RESOURCE PARTITIONING IN A VIVERRID ASSEMBLAGE

by

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PREFACE

This research was carried out while I was a student in the Department of Zoology and Entomology, University of Natal, Pietermaritzburg, from January 1984 to April 1988. The project was supervised by Professor M.R. Perrin and co-supervised by Dr. D.A. Melton.

This research is my original work and has not been submitted in any form to another university.

A.H. MADDOCK

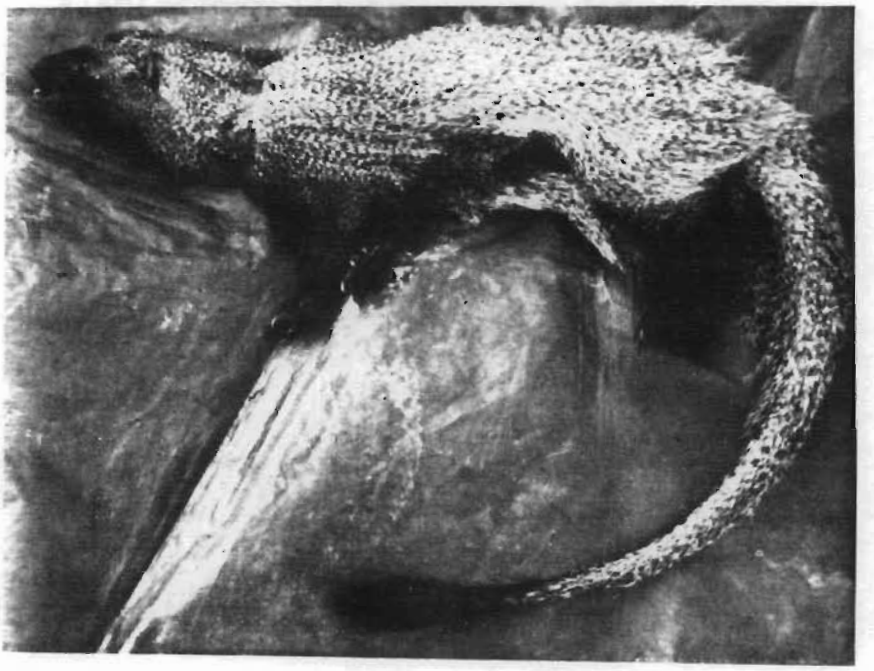
To my parents and Caroline

and in memory of all the animals

that died during this project

A

B



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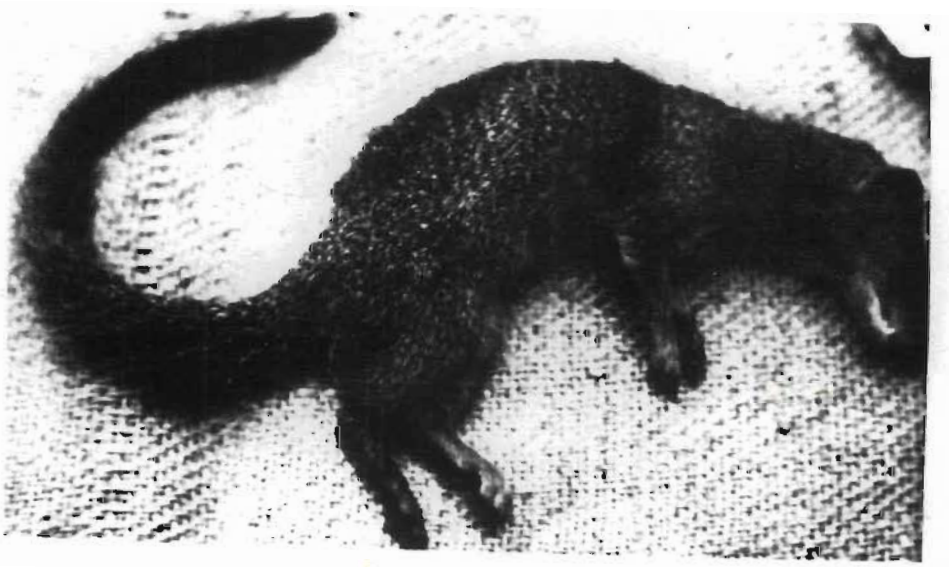

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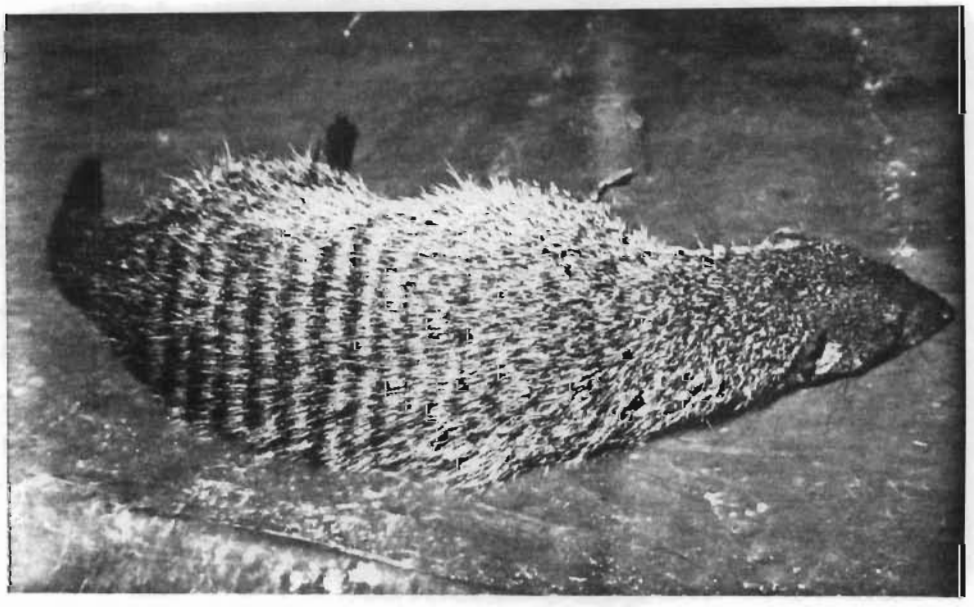

FRONTISPIECE. The viverrid assemblage. Photographs taken of anaesthetised viverrids prior to attachment of radio transmitters. A =Genetta tigrina, B =Herpestes ichneumon, C =Galerella sanguinea, D =Atilax paludinosus and E =Mungos mungo.

ABSTRACT

Viverrids are small carnivores that achieve high species richness throughout their range. This study investigated the ecology and resource partitioning of five members of this family (Genetta tigrina, Herpestes ichneumon, Galerella sanguinea, Atilax paludinosus and Mungos mungo) that coexist in Vernon Crookes Nature Reserve on the south coast of Natal, South Africa.

Emphasis was placed on differences and similarities within this assemblage. Diets of the viverrids were determined by scat analysis and prey abundance was revealed by means of a monthly trapping programme.

The spatial ecology of the assemblage was assessed using radio-tracking and habitat utilisation was compared with habitat availability. The activity regimens of these viverrids were also determined from radio-tracking.

Consideration of all three major niche dimensions (food, habitat and time) revealed important differences within this assemblage. Each species used different resources, along at least one niche axis, from other members in the assemblage. Consequently, the three niche dimensions segregated all five species. These differences may reduce interactions and facilitate coexistence.

ACKNOWLEDGEMENTS

As with most scientific work, much of the research presented in this thesis would not have been possible without contributions from a variety of people. To everyone who has helped with this thesis, I extend my appreciation and thanks.

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Prof. G. Maclean identified feathers and translated manuscripts; Prof. E. van Dijk helped with the frog identifications; Prof. D. Brothers identified insect remains and lent equipment while reptile identifications were done by Mr. L. Raw who also advised on trapping. Mrs. N. Rayner contributed to the identification of various invertebrates; Dr. R.F. Lawrence identified the Myriapoda and Mr. P. Croeser the Arachnida. Drs. R. Smithers and N. Rautenbach from the Transvaal Museum and Prof. J. Meester from the University of

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My co-supervisor, Dr. Derek Melton, gave help, advice and encouragement throughout the project and greatly improved the quality of the thesis with his criticisms of numerous early drafts.

My supervisor, Prof. Mike Perrin, competently ensured the smooth running of the project by helping with funding, access to equipment and other logistics while his criticisms of earlier drafts of the thesis also greatly improved the final product. His interest stimulates my research.

My parents, Marge and Arthur, financed my early years at university and encouraged and supported me throughout. My father, competently corrected the grammar, proof read the thesis and offered professional advice. To them I extend special thanks.

And finally, I am indebted to Caroline, who for three years spent two weeks of every month alone and for the last eight months has put up with a closed study door and all the aggrevations of being a Ph.D candidate´s wife. She criticised innumerable drafts of the thesis, typed and checked the references, professionally pasted-up all the figures, tables and maps and did countless other tasks. To her I express my deepest appreciation and thanks for her encouragement, love and understanding.

Despite the help, advice and checking of the thesis by a number of people, all errors are my own.

CONTENTS

CHAPTER 1

INTRODUCTION TO STUDY

Background and reasons for study

Community ecology is a young science (Pianka 1983) that is attracting the attention of many ecologists (Cody & Diamond 1979; Strong, Simberloff, Abele & Thistle 1984; Kikkawa & Anderson 1986). Broadly, community ecology research can be divided into two parts; first, fundamental questions are being raised about community structure, organisation and patterns (Pianka 1983; Wiens 1984). The second part, a progression from the first, attempts to discern the causal processes underlying these patterns (Wiens 1984).

