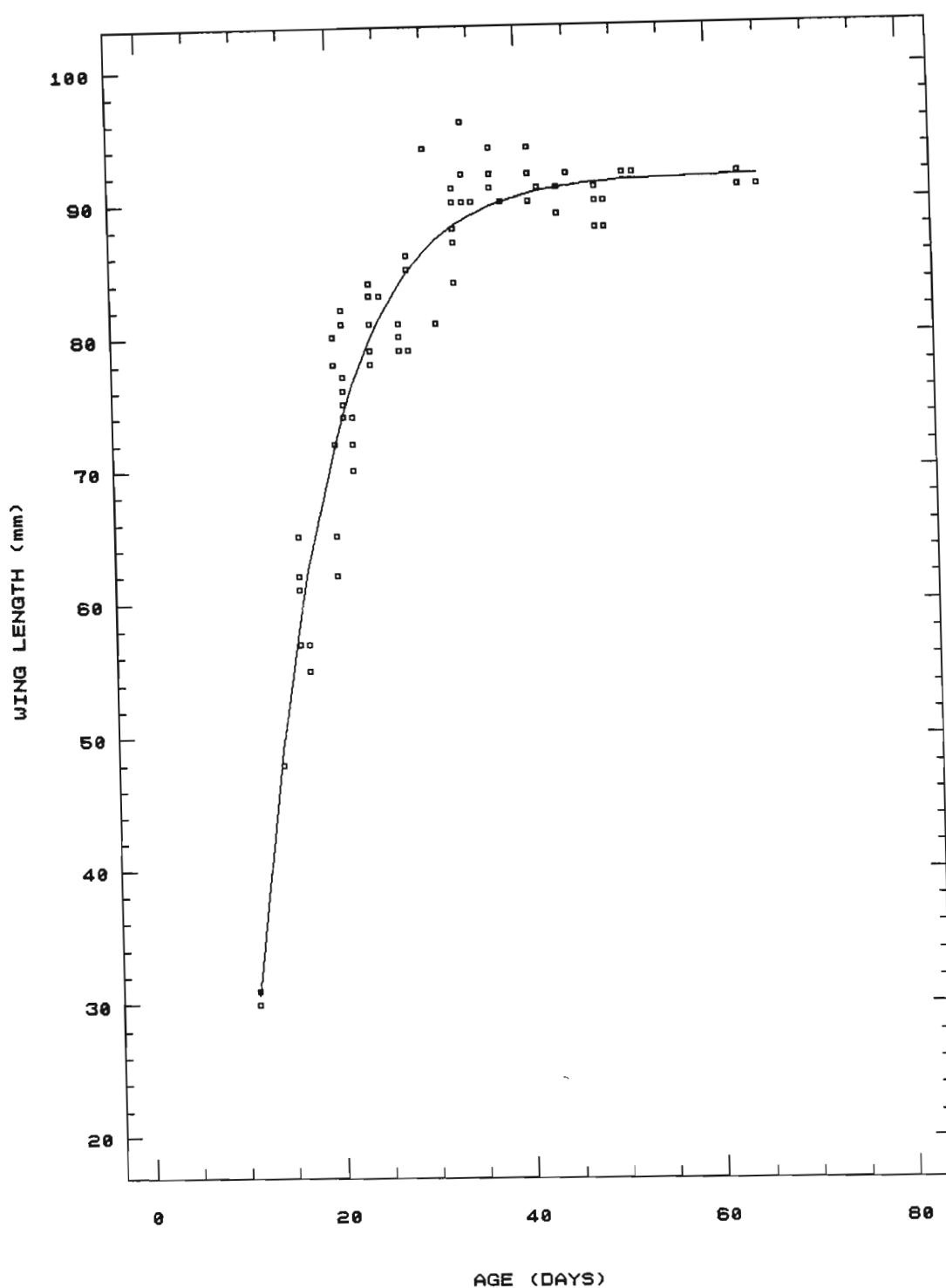
**Fig. 9.15** Individual growth curves of five birds for which three or more measurements of mass were obtained.



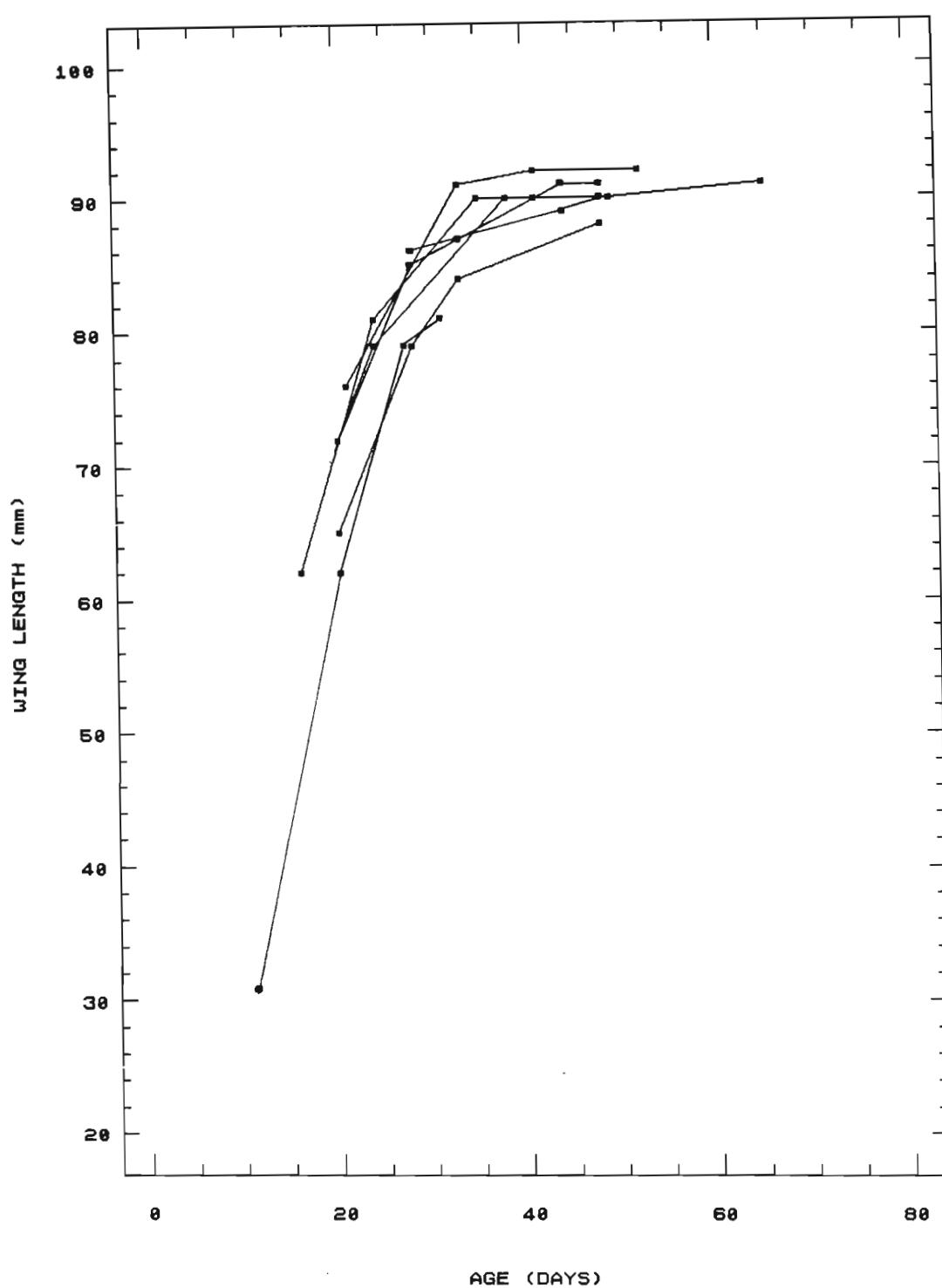
**Fig. 9.16** Increase in the bill length of young Buffspotted Flufftails with age ( $n = 77$  measurements), with a fitted growth curve.



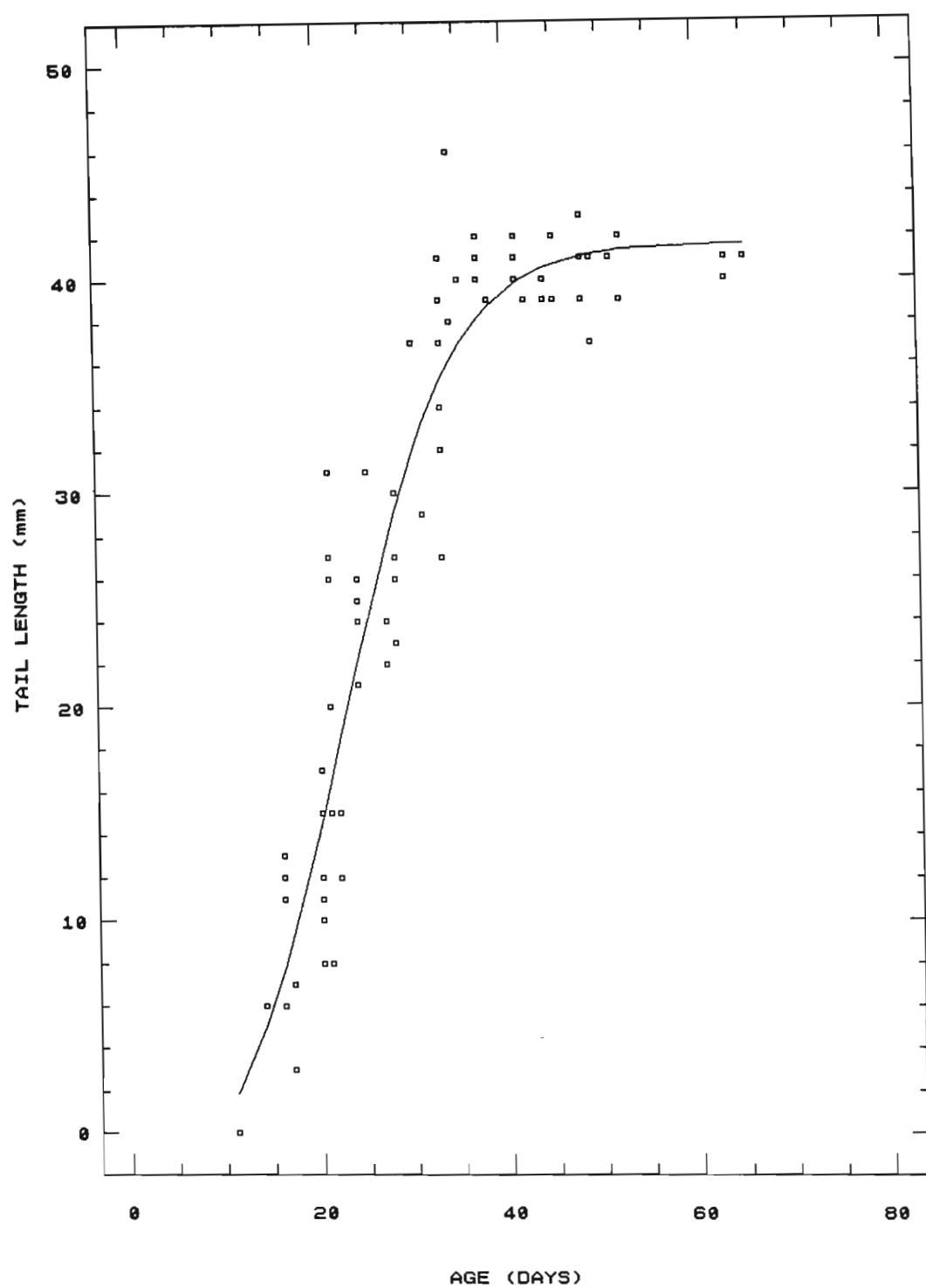
**Fig. 9.17** Individual growth curves of six birds for which three or more measurements of bill length were obtained.



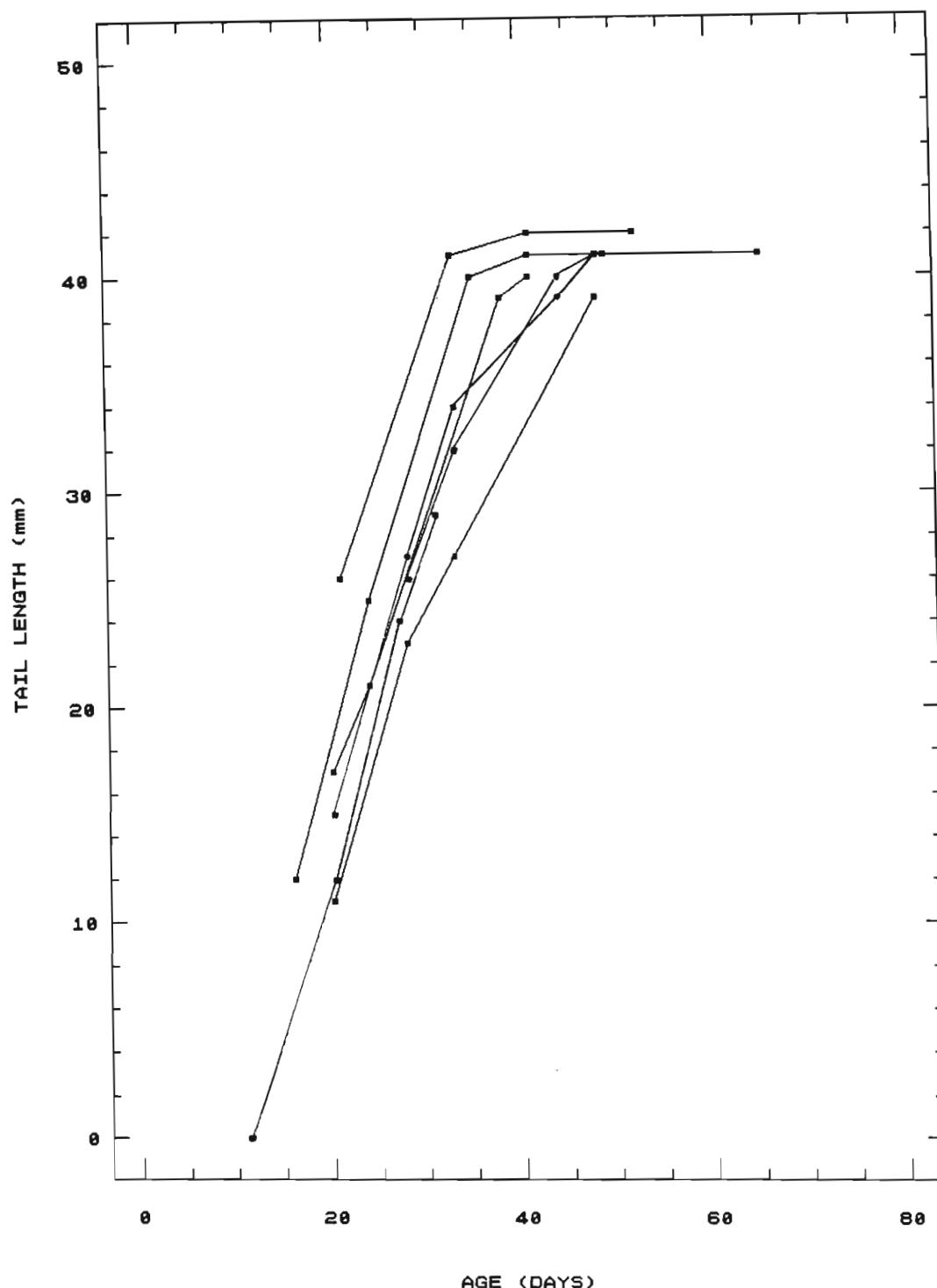
**Fig. 9.18** Increase in the wing length of young Buffspotted Flufftails with age ( $n = 78$  measurements), with a fitted growth curve.



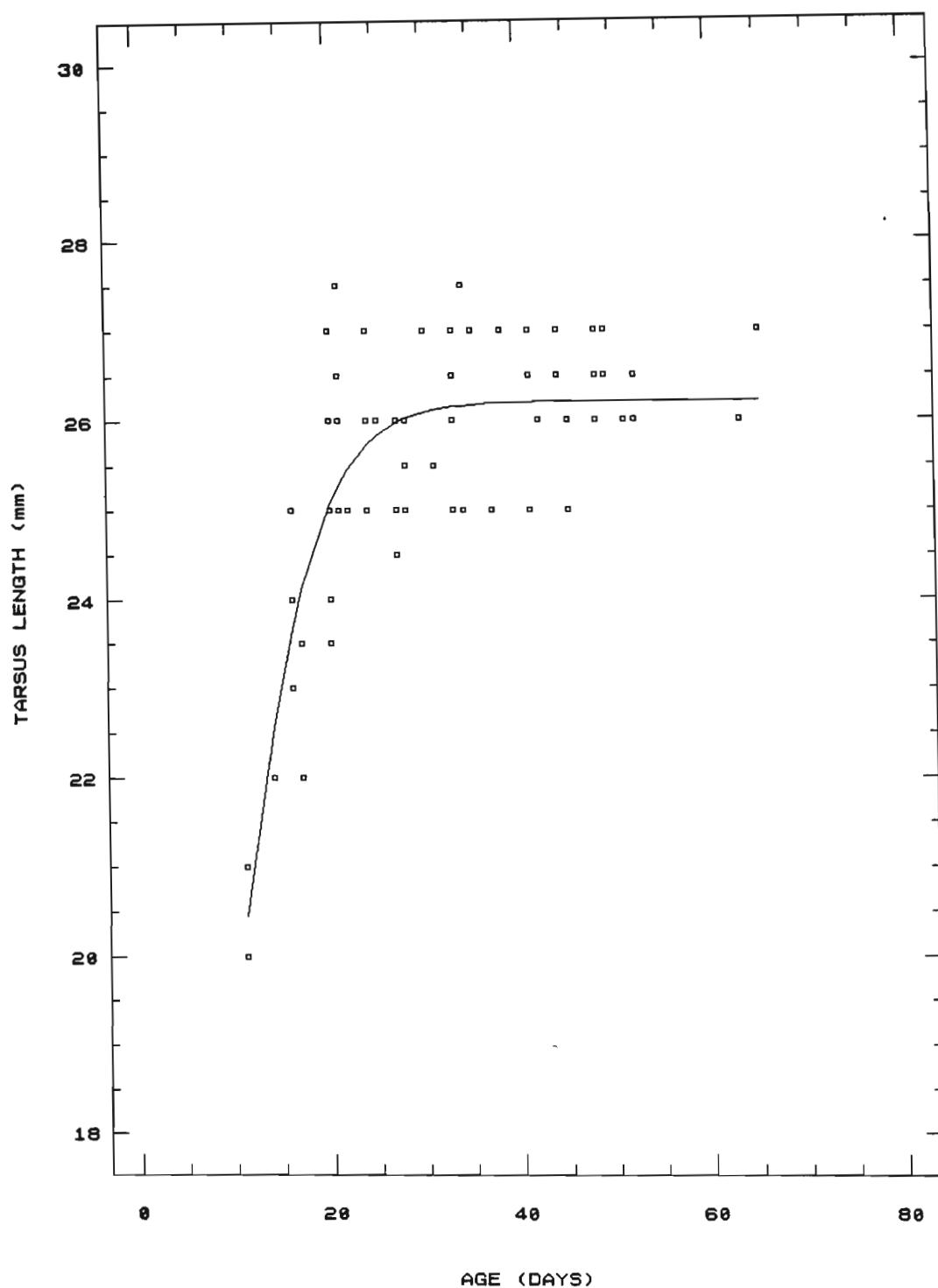
**Fig. 9.19** Individual growth curves of seven birds for which three or more measurements of wing length were obtained.