Investigation of how ecologically similar species in a community partition resources is one way in which certain patterns, particularly the ratio of resource demand and supply, can be identified and described (Jaksic, Greene & Yanez 1981; Hayward & Garton 1988). Central to the study of resource partitioning, is the niche concept (see reviews in Vandermeer 1972; Glasser & Price 1982; Pianka 1983; Giller 1984) which, prior to 1957, was defined in a variety of ways (Vandermeer 1972; Pianka 1983). But in 1957, Hutchinson placed the concept on a sound footing using set theory, formally defining and unifying the niche as an n-dimensional hypervolume.

Although Hutchinson´s n-dimensional niche has been

conceptually beneficial, it is too abstract for practical use (Hudson 1976; Pianka 1983) as there is a limit to the number of resource (niche) dimensions that can be studied. Even if all dimensions could be examined, it would be impossible to display them coherently (Hudson 1976). A reduction in niche dimensionality in field studies was required but niche complementarity (Schoener 1974a) indicates that more than one niche dimension should be examined. Consequently workers have concentrated on the investigation of habitat, food and time of activity to show segregation among species, an approach that has been used to advantage (Cody 1974; Hudson 1976; Pianka 1980, 1983; Jaksic et al. 1981; Hayward & Garton 1988).

To address hypotheses concerning community patterns and degree of resource partitioning, data from diverse communities are required (Hayward & Garton 1988). Schoener (1974a) surveyed 81 studies and found that species segregate by habitat differences more often than by food differences - temporal segregation was rare. Very generally, this conclusion has been supported (Cody 1974; Simms 1979; Cody & Diamond 1979; Jaksic et al. 1981; Huey & Pianka 1983; van Hensbergen 1984; Strong et al. 1984; Kikkawa & Anderson 1986; Hayward & Garton 1988; and references therein). In Africa relatively few similar studies have been published and it would appear that a resource partitioning study in Africa would provide important new data.

Theoretical and empirical work has indicated that closely related species as well as members of predatory guilds are more likely to compete than other groups of organisms (Pontin 1982; Connell 1983; Schoener 1983). Coexistence among these

species implies that resource partitioning is important. Thus, an examination of an assemblage of closely related carnivores may be rewarding.

A number of studies on coexistence in carnivores have been conducted but many were general (Rosenzweig 1966, 1968; Erlinge 1972; Rautenbach & Nel 1978; Waser 1980; Powell & Zielinski 1983; Delibes 1983) or related to a single niche dimension (Erlinge 1969; Simms 1979; Shepard, Lerman & Hartwig 1983), mainly feeding (Rowe-Rowe 1977; Stuart 1977; Wise, Linn & Kennedy 1981; Bothma, Nel & MacDonald 1984; MacDonald & Nel 1986). Only one study has investigated small carnivore resource partitioning in detail (van Hensbergen 1984) but few studies deal with Southern African species, particularly viverrids.

Viverrids are small carnivores with an almost ubiquitous occurrence in Africa. Taylor (1986) remarked on their great diversity, generally (37 species in Africa) and locally. A random survey of mammal checklists supports Taylor's (1986) observations and a mean of 5,8 (range 3 - 10) viverrids are sympatric in 10 sites in South Africa (Table 1.1). Figures for canids, felids and mustelids in South Africa are much lower (Tables 1.1 & 1.2). Because of this high species richness and the belief that competition is likely in predatory guilds (above), viverrids were ideal candidates for a resource partitioning study.

In a reserve on the south coast of Natal, South Africa there are five species of the family Viverridae (the genet, Genetta tigrina, the Egyptian mongoose, Herpestes ichneumon, the

TABLE 1.1. Species richness of Viverridae from various sites in South Africa.

Species	Sites (key below) 1	2	3	4	5	6	7	8	9	10
Civettictis civetta				X	X					
Genetta genetta		X		X			X	X	X	
G. tigrina	X		X	X	X	X				X
Suricata suricatta							X	X	X	
Paracynictis selousi		X								
Cynictis penicillata							X	X	X	
Herpestes ichneumon			X	X	X			X		X
Galerella sanguinea	X	X	X	X	X	X				X
G. pulverulenta							X	X		
Rhynchogale melleri				X						
Ichneumia albicauda	X	X	X	X	X	X				
Atilax paludinosus	X	X	X	X	X		X			X
Mungos mungo	X	X	X	X	X	X				X
Helogale parvula				X	X	X				
Total	5	5	6	10	8	5	5	5	3	5
Mean 5,8±1,9										

1 =Whateley & Brooks 1985; 2 =Sadie 1983; 3 =Bourquin & Mathias 1984; 4 =Pienaar *et al.* 1980; 5 =Dixon 1964; 6 =Hiscocks pers. comm. 7 =Du Toit 1980; 8 =Perrin & Campbell 1980; 9 =Mills 1981; 10 =Bourquin & Sowler 1980; Maddock & Zaloumis 1987.

TABLE 1.2. Species richness of Canidae, Felidae and Mustelidae from various sites in South Africa.

Species	Sites (key below) 1	2	3	4	5	6	7	
Canidae								
Otocyon megalotis					X		X	
Lycaon pictus		X			X		X	
Canis adustus				X			X	
C. mesomelas	X	X	X	X	X	X	X	
	1	2	1	2	3	1	4	mean 2,0±1,2
Felidae								
Acinonyx jubatus		X			X		X	
Panthera pardus	X	X	X		X		X	
P. leo		X	X		X		X	
Felis caracal	X						X	
F. serval	X	X	X	X			X	
F. lybica			X				X	
	3	4	4	1	3	0	6	mean 3,0±2,0
Mustelidae								
Aonynx capensis	X	X	X			X	X	
Mellivora capensis		X	X	X			X	
Poecilogale albinucha				X		X		
Ictonyx striatus	X	X	X	X			X	
	2	3	3	3	0	2	3	mean 2,3±1,1

1 =Bourquin & Mathias 1984; 2 =Whately & Brooks 1985; 3 =Bourquin *et al.* 1971; 4 =Dixon 1974; 5 =Mills 1981; 6 =Bourquin & Sowler 1980; Maddock & Zaloumis 1987; 7 =Pienaar *et al.* 1980; pers. obs.

slender mongoose, Galerella sanguinea, the water mongoose, Atilax paludinosus and the banded mongoose, Mungos mungo). Little ecological research had been conducted on these species in Africa and their inter-relationships are unknown. Most of our understanding of these species is derived from behavioural studies (Baker 1980, 1981, 1982, 1984, 1987a,b,c, 1988a,b; Baker & Meester 1986 - on the slender and water mongooses) and short-term reports of their feeding ecology (Stuart 1977; Macdonald & Nel 1986; Louw & Nel 1986). The feeding ecology of M. mungo was the subject of an M.Sc. thesis (Sadie 1983) but very little is known about the Egyptian mongoose and the genet.

There was therefore a clear need for research on these viverrids and they were selected for study. The fundamental aim was to provide information on the basic ecology of this viverrid assemblage. Thus, the search for patterns and organisation, or the first part of the investigation of community ecology outlined above, was conducted on these small carnivores. The study complements previous resource partitioning investigations (see references above), particularly that of van Hensbergen (1984), by providing new data on community organisation from a species assemblage from which data are lacking.

Layout of the study

The approach was to divide the research into the spatial, trophic and temporal niche dimensions and gather comparative data for each species. (From these niche dimensions, others that may be found important as the study progressed, could

then be included; Hudson 1976). Resource availability was quantified and compared with resource use by the five species.

The trophic niche represented feeding ecology in its broadest sense and included quantification and comparison of prey taxa and prey size (Chap. 4) as well as foraging behaviour and prey availability (Chap. 5). These two chapters evaluate the importance of trophic partitioning among viverrids (Hypothesis I; see Schoener 1974a), in the light of the finding that carnivores often separate by diet (Rosenzweig 1966; Erlinge 1969, 1972; Rowe-Rowe 1977; Wise et al. 1981; Bothma et al. 1984; Powell & Zielinski 1983; Sadie 1983; Bekoff, Daniels & Gittleman 1984; Macdonald & Nel 1986).

In Chapter 6, the spatial and temporal niche dimensions are considered together because data were collected simultaneously using radio-tracking and observations. Macrohabitat (vegetation zone) and microhabitat use among the viverrids is compared and evaluated in terms of habitat availability. In this way, Schoener's (1974a) finding that species most often separate by differences in habitat use (Hypothesis II) is examined.

Hypothesis III investigates whether the viverrids segregate along the temporal niche. Diel activity of the viverrids is quantified in Chapter 6 and, in Chapter 7, is used to examine the effect of differing periods of activity on prey and habitat use.

Thus, Chapters 4 to 6 view the three niche dimensions as independent (orthogonal) and they are treated separately. In

Chapter 7, the interaction among these three dimensions are examined and their importance assessed. An overall multivariate, rather than univariate explanation of resource partitioning (Schoener 1986) in this viverrid assemblage is proposed using Hypotheses I,II and III.

Throughout the thesis, the idea that communities (assemblages) are at equilibrium (i.e. ecologically saturated, resource limited and governed by competition) and that differences in resource use is necessary for coexistence, is assumed (Cody 1974; Schoener 1974a; Pianka 1976). This facilitates presentation of the data. However, some researchers have found that this may not be realistic (Wiens 1977, 1984; Connell 1980; Price 1984) and in Chapter 7 this assumption is questioned.

Statistics

Initially, the data were drawn into various community matrices from which trends and statistical analyses were computed. Mainly non-parametric statistics were used and all procedures followed Zar (1974) and Nie, Hull, Jenkins, Steinbrenner & Bent (1975). Tests for independence were made using chi-square analysis when sample sizes were large and more than five observations per cell were recorded. For smaller sample sizes the Kolmogorov-Smirnov test was used (Zar 1974). Although the G statistic is more robust than chi-square analysis, most computer programmes routinely provided chi-square values and for continuity this method of analysis was used throughout. However, care was taken not to violate the assumptions of this model (Zar 1974) and all results were critically evaluated.

The Bonferroni confidence intervals based on the **z** statistic (Neu, Byers & Peek 1974; Byers, Steinhorst & Krausman 1984) were used to identify those variables responsible for the significant differences determined by independence tests. The confidence intervals indicate whether the observed resource is used more than, less than or in proportion to an expected distribution based on resource availability (Neu et al. 1974; Byers et al. 1984). This test has been used successfully in a number of resource preference studies (Litvaitis, Sherburne & Bissonette 1985a; Rolley & Warde 1985) and was considered a valuable technique when compared with three other methods (Alldrede & Ratti 1986).

Justification for using various statistical models and tests of their assumptions are provided in Appendices 1 to 3. Except were otherwise stated, significance was considered when $P<0,05$. Percentages are given to one decimal place in the tables but are rounded off in the text.

Niche breadth and overlap

To further describe community structure, niche breadth and pairwise niche overlaps were calculated (Petraitis 1979). A number of different measures have been proposed but many are inadequate because resource availability is not quantified; therefore limited and abundant resources are given equal status (Hurlbert 1978; Johnson 1980; Feinsinger, Spears & Poole 1981). Although, resource availability is difficult to quantify, especially food (Hurlbert 1978), indices that included resource use and abundance were used to give a more biologically meaningful representation of niche breadth and overlap.

Niche breadth is, therefore, used as an index of the breadth of resources used in proportion to their availability. Overlap, is not used as an indication of competition (Cody 1974; Abrams 1980) but as a measure of similarity in resource use between species in comparison with resource availability. That this similarity may be a result of competition, or any other biotic or abiotic factor, is debatable and requires experimental research beyond the scope of this thesis.

Niche breadth was measured using Feinsinger et al.'s (1981) Proportional Similarity Index:

$$PS = 1 - 0,5 \Sigma (pi - ai)$$

where: pi = proportion of resource items i in use
and ai = proportion of resource items i available

and niche overlap was measured using Hurlbert's (1978) modified formula L:

$$L = E/E'$$

where: $E = \Sigma (xiyi/ai)$
$E' = XY/A$
xi = proportion of resource items i used by species x
yi = proportion of resource items i used by species y
ai = proportion of resource items i available
X = sum of resource items used by species x
Y = sum of resource items used by species y
A = sum of resource items available

Techniques are not considered further here as each chapter has its own Materials & Methods section.

CHAPTER 2

STUDY AREA

Location and topography

The study was conducted from March 1984 to November 1986 at Vernon Crookes Nature Reserve (VCNR) which is under the jurisdiction of the Natal Parks Board (NPB). The reserve is on the south coast of Natal, 20 km inland from Park Rynie and approximately 70 km from Durban, between $30^{o}15'$ and $30^{o}19'$ south and $30^{o}33'$ and $30^{o}38'$ east (Fig. 2.1). It was proclaimed on 4 January 1974 and is 2 189 ha in extent (Bourquin & Sowler 1980; Sandwith & Brown 1981).

The reserve is surrounded by private farmland which is mainly under timber (Eucalyptus spp.) or sugar cane but is bordered in the north by Mysieland, KwaZulu (Fig. 2.1). The reserve slopes from a high point of 546 m above sea level in the northwest to 200 m above sea level in the southeast. The land also falls away sharply from Mankungwane and Velaname, on the northern boundary, northwards to the Mpambanyoni River outside the reserve (Fig. 2.1).

There are four main streams flowing from the northern highlands (Fig. 2.1). These are fed by numerous small tributaries (Fig. 2.1) whose drainage lines have cut deep valleys into the landscape causing steep or undulating topography (Fig. 2.2). The four streams include the Mthakathi Stream in the east, flowing past the Table Mountain Sandstone

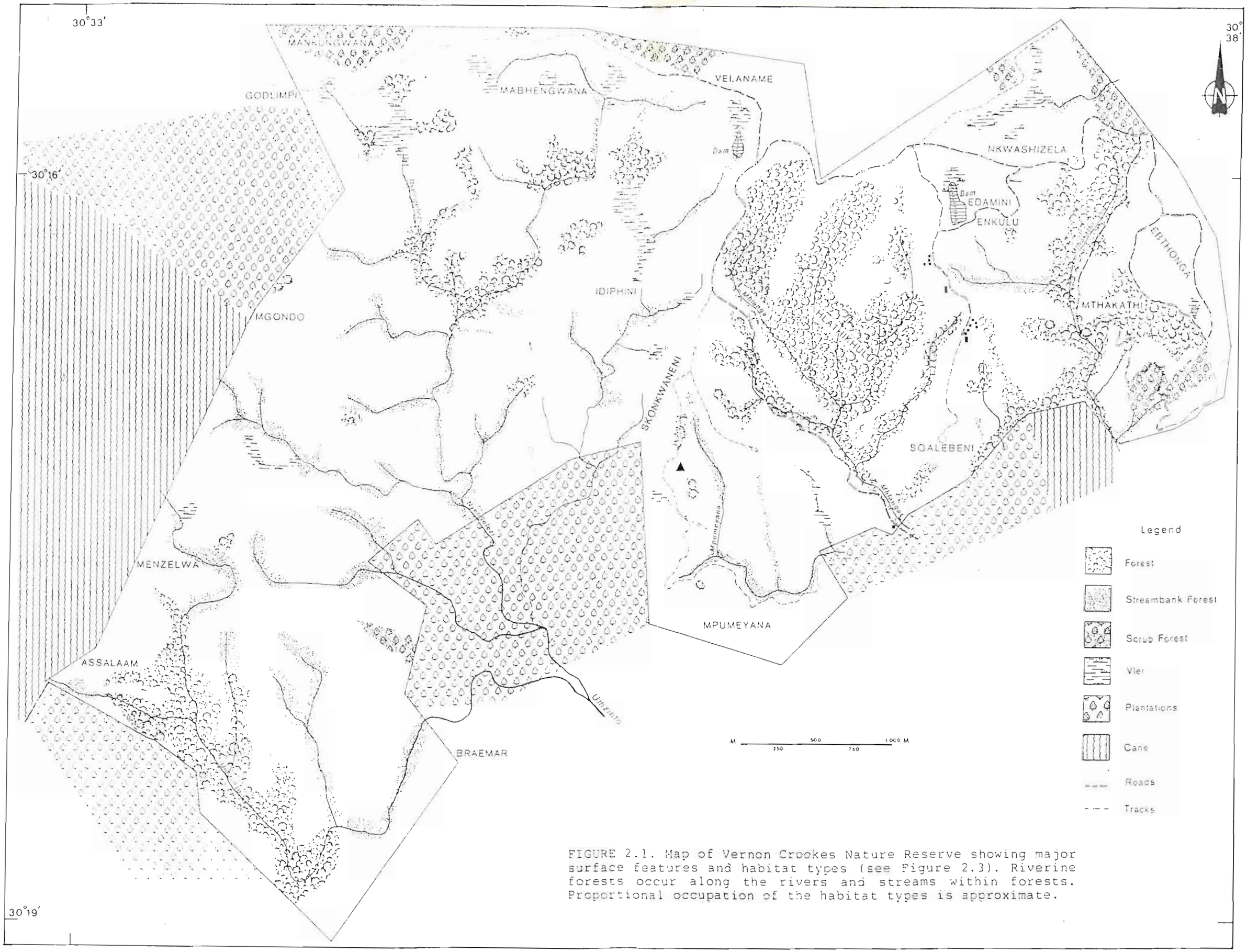

FIGURE 2.1. Map of Vernon Crookes Nature Reserve showing major surface features and habitat types (see Figure 2.3). Riverine forests occur along the rivers and streams within forests. Proportional occupation of the habitat types is approximate.

FIGURE 2.2. View north across Vernon Crookes Nature Reserve showing the undulating topography characteristic of the Natal south coast.

cliffs below Ebthonga and the Mhlanga River which runs parallel to the main entrance road and is joined by four small tributaries (Fig. 2.1). The Nyengelezi River which drains the main part of the wilderness area in the western half of the reserve receives numerous small tributaries, including the Nguduza Stream (Fig. 2.1). This river flows through more open habitats than the other three (Fig. 2.1). The Umzinto River occurs in the extreme southeast corner of the reserve (Fig. 2.1).

There are two man-made dams - a large one at Edamini Enkulu and a smaller one at Idiphini (Fig. 2.1). Both are in open grassland or bushclump and have little shallow water and few dense reeds. There are at least 12 vleis of which two are associated with the dams although most occur in the north, particularly at the headwaters of the Nyengelezi River and Nguduza Stream (Fig. 2.1).