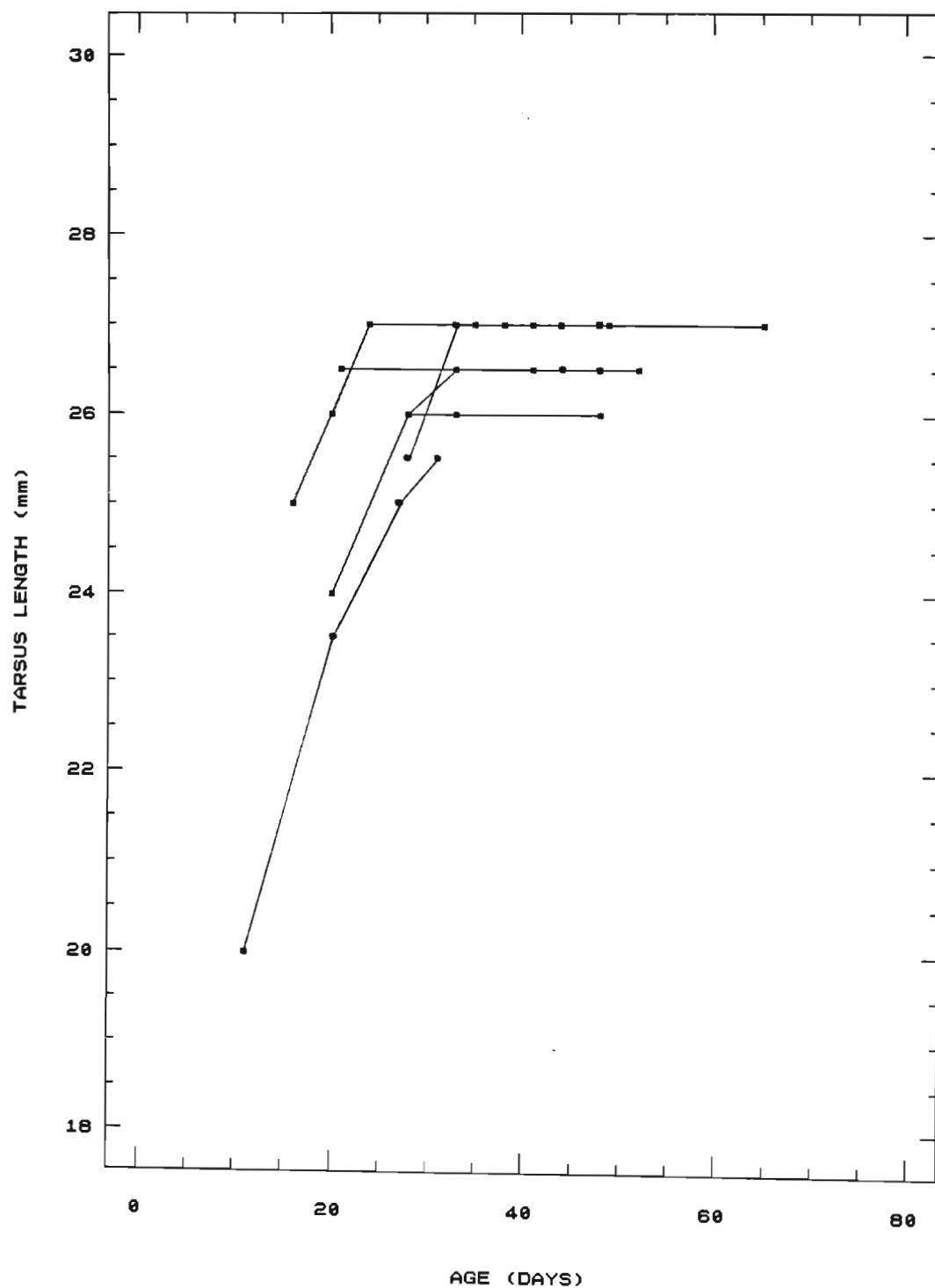
**Fig. 9.20** Increase in the tail length of young Buffspotted Flufftails with age ( $n = 77$  measurements), with a fitted growth curve.



**Fig. 9.21** Individual growth curves of seven birds for which three or more measurements of tail length were obtained.



**Fig. 9.22** Increase in tarsus length of young Buffspotted Flufftails with age ( $n = 77$  measurements), with a fitted growth curve.



**Fig. 9.23** Individual growth curves of seven birds for which three or more measurements of tarsus length were obtained.

the others being contact or alarm calls, and the young had a repertoire of 16 calls (Table 9.3). Five of the calls developed during this period, including the trill and two other soliciting calls, were also heard after independence, until the young were 25-34 days old. From the fourth week of age the young developed 19 more vocalizations (Table 9.2), to give them a repertoire of 26 calls, principally alarm, aggressive and contact calls (Table 9.3). The development of aggressive calls began at about 24 days, when the independent young had been rejected by the parents and had to fend for themselves. Of the calls used during this period, seven (six of them aggressive) were similar to those used by adults, in contrast to the pre-independence period, when only one call (Y17) also had an adult equivalent.

Before they became independent, young birds appeared to ignore taped playback of most Buffspotted Flufftail calls, occasionally listening to contact calls. After independence they became more aware of taped playback, reacting as they would when hearing calls from the parents, i.e. normally seeking to avoid contact with the source of the call.

#### **9.4.10.4.4 Behavioural development**

The main developments in behaviour may be summarized as follows.

**1 day.** Movements are relatively feeble; chicks remain in or close to the nest.

**2 days.** Chicks run, but not strongly; they may leave the vicinity of the nest.

**3 days.** Chicks run more strongly and accompany the parents everywhere, keeping close to them. They accompany either parent, the relative numbers looked after by each parent varying with the pair concerned. Although chicks frequently solicit food they are already capable of foraging for themselves. At feeding stations they usually stay in cover while parents carry food to them. They jump well, and land unharmed after a fall of 1 m.

**4 days.** When foraging the chicks make short runs with pauses (the parents usually walk). They emerge briefly from cover at feeding stations.

**5 days.** Chicks run very strongly and make their first bathing actions (dipping the body and fluttering the wings) near water. They are more confident at feeding stations, remaining out of cover for long periods.

**6-7 days.** They gain confidence for forays away from the parents but usually stay close, and are confident enough to cross open areas (lawns, etc.) unaccompanied. They avoid a model female but ignore a model 11-day-old chick.

**8-9 days.** When foraging, chicks move dead leaves around like adults. They still make bathing actions on dry land.

**10-11 days.** Young gain confidence from the presence of the stuffed chick at the feeding station and stay in the open for longer periods, feeding near it. They still actively solicit food from parents, but are often seen on their own. The first proper bathing, and the first attempts to take food from water (often unsuccessful) are seen.

**12-13 days.** They continue to gain confidence and forage more independently.

**14 days.** Some are adept at feeding in water, others are not: one bird, after many failures to catch prey, persistently solicited food from a successful sibling by pushing its head forwards between the sibling's legs in the typical soliciting action of a chick (see below), and ate a mealworm which the other eventually dropped.

**15 days.** Young are almost independent, performing all activities on their own; they bathe and preen efficiently. They begin to climb around in low branches. The typical chick soliciting action of pushing the head forward between the adult's legs is still occasionally seen at this age.

**16 days.** Although independent of adults when foraging, the young still solicit food from adults and are often fed frequently. One brood (Pair 1, brood 2, January 1991) was abandoned at this age.

**17 days.** Many young are still inefficient at taking food from water, requiring several attempts before grasping submerged prey.

**18 days.** Young jump up and down and run around with flapping wings, preparing for flight; they jump on to low branches and walk around in bushes.

**19 days.** The first proper flights occur, usually vertically up into the low branches of an overhanging bush. Young still solicit food from parents occasionally, but are fully independent and are usually rejected at 19-21 days of age, after which they are very wary of the adults and avoid them actively although staying in the area for some time (Section 9.4.11). Young are more sensitive than adults to normal background noises such as people talking, farm machinery, vehicles, etc.

**20+ days.** All young are adept at feeding in water. Female young of the final brood of the season were seen to be fed occasionally by the adults until 28 days old, but males did not feed young males older than 19 days. After the adults left in March 1991 all the third brood young fed together amicably until they left the area in April at ages 48-59 days, although a dominance hierarchy was apparently established, involving a little low-intensity chasing by dominant males and submissive behaviour by females. Allopreening between young was never seen. Birds 20-22 days old occasionally solicited food from siblings.

Young birds have three principal methods of soliciting food from the parents. They frequently stand still, especially when very young (up to 4-5 days old), and repeatedly give soliciting calls (see Section 9.4.10.4.3.), often crouching with the neck retracted and the head horizontal. The parent approaches with prey and stands motionless in front of the chick, which pecks upwards to take the

food from the parent's bill; the food is not actually offered to the chick. Young chicks frequently make several attempts to grab the prey before succeeding and the parent sometimes drops the food for the chick to pick up. When the family is foraging together, chicks often run to a parent which has found food and perform the same begging action in front of it, or stand alongside the parent, head to head, and reach forward to take prey from the parent's bill. The third method is practised from 4-15 days of age and consists of the young bird approaching from behind, pushing its head and body under the parent's belly and forwards between its legs to stretch the neck up and take food from the parent's bill. When the young are 10-11 days of age their large size makes this action rather more difficult and, in their attempts to squeeze beneath the parent, they may raise the parent off the ground or cause it to overbalance. Young chicks occasionally solicited food from any independent females of the previous brood which might have remained in the vicinity, and very occasionally one of these birds would drop a mealworm, which the chick would then eat. They appeared to be very wary of immature males.

The chicks normally sleep in a crouched position, the wings drooped and the bill almost touching the ground. The female was seen to brood young chicks under both her body and her wings, fluffing out her feathers while doing so.

On three occasions young birds aged 49-52 days were seen to give a typical spread-wing aggressive display (Section 9.4.5.3) to Olive Thrushes and Cape Robins which approached the feeding station, successfully scaring off these birds. When released on the ground after trapping and measuring, flufftails as young as 21 days sometimes crouched with open and drooped wings before running into cover.

#### **9.4.10.4.5 Parental behaviour**

The male is bold in the defence of the nest against human intruders, standing in the small cleared space in front of the entrance and making loud snake-like hisses. Males with dependent young will threaten or attack any potential source of danger, from a rat to a human intruder, using either the full spread-wing display (described in Section 9.4.5), in which the wings are raised over the back, or a low-intensity variant in which the wings are extended to the side and drooped so that the primary tips touch the ground. During such displays the birds utter *CHEK-CHEK* calls (Table 9.2, Call M25) and often rush towards the intruder, occasionally even striking it with the wings or bill. The spread-wing display is also sometimes used in defence of the nest. Females were not seen to be so strongly aggressive to intruders, and were not seen to chase rats, but in defence of the chicks against observers at Scotston they ran around with open drooping wings, uttering Call F16, the equivalent of the male's

Call M25 (Table 9.2). They also performed this display, with Call F12, towards unseen intruders (possibly rats).

On one occasion when I surprised three seven-day-old young feeding in an open trap, the male parent made a silent low-intensity spread-wing display while the female entered the trap, gathered the chicks together and herded them out.

The adults are particularly attentive towards chicks less than 7 days old, spending much time ensuring that the young do not wander too far away from the family group. When moving across open ground such as lawns, adults will pause frequently to allow young chicks to catch up before proceeding. The methods of feeding and brooding young have already been described (Section 9.4.10.4.4).

When the three-day-old young were ready for release after being found abandoned and weak (Section 9.4.10.4.6), they were taken to the feeding station, when their loud *ZEEK* calls immediately attracted the female, which walked around agitatedly in cover until I placed the chicks on the ground, when she immediately approached and led them into cover.

#### **9.4.10.4.6 Breeding success and survival**

Excluding the Scotston breeding data (Fig. 9.13), of the 36 other breeding records obtained during the study, 18 involved sightings of adults with 1-4 young birds ranging in age from about 3 to 20 days. The mean number of young seen was 2.06 (S.D. = 0.94) and, although some young may have been overlooked (they are often difficult to see and to count accurately), the fact that the normal clutch size is 4 or 5 eggs (Section 9.4.10.3) suggests that some broods may suffer substantial reductions from either infertility or chick mortality. Of the five records involving clutches (two of four and three of five eggs) only one egg failed to hatch in one clutch of each size and this suggests that chick mortality is the more important factor in reducing brood size.

Of the nine clutches laid in the Scotston garden during the study, one was destroyed soon after incubation commenced (Fig. 9.13) and eight hatched successfully. Although these clutches were not seen before hatching, it was considered probable that all the eggs hatched in each case (Section 9.4.10.3). Pair 1's first two broods (four and five young respectively) in the 1990-1991 season were reared under normal conditions, the adults not becoming accustomed to taking mealworms until the second brood was ten days old. Only two young from each brood survived to maturity and this supports the suggestion that mortality is normally high among chicks. However, all chicks of Pair 1's third brood, and all chicks of the five broods hatched by Pairs 1 and 2 in the 1991-1992 season,

survived to maturity. All were fed frequently on mealworms and it is probable that the success of these six broods was influenced by the artificial food supply.

At Underberg several indications were obtained of the type of predation to which eggs and young are subjected. Adults were very aggressive towards rats (Section 9.4.10.4.5) and one seven-day-old chick in another garden was killed and partly eaten by a rat (N. Treleaven pers. comm.); rats are numerous in these gardens and may take a considerable toll of young chicks, and perhaps also of eggs. Striped Mice *Rhabdomys pumilio* at Scotston frequently attempted to chew the stuffed flufftail skins used as models and they may eat eggs, although they would be easily repulsed by the adult flufftails. A Southern Boubou *Laniarius ferrugineus* at Scotston ignored adults and fully grown young but would have attacked calling 10-day-old young had the observer not scared it away. The reactions of adults to snakes (Section 9.4.12) suggest that they regard these reptiles as a danger. The fourth clutch of Pair 1 at Scotston was destroyed, and the female slightly injured, just after a Large-spotted Genet *Genetta tigrina* appeared temporarily in the garden. Domestic and feral cats kill many adults in other gardens, and must also kill chicks.

Several observers noted that very young chicks (less than 6-7 days old) occasionally stray from the family group and enter houses or verandas, and two such occurrences were noted at Scotston; in both cases the young were released in the garden to rejoin the family. Small young also occasionally fell into ditches and holes from which they could not escape, and were rescued by observers. Under natural conditions the chances of straying young surviving accidents or escaping predators must be small.

Very young chicks are also vulnerable to bad weather, as was seen at Scotston in 1992. Pair 2's second brood appeared on 7 February, the day after hatching, which suggested that they had been forced to vacate the nest early, possibly after disturbance. That night it rained heavily and at 07:00 the next morning three of the chicks were found under bushes in a flowerbed where the family had probably roosted. The chicks were wet and very weak, and called feebly. After being dried, kept warm and fed on small mealworms, they recovered fully and became very active. They were released at 08:30, when the female took them to join the other young (Section 9.4.10.4.5), and the entire brood survived to maturity.

The Scotston young also suffered several other accidents. A 38-day-old female suffered a broken leg and was kept in captivity for a week while the break healed. On release she appeared to fare well. Another female became ill when 26 days old and remained quietly at the feeding station for three days, even entering the hide. She recovered and remained in the garden for another month. A 32-day-old female suffered a broken wing and, although the break healed in captivity, she was unable to fly properly so she was removed to an outdoor aviary in Durban, where she subsequently

died from an unknown cause. Such birds would probably not have survived under completely natural conditions.

No information was obtained on the longevity of adults but this bird's migratory tendencies must result in a greater mortality than that suffered by purely sedentary species such as the Redchested and Whitespotted Flufftails, while both adults and young also appear to suffer a relatively high level of predation (see Section 9.4.12). Thus it is to be expected that this species is not as long-lived as the more sedentary flufftails.

#### **9.4.11 Dispersal of young birds**

Dispersal of young birds during and after the breeding season was monitored at Scotston, while evidence for dispersal elsewhere in Natal was obtained from the casualties acquired during the study. At Scotston nine unknown immatures were recorded in the garden (Table 9.12), these birds being easy to identify as strangers because of their initially retiring behaviour and the fact that all the resident birds in the garden had been colour-ringed. Two of the February 1991 arrivals were also colour-ringed for ease of identification. Most arrivals occurred in January and February, and both the pattern of occurrence and the ages of the young on arrival (45–60 days; mean 52,5 days) approximate to those of the garden immatures when they finally moved away from the parental territories. The three birds which arrived on 21 February 1991 stayed for extended periods but all birds arriving in early 1992 were transient visitors. The reason for this difference may be that in February 1991 the garden contained only one breeding pair of flufftails, which occupied less than half its area, so that the immigrants came into contact with the territory holders much less frequently than in the following season, when two breeding pairs occupied the entire garden and probably harassed the immigrants considerably.

Of the 31 young reared to independence in the Scotston garden during the two seasons, the disappearance of 18 (nine males and nine females) was considered to involve normal dispersal as opposed to harassment or mortality. Of these birds, one left as early as 13 December, four in January, six in February, two in March and five in April. Their residence periods ranged from 37 to 69 days (mean 55,9 days). Comparing both the means and medians of the residence periods of males and females showed no statistically significant difference between the sexes ( $t = 0,538$ ;  $P > 0,5$ ; d.f. = 16, and  $U = 32$ ;  $P > 0,05$ , Mann-Whitney  $U$ -test).