Vegetation

The vegetation in the reserve is classed as typical coast belt forest; Type 1(a) (Acocks 1975). Dominant forest species include Milletia grandis, Protorhus longifolia, Strelitzia nicolai, Croton sylvaticus, Macaranga capensis, Schefflera umbellifera and Syzygium cordatum. Open savanna is rare but bushclump and various successional stages between grassland and forest are present. Grasses are usually tall with Themeda triandra, Digitaria spp., Hyparrhenia filipendula and Cymbopogon excavatus being representative (Acocks 1975; Sandwith & Brown 1981). Stands of bracken, Pteridium aquilinum, occur within the grassland near forest margins.

Land use practices prior to proclamation in 1974 caused vegetation changes that are in evidence today (Sandwith & Brown 1981). Cattle ranching resulted in the formation of 'Ngongoni veld' (Aristida junciformis), particularly in the west of the reserve while kraal building and localised cultivation were partly responsible for the introduction of many alien plants (Psidium guajava, Lantana camara, Chromalaena odoratum, Solanum mauritanium, Cestrum laevigatum, Opuntia spp., Euphorbia tirucalli, Caesalpinia decapetala, Melia azedarach, Mangifera indica and Eucalyptus spp. (Sandwith & Brown 1981). Reclamation of old sugar cane lands in Mthakathi valley (Fig. 2.1) and elsewhere has resulted in large areas of C. odoratum-dominated scrub. Many of the management policies at VCNR are centred on the control or eradication of these invaders (Anon 1986).

Sandwith & Brown (1981) analysed the vegetation at VCNR in detail and recognised several different habitat types which I adopted with minor modifications (Table 2.1). I pooled their four types of forest, two types of streambank forest and their two wetlands due to life-form similarities and frequent co-occurrence. In this study these were considered as three separate habitats - forest, streambank forest and vlei (Table 2.1). Sandwith & Brown (1981) also subdivided the grassland but I considered this as a single large habitat (Table 2.1). Thus, ten habitat types were recognised in the reserve (Fig. 2.1). Sampling was also conducted in a 50 ha sugar cane field adjacent to the reserve which was therefore included in the study area (Fig. 2.1). The proportional area occupied by these physiognomic categories is shown in Figure 2.3.

TABLE 2.1. Description of the ten habitat types at VCNR (after Sandwith & Brown 1981). * = data from Sandwith & Brown (1981).

Physiographic type	Height (m)	%Canopy closure	%Ground cover	Canopy levels	Characteristics
Forest	10*	closed* 59,6±15,4	open-semiclosed* 11,8±18,3	2-3 woody 1 ground* 2,1±0,7	Tall Protorhus longifolia, medium Bequaertiodendron natalense - P. longifolia and tall Vepris lanceolata were pooled into one category. Evergreen and partly deciduous broadleaf. Lianes Dalbergia armata and D. obovata had a 12,1% frequency of occurrence.
Streambank forest	6*	open-closed* 50,9±20,2	closed* 28,8±20,6	1-3* 2,0±0,7	Streams and rivers Syzygium cordatum - Macaranga capensis evergreen broadleaf. Present among boulders of drainage lines. Bridelia micrantha, Phoenix reclinata, Strelitzia nicolai obvious. D. armata and D. obovata at all levels with a 5.9% frequency of occurrence.
Riverine forest	15*	closed* 51,5±23,8	semiclosed - closed* 17,7±26,6	2-3* variable* 2,0±0,8	Occurs within forests along streams and rivers. Lianes D. armata and D. obovata occurring in 10,5% of the samples. Epiphytic ferns abundant. Stratification dependant on size of river or stream. Evergreen and partly deciduous broadleaf.
Scrub forest	3-5*	semiclosed - closed* 57,9±15,5	closed* 44,8±26,4	1-2 woody* 2,3±0,6	Infested with Chromalaena odoratum and Lantana camara due to broken canopy. Very dense ground cover forming open thickets. Forest precursors Albizia adianthifolia, Trema orientalis present and Ziziphus mucronata. Lianes occurring with 8,2% occurrence.
Scrub	2-5*	open-closed*	closed*	1-2*	
Bushclump	<2*	- 30,7±29,9	closed* 46,6±32,4	1-2* 1,4±0,6	Bushclumps less than 30 m diameter. Occurs within grassland and possibly maintained by fire. Dominated by either P. longifolia or P. reclinata which occur among rocky outcrops or in moist locations.
Grassland	-	0,7± 0,7	73,5±33,5	1,0±0,0	Exceptionally diverse; grasses, forbs and herbs including Ngongoni veld (Aristida junciformis) and stands of bracken occur (Pteridium aquilinum).
Disturbed grassland	-	0,0	88,3±13,0	1,0±0,0	Similar to scrub with high incidence of exotic plants and precursors like Burkea spp. Reclaimed sugar cane plantations.
Vlei	-	0,0	closed* 93,3±9,1	1,0±0,0	Surface waters or moist locations on flat areas or at head regions of streams or rivers; contains Phragmites australis and Cyperus spp.
Forest margin	-	36,9±32,2	56,6±33,3	1,8±0,7	Dependent on forest type. Fairly closed ground layer.

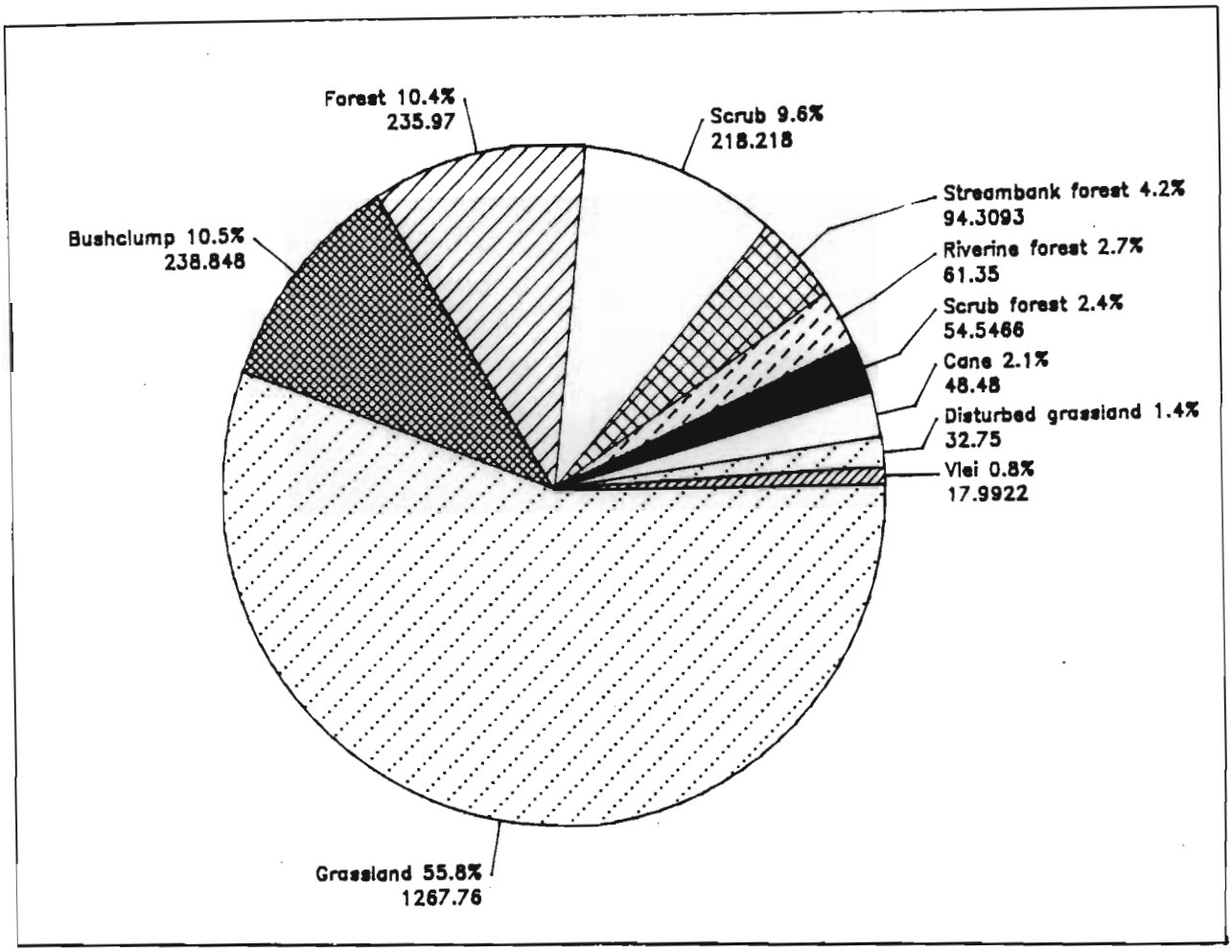

FIGURE 2.3. Area in hectares of the ten habitats recognised in the study. Habitat divisions were based on Sandwith & Brown (1981). See Table 2.1.

Climate

The climate is mild with mean maximum and minimum temperatures during January of 27,3°C and 20,7°C, and 22,5°C and 10,4°C in July. Mean monthly temperatures are shown in Figure 2.4. A mean annual rainfall of 1 218 mm was recorded between January 1984 and December 1986 occuring mainly between spring and autumn with little rain in winter (Fig. 2.5). Winds predominate from the northeast and southwest (Bourquin & Sowler 1980).

The year was divided into four seasons based on the weather data presented in Figures 2.4 and 2.5; summer - December to February, autumn - March to May, winter - June to August and spring - September to November (see Rowe-Rowe 1977). It is recognised that such subdivisions are artificial, varying from year to year, but the convenience of this categorisation was considered to outweigh the inflexibility of the method.