The departure dates of the last nine young hatched in 1992 were not determined because observations were discontinued on 8 March. On this date, Pair 1's third brood ( $n = 4$ ) was 49 days old and Pair 2's second brood ( $n = 5$ ) was 31 days old. Of the other four birds, three left when

TABLE 9.12

Occurrences of unknown young Buffspotted Flufftails in the Scotston garden during the 1990-1991 and 1991-1992 breeding seasons. Abbreviations: F = female; M = male; ? = age not estimated.

Season	Sex	Estimated age (days)	Arrival date	Length of stay (days)	Date last seen
1990-1991	M	53	21 February	36	28 March
	F	50	" "	11	3 March
	F	60	" "	8	28 February
	F	?	6 April	1	6 April
1991-1992	M	45	17 January	1	17 January
	F	?	21 January	1	21 January
	M	55	22 January	1	22 January
	M	52	2 February	1	2 February
	F	?	13 February	1	13 February

20-27 days old, apparently because of severe harassment from their male parent, while the other suffered a broken wing at 32 days of age and was taken into captivity.

Thus the pattern at Underberg appeared to involve the dispersal of young from breeding territories from mid-December to late April, such birds being about 6-10 weeks old when they finally moved away. This pattern is to be expected in a region where the normal breeding season appears to run from October to March (Table 9.9). In the 1990-1991 season the young of the last brood remained until April, leaving between 6th and 23rd, although their parents had left on 9 and 13 March. The stay of the young was probably lengthened by artificial feeding: the supply of natural food at the site fell rapidly during April (Chapter 10), when the birds visited the feeding station very frequently.

Evidence obtained from casualties for the movements of immatures is summarized in Section 9.4.3.3 and Fig. 9.4, most instances involving birds with appreciable fat deposits and most records coming from the coast. Such records are probably indicative of large-scale, and possibly long-distance, postbreeding and prebreeding movements, and should not be placed in the same category as simple dispersal from the breeding territories. However one May bird without fat deposits was probably undergoing dispersal as opposed to more prolonged movement (Section 9.4.3.3).

It is interesting that, although the Scotston Pair 1 adults both returned to the same territory to breed in the following season, none of the 28 young colour-ringed in the garden, nor the two immigrant immatures which were also colour-ringed, were seen in the subsequent two seasons, either at Scotston or at other gardens at Underberg. This suggests that, after dispersal, most immatures may not return to breed at or near the place where they were hatched.

#### **9.4.12            Predation and mortality**

Of the 53 casualties examined (Section 9.4.3.3), the cause of death was uncertain in 15 (28%), six (11%) had flown into walls or windows, two (4%) were road casualties, one (2%) was killed in a trap and two (4%) were killed by dogs. The remaining 27 (51%) were killed by cats and this form of predation is undoubtedly a significant cause of mortality where the birds occur close to human habitation. Such birds are usually killed in gardens, where they are often occupying artificially created habitats with alien vegetation, which may compensate for the loss of forested habitat in those areas (e.g. in Durban and Pietermaritzburg) or may have created habitat where none existed before (e.g. in high-altitude areas like Underberg). On balance the birds have possibly benefitted from their ability to colonize such habitats, even though the predation level may be high.

Although rats are known to kill young birds (Section 9.4.10.4.6) they probably do not normally pose a threat to healthy adults, which are able to chase them away (Section 9.4.10.4.5). The

Scotston female which was injured when her clutch was destroyed (Section 9.4.10.4.6) was probably attacked by a Large-spotted Genet and this viverrid was once attracted to taped playback of Buffspotted Flufftail calls, as was the Slender Mongoose *Galerella sanguinea*. At Scotston a female Redbreasted Sparrowhawk *Accipiter rufiventris* once flew low over the hedge above Hide 2, causing the adult flufftails to rush into dense cover, making an uncharacteristically noisy passage over the leaf litter. Although accipiters may pose a threat, it is doubtful whether they could often catch adults in cover.

The reactions of adults to a snake were observed at Scotston, when a Berg Adder *Bitis atropos* appeared one midday at a feeding station. The female crept slowly out of cover, with her head low and her neck stretched out, approached to within 30 cm of the snake's head and followed it as it moved around, until it became aware of the observer and disappeared. The pair had no dependent young at the time. This behaviour resembles that shown by captive Redchested Flufftails to a model snake (Chapter 4, Section 4.4.12).

#### 9.4.13 Moult

All descriptions of moult concern birds from Natal, from which region most material is available. A full description of the stages of postjuvenile moult is given in Section 9.4.10.4.2, from which it is apparent that this moult normally involves replacing plain juvenile feathers on the head and body, plus the direct replacement of down on the head (in some birds), thighs and tail, and feather growth on initially bare tracts, namely the lores and ear-coverts, the lesser and marginal upperwing coverts and all the underwing coverts. The rest of the upperwing coverts, the alula and the remiges are not replaced during this moult.

No field observations were made of the progress of moult between the age of 70 days and the start of the next breeding season, but specimens indicate that the unspotted juvenile median upperwing coverts are progressively replaced during the winter, while all or most of the greater upperwing coverts are retained into the following breeding season, making it possible to identify birds hatched in the previous breeding season. Two immature specimens, a female from St Lucia in May and a male from Richmond in July, are in active remex moult, suggesting that immatures normally moult the remiges during the winter. Both birds are moulting the primaries sequentially, one ascendently and the other descendently. The greater primary coverts are apparently replaced during this remex moult. No dated material is available to show the extent and timing of any pre-breeding body moult in first-year birds.

Adults normally have a complete postbreeding moult, four specimens being in active remex and body moult in the April-July period. On 7 March 1992 the Scotston Pair 1 male had started body moult but not remex moult. Primary moult is sequential; in two specimens it is descendent and in one ascendent. One June bird, and one from December, show arrested moult where 3-4 of the central primaries have not been moulted. Secondaries are apparently moulted during or just after primary moult. Several adult specimens show signs of prebreeding body moult in the last four months of the year.

## 9.5 Discussion

### 9.5.1 Distribution, status and habitat

Because of its retiring habits the Buffspotted Flufftail is often overlooked and it is certainly under-recorded, although perhaps not to the same extent as the Redchested Flufftail (Chapter 4, Section 4.5.1) which, because of its association with wetlands and its less distinctive and conspicuous breeding-season calling, is less obvious to the casual observer. In common with the Redchested Flufftail, the Buffspotted Flufftail is more widespread and numerous in southern Natal than in any area which I have surveyed in central and East Africa (Zambia, Zimbabwe, and Kenya). Its distribution in Zimbabwe is restricted in extent (Section 1.2.1.1; SABAP data) and in Zambia I found it sparsely distributed and apparently seasonal in occurrence. I also found it to be localized and relatively uncommon in Kenya, and even at Kakamega Forest in western Kenya, where it was sometimes locally numerous, its occurrences in the early 1980s were erratic and unpredictable (Taylor & Taylor 1986). It was also occasional and unpredictable in occurrence in the central Kenya highlands, where it was rarely recorded from forests in the Nairobi area and was never encountered at the extensive Kikuyu Escarpment Forest, where an intensive four-year study of forest birds was made (Taylor & Taylor 1988), despite the presence of apparently suitable habitat and the occurrence throughout the year of ground-feeding passerines which exploited its terrestrial foraging niche. In the Nairobi area it did not apparently occur in gardens to any significant extent, despite the presence of apparently suitable habitat. In South Africa its restricted distribution in the Transvaal, and its mainly coastal distribution in Cape Province (Section 1.2.1.1), suggest that the southern and coastal regions of Natal hold a significant part of the country's population.

In Natal the Buffspotted Flufftail is a widespread and successful colonist of exotic vegetation associated with human habitation and is not seriously threatened by habitat loss, in contrast to the wetland and grassland flufftail species discussed elsewhere in this thesis. It is probably holding its own and may even have increased in numbers locally in recent years. However at some localities it

has decreased in recent years, for example at some sites in Durban where birds inhabiting undisturbed tracts of dense vegetation in residential areas have apparently been eliminated by cats which come from the increasing number of households in the vicinity (R. Davidson pers. comm.). In many suburban gardens the species must also be exposed to the effects of insecticides as well as to the depredations of cats. Continued destruction of forests and deciduous thickets will also affect its numbers adversely and the poor ground cover and relatively sterile terrestrial feeding niche offered by conifer, wattle and eucalyptus plantations render these vegetation types unsuitable for occupation.

#### 9.5.2 Movements

The information obtained from field observations in Natal during this study suggests that Buffspotted Flufftails will remain permanently in any area as long as conditions are suitable, at any altitude from sea level to at least 1 600 m a.s.l. In mid-altitude areas, when conditions deteriorate below an acceptable level (Chapter 10) the birds may respond with purely local movements, for example to damper areas near streams, possibly at a somewhat lower altitude, either within or beyond the tract of habitat occupied during the breeding season. However, under normal conditions of habitat and precipitation, seasonality of occurrence is usually well marked and regular at altitudes above c. 950 m a.s.l., birds being present only during the breeding season (September to March).

This pattern of occurrence applies to both adults and immatures, and both field observations and data from casualties suggest that the two age-groups regularly undergo movements which are more than purely local, but that immatures are less sedentary than adults, a significant number of them probably undergoing movements at all altitudes. Observations suggest that all immatures undergo dispersal from the breeding site but that many subsequently make what is possibly a long-distance seasonal movement away from the breeding area. It is quite possible that movements to and from the higher-altitude areas of Natal are predominantly altitudinal and over 70 bird species are known or believed to show altitudinal migrations in Natal, moving to lower altitudes from about March to September (Johnson & Maclean in press). These include the Olive Thrush, the Cape Robin and the Starred Robin, forest species which sometimes feed in leaf-litter (Oatley 1966, 1982). However there is no evidence from any coastal or other low-altitude areas of Natal (or anywhere else in South Africa) that the Buffspotted Flufftail either occurs only during the winter or that its numbers are higher in the winter than the summer. Although such occurrences would probably be overlooked in most areas because of the birds' secretive habits and their lack of calls in the nonbreeding season, during this study I never found that any coastal or low-altitude locality which I visited regularly held this species only during the nonbreeding season, nor was I ever aware of any significant increase in

the population at any such locality. Thus the destination of birds moving down from high altitude regions is unclear, but it is possible that the occasional occurrence of winter advertising calling, noted in some areas during the study (Sections 9.4.5.2 and 9.4.8), may be indicative of territorial behaviour in response to the arrival of birds from other areas.

There is evidence, from both casualties and field observations, for coastal movements in Natal, both at the end of the breeding season (predominantly in May) and at the beginning of the breeding season (possibly peaking in October). The postbreeding movement appears to involve a large proportion of immature birds, as is to be expected, and first-year birds were also more numerous among the smaller number of casualties obtained in the spring (August-October) movement period (Fig. 9.4). It is possible that birds undergoing coastal movements may migrate northwards beyond Natal to winter in the coastal lowlands of Mozambique or further north, as is thought to occur in species such as the Pygmy Kingfisher *Ispidina picta* and Paradise Flycatcher *Terpsiphone viridis* (Berruti *et al.* in press), and also that birds moving down from higher altitudes in the Natal interior may join this coastal migration. In view of the unobtrusiveness of the species and the difficulties involved both in ringing large numbers of the birds in the breeding areas and in recovering ringed individuals on passage or in wintering areas, it is unlikely that movement patterns in this flufftail will be resolved in the foreseeable future.

### **9.5.3 General behaviour**

The study produced good evidence that the Buffspotted Flufftail, like the Redchested Flufftail (Chapter 4, Section 4.5.2), is entirely diurnal and crepuscular in all its activities except movements and advertising calling, and avoids prolonged exposure to direct sunlight. The daily activity patterns noted during the breeding season resemble those observed in the Whitespotted Flufftail (Taylor & Taylor 1986) except that the latter's foraging activity apparently extended over less of the day, the most intensive feeding being observed for three hours after sunrise and 2-3 hours before sunset, even in pairs with chicks. However, as Whitespotted Flufftails lay only two eggs and probably breed only once per season (Keith 1986; Keith *et al.* 1970; Pye-Smith 1950; Taylor & Taylor 1986), they presumably need to spend less time per day in foraging with the young.

The absence of communal play activities in the Buffspotted Flufftail is in striking contrast to the behaviour of the Redchested Flufftail and is one example of the different relationship between pair members, and between adults and offspring, in the two species. Other examples of the less amicable co-existence between Buffspotted Flufftail pair members are the lack of allopreening and the breeding-season sexual harassment of the female by the male. There was no indication of such harassment in

the Redchested Flufftail, although I made relatively few prolonged observations of breeding pairs in the wild. Allopreening is associated with prolonged maintenance of the pair bond (references reviewed by Kunkel 1974) and its absence in the Buffspotted Flufftail may indicate that the pair bond is not normally permanent; this may also be indicated by the complete absence in this species of social play, which in the Redchested Flufftail may be beneficial in consolidating long-term relationships within the pair or family group (Chapter 4, Section 4.5.2). Captive birds coexisted amicably in pairs (one pair per aviary) throughout the year (R. Davidson pers. comm.) but no information was obtained on the nature, strength or duration of the pair bond in captivity, or of the existence of territorial behaviour in the nonbreeding season.

The Buffspotted Flufftail adults' early rejection, and subsequent intolerance, of independent offspring in the wild was mirrored in captivity, where pairs would eventually kill independent young which were not removed (R. Davidson pers. comm.). The early rejection of young is indicative of a reproductive strategy geared to maximizing the number of offspring produced in a season, presumably to offset the apparently high level of mortality experienced by this species, not only among chicks but also among immatures and adults as a result of their migratory tendencies (Section 9.4.10.4.6). This topic is discussed further in Chapter 11.

#### **9.5.4 Territoriality**

Too little information was collected on the behaviour of females outside the breeding season to allow any firm conclusions to be drawn concerning the role of the female in territorial defence at this time of the year, and it was never established conclusively that any pair remained together throughout the year in a permanent territory. In view of the differences in the relationship between pair members compared with the permanently territorial Redchested Flufftail (Section 9.5.3) it is possible that the pair bond is often not permanent and thus that nonbreeding males may defend individual territories in the nonbreeding season. However, given stable conditions conducive to permanent residence within a territory, it is also possible that the pair bond could be maintained permanently. Intensive studies at a site such as that at Franklin (Section 9.4.3.2) would easily establish this beyond doubt.

#### **9.5.5 Vocalizations and calling patterns**

The results of the analysis of the influence of time of day and weather on advertising calling are in broad agreement with the subjective assessments made of the bird's calling patterns by the observers who participated in the survey. However it was clear to some observers (including me) that

some birds did not always conform to the expected pattern of calling; for example the occasional individual male might call throughout the night for several mild, clear nights in hot weather, and yet not call in subsequent cool, cloudy weather. There is an obvious danger in oversimplifying the factors affecting calling and it must be borne in mind that the frequency and duration of calling also vary at different stages of the breeding cycle, as is shown in Table 9.8 and described in Section 9.4.8. Thus an unmated male when establishing a territory may call almost continuously, independent of weather conditions, while later in the breeding season he may be stimulated to begin a period of calling at any time when threatened by an intruder, after the loss of his mate, or as a result of some hitherto unknown factor in the breeding cycle. However at most times the duration and timing of calling may be influenced primarily by weather and time of day.

The pure-toned advertising call of strongly calling birds was normally given at a constant frequency throughout all calling periods but usually differed sufficiently from the frequencies used by adjacent territory holders to make individual recognition easy, as was also the case in both the Striped Flufftail (Chapter 7, Section 7.4.3) and the Redchested Flufftail. Apart from this, and from the frequency differences associated with the territorial status of the individual (Section 9.4.8), the simple nature of the call provides little scope for the inclusion of information about the individual. Assuming that the acoustic properties of the call and the behaviour of calling birds have evolved primarily to maximize signal transmission (Section 9.4.8), any advantages conferred by calling at night and in cloudy or misty weather are presumably related to this function. It has already been mentioned that signal attenuation by atmospheric turbulence is least at night (Section 9.4.8) and there appears to be an additional advantage in calling during cloudy or misty weather in that signal attenuation by absorption decreases as humidity increases (Wiley & Richards 1978, 1982). This effect, although small, is greatest for frequencies below 8 kHz and at temperatures from 0-15°C (Wiley & Richards 1982).

A study by Wilkinson & Huxley (1978) on the development of calls in young Aldabra Whitethroated Rails *Dryolimnas cuvieri aldabranus* provides an interesting comparison with this study's observations of call development in the Buffspotted Flufftail. Whitethroated Rail chicks have a much less extensive vocabulary than the young flufftails, but the pattern of call development shows some similarities. As in the flufftail, the rail's earliest vocalizations are used only for contact and location (three calls), and to indicate alarm or distress (two calls), while most of the adult-type calls begin to develop only when the young are ejected from the parental territory, in this species at the age of about 12 weeks. Unlike the flufftail no calls were thought to have a purely food-soliciting function, while the young rails began to give a simple version of the adult's song from as early as ten days of age.

### 9.5.6 Development and rejection of the young

Observations of the development of the young and of the behaviour of the parents show that the age of the young when they are rejected (normally 19-22 days; once 16 days) coincides with the time at which the first adult-type plumage characters begin to become obvious, namely the spotting on the scapulars, mantle and remiges and, in some males, the appearance of the first rufous feathers on the head or breast. Captive birds also attacked young as soon as the first signs of adult plumage began to appear (R. Davidson pers. comm.). Such plumage changes may be the proximate factor stimulating the appearance of aggressive behaviour in the parents. Breeding adult Buffspotted Flufftails ignored, or showed only mild interest in, both an 11-day-old stuffed chick and life-sized two-dimensional wooden flufftail models painted in plain colours to resemble birds in juvenile plumage. Two-dimensional models with adult-type plumage colours and patterns were attacked by breeding males, which showed weaker and less prolonged reactions to them than to three-dimensional wooden models and stuffed adults, presumably because the two-dimensional models were not so lifelike.

The young are well able to fend for themselves by the age at which they are usually rejected, having attained foraging independence at about 15 days of age and being able to fly at 19 days. However they are not fully grown when rejected, the growth curves showing that at 21 days of age the bill and tarsus are about 95% grown, the wing averages 74 mm (83% of the mean adult length) and the mass averages 36 g, 76% of the mean adult mass. It has already been mentioned (Section 9.4.10.4.2) that most birds do not finally leave the vicinity of the natal territory until they are fully grown.

In the young of two wetland rallid species, the Sora *Porzana carolina* and the Virginia Rail *Rallus limicola*, the tarsus is fully grown, and full juvenile plumage has been attained, at 28 days of age (Kaufmann 1987b; Johnson & Dinsmore 1985), this being comparable with tarsus and plumage development in the Buffspotted Flufftail. However postjuvenile moult in these two marsh species apparently does not begin until the young are at least three months old (Kaufmann 1987b), much later than in the young of both Buffspotted and Redcheasted Flufftails, which have completed this moult at 10-11 weeks of age (Section 9.4.10.4.2; Chapter 4, Section 4.4.10.3).

## CHAPTER 10

### THE SEASONAL OCCURRENCE OF THE BUFFSPOTTED FLUFFTAIL IN NATAL IN RELATION TO VEGETATION COVER AND THE AVAILABILITY OF INVERTEBRATE FOOD

#### 10.1 Introduction

During observations of Buffspotted Flufftails at the long-term study sites in southern Natal (Chapter 9) it became clear that considerable differences in the periods of occurrence and migratory status of the species existed at different sites, birds occurring throughout the year at some sites but only during the breeding season at others (Section 9.4.3.1). The pattern at a study site was often reflected in observations made at nearby localities, but could also differ markedly between localities within a short distance of each other (Sections 9.4.3.1 and 9.4.3.2). It was concluded (Section 9.5.2) that patterns of occurrence in Natal are complex and that both local and long-distance movements probably occur.

In an attempt to establish what factors might affect the birds' pattern of occurrence it was decided to measure the two environmental variables which might be expected to have the greatest influence on the suitability of any site for residence outside the breeding season, namely vegetation cover and the availability of food. The importance of these two variables is discussed in Chapter 3, Sections 3.6 and 3.7, and the dependence of the Buffspotted Flufftail on dense cover has already been emphasized (Chapter 1, Section 1.2.1.2 and Chapter 9, Section 9.4.2). Although it was concluded (Chapter 9, Section 9.5.2) that immatures are less sedentary than adults and may make long-distance movements away from breeding areas at all altitudes, while adults may remain until forced to move by deteriorating local conditions, the proximate factors influencing the time of movement are probably the same for both age classes and it should be possible to suggest correlations between patterns of occurrence and variations in the availability of food and cover.

#### 10.2 Study sites

The study was conducted at four long-term study sites, full details of which are given in the relevant sections of Chapter 2: Danville Park, Durban (Section 2.2.9), Ferncliffe Forest and Bisley Valley, Pietermaritzburg (Sections 2.2.6 and 2.2.8) and the garden of Scotston Farm, Underberg (Section 2.2.10). These sites provided examples of the major habitat types and climatic conditions

encountered by the species in Natal, namely coastal forest with high rainfall and a mild climate (Danville), mid-altitude forest with high rainfall and cool winter conditions (Ferncliffe), relatively low-rainfall deciduous bush with cool winters (Bisley) and exotic vegetation in gardens at high altitude where winters are very cold (Underberg).

### 10.3 Methods

Monthly measurements of vegetation cover were made in territories of Buffspotted Flufftails at the four study sites for one year (July 1991 to June 1992), using a density board as described in Chapter 3, Section 3.6.1.3. At Scotston measurements were made twice during October 1991, to monitor more accurately the development of vegetation during the birds' arrival period in the area. All measuring sites were in flufftail territories, indigenous vegetation types being sampled at Danville and Ferncliffe (forest) and at Bisley (dense deciduous bush). At Scotston all vegetation was exotic and that of the vegetable garden was largely cleared during the winter so that the only extensive permanent cover which could be measured was the deciduous hedgerows of *Chaenomeles lagenaria* and *Kerria japonica*, which also had some ground cover of *Vinca*, *Lamium* and grass. During the breeding season these hedgerows were continually frequented by the flufftails, which nested on ground within or adjacent to them (Chapter 2, Fig. 2.21), while all leaf-litter samples were collected within or near them.

The Buffspotted Flufftail's diet consists principally of insects and other invertebrates, and no clear evidence was found that plant material forms a significant part of its diet at any time of the year (Chapter 9, Section 9.4.6), unlike the Redchested Flufftail, which sometimes eats a considerable quantity of grass seeds, especially during the winter (Chapter 4, Section 4.4.6). The degree to which the fruits of two trees, the Bugweed *Solanum mauritianum* and the Pigeonwood *Trema orientalis* might form part of the diet (Chapter 9, Section 9.4.6) was not considered to be significant because the birds were never seen feeding on these fruits, while only seeds, never other parts of the fruit, were found in gizzard samples. To obtain an indication of seasonal variations in food availability it was therefore considered sufficient to sample terrestrial invertebrates. Sampling was confined to leaf litter, the bird's principal feeding substrate, observations indicating that the garden birds did an insignificant amount of foraging in short vegetation, on mossy rocks, in water or by probing in bare soil and mud. Monthly counts of invertebrates from leaf-litter samples were made at the four sites for one year (July 1991 to June 1992), as described in Chapter 3, Section 3.7.3. All the samples were taken from ground where Buffspotted Flufftails were regularly seen to forage.

Regular observations were made of Buffspotted Flufftails at the four study sites throughout the sampling period and, at all sites except Bisley, for periods of 7-25 months before sampling began (see Chapter 2 for full details of the observation periods at these sites). Birds were colour-ringed at all sites and details of the observed patterns of occurrence and movements are given in Chapter 9, Section 9.4.3.1, as is other relevant information obtained in the study area (Sections 9.4.3.2 and 9.4.3.3).

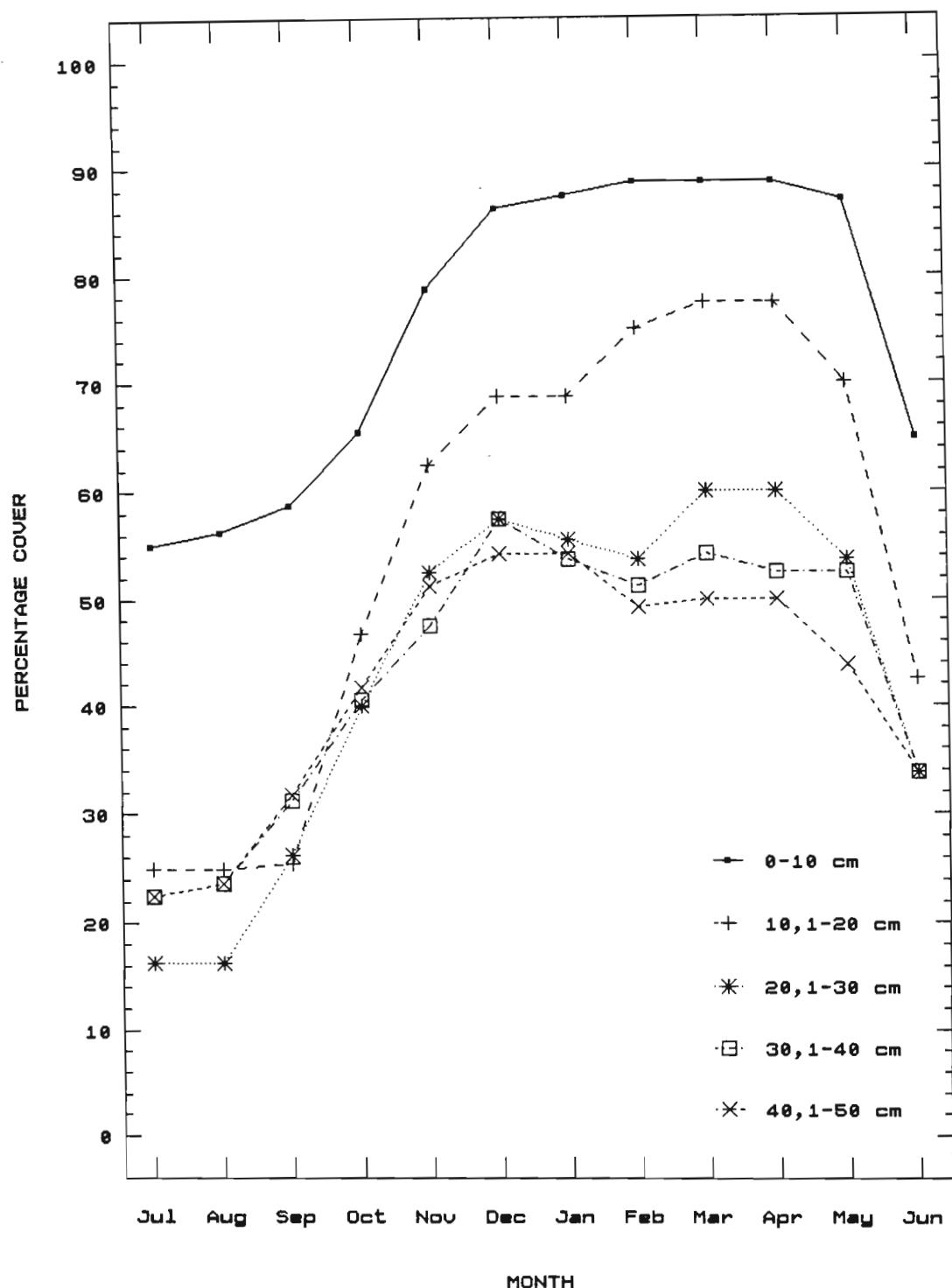
## 10.4 Results

The one-year period selected for the measurements of cover and invertebrates coincided with the onset of the drought which affected much of Natal in 1992 but which did not have equally severe effects at all the study sites. Thus Ferncliffe Forest and Scotston were hardly affected during the measuring period, but severe effects were noted at Danville Park from June 1992 while at Bisley Valley some effects were noticeable from March 1992. Further details are given in the relevant section on each site.

### 10.4.1 Vegetation cover

#### 10.4.1.1 Danville Park

Fig. 10.1 shows the monthly mean percentage vegetation cover measured at the four locations within the forest. Cover remained at close to its maximum density for six months (December to May) during the summer and autumn at all five levels, a longer period than at any other site. The densest cover throughout the year occurred at the lowest measuring level (up to 10 cm above the ground) and never fell below 55% at the observation distance of 5 m. This cover, largely ground herbs, grasses and tree seedlings, increased rapidly from late August to December, remaining dense well after dieback began in late April. This vegetation also contributed to the relatively high summer density of cover at the second level (10,1-20 cm above the ground). However in May and June there was almost complete dieback of those parts of the ground vegetation which extended into the second level, where winter cover consisted only of the stems and leaves of the woody vegetation (trees, creepers and woody herbs) which also formed the cover at higher levels. The secondary increase in cover, in February-March at the 10,1-20 cm level, and in March at the 20,1-40 cm levels, was largely caused by vertical growth and flowering of grasses and by a small proliferation of leaves on saplings and the lower branches of creepers. Throughout the year the density and seasonal variation in cover were comparable at the three highest levels, autumn reductions being caused largely by dieback of woody



**Fig. 10.1** Monthly mean percentage vegetation cover, over 10-cm sections, for 50 cm above ground level in coastal forest (15 m a.s.l.) at Danville Park, Durban, July 1991-June 1992.

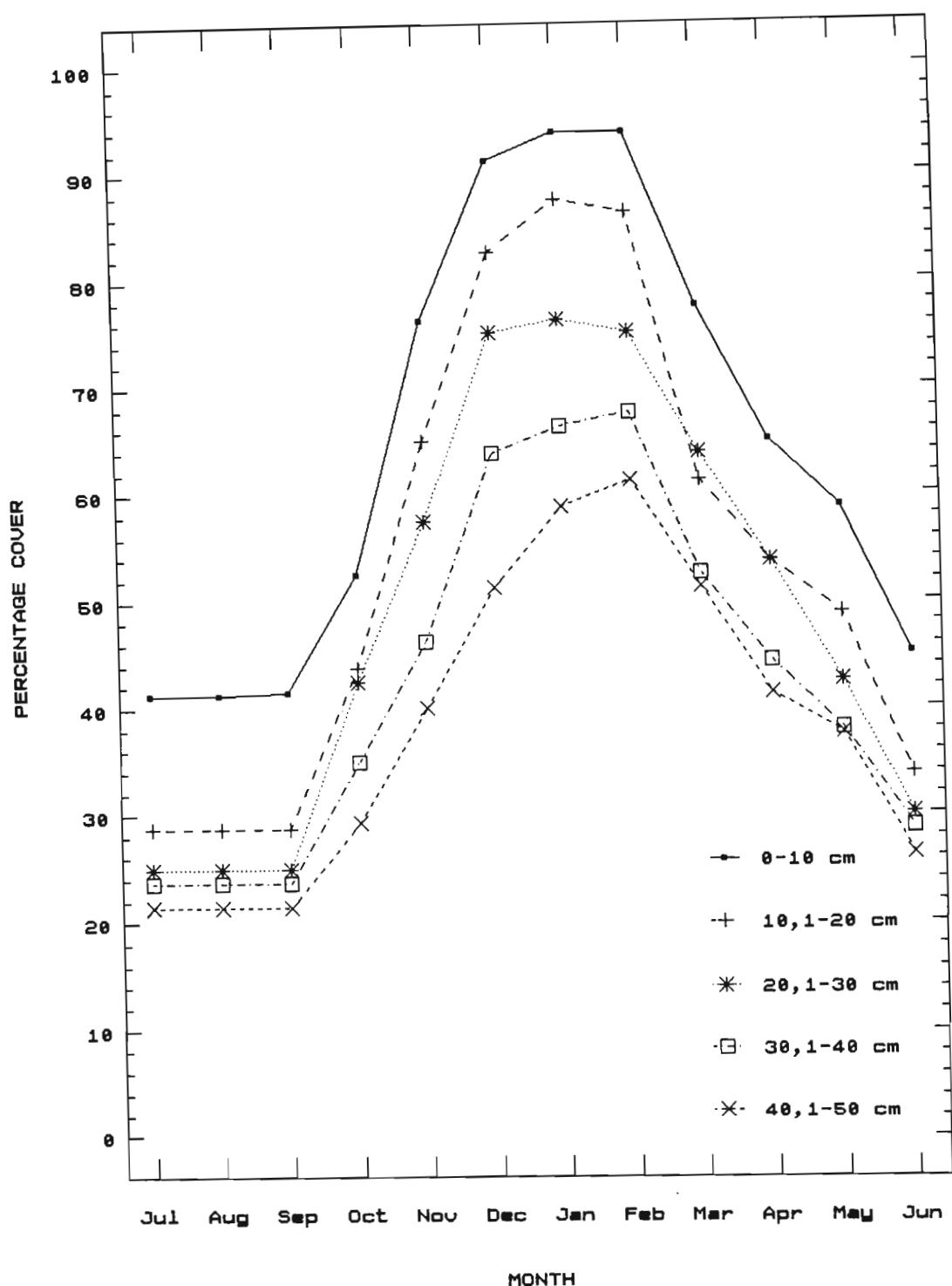
herbs but also by leaf fall from some forest trees and creepers, and spring increases being caused by the regrowth of woody herbs and the growth of new leaves on saplings, trees and creepers.

Rainfall was very low after November 1991 (Chapter 2, Fig. 2.20B) and there was no rain in May and June 1992. The effects of the drought on the forest vegetation were not seen until June, when much leaf fall from trees occurred, all leaves on the woody herbs wilted and the ground cover began to die. In the following months, after detailed measurements ceased, overall cover at this site became very poor, and the thickets became very open after the death of almost all the low cover.

#### **10.4.1.2 Bisley Valley**

The seasonal variation in mean percentage vegetation cover at the four deciduous thicket measuring locations at Bisley Valley (Fig. 10.2) showed two major differences from that at the forest sites of Danville (Fig. 10.1) and Ferncliffe (Fig. 10.3). Firstly, it was at its peak for only a relatively short three-month period (December to February) and secondly, growth did not start until late September, a month later than at the forest sites. The short period of peak density may not be typical of the site because of the very low rainfall after November 1991 (Chapter 2, Fig. 2.16B): by late March 1992 the entire site was very dry, most ground herbaceous vegetation was wilting rapidly and leaf fall was at its maximum. However by June the very dry conditions had not reduced cover below the minimum level recorded in the previous winter, because leaf fall from the deciduous thickets, and dieback of ground herbs, were almost complete every winter. The pattern of a short period of maximum cover and an early start of dieback is comparable with that shown by the exotic deciduous cover at Scotston (Section 10.4.1.4).

Throughout the year the densest cover was at the lowest measuring level (0-10 cm) and there was a somewhat more constant and equal difference between cover at the five levels throughout the year than was seen at the forest sites. This was partly because (a) the leaves of creepers and low bushes contributed a significant amount to cover at all levels, creepers even growing at ground level in some places, and (b) the common perennial forb *Protasparagus virgatus* was sometimes an equally important constituent of cover at all heights up to 50 cm. All vegetation, whether short grass or forbs, creepers or bushes, grew most rapidly and developed most new leaves in November and December, growth continuing at a much reduced level into January or February. During the winter much of the low cover was provided by the bare stems and branches of creepers and low bushes, and by the clumps of *Protasparagus*, relatively little being provided by persistent leaves of bushes such as *Lantana*.



**Fig. 10.2** Monthly mean percentage vegetation cover, over 10-cm sections, for 50 cm above ground level in deciduous thickets (710 m a.s.l.) at Bisley Valley, Pietermaritzburg, July 1991-June 1992.