Fauna

The vertebrate fauna of VCNR has been described by Bourquin & Sowler (1980), Bourquin & van Rensburg (1984) and Maddock & Zaloumis (1987) and now total 119 species (Maddock & Zaloumis 1987). Many of the smaller vertebrates and some of the invertebrates are discussed in the chapter dealing with prey abundance (Chap. 5). Potential prey not dealt with in that chapter include the blue duiker, Philantomba monticola, the rock dassie, Procavia capensis and two species of hare; the scrub hare, Lepus saxatilis and the Natal red hare, Pronolagus crassicaudatus which are common in the reserve.

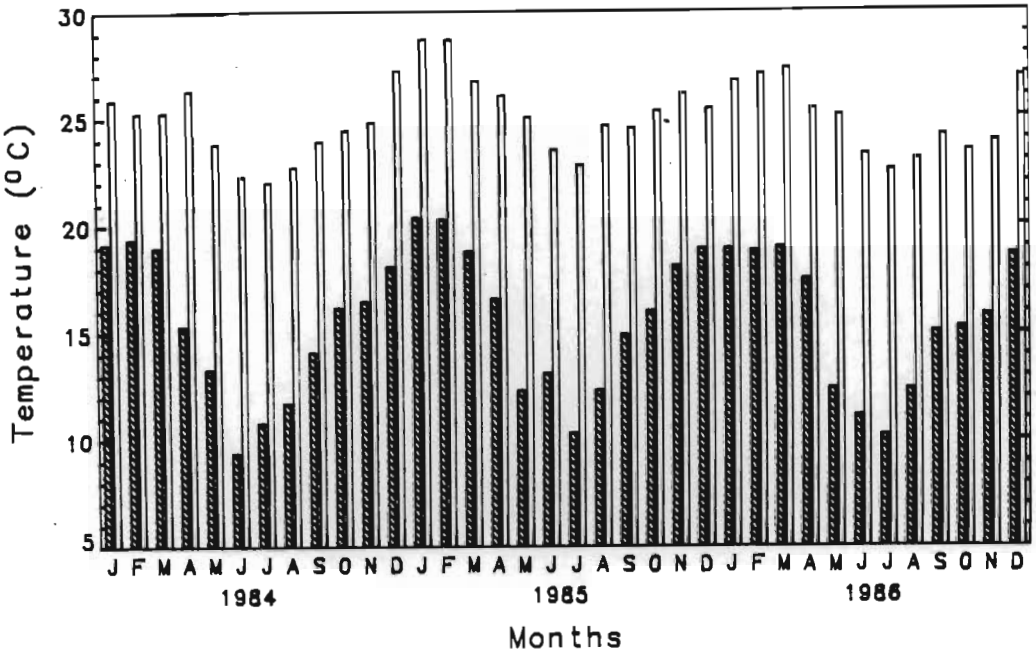

FIGURE 2.4. Mean monthly maximum and minimum temperatures recorded at Esperanza weather station near VCNR during the three year study.

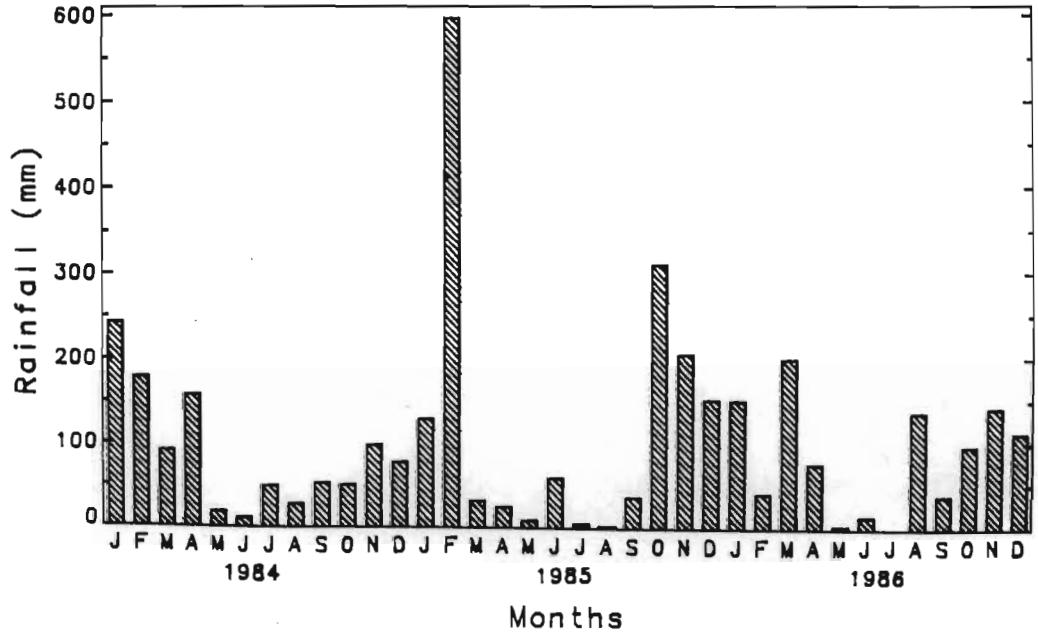

FIGURE 2.5. Mean monthly rainfall recorded at Vernon Crookes Nature Reserve during the three year study. Floods were experienced in February 1985.

Species that have diets that may overlap with the viverrids studied include the Cape clawless otter, Aonyx capensis, the black backed jackal, Canis mesomelas, the white-naped weasel, Poecilogale albinucha, seven species of shrew (Maddock & Zaloumis 1987), the Hottentot golden mole, Amblysomus hottentotus and numerous bats (Bourquin & Sowler 1980). The three carnivores mentioned above occur at low numbers in the reserve (Maddock & Zaloumis 1987).

A range of reptiles (Broadley 1983), particularly the water leguaan, Varanus niloticus, and birds (Maclean 1985) prey on similar food to the viverrids although the low metabolic rate of reptiles and low food intake probably results in minimal competition with viverrids (Sadie 1983). Birds on the other hand, have higher metabolic rates and may have a pronounced ecological effect on the viverrids (see Andersson & Erlinge 1977; Jaksic et al. 1981). Most important of these are probably the Yellowbilled Kite, Milvus migrans parasitus, Longcrested Eagle, Lophaetus occipitalis, the Steppe Buzzard, Buteo buteo, Grass Owl, Tyto capensis, the Wood Owl, Strix woodfordii and Marsh Owl, Asio capensis which are abundant in the reserve. The Martial Eagle, Polemaetus bellicosus and the Crowned Eagle, Stephanoaetus coronatus may be important not only because of diet similarity but because they also eat viverrids (Maclean 1984).

No effort is made to quantify interactions between viverrids and non-viverrids but, as the list above suggests, resource partitioning may occur between unrelated taxonomic groups. I am well aware of this.

CHAPTER 3

STUDY ANIMALS

INTRODUCTION

The Viverridae, with the Felidae, Hyaenidae, and Protelidae, belong to the Superfamily Feloidea (Meester, Rautenbach, Dippenaar & Baker 1986). The Viverridae is the oldest carnivore family (Hinton & Dunn 1967; Smithers 1983), whose earliest fossils are nearly indistinguishable from the ancestral Miacidae (Savage 1977). Viverrids are distributed in Africa, Asia and Europe but only two species, Herpestes ichneumon and Genetta genetta, occur in Europe while most are found in Africa and Madagascar (Michaelis 1972; Ewer 1973; van Hensbergen 1984).

There is much taxonomic uncertainty within the Viverridae (Rosevear 1974; Smithers 1983) but no attempt is made to revise their systematics and, as with all other mammalian taxonomy in this thesis, the classification of Meester et al. (1986) is followed. The viverrids at VCNR are represented by five species: the large- or rusty-spotted genet Genetta tigrina; the large grey or Egyptian mongoose Herpestes ichneumon; the slender mongoose Galerella sanguinea; the water or marsh mongoose Atilax paludinosus and the banded mongoose Mungos mungo (Bourquin & Sowler 1981; Maddock & Zaloumis 1987).

The genets belong to the subfamily Viverrinae while the other four species are classed as Herpestinae (Meester et al. 1986). According to the taxonomy adopted in this study, each species belongs to a separate genus (Meester et al. 1986) thus, the study animals are referred to by their generic name only, as outlined below.

This chapter describes the methods used to capture the viverrids and the data obtained from captured animals. As intraspecific variation in size may occur from area to area (Smithers 1983) it was considered more accurate to use measurements of these captured animals in this thesis rather than published data. Consequently, these data are listed in Tables 3.1 and 3.2. A brief description is given of each of the five species of viverrid but for more detail consult the general texts of Smithers & Wilson (1979), Stuart (1981), Rautenbach (1982), Smithers (1983) or Meester et al. (1986).

Viverrids are a primitive and diverse group, both ecologically and behaviourally and many differences can be ascribed to primitive or advanced traits (Kruuk 1975; Gorman 1979; Rood 1983; Waser & Waser 1985; Baker 1987c). Characteristics such as tooth specialisation (Petter 1969), solitary versus social organisation (Baker 1987c) and the association of increased Encephelisation Quotient with various behavioural, social and ecological adaptations (Sheppey & Bernard 1984; Gittleman 1986) have been studied. Viverrids show the general carnivore trend from primitive (solitary, highly predacious, nocturnal) through to advanced (social, insectivourous, diurnal) species (Rautenbach & Nel 1978; Waser & Waser 1985; Baker 1987c). Although a detailed examination of viverrid evolution is

beyond the scope of this work, some of these traits will be mentioned below as they are useful when explaining resource partitioning.