#### **10.4.1.3 Ferncliffe Forest**

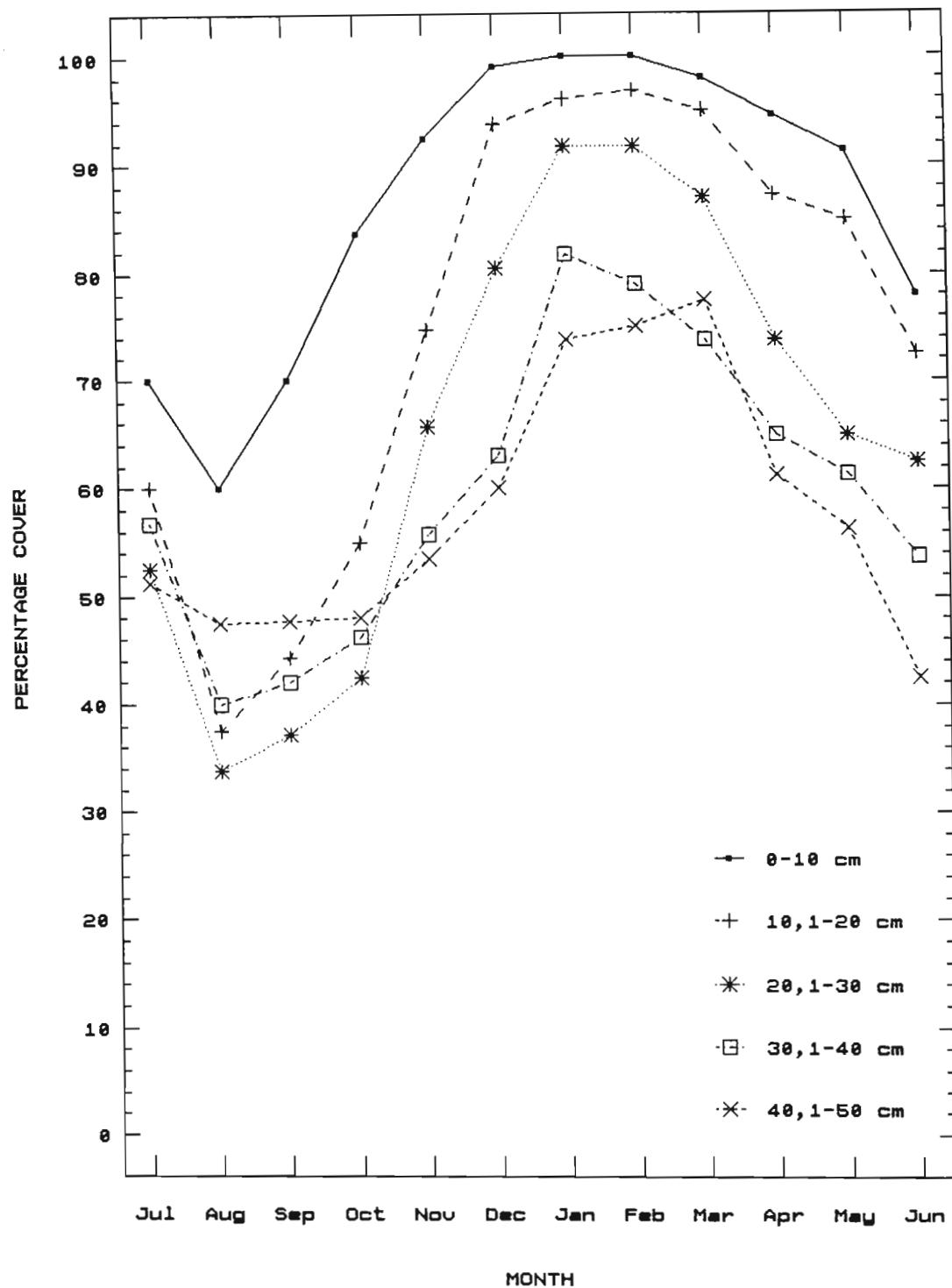
Throughout the year the vegetation cover at Ferncliffe (Fig. 10.3) remained at a higher density than at any other site, persisting at about 100% at the lowest level (0-10 cm) for three months in summer (December to February) and never falling below 34% at any level in winter. As at Danville, cover density was high for a relatively long period in the summer, that at the lowest level not falling below 90% for six months (December to May). Cover up to 30 cm above the ground was very dense in the summer because of a luxuriant growth of ferns, grasses and forbs (Chapter 2, Section 2.2.6), reasons for this lushness possibly including the high rainfall at the site (Table 2.1) and the relatively large amount of light penetrating to the ground as a result of the secondary nature of the forest's structure (Section 2.2.6). The lowest vegetation, including grasses, forbs, creepers and tree seedlings, began growing well in early September and maintained a fairly constant rate of growth until December, growth at higher levels (210, 1-40 cm) continuing until January, while cover at the highest level (40, 1-50 cm) continued to increase until March, principally because of the growth of the taller ferns. Leaf fall from forest trees was appreciable in April, when grasses seeded and ground vegetation began to die back, and by June the lowest cover was largely all grass, some of it still growing.

The growth pattern at Ferncliffe during the measuring period was probably fairly normal, total rainfall being 90% of the mean (Chapter 2, Section 2.2.6; Fig. 2.11B). The leaf litter was still moist in places in April 1992 but was almost all dry in May.

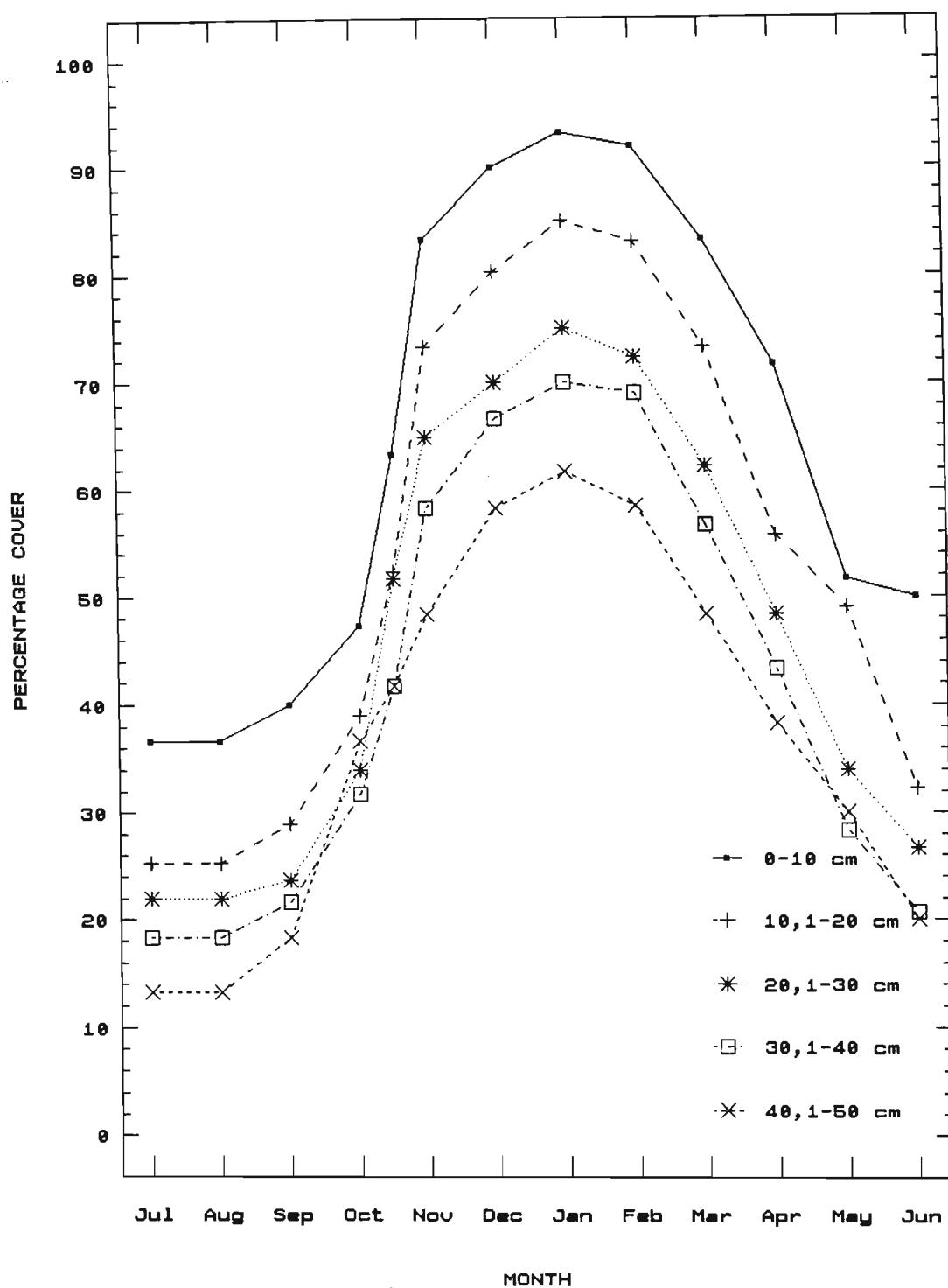
#### **10.4.1.4 Scotston Farm**

The development of new cover at the Scotston hedgerows started in September and was very rapid during October and November, continuing at a reduced rate until the end of January, after which leaf fall commenced (Fig. 10.4). Leaf fall was rapid from mid-March, while good ground cover persisted until late April when the first frosts began to affect the vegetation. As at all other sites, the lowest level (0-10 cm) had the densest cover throughout the year. During the winter months most cover above 10 cm was provided by the stems and branches of the woody vegetation. As at Bisley, there was a relatively constant and equal difference between cover at the five levels throughout most of the year and the period of peak cover spanned only the three months from December to February.

The Scotston site was unique among those studied in not having woody vegetation as the dominant cover over its entire area. The vegetation types in which measurements were made covered no more than 0.145 ha (17%) of the garden's total area and it was clear that the cover provided by



**Fig. 10.3** Monthly mean percentage vegetation cover, over 10-cm sections, for 50 cm above ground level in mid-altitude mistbelt forest (960 m a.s.l.) at Ferncliffe, Pietermaritzburg, July 1991-June 1992.



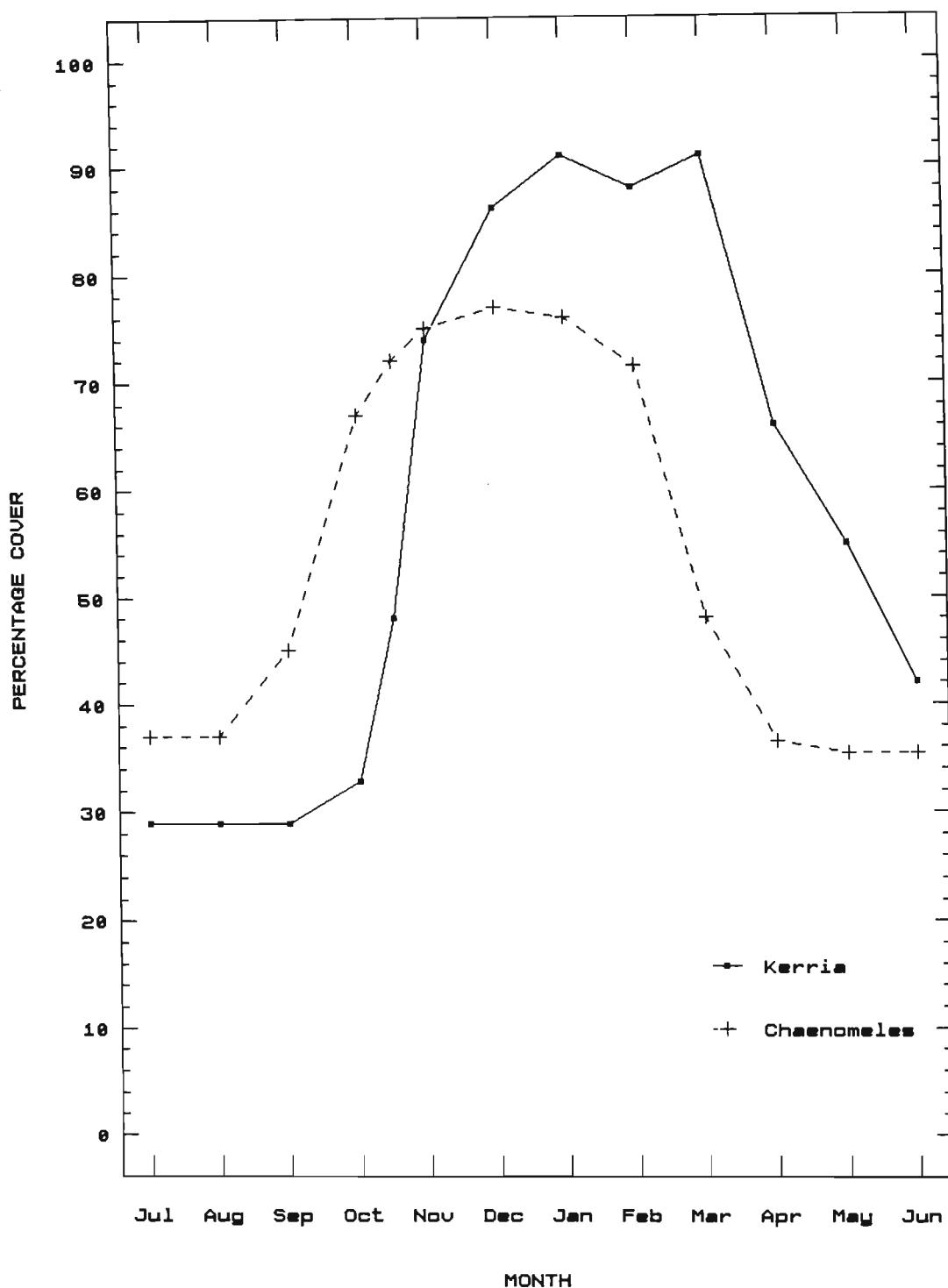
**Fig. 10.4** Monthly mean percentage vegetation cover, over 10-cm sections, for 50 cm above ground level in exotic hedgerows at Scotston farm garden, Underberg, at 1 500 m a.s.l., July 1991-June 1992.

flowerbeds, isolated low shrubs and vegetable beds was also important to the flufftails for shelter and foraging. Although no measurements were made in these vegetation types, regular observations showed that the cover provided by shrubs and flowerbeds persisted for at least as long as that measured in the hedgerows, while most of the vegetable garden continued to provide cover until early May when the ground was cleared. During the winter months (June to August) the flowerbeds and vegetable beds provided no cover for secretive terrestrial birds, but by early October cover in some of these areas was sufficient for them to be used by the flufftails.

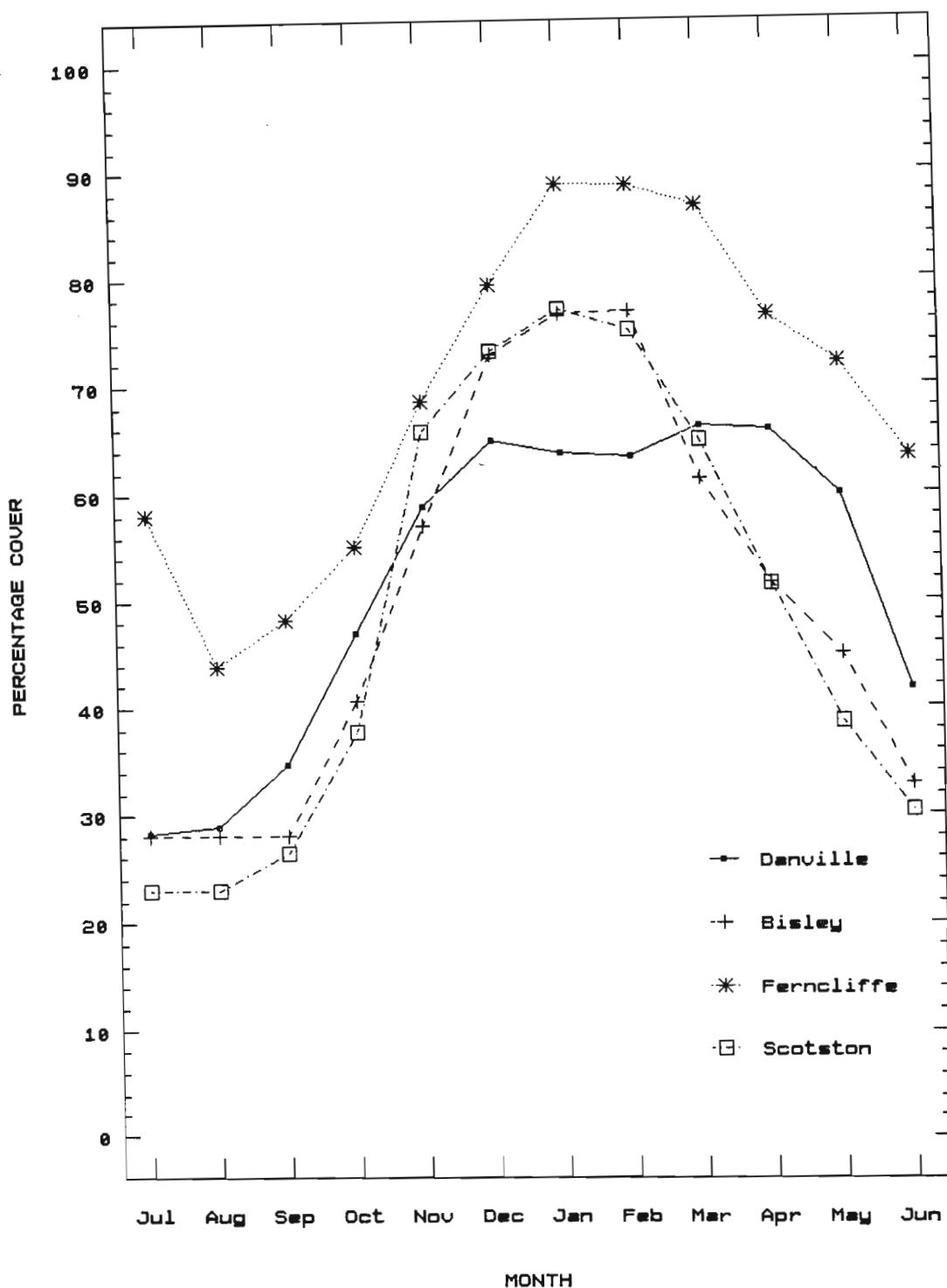
The graph of mean percentage cover (Fig. 10.4) shows average values for all four measuring locations in the garden and therefore gives no indication of significant differences in cover development between locations. However there was a noticeable difference in the timing of overall cover development at the measuring locations inside the *Kerria* hedgerow near Hide 1 (Pair 2's territory) and the *Chaenomeles* hedgerow and thicket near Hide 2 (Pair 1's territory), and in the reduction of cover at the end of the summer at these locations, which were near nest sites. The mean percentage cover throughout the year is plotted in Fig. 10.5, which shows that cover developed noticeably earlier at the *Chaenomeles* location, showing the greatest increase in October, while the greatest increase in the *Kerria* hedgerow cover took place in November and December. The *Chaenomeles* cover did not reach the maximum density attained by the *Kerria* cover, and most leaf fall occurred in March and April as opposed to April-June in the *Kerria*.

#### 10.4.1.5 Comparisons between the four sites

From a comparison of Figs 10.1 to 10.4 it is clear that (a) throughout the year at all sites cover tended to decrease with height above the ground and (b) cover was always greater at the lowest level (0-10 cm) than at any other, especially in winter. A graph of the overall monthly mean percentage cover for the first 50 cm above ground level at all four sites (Fig. 10.6) shows that the deciduous bush at Bisley Valley and the exotic deciduous hedgerows at Scotston had a very similar pattern of overall cover availability throughout the year. Scotston had a lower level of cover in the winter months, while the minimum winter cover at Bisley was similar to that at Danville, primarily because the Bisley site had a relatively high density of woody stems and branches at low levels, as well as extensive patches of *Protasparagus*. Ferncliffe had a higher density of cover throughout the year than any other site, particularly in the winter even though the ground was very dry. At this site the leaves of *Piper capense* provided good cover at low levels throughout the year. Fig. 10.6 shows that the 1992 drought had no appreciable effects on cover availability by the end of the sampling period (June) when, even at Danville, overall cover was still higher than in July 1991.



**Fig 10.5** Overall monthly mean percentage vegetation cover for the first 50 cm above ground level at *Chaenomeles* and *Kerria* hedgerows at Scotston farm garden, Underberg, showing the differences in the timing of cover development and dieback in the two vegetation types.



**Fig 10.6** Overall monthly mean percentage vegetation cover for the first 50 cm above ground level at four long-term study sites in southern Natal, July 1991-June 1992: coastal forest at Danville Park, Durban; deciduous bush at Bisley Valley and mid-altitude mistbelt forest at Ferncliffe (both Pietermaritzburg); exotic vegetation in an upland region at Scotston farm garden, Underberg.

## 10.4.2 Invertebrate abundance and diversity

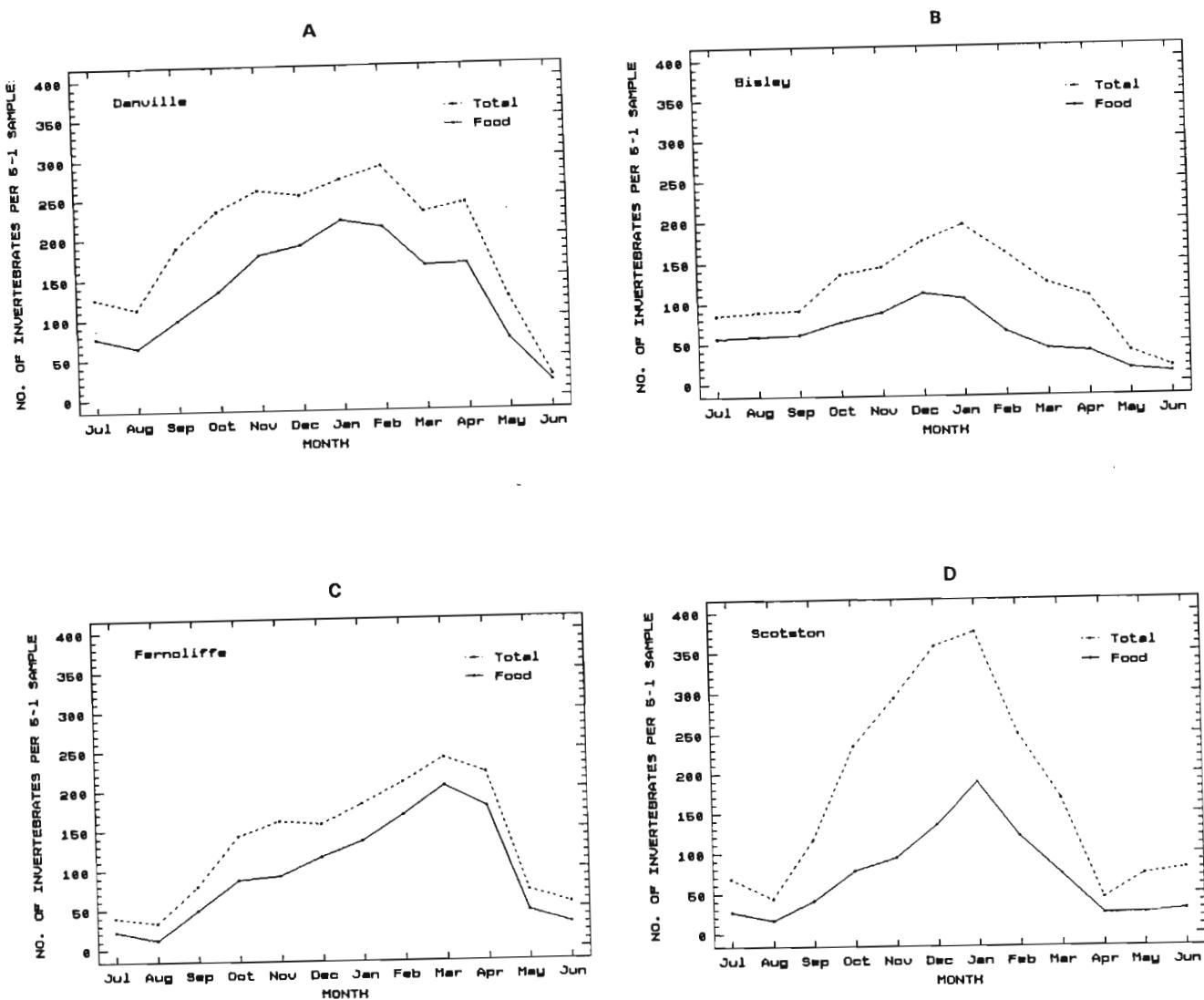
### 10.4.2.1 Potential food items

The total number of potential food items in a sample was calculated by adding together the number of invertebrates belonging to each group which is known to form part of the diet of the flufftail, information on prey having been obtained by observation and from the examination of gizzard contents (Chapter 9, Section 9.4.6). As there is no evidence that the birds regularly take prey less than 1,5 mm long (Section 9.4.6), all invertebrates smaller than this were excluded from the total of potential food items. The overall total and the total of potential food items were then plotted for each month (Fig. 10.7), while the differences in the availability of potential prey in winter and summer were shown by a comparison of the July 1991 and January 1992 numbers of each invertebrate group in the sample (Figs 10.8 and 10.9).

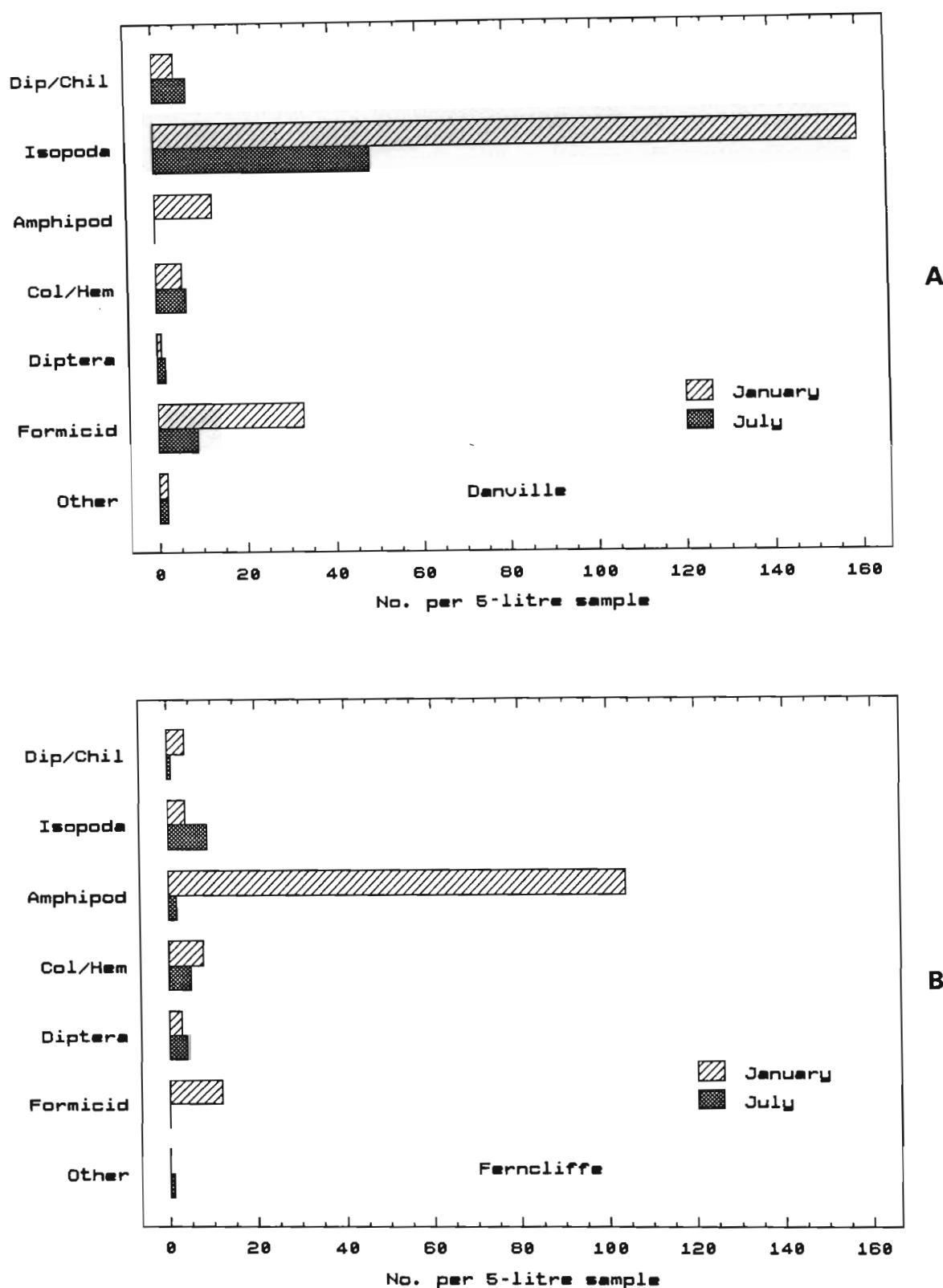
### 10.4.2.2 Danville Park

Danville had a higher summer total of potential food items (Fig. 10.7A) than any other site (Fig. 10.7B-D), the great majority of these being woodlice (Isopoda) (Fig. 10.8A) and in every month before June 1992 more food was available per unit volume of leaf litter than at any other site, the overall mean monthly availability of food items (132,5 per 5-l sample) being appreciably higher even than at Ferncliffe (mean = 94,58), while the mean values for Bisley and Scotston were 60,33/5 l and 70,83/5 l respectively. The lowest number of food items recorded in the 1991 winter was 64 in August and invertebrate numbers began to increase when the ground became moist in September. By late September the sample total of food items had reached 100 and it remained well above this figure until May, although rainfall during the summer was very low (Chapter 2, Fig. 2.20B) and the ground became predominantly dry from March. In May 1992 conditions were very dry and there was a sharp drop in the invertebrate population, while the final 5-l sample, taken on 25 June 1992 when the effects of the drought on the vegetation were obvious, yielded only 25 invertebrates, 18 of them potential food items.

Some variation occurred in the seasonal composition of the potential food supply (Fig. 10.8A). Isopoda were the most abundant group in both summer and winter, although their numbers were much lower from May to August. Formicidae and Amphipoda were also much more numerous in summer than in winter, the latter being absent from all samples in July, August and September. Diplopoda and Chilopoda reached their highest numbers in early summer (October-December) and were less numerous in January.



**Fig. 10.7** Numbers of invertebrates per five-litre sample of leaf litter at four long-term study sites in southern Natal, July 1991-June 1992, showing total number (solid line) and number of potential food items (dashed line). A: coastal forest, Danville Park, Durban. B: deciduous bush, Bisley Valley, Pietermaritzburg. C: mid-altitude mistbelt forest, Ferncliffe, Pietermaritzburg. D: exotic vegetation in an upland region at Scotston farm garden, Underberg.



**Fig. 10.8** Number of potential invertebrate food items in midsummer (January 1992) and midwinter (July 1991) leaf litter samples from (A) Danville Park, Durban and (B) Ferncliffe Forest, Pietermaritzburg. Abbreviations: Amphipod = Amphipoda; Col/Hem = Coleoptera & Hemiptera; Dip/Chil = Diplopoda & Chilopoda; Formicid = Formicidae.

#### **10.4.2.3 Bisley Valley**

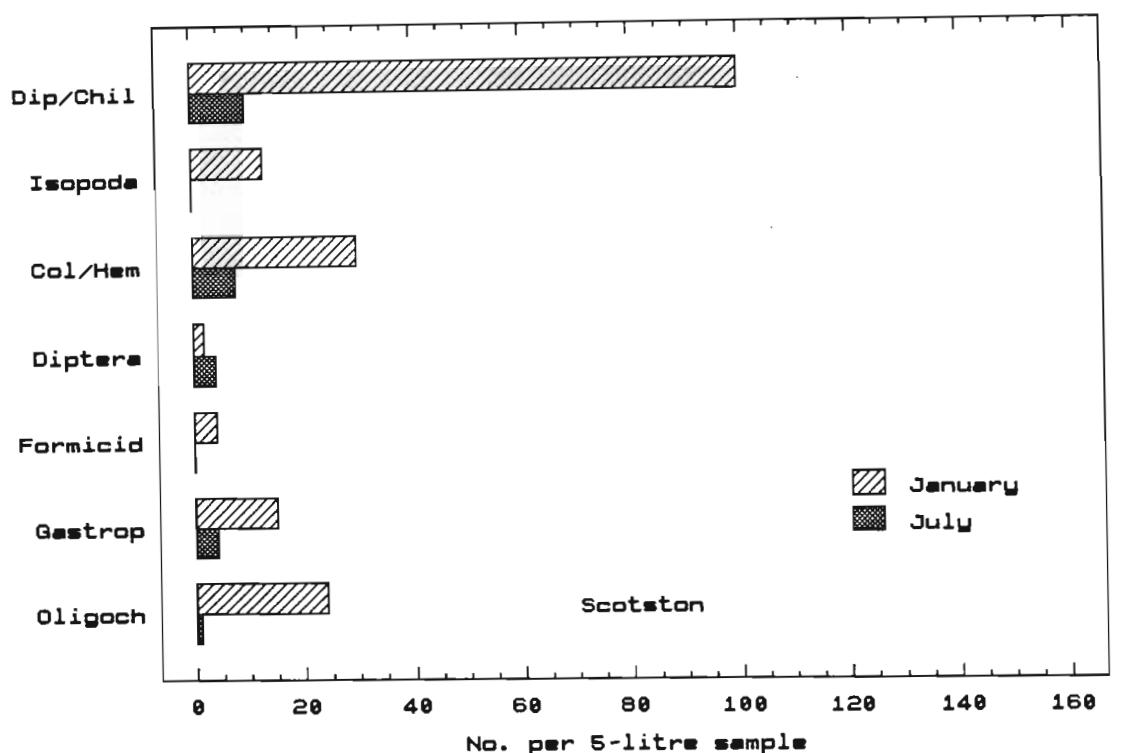
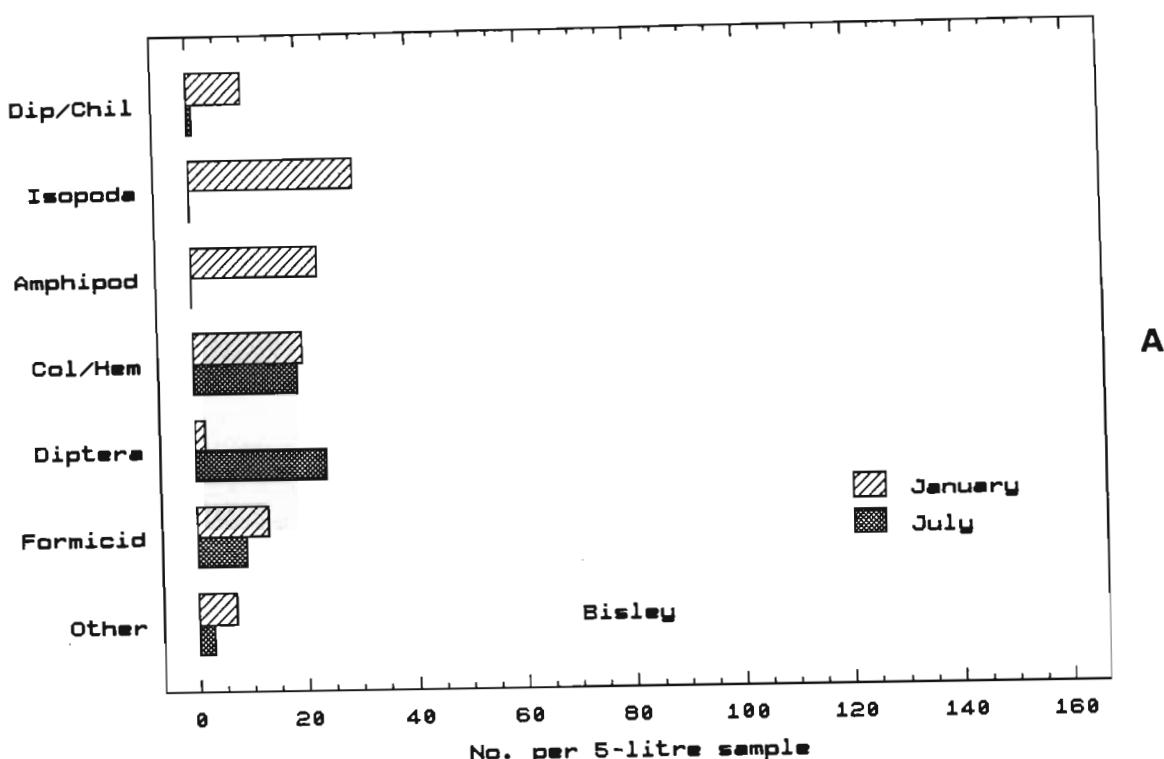
Bisley did not have as great an abundance of potential food items during the summer months as did the two forest sites, the maximum monthly total (111/5  $\ell$  in December 1991) being only about half that attained at Danville and Ferncliffe. However, the very low rainfall experienced from December 1992 to March 1993 (Chapter 2, Fig. 2.16B) may have adversely affected invertebrate numbers: at the four measuring locations the leaf litter was very dry from February to June, and in every month from March fewer invertebrates were found in samples than were present in the previous July (Fig. 10.7B). The May and June totals of potential food items (16/5  $\ell$  and 11/5  $\ell$  respectively) were less than the lowest recorded Danville total of 18/5  $\ell$  in June 1992, when that site began to be severely affected by the drought (Section 10.4.2.2). The decrease in Bisley's invertebrate numbers from January to March 1992 was largely because of drastic reductions in sampled numbers of Formicidae in January and of Coleoptera, Amphipoda and Chilopoda in February-March.

Unlike the samples from the forest sites, the Bisley summer samples did not reflect the predominance of any one potential food group, the January 1992 figures (Fig. 10.9A) showing a relatively well balanced mix of the five commonest groups. In winter, however, the situation was very different, as is shown by the July 1991 sample (Fig. 10.9A) in which Diptera, Coleoptera and Formicidae predominated. Adult and larval Diptera were much more numerous from July to October 1991 than during the summer, while Isopoda and Amphipoda were absent from the early samples, being first recorded in September and October 1991 respectively.