MATERIALS AND METHODS

Capture methods

Small carnivores are secretive and difficult to study in the wild, particularly if they are nocturnal or live in dense undergrowth (King & Edgar 1977; Baker 1980; Waser 1980; van Hensbergen 1984). Viverrids are also relatively infrequently seen and consequently, many data in this study were derived from trapped animals (see King & Edgar 1977) fitted with radio transmitters. Twenty four, 30 X 14 X 14 cm "Havahart" traps (Tomahawk, USA) and thirty one 100 X 30 X 30 cm self-made drop-door weld-mesh traps were used. These traps were chosen because they have been used successfully by a number of workers in Southern Africa (Baker 1980, 1987c; Rautenbach 1982; Bowland 1985; Smithers pers. comm.[1]) with no trap mortalities.

Initially traps were set about 200 m apart, where spoor suggested viverrid presence. As the habits of the study animals became known, trap sites were more critically selected, generally without regard to spacing (c.f. King 1980b). Where possible, sets were situated in natural dead ends (between large rocks or logs, under fallen trees) and along roads or paths which are often used by viverrids

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1. Smithers, R.H.N. Transvaal Museum, Paul Kruger St., Pretoria

(Smithers 1983). Traps were set to blend with the environment and were covered with natural materials (logs, leaves, grass, branches etc.) for camouflage and to darken the interior. Incompletely covered traps were never successful nor were those that were uncovered at both ends (see King 1973). The trap entrance was cleared and checked for easy access by the animal (Linn pers. comm.[2]).

Different baits were tried including dead wild rodents and birds, also a rotten fishmeal, sheep blood and water mixture. But dead day-old chicks were most practicable. They were readily available, easy to store in the deep freeze and resulted in a relatively successful capture rate. Chicken guts were wiped on the trap door to try to disguise the human smell, one or two chicks were placed around the trap entrance and one attached to the trigger mechanism. Traps were set for approximately 10 days each month, checked daily at dawn and locked open between trips. Unsuccessful traps were moved to new sites.

When a viverrid was caught, the trap was immediately covered with sacks which quietened the animal. An injection of ketamine hydrochloride (Parke Davis; range 36 to 64 mg/kg; Maddock 1988) was administered by constricting the animal against the rear of the trap by means of a wooden plunger (with the same area as the inside cross section of the trap) entered through the door. The plunger was then withdrawn and the animal left until tractable.

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2. Linn, I. Zoology Department, University of Exeter, Exeter, England.

While tractable, the animal was measured (Ansell 1965; Table 3.1) and tooth impressions, hair samples (Chap. 4) and ectoparasites collected. Age determination of animals was based on tooth wear and mass. Viverrids with badly worn teeth were considered to be "old"; "adults" were those with sharp, or slightly worn, teeth and approximate adult mass; while "juveniles" were those animals with emerging or sharp teeth and low mass (Table 3.2). This method was consistent as recaptured animals were correctly aged.

Initially an AVM radio transmitter (Chap. 6) was attached to the animal by means of a sterkolite collar but this was modified to a 10 mm diameter plastic hose collar or harness. All animals were ear-notched. Those not radio-marked were given coloured sterkolite collars but none of these marked animals was resighted and the method was abandoned. Animals were returned to the covered traps once processing was finished and the transmitter tested and were left to recover for six to seven hours.

A brief profile of each species, based on field observations, is given below. The distribution maps are compilations of capture and observational data provided by Stuart (1981; Cape Province), Lynch (1983; Orange Free State), Rautenbach (1982; Transvaal), Pringle (1977) and Rowe-Rowe (1978; Natal) supplemented by personal observations. These maps are thus more detailed than the other information provided in the profiles.

RESULTS AND DISCUSSION

Trapping

Monthly trapping data, including captures per 100 trap nights, and total number of traps set each month, are shown in Figure 3.1. There was no difference in the capture rates of the two sizes of traps (P>0,05; see Baker 1980); capture rates of 1,3 animals per 100 trap-nights (39 animals in 2 967 large carnivore trap-nights) and 1,2 animals per 100 trap-nights (8 animals in 696 Havahart trap-nights) were obtained (Fig. 3.1). Neither was there a significant difference in the monthly captures of each species considered separately or of all viverrids considered together (Kolmogorov-Smirnov; P>0,2). These results exclude captures of non-target species, such as leguaans (V. niloticus), porcupines (Hystrix africae-australis), wild birds and domestic dogs. Galerella were caught in both traps (see Baker 1980) but the other four species were caught only in the larger traps.

Figure 3.2 shows viverrid captures versus the age of the bait. Differences were not significant when each species was considered separately (P>0,2). This could be a result of small sample sizes because when all captures were pooled (Fig. 3.2) differences were highly significant (P<0,001) and indicated that animals were most often caught on the second day (range 1 - 3) after baiting the traps. Rowe-Rowe & Green (1981) also found that success rate tailed off rapidly and suggested that if no captures were made after five days, traps should be moved.

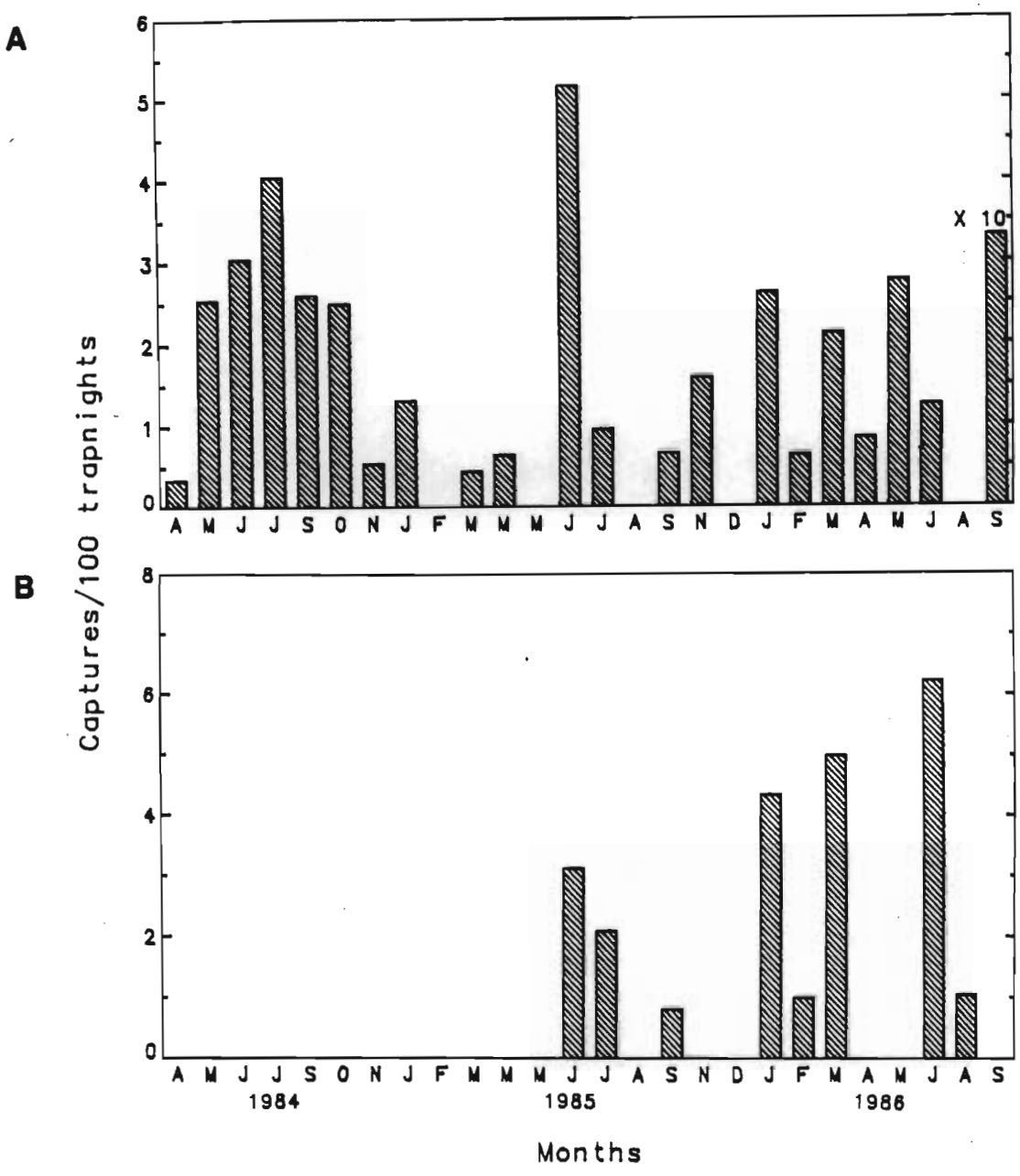

FIGURE 3.1. Monthly success rates of viverrid captures at VCNR using live traps. A=large, self-made traps, B=small, Havahart traps. Note: due to few large traps being set in September 1986 and a capture on the second night, a high success rate was achieved.

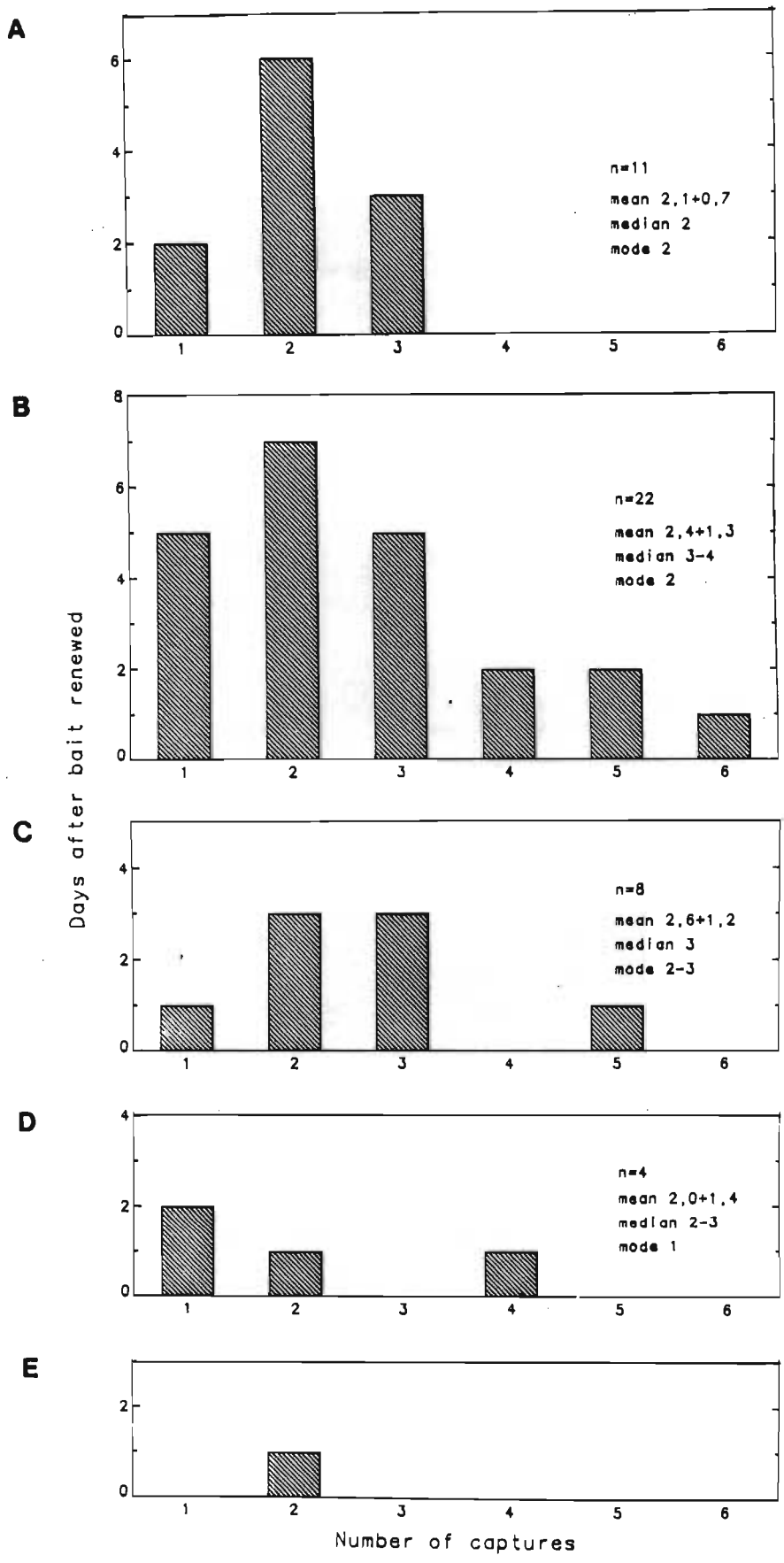

FIGURE 3.2. Number of viverrid captures at VCNR as a function of the age of bait in the small and large carnivore traps. Statistics of location are indicated. A =Genetta, B =Herpestes, C =Galerella, D =Atilax and E =Mungos.

Measurements

Measurements of the viverrids are provided in Table 3.1. Interspecific size differences were examined for all species pairs except Mungos, of which only one animal was caught. Atilax and Genetta had similar body mass (P>0,2) but all other pairs were significantly different in mass and head and body length (P<0,005; Table 3.2).

TABLE 3.2. Comparison of body mass among four species of viverrid caught at VCNR. Differences were determined using the Mann Whitney U test. The first mentioned species is the heavier.

Species pairs	Significance
A. paludinosus and G. sanguinea	P<0,005**
H. ichneumon and A. paludinosus	P<0,002**
A. paludinosus and G. tigrina	P<0,2 NS
H. ichneumon and G. tigrina	P<0,001***
H. ichneumon and G. sanguinea	P<0,001***
G. tigrina and G. sanguinea	P<0,001***

Trapping was biased in favour of females for all species, the greatest difference being shown by Galerella and Genetta (Table 3.3). Overall there were more than twice as many females caught as males (Table 3.3).

Generally, more adults were caught than juveniles although data for Atilax approached parity (Table 3.3). Genetta and Herpestes were the only viverrids with "old" classes, and no "juvenile" Galerella were caught (Table 3.3). "Juveniles" were caught in March (Atilax), May (two Genetta and one Herpestes) and September (Mungos and Atilax). Although the sample is small it does suggest a breeding period in mid to late summer and one in mid winter. Viverrids are known to have two breeding seasons (Taylor 1969; Sadie 1983).

TABLE 3.1. Measurements of the 37 viverrids caught at VCNR between May 1984 and September 1986. Species are listed in order of decreasing body mass.

	Mass (g)	H/B (mm)	Tail (mm)	H/F (mm) (c.u.)	H/F (mm) (s.u.)	Ear (mm)	Shoulder (mm)
Herpestes ichneumon	Male n=4						
x	3307,5	584,5	526,8	108,0	101,1	37,0	249,3
±SD	400,9	30,5	31,1	3,8	5,0	1,4	13,5
H. ichneumon	Female n=7						
x	2781,6	548,83	492	105,2	96,7	34,4	255
±SD	351,2	25,9	40,9	4,5	3,7	2,1	13,1
Genetta tigrina	Male n=3						
x	1675	463,5	414,5		82,2	42,1	204,5
±SD	106,1	48,8	10,6		0,8	0,6	10,6
G. tigrina	Female n=8						
x	1630,3	467,3	389,7		81,1	45,7	211,3
±SD	145	6,9	41,2		1,6	2,1	12,9
Atilax paludinosus	Male n=2						
x	1765	481,5	292,5	101,4	94,5	32,4	186
±SD	120,2	29	10,6	0,9	2,1	1,9	59,4
A.paludinosus	Female n=3						
x	1600	453,3	272,6	99,3	91,2	32,7	219
±SD	130,8	46,3	24,0	7,0	4,4	2,1	18
Mungos mungo	Female						
	960	350	180	70,5	63,4	21,0	165
Galerella sanguinea	Male n=2						
x	750	327,7	278	65,8	63,2	27,7	150,1
±SD	70,7	10,4	16,9	0,7	4,0	0,4	0,1
G. sanguinea	Female n=7						
x	401.4	299,2	249	56,2	52,2	22,5	124,0
±SD	63,6	19,8	10,0	1,5	1,7	3,5	9,7

TABLE 3.3. Sex and age ratios for the five species of viverrid caught at VCNR.

Species	M	F	Ratio	Juvs	Adults	Old	Ratio
G. tigrina	3	8	1:2,7	2	6	3	0,3:1:0,5
G. sanguinea	2	7	1:3,5	0	9	0	0:1:0
H. ichneumon	4	7	1:1,8	1	8	2	0,1:1:0,3
A. paludinosus	2	3	1:1,5	2	3	0	0,7:1:0
M. mungo		1		1			
Totals	11	26	1:2,4	6	26	5	0,2:1:0,2

Species profiles

Genetta tigrina (Schreber 1776)

The taxonomy of this species, the only Viverrinae at VCNR, is confused (Smithers 1983; Meester et al. 1986) with the greatest confusion being found among tigrina, pardina and felina (Rosevear 1974). Within Natal, Pringle (1977) recognised two subspecies; G. t. tigrina south of a line drawn from Oliviershoek Pass through Nottingham Road to Port Shepstone and G. t. rubiginosa to the north. Following Meester et al. (1986), I have classified Genetta at VCNR as G. tigrina, sensu lato.

Genetta tigrina (hereafter Genetta) are short-legged with elongate bodies and long, ringed tails (Table 3.1). Genetta is small, with a mass of about 1 640 g, standing just over 200 mm at the shoulder with a head and body length of 465 mm and a tail about 90% of head and body length (Table 3.1; Frontispiece). No sexual dimorphism was noted (Table 3.1). The claws are sharp and partly retractile to aid climbing (Taylor 1974, 1979). The coat is short and greyish-white with rusty,

black-ringed spots merging into lines at the neck. White patches occur below the eyes and around the nose (Frontispiece).

The head has a pointed muzzle and the profile from forehead to rhinarium is concave; the ears are large and ovoid. The dental formula is:-

$$\frac{3\ 1\ 4\ 2}{3\ 1\ 4\ 2} = 40$$

The carnassials have good cutting blades but are not particularly specialised in that the protocone on P^4 and talonid on M_1 are large (Ewer 1973). This dentition characterises Genetta as an ancestral viverrid (Petter 1969), a conclusion supported by its solitary and nocturnal habits (Rautenbach & Nel 1978; Baker 1987c). The Encephalisation Quotient (EQ) at 0,5, is well below the hypothetical carnivore average of unity and was intermediate among 11 species of Cape Viverridae (Sheppey & Bernard 1984).