#### **10.4.2.4 Ferncliffe Forest**

During the summer the Ferncliffe samples (Fig. 10.8B) yielded fewer invertebrates in most of the food groups than did those from Danville (Fig. 10.8A), apart from Amphipoda, which were present in large numbers from December to April. The total number of potential food items (Fig. 10.7C) increased when the leaf litter became damp with the first good rain in September 1991 and rose at a fairly constant rate to a peak in March 1992. A large drop in invertebrate numbers occurred in May, when the leaf litter became dry. Although Ferncliffe had the second highest mean monthly availability of food items (Section 10.4.2.2), winter numbers of invertebrates were very low, the number of potential food items per sample in June, July and August being only 30, 22 and 11. As Ferncliffe was hardly affected by the 1992 drought (Section 10.4) the low winter food level was probably a normal occurrence at this site.

Seasonal variations in the composition of the potential food supply were noticeable (Fig. 10.8B). Amphipoda and Formicidae almost disappeared from May to August, while Isopoda were



**Fig. 10.9** Number of potential invertebrate food items in midsummer (January 1992) and midwinter (July 1991) leaf litter samples from (A) Bisley Valley, Pietermaritzburg and (B) Scotston farm garden, Underberg. Abbreviations: Col/Hem = Coleoptera & Hemiptera; Dip/Chil = Diplopoda & Chilopoda; Formicid = Formicidae; Gastrop = Gastropoda; Oligoch = Oligochaeta.

commoner in winter than in summer, their numbers increasing in March and remaining relatively high until October, when a corresponding decrease occurred.

#### 10.4.2.5 Scotston Farm

During the measuring period the Scotston Farm garden was not affected by the drought (Section 10.4), so the observed pattern of invertebrate abundance (Fig. 10.7D) may be taken as representative of the normal situation. Invertebrate numbers in winter were very low in the leaf litter at all locations, potential food items never exceeding 30/5 l from April to August. Invertebrate numbers increased when the leaf litter became moist after the first rain in September 1991 and rose at a fairly constant rate to a peak in January 1992 (Fig. 10.7D). From February there was a sharp drop in numbers to a minimum in April, although the leaf litter remained quite moist in February and began to dry out only in March. Numbers of Coleoptera, Isopoda, Diplopoda and Chilopoda all fell sharply in February, followed by similar decreases in March and April. There was an almost twelve-fold increase in the numbers of potential food items per 5-l sample (16 to 188) between August and January, while the numbers of non-food items rose from 28 to 187 (a 6.75-fold increase). The increase in food items largely involved the proliferation of Diplopoda and Chilopoda (Fig. 10.9B) but substantial increases in Gastropoda and Oligochaeta were also recorded and both Isopoda and Formicidae were present in summer and absent in winter. The organisms primarily responsible for the large increase of non-food invertebrates during the summer were minute Collembola, which were numerous in rotting leaves from November to February; at no other site was a comparable increase noted.

#### 10.4.3 Flufftail occurrence patterns

The patterns of occurrence of the Buffspotted Flufftail at all four study sites, both before and during the sampling year, are described in detail in Chapter 9, Section 9.4.3.1. At Danville birds were normally present throughout the year, but in 1992 they disappeared in May. At Bisley, flufftails were seen at the sampling site from April 1991 to late February 1992, but none was recorded from March to June 1992. The Ferncliffe birds were present only from September to April in the sampling year and from September to March in the year preceding it. At Scotston, birds arrived in early October 1991 at the *Chaenomeles*-dominated cover at Hide 2 (Pair 1) but not until mid-November in the *Kerria*-dominated cover at Hide 1 (Pair 2). The exact departure time was not established in

early 1992, but the adults and young of both pairs were not seen after 8 March; in 1991 the Pair 1 adults left in mid-March and the last-brood immatures during April (the latest date being 23rd).

## 10.5 Discussion

### 10.5.1 Danville Park

The observed status of the Buffspotted Flufftail throughout the year at Danville (Chapter 9, Section 9.4.3.1) indicates that the minimum levels of both food and cover measured in July and August 1991 (Figs 10.1, 10.6 and 10.7A) are sufficient to support at least the resident adults during the winter months, when dense cover occurs only up to 10 cm above the ground, where it is twice as dense as the cover at 10.1-50 cm (Fig. 10.1), and the number of potential invertebrate food items (77/5  $\ell$  and 64/5  $\ell$  in July and August 1991) may be a little as 30% of the midsummer total (220/5  $\ell$  and 211/5  $\ell$  in January and February 1992).

The onset of drought conditions in early 1992 was fortuitous in that it enabled me to compare the cover and food availability when the resident birds left with those in a normal season at Danville and also with those in areas where seasonal movements were regular. When the Danville birds disappeared in May, cover density was still almost at its summer maximum (Fig. 10.1) but the number of potential food items had decreased sharply (Fig. 10.7A); by June 1992 the number ( $n = 18/5 \ell$ ) had fallen to the approximate level of that measured at Ferncliffe and Scotston in midwinter, when the flufftails were absent (Sections 10.5.3 and 10.5.4). A preliminary 5- $\ell$  leaf-litter sample taken at Danville in June 1991 gave a potential food total of 75 invertebrates, close to the numbers recorded in the following two months, which indicates that the June 1992 total was exceptionally low.

In the absence of any other factors which could obviously have affected the birds' residential status at Danville in mid-1992, it appears that departure was probably caused by the drop in invertebrate food availability. With regard to plant food, although no measurements were made I judged that the production of seeds by the forest grasses was not significantly less than normal, so that this potential food supply was available to the birds at the end of the summer.

### 10.5.2 Bisley Valley

The available evidence suggests that the Buffspotted Flufftail occurs throughout the winter at Bisley in years when conditions are normal, as in the 1991 winter when the overall abundance of

potential food in July, August and September (counts of 56, 58 and 60 items per 5-l sample respectively) was similar to that at Danville in August. The density of cover in July-September 1991, although not as great as at Danville at the lowest level, was slightly higher at some upper levels (compare Figs 10.1 and 10.2), giving a very similar overall mean level of winter cover (Fig. 10.6). As at Danville, the onset of the drought in early 1992 enabled me to assess the deterioration in conditions which had occurred when the birds left the area. No flufftails were seen at Bisley after February 1992, and it is significant that, although cover at all levels in March-June 1992 was still greater than that measured in July-September 1991 (Fig. 10.2), by March 1992 the number of potential food items ( $n = 42/5 \ell$ ) had dropped below the minimum recorded in the previous winter ( $n = 56/5 \ell$ ), and continued to fall to a very low level ( $n = 11/5 \ell$ ) in June (Fig. 10.7B; Section 10.4.2.3). Thus it appears that, as at Danville, it was the decrease in food availability, rather than any decrease in cover, which was a major factor influencing the timing of the birds' departure.

#### **10.5.3 Ferncliffe Forest**

Throughout the measuring period the density of vegetation cover at Ferncliffe was higher than that at the sites where the birds normally occurred throughout the year (Figs 10.3 and 10.6) and therefore the pattern of occurrence of the birds should not have been affected by variations in cover. However a factor very likely to be relevant to the birds' absence in the May-August period is the number of potential food items (Fig. 10.7C), which fell very sharply in May to reach a level of only 30/5  $\ell$  in the June 1992 sample, while numbers in July and August 1991 were even lower (Section 10.4.2.4). In September 1991, when the birds reappeared, invertebrate numbers were rising, the sample that month giving a count of 49 potential food items per 5  $\ell$ , and before the end of October the invertebrate food count equalled that recorded at Bisley in November (Fig. 10.7). Thus invertebrate food availability may influence both the arrival and the departure times of the flufftails at this site.

#### **10.5.4 Scotston Farm**

The situation at Scotston is complicated by the fact that the measured vegetation types (hedgerows) provided only a fraction of the site's cover (Section 10.4.1.4), but it is still possible to assess the overall influence of cover on the birds' arrival and departure times because it was judged that the cover in other vegetation types was adequate for as long a period as it was in the hedgerows. When the last birds left the garden in late April 1991, overall hedgerow cover was approximately

equivalent to that measured in April 1992, when it was still denser than that measured when the first birds arrived in October 1991 (Figs 10.4 and 10.6). Thus deterioration in cover is unlikely to have been a major factor influencing the birds' departure time in 1991 (departures in 1992 were not timed). However the sample count of invertebrate food had dropped to 24/5 l in late April 1992 (from 73/5 l in March), a total almost as low as that at Ferncliffe in July 1991 ( $n = 22/5 l$ ), and this indicates that by the end of April the natural food supply is insufficient to support the birds. From May onwards, although overall cover in the hedgerows was higher than that recorded at Bisley in winter months when the birds were resident (Fig. 10.6), the lack of cover elsewhere in the garden (Section 10.4.1.4) meant that insufficient foraging areas were available to the birds.

When the first birds returned in early October 1991 the natural food supply had risen to a level (78 items in the 5-l sample) which exceeded that at Ferncliffe at the time of the birds' return (Section 10.5.3) and it was judged that sufficient cover had developed in flowerbeds and vegetable beds to allow them to be used by foraging birds. However the development of cover differed markedly in the two types of hedgerow measured (Fig. 10.5) and it is interesting that, when Pair 1 returned to its territory in the *Chaenomeles* hedgerow in early October 1991, the overall cover in that vegetation type had reached about 60% whereas it was only about 30% in the *Kerria* hedgerow. When Pair 2 occupied the *Kerria* hedgerow in mid-November, overall cover there had also reached about 60% (Fig. 10.5), this suggesting that return times at Scotston are influenced by development of cover in the woody vegetation rather than by food availability. In the 1991-1992 season, the first breeding nest of each pair was situated within the dominant hedgerow type in its territory.

#### 10.5.5 Conclusions

The results of this study indicate that food availability is normally the major factor influencing the pattern of occurrence in any area. Measurements showed that no birds occupied habitat at any site when the invertebrate count was less than c. 50 potential food items per 5-l sample of leaf litter, and it is clear that, at sites where movements were noted (either regularly or as a result of drought conditions), departures normally occurred at times when cover was adequate for continued occupation but invertebrate numbers were not. At Ferncliffe, arrival time was also apparently related to food availability, but at Scotston, although the natural food supply was adequate in all vegetation types from early October, one breeding site was not occupied until five weeks later, apparently because of inadequate cover in October. Thus development of cover may affect arrival time in different patches of the same deciduous habitat and the birds which succeed in establishing themselves in early-developing cover may be able to begin breeding at least a month earlier than late arrivals or

subordinates forced to wait until other patches have developed. At Scotston, the early occupation by Pair 1 enabled them to lay four clutches in the 1991-1992 breeding season, as opposed to the two laid by the late-established Pair 2 (Chapter 9, Fig. 9.13).

The differences in the timing and duration of high numbers of invertebrate food items at the different sites are interesting when compared with the flufftail's known breeding season in the areas concerned (Chapter 9, Table 9.9). Breeding is not known to occur earlier than September in any part of Natal, and it is clear from this study that invertebrate numbers did not increase significantly at any site until September (Fig. 10.7). The high level of potential food late in the summer at Danville (Fig. 10.7A) suggests that a more extended breeding season might be possible in coastal forest than at inland sites and Table 9.9 shows that coastal breeding is recorded as late as May. During the drought period in 1992, cover and food at Danville fell rapidly in May (Figs 10.6 and 10.7A), but in more normal years conditions might remain suitable into June, allowing the successful rearing of chicks from clutches laid in May. The peak laying months at Underberg are November to January (Table 9.9) and thus the majority of young should be present from late November to February, coinciding with the December-February peak period of food availability measured at Scotston (Fig. 10.7D).

Figure 10.7 shows a considerable difference in the timing of peak invertebrate availability at the two Pietermaritzburg sites, the peak in forest at Ferncliffe occurring in February-April, while that in deciduous bush at Bisley occurred in December and January. In view of the drought conditions it is not clear whether the 1992 Bisley peak reflects the normal situation or whether, in years of more normal rainfall, invertebrate numbers remain high (or continue to rise) during or after February. The pattern of precipitation at both sites is similar (Chapter 2, Figs 2.15 and 2.10), most rain falling between September and April with a peak in January, and it is not immediately obvious why the 1991-1992 invertebrate peak at Ferncliffe should fall so late in the season, especially since there was very little rain in February and March 1992 (Chapter 2, Fig. 2.11B). However, the Ferncliffe peak was caused by high numbers of Amphipoda, especially of young individuals (in March, for example, the 5-l sample contained 168 Amphipoda, 136 (81%) being less than 6 mm long and 32 (19%) being 6-10 mm long). If this reflects the normal population-recruitment pattern for this crustacean, it would have a much smaller effect on the overall leaf-litter-invertebrate abundance at other sites, where Amphipoda are not the dominant group (Figs 10.8 and 10.9). For example, the peak numbers of the commonest invertebrates at Danville (Isopoda) occurred in January-February, when young individuals also predominated in the samples.

Although few data are available on breeding times at Ferncliffe and Bisley, the invertebrate counts suggest that breeding at Bisley may follow a pattern similar to that for the Pietermaritzburg area as a whole (Table 9.9), peak laying probably occurring in November to take advantage of the December food peak, while at Ferncliffe it is possible that the laying peak may be later in the season

(or that the breeding season may be prolonged into April) to coincide with the high invertebrate numbers. However, this assumes that the flufftails will feed largely on whatever prey type is most abundant in the population, and there is no evidence for this with regard to organisms such as Amphipoda. The birds are known to take many Formicidae, Isoptera and Oligochaeta in the breeding season (Chapter 9, Section 9.4.6) and, as these prey types were often not significantly represented in leaf-litter samples, it is unwise to infer too much from invertebrate counts which do not reflect variations in abundance of these important prey items during the breeding season.

## CHAPTER 11

### CONCLUSION

#### 11.1 Introduction

This study has been largely successful in achieving the primary aims listed in Chapter 1, the only exception being my failure to discover more about the Whitewinged Flufftail's distribution, status and breeding. As mentioned in Chapter 8 the limitations of time and finance, coupled with the often erratic and unpredictable nature of the bird's occurrences, made it impossible to concentrate my research effort on this species. However, I believe that the information obtained on the other three species, coupled with data from previous work on the Whitespotted Flufftail (Taylor & Taylor 1986) is sufficient to give a detailed insight into the biology and ecology of the genus *Sarothrura* as a whole, over all the biomes in which flufftail species occur. In the light of this knowledge, the limited number of data collected on the Whitewinged Flufftail permit a more reasoned assessment to be made of this bird's ecology and behaviour than was possible before.

This concluding chapter concentrates on two aspects of the study: the conservation of flufftails and their habitats, and the contribution of my results to an appreciation of the life-history traits evolved by flufftail species in response to differing environmental pressures in different biomes.

#### 11.2 Conservation of flufftails and their habitats

##### 11.2.1 The Redchested Flufftail, sympatric wetland rallids and their habitats

The results discussed in Chapters 4-6 provide the first comparative assessment of post-burn regrowth in different vegetation types on substrates of different degrees of saturation, and also the first real insight into the effects of wetland burning on terrestrial rallids of such habitats. It is clear that the Redchested Flufftail is a successful species not only because of its ability to colonize a wide variety of wetland vegetation types (Chapter 4) but also because it has evolved an effective means of minimizing the risk of temporary emigration caused by catastrophic and unpredictable seasonal reductions in its habitat (Chapter 5). As an insurance against such reductions in usable habitat, which are caused principally by burning but also by grazing, trampling and wind damage, it holds territories much larger than the minimum required for survival during the nonbreeding season. The advantages to the species of holding permanent territories are discussed in Chapter 5. The sympatric Black Crake

and African Rail are only seasonally territorial and I have suggested that the maintenance of permanent territories would not be similarly advantageous to these species because of their less rigorous requirements for dense cover, the relative stability of their more permanently flooded habitats and their ability to exploit a wider range of food items (Chapters 4 and 5). Optimal habitat for this flufftail appears to be provided in situations where burning occurs, suggesting that the bird has been subjected to the environmental impact of fire throughout recent geological time and has become adapted to take advantage of fire-modified wetland habitats. It has been shown (Chapter 6) that partial and/or biennial burning of the flufftail's habitats results in improvements in habitat quality expressed in terms of the increased availability of suitable habitat and, in large areas, the possible increase in the density of permanently territorial pairs. It was not possible to investigate whether burning confers corresponding improvements of quality to the other rallid species' wetland habitats but it is likely to do so, particularly in terms of vegetation structure and the availability of invertebrate food.

Thus any management strategy for such rallids of dense wetland vegetation should include periodic burning, and the best management strategies for Redchested Flufftail habitats are discussed in Chapter 6, Section 6.6. These could also be applied effectively to the more permanently flooded habitats occupied by the Black Crake and the African Rail, while my field experience of other wetland species such as the potentially endangered Baillon's Crake and Striped Crake (Brooke 1984), and the Streakybreasted Flufftail, suggests that these birds are also well adapted to fire-modified wetland vegetation. It is recognized that disturbance increases the heterogeneity of environments and of the communities which occupy them (Wiens 1989b), and patch burning is a good example of a disturbance factor which can improve wetland environments in this way.

It has been shown (Chapter 4) that the Redchested Flufftail is a successful colonist of very small, often isolated, wetland patches, and my observations during this study suggest that the Black Crake, African Rail and Baillon's Crake will also inhabit wetland patches as little as 0.1-1 ha in extent. Small areas of marginally suitable habitat are also potentially important, both as winter refuges for temporarily displaced birds (Chapter 5) and as more permanent habitat for nonbreeding "floaters" (Perrins & Birkhead 1983; this study, Chapter 5). In the USA the importance of small wetland patches to rails and other small vertebrates has been mentioned by several authors. Johnson & Dinsmore (1985) suggest that small wetland patches are important to Soras and Virginia Rails, which undergo postbreeding (pre-migratory) dispersal from breeding territories to such areas, while Brown & Dinsmore (1986) found that, of 25 bird species breeding in Iowa marshes, these two rails were among only seven species whose occurrence was independent of marsh size and which bred in marshes smaller than 1 ha in area. Gibbs (1993) simulated the loss of small freshwater wetlands in Maine and found that the loss of wetlands of 0.1-4 ha in area reduced the total wetland area by 19% and the total number of wetlands by 62%, and increased mean inter-wetland distance by 67%. His

spatially structured demographic model revealed that previously stable local populations of turtles, small birds and small mammals faced a significant risk of local extinction after the loss of these small wetlands.

Such evidence shows that the conservation of small wetlands is important. My experience during this study has been that farmers may be unaware of the value of very small wetland patches, and may burn and/or graze them indiscriminately in winter or spring. However, when appraised of their potential value, some farmers are willing to preserve such patches by excluding stock (the loss of grazing is very small), and it has also been possible artificially to create small wetland patches (Chapter 4, Section 4.4.2) which have been occupied by Redchested Flufftails and Baillon's Crakes.

Another method of improving wetland habitats for rallids is the artificial regulation of water levels to encourage the sequential zonation of wetland vegetation and to maximize the extent of moist-soil and shallow-marsh habitats (Eddleman *et al.* 1988; Johnson & Dinsmore 1986). To my knowledge this method is not practised in South African wetlands but it might be feasible in some situations, especially in wetlands at the intake areas of small dams, as my own experience has shown. In the mid-1980s I made a study (P.B. Taylor, unpublished ms) of Baillon's Crake on the Del Monte pineapple estates at Thika, Kenya, where this species is a nonbreeding visitor to wetlands at two irrigation dams. Periodic gradual reductions in one dam's water level resulted in a significant increase in the availability of suitable nonbreeding habitats (exposed mud, shallowly flooded marsh and moist grass) and encouraged the prolonged occurrence of good numbers of this species, and also of commoner wetland rallids, in the nonbreeding season.

With regard to the conservation, management, restoration and creation of wetlands in Natal, I fully support the recommendations made by Begg (1990: pages xiv and xvi), especially with regard to the importance of conserving the diversity of plant and animal species in wetland areas, the need to encourage the rehabilitation and restoration of wetlands (especially on private land) and the importance of seeking professional advice before the alteration of any wetland is undertaken (see comments on the Whitewing Flufftail, Section 11.2.3). My study has shown that small wetlands are valuable, especially to rallids, and should be considered when formulating management and conservation strategies.

### **11.2.2      The Striped Flufftail and its grassland habitats**

Section 7.5.1 discusses in detail the results of my survey work on the Striped Flufftail. In Natal this species may still be locally numerous in suitable upland grassland habitats of the Natal Drakensberg Park but its status needs more clarification in this region and it has certainly disappeared

from many lower-altitude areas during this century. There is an urgent need to establish the extent to which the upland populations move seasonally, and where they might spend the nonbreeding season, although there are considerable practical difficulties involved in locating wintering populations if they occur at any distance from the breeding areas. The best initial approach would be to look for suitable habitat in the mildest climatic conditions at the lowest elevations within the Natal Drakensberg Park region, to establish whether significant numbers of birds winter within protected areas. If they do, then the future of the nominate race in Natal is more assured.

With regard to the situation in the rest of southern Natal it is possible that, in farming areas, an approach to landowners could result in the protection of existing habitat patches and even the creation of small patches of suitable habitat on ground which does not make an economically significant contribution to the grazing potential of farms. Thus simply practising good veld management could result in the creation of more habitat (Section 7.5.1). Ensuring that grazing and annual burning do not occur in some small areas (1,5-2 ha) of grassland, *Protea* savanna, bracken-briar, *Leucosidea/Buddleja* patches, etc., especially on slopes in stream valleys and adjacent to moist depressions, would create breeding habitat both for the flufftails and for other small bird species.

Although the status of the Striped Flufftail in the Transvaal and Cape Provinces is unclear, recent observations (E.P. Smith pers. comm., August 1994) indicate that the birds are locally numerous in some fynbos- and *Protea*-dominated areas of the extreme southwestern Cape, in which habitats they may occur on ground with a greater percentage cover of rocks than was tolerated at the Mt Currie Reserve study site in Natal (Chapter 7). It is possible that the southwestern Cape may support significant numbers of this species and detailed surveys of the birds and their habitats in this region would be of great value.

My studies at Mt Currie have shown that burning has the immediate effect of reducing the density of breeding birds but that the breeding population increases during the second breeding season after a burn. Like the Redchested Flufftail (Section 11.2.1) this species must have been continually subjected to the environmental impact of fire during recent geological time and is therefore, like other grassland vertebrates (Tainton & Mentis 1984), well adapted to frequent burning. The bird's adaptation to fire-climax grassland (Section 7.5.2) means that periodic burning or grazing is necessary in some of its habitats to maintain this vegetation type but my study provides no information on the frequency of burning which should be practised to provide optimum grassland habitat for the species. However it is known that frequent fire (i.e. annual or biennial burning) has no long-term detrimental effect on grassland herbage production (Tainton & Mentis 1984), while in the Natal Drakensberg area, habitats which are not burned for 3-4 years contain more dead than growing grass and have a dense layer of moribund grass at ground level (Rowe-Rowe & Lowry 1982). The diversity and

abundance of small mammal and bird species in such grasslands are greatest for up to three years after a fire, fall thereafter (as moribund vegetation increases) and then rise after about ten years as grass tufts become larger and vegetation becomes less impenetrable (Mentis & Rowe-Rowe 1979; Rowe-Rowe & Lowry 1982). This bimodal distribution reflects a separation of the animals into those of the fire climax and those of the postfire climax vegetation (Tainton & Mentis 1984).

The Striped Flufftail requires dense cover with clear ground for foraging and it may therefore be adapted to both fire and postfire climax vegetation: it occurs in both pure short grassland and longer grass associated with scrub and forest edge at Mt Currie. Depending on the habitat type which managers desire to encourage in the region or reserve concerned, an optimum burning schedule to encourage good habitat for this species could be either frequent (biennial) burning of fire-climax grassland or long-term protection from burning to encourage the development of post-fire climax rank grass and of scrub and forest patches, the margins of which are also accessible to the flufftail. As with the Redchested Flufftail in wetlands, the best solution is to simulate natural conditions as much as possible, by the irregular and patchy burning of the grassland to encourage a mosaic of burned and protected areas, when the variety of animals supported should be at its greatest (Edwards 1984).

### 11.2.3      The Whitewing Flufftail

The results of this study confirm the great need for concern about the small size of this bird's southern African population, its sensitivity to habitat loss and disturbance, and the continuing decrease in its wetland habitats in South Africa (Chapter 8). Although my definition of the two habitat types preferred by this species in southern Africa (Section 8.5.2) is rather unsatisfactory in its generalized nature, it does permit an assessment of the amount of suitable habitat available in the wetlands which I have surveyed in southern Natal and the eastern Transvaal. My surveys indicate that the amount of such habitat is very limited and this makes it imperative to protect all sites where the species is known to occur. Threats to the bird's habitats are summarized in Chapter 8, Sections 8.4 and 8.6. In view of the rarity of the species, it is strongly recommended (Section 8.6) that any significantly large wetland under consideration for alteration should be surveyed for the possible occurrence of Whitewing Flufftails and their habitat. This proposal is in line with Begg's (1990) wildlife management policies for wetlands.

Section 8.6 also summarizes the urgent need for intensive surveys of wetlands to provide more information on the Whitewing Flufftail's distribution and status in South Africa. There is no good evidence that the species breeds in South Africa, but it may do so, and there is an urgent need to search for possible breeding sites, not only in South Africa but also in Zimbabwe and Zambia. In South Africa it would be worthwhile to survey ephemeral breeding habitats such as seasonally

flooded, largely grass-dominated vegetation (including pans) similar to those preferred by the Streakybreasted Flufftail and the Striped Crake further north in southern and central Africa (Keith 1986; Taylor *et al.* 1994). The need for surveys in the Ethiopian highlands, the only area where breeding has been proved to occur, is even more urgent.

In the light of the bird's apparent preference for vegetation which has been spring-burned (Section 8.5.2) it may be possible to increase the amount of habitat suitable for the species, especially at sites where it is known to occur regularly, by ensuring that at least a portion of the potentially suitable vegetation is burned each year. It may even be possible to create suitable areas of Habitat Type 1 at wetlands above dams (such as that at Dullstroom), especially in upland areas where *Carex acutiformis*, *Typha*, *Leersia* and *Phragmites* occur together, by regulating summer flooding to increase the area of dry to moist vegetation of this type; at some sites this might necessitate decreasing the depth of summer flooding to prevent the development of this vegetation into other types.

Section 8.6 also mentions the value of a captive-breeding programme as the quickest and most practical means of establishing the basic facts about this bird's biology, especially its breeding. Captive breeding of Redchested Flufftails and other rallids, although difficult, has been very successful (Chapter 4; Wintle 1988; Wintle & Taylor 1993) and it is recommended that a captive breeding study of the Whitewing Flufftail be established at Bromley, Zimbabwe, as soon as possible. Birds reared during this study could be released at local wetlands where the species is known to have occurred (Hopkinson & Masterson 1977, 1984). A suggestion by Collar & Stuart (1985) for a programme to catch, mark and radio-tag Whitewing Flufftails is considered impractical (Chapter 3).

### 11.3 Flufftail life histories

An animal's life history is a set of coadapted traits evolved through natural selection to adapt to particular ecological requirements (Stearns 1976). These traits represent the differential allocation of the organism's time and resources to the three types of activity which best enhance the rate at which genes are propagated to the next generation, namely (a) the enhancement of the animal's own survival, (b) the production of animal's own (or closely related) offspring at a faster rate, and (c) the enhancement of the survival and reproduction of those progeny already produced (Wittenberger 1981). In simple terms, an animal's overall life-history pattern apportions time and resources to fecundity, parental care and survival, the optimal pattern being that which best enhances fitness.

The aim of this section is to compare the relative investments made by different flufftail species in these types of activity, and to relate these patterns of investment to the habitats occupied

by the species, in an attempt to show how their life histories are adapted to the conditions which they encounter in their environments.

Relevant information on breeding is available for four African flufftail species (Whitespotted, Buffspotted, Redchested and Streakybreasted) (Keith 1986; this study), which occur in wetland and forest biomes. All are monogamous and some form permanent pair bonds (Keith *et al.* 1970; Wintle 1988; this study). They are solitary nesters and are territorial at least when breeding. Both parents incubate the eggs and care for the young. This study and that made in Kenya by Taylor & Taylor (1986) show that breeding behaviour, social behaviour and reproductive strategy may differ considerably between species in different biomes. The main factors to be considered are described for each species and are summarized in Table 11.1.

### **11.3.1      The Whitespotted Flufftail**

Whitespotted Flufftails inhabit chiefly lowland rain forest, where they are usually associated with water, especially forest streams (Keith 1986). At Kakamega Forest, Kenya, they forage for invertebrates in shallow water, on mud and in leaf litter, and they are entirely sedentary: their environment is very stable, the food supply is always adequate and cover is always good (Taylor & Taylor 1986). The species is long-lived and maintains a strong permanent pair bond, the territory is defended throughout the year by both sexes and suitable habitat appears to be permanently saturated with territorial pairs (Taylor & Taylor 1986). At Kakamega breeding occurs during the main rainy season (Taylor & Taylor 1986).

Under these very stable environmental conditions, Whitespotted Flufftails have a low breeding rate. The clutch size is two eggs and I have no evidence that more than one brood is reared per season. I have no information on clutch losses, but mortality among young birds is probably low. The young are unique among flufftails in having the juvenile plumage patterned like that of the adults (other species have a plain juvenile plumage), and from an early age they appear to form a close association with the parent of the same sex (Taylor & Taylor 1986). The young frequently remain in the parental territory throughout the nonbreeding season, helping to defend it from intruders, but they are ejected at the start of the next breeding season.

### **11.3.2      The Redchested Flufftail**

This study has shown that Redchested Flufftails inhabit a wide range of wetland vegetation types, are entirely sedentary, maintain a strong permanent pair bond and are permanently territorial,

TABLE 11.1

Comparison of the habitat, status, behaviour, breeding and mortality of four flufftail *Sarothrura* species. Unconfirmed statements are given in parentheses.

	<b>Whitespotted <i>S. pulchra</i></b>	<b>Redcheasted <i>S. rufa</i></b>	<b>Buffspotted <i>S. elegans</i></b>	<b>Streakybreasted <i>S. boehmi</i></b>
<b>Habitat type</b>	Forest with water	Wetland	Forest, bush, gardens	Wetland
<b>Habitat stability</b>	Very stable	Stable, some variations	Stable to seasonal	Seasonal
<b>Status of species</b>	Sedentary	Sedentary; some local movements	Sedentary to migratory	Migratory
<b>Territoriality</b>	Permanent	Permanent	Seasonal, possibly sometimes permanent	(Seasonal)
<b>Pair formation</b>	Permanent	Permanent	Seasonal, possibly sometimes permanent	Seasonal
<b>Clutch size</b>	2	2-3	4-5	4-5
<b>Clutch losses</b>	(Low)	Sometimes high	Low	High
<b>No. of broods</b>	1	1-3	3-4	(As many as possible)
<b>Age of young when rejected</b>	Up to 9 months	11 weeks to 6 months	21 days	(As in <i>S. elegans</i> )
<b>Mortality of young</b>	Low	(Low)	High	(High)
<b>Mortality of adults</b>	Low	Low	High	(High)

both sexes being active in territory defence. Although their environment appears relatively stable, seasonal fluctuations in habitat availability occur regularly. In the nonbreeding season, vegetation dieback and the drying out of seasonally wet areas regularly cause small reductions in territory area, which are tolerated by the birds. Irregular severe reductions also occur, especially through burning, and these often force emigration. Displaced pairs probably move as short a distance as possible, occupy habitat often only marginally suitable and move back after 2-3 months when the burned vegetation has grown again.

This species breeds during the rains. The clutch size is normally 2-3 eggs and clutch losses (from predation and temporary flooding) may be high. I have little information on the level of chick or juvenile mortality. From 1-3 broods are reared per season. Captive birds lay repeat clutches after failures, and under optimum conditions may lay clutches of 3-4 eggs up to five times per season. Early broods help to feed the chicks of subsequent broods, and young are normally tolerated in the territory until they are about 11 weeks old. However the last brood is often allowed to remain throughout the nonbreeding season, being ejected from the territory when breeding starts again. Family groups indulge in allopreening and social play, which probably serve to consolidate relationships and to redirect the adults' aggression.

The Redchested Flufftail is long-lived and the available permanent habitat may normally be saturated with territorial pairs. In this habitat, where regular seasonal changes are tolerable, the species adopts a strategy of producing a relatively small number of young which are cared for as long as possible.

### **11.3.3        The Buffspotted Flufftail**

Like the Whitespotted Flufftail this species inhabits forest, but it tolerates a wider variety of forested habitats, particularly disturbed or secondary growth, and it also occurs in dense deciduous bush and in thick cover of alien woody vegetation. It forages mainly in leaf litter and is not normally associated with water. It is unique among flufftails (and among other rallids) in having adapted to exotic vegetation around human habitations: in Natal it is a successful colonist of suburban gardens.

My studies have shown that this species may have regular migrations, in Natal probably both altitudinal and coastal, and possibly over long distances. The food supply, in habitats such as exotic vegetation and high-altitude forests, falls in winter to a level insufficient to support the birds, forcing emigration. Birds will stay in the breeding areas if possible, but many immatures, and some adults, migrate each year.

Breeding takes place during the rains. A pair bond is formed for the duration of the breeding season but there is inconclusive evidence for its existence at other times. Pair members do not

associate amicably with each other: there is no allopreening and the female is frequently harassed by the male's perpetual courtship behaviour. Pairs are strongly territorial and both sexes are active in territory defence. The clutch size is 4-5 eggs and clutch losses are low, but chick mortality is high, no more than two young of a brood usually surviving to maturity. The young are rejected as soon as they are independent, usually at 19-21 days of age, by which time laying may have started again, and 3-4 broods may be reared per season.

Given this bird's migratory tendencies as a result of its less stable habitat, mortality among both adults and immatures must be much higher than in the sedentary species, while mortality among chicks is apparently also higher. This species produces as many young as possible during the breeding season and there is a very limited period of parental care for the young.

#### **11.3.4      The Streakybreasted Flufftail**

The strongly migratory Streakybreasted Flufftail is unique among flufftails in that its breeding habitat is ephemeral: short grass temporarily inundated during the rains (Keith *et al.* 1970). The birds are often present in breeding areas for a very short time and captive males have a primitive communal display to attract mates (Wintle 1988). The bird's migratory habits and its reliance on unpredictable habitats must give rise to a higher adult mortality than in other *Sarothrura* species. The clutch size is 4-5 eggs and clutch losses may be heavy (Keith 1986). Chicks are probably rejected at an early age to allow as many broods as possible to be reared (C.C. Wintle pers. comm.). This bird's habitat is shared by the equally migratory Striped Crake *Aenigmatolimnas marginalis* which is unique among rallids in having (at least in captivity) a sequentially polyandrous mating system (Wintle & Taylor 1993). The Striped Crake's polyandry may have evolved in response to the great interyear variability in breeding conditions and/or the availability of abundant food; these are characteristic of the bird's ephemeral breeding habitat and are recognized ancestral conditions favouring polyandry (Oring 1985; Wittenberger 1981).

#### **11.3.5      Discussion**

These comparisons show that stable and unstable habitat types occur in both wetland and forest biomes, and that flufftail species differ widely in their migratory tendencies, social behaviour and reproductive strategies depending on whether they occupy stable or unstable habitats in either biome. Table 11.1 shows that, matching the transition from stability to seasonality of habitat there is a distinct change in (a) species status from sedentary to migratory, (b) territoriality and pair

formation from permanent to seasonal, and (c) adult mortality from low to high. In seasonal or unpredictable habitats clutch sizes tend to be larger, juvenile mortality higher, and the number of broods per season greater, than in stable habitats. It is clear that, for these entirely terrestrial birds, clutch losses are higher in wetland habitats than in forest habitats. The variation in the duration of parental care and protection is striking, ranging from only 21 days in the Buffspotted Flufftail, which experiences high juvenile mortality and often occupies seasonal habitat, to 11 weeks to nine months in the two permanently territorial species of stable habitats. As far as social interactions are concerned, this study has shown that the permanently territorial and sedentary Redchested Flufftail has a much more stable and interactive relationship between the members of a pair, and between adults and young, than does the Buffspotted Flufftail, exhibiting courtship feeding, allopreening, and social play activities (Chapters 4 and 9).

In these flufftail species, deteriorating habitat stability and the assumption of migratory tendencies, and the concomitant decrease in longevity and increase in juvenile mortality, are accompanied by a greater investment in fecundity and a reduction in parental care. The Redchested Flufftail, at least, is able to increase its reproductive rate when conditions favour juvenile survival, as occurs in years of good rainfall when suitable habitat is at its most extensive.

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