Genets are widely distributed; occurring throughout Africa (except in the Sahara) and in Southern Europe and the Eastern Mediterranean (Wenzel & Haltenorth 1972; van Hensbergen 1984)). G. tigrina, sensu lato, is widespread south from the Sahara to the Cape (Wenzel & Haltenorth 1972). Rosevear (1974), suggests that the east African specimens belong to the pardina and not tigrina group, thereby limiting the distribution to western parts.

Genetta occurs mainly in the eastern woodlands of South Africa which receive more than 450 mm of rain annually (Stuart 1981;

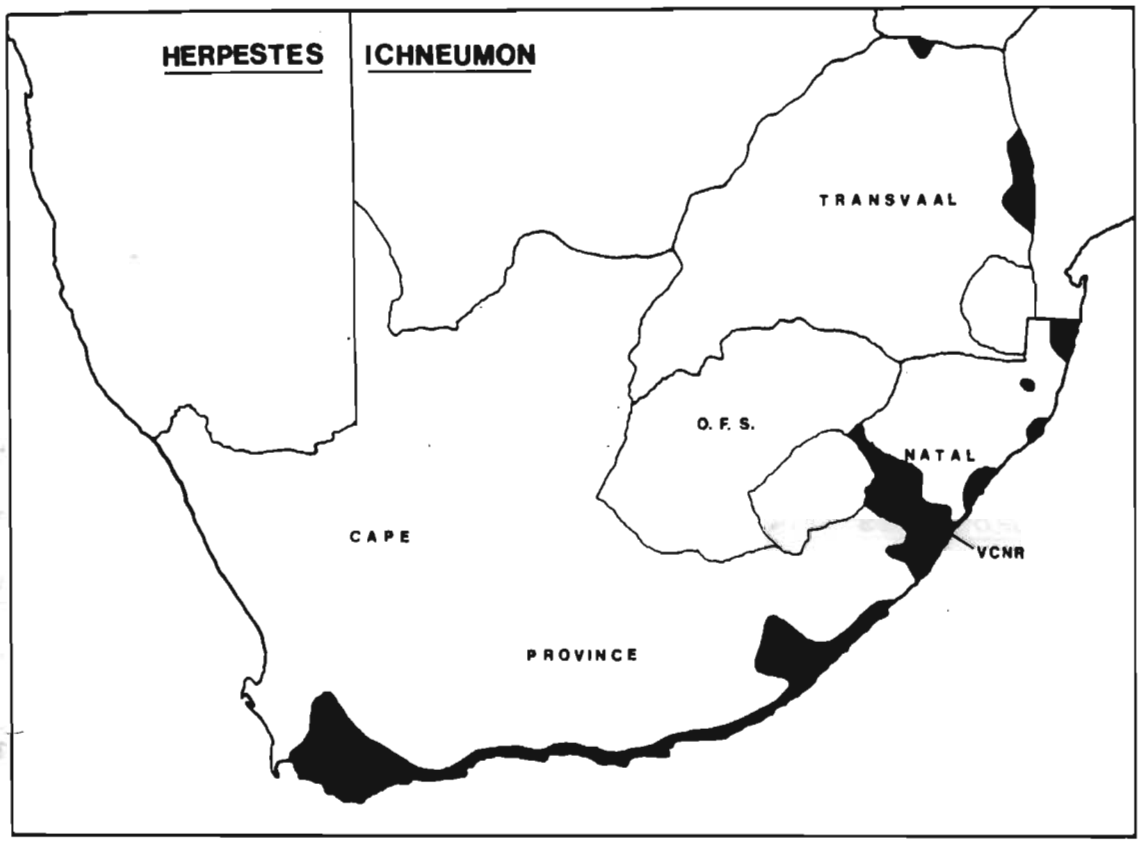

FIGURE 3.4. Distribution of H. ichneumon in South Africa. Otherwise legend as for Figure 3.3.

adpressed ears and slightly convex profile from forehead to rhinarium. The dental formula is:-

$$\frac{3\ 1\ 4\ 2}{3\ 1\ 3\text{-}4\ 2} = 38\text{-}40$$

The molars are broad and the carnassials high-cusped indicating a crushing adaptation (Smithers 1983) although Ewer (1973) suggests that Herpestes has an all-purpose dentition with a moderately well-developed carnassial blade. Petter (1969) considers Herpestes an ancestral viverrid, based on the carnassial dentition which facilitates slicing rather than crushing. The EQ for Herpestes, at 0,7, was second only to Atilax among Cape Viverrids (Sheppey & Bernard 1984).

Herpestes is widely distributed from the Cape through central and East Africa, west across the continent and north to Egypt and the Eastern Mediterranean (Wenzel & Haltenorth 1972). Also in North Africa and into Spain and Portugal but they are absent from the Sahara and Central African equatorial forests (Wenzel & Haltenorth 1972; Smithers 1983).

In Southern Africa, Herpestes is uncommon, although widespread in the Western and Eastern Cape (Stuart 1981; Fig. 3.4). They extend along the coast, through the Transkei, into Natal (Stuart 1981), mainly in the southern region from the coast to the Drakensberg (Rowe-Rowe 1978; Fig. 3.4). Herpestes has a patchy distribution along the Natal coast to Northern Zululand (Pringle 1977; Rowe-Rowe 1978; Fig. 3.4) and is rare in this province (Pringle 1977) although Rowe-Rowe (1978) found them to be common in the south. In the Transvaal, this species is limited to the southeastern lowveld and around the Limpopo

river near Messina (Rautenbach 1982; Fig. 3.4).

Galerella sanguinea (Ruppell 1836)

Although some authorities consider Galerella a subgenus of Herpestes (Ellerman, Morrison-Scott & Hayman 1953; Coetzee 1977 in Meester et al. 1986), Rosevear (1974) and Meester et al. (1986), following Allen (1924), elevated Galerella to genus status to distinguish the small G. sanguinea and G. pulverulentus from H. ichneumon (Smithers 1983). Among the species, the problem is whether all small sized, variously coloured, Galerella belong to a single species complex or if valid specific differences exist (Rosevear 1974). Meester et al. (1986) considers VCNR specimens as G. sanguinea, sensu lato.

Galerella sanguinea (hereafter Galerella) is characterised by small size and slender build, short, red pelage and long, blacked-tipped tail approximately 84% of the head and body length (Table 3.1; Frontispiece). This was the only viverrid at VCNR to exhibit sexual dimorphism (Mann Whitney; $P<0,05$; Table 3.1). Females were almost half the male mass but only 10% shorter (Table 3.1). The legs of this species are short; the males standing 150 mm at the shoulder and the females 124 mm (Table 3.1). A distinguishing feature is that the pollex and hallux are reduced and the claws are short and curved. Like Herpestes, the limb structure is primitive and generalised (Taylor 1974, 1979).

Like Herpestes, the head of Galerella is typically mongoose-like but is small and pointed. The dental formula is:-

$$\frac{3\ 1\ 4\ 2}{3\ 1\ 3\ 2} = 38$$

with high-cusped premolars being primarily adapted to an insectivorous diet (Smithers 1983). In contrast, Rosevear (1974) states the carnassials are well developed and relatively, are among the largest in the Subfamily, facilitating predation on vertebrates. Petter (1969) regards the species as primitive because of its sectorial dentition. Their EQ was the lowest of 11 Cape viverrids (Sheppey & Bernard (1984).

Galerella is common throughout Africa south of the Sahara except for the extreme southwestern coast (Rosevear 1974), the Central African equatorial forests and southern South Africa (Stuart 1981; Smithers 1983).

In Southern Africa, Galerella occurs in the arid regions of South West Africa/Namibia (excluding the Namib Desert), in the Kalahari Gemsbok National Park and are widespread in Botswana and Zimbabwe (Smithers 1983). They do not appear to be limited by rainfall or vegetation type (Smithers 1983) and are also common in well-watered areas of Natal (Pringle 1977; Rowe-Rowe 1978), along the Vaal River in the Orange Free State (Lynch 1983) and in the Transvaal (Rautenbach 1982; Fig. 3.5). They appear to be absent from much of the Cape Province (Stuart 1981; Fig. 3.5).

Atilax paludinosus (G. Cuvier 1826)

Although up to ten subspecies have been described for this monospecific genus (Allen 1924), with three or four being

recognised in Southern Africa (Roberts 1951; Ellerman et al. 1953), most recent work disregards all subspecies (Smithers 1983; Meester et al. 1986). Rosevear (1974) states that this is one of the few mongooses about whose generic independence and identity there is no dispute.

Atilax paludinosus (hereafter Atilax) is a stocky, animal (Table 3.1). Both Smithers (1983) and Baker (1987c) consider Atilax heavier than Herpestes but my data agree with Rosevear (1974), Smithers & Wilson (1979) and Stuart (1981) in finding Herpestes heavier (Table 3.1). Three adult Atilax had a mean mass of 1 740 ± 95,4 g (Table 3.1). This partly aquatic animal is unique in that it is the only viverrid with unwebbed feet causing the toes to splay and leave a distinctive spoor - an adaptation for walking on soft mud (Taylor 1974, 1979). The ears are adpressed against the head and, like the rest of the body and the relatively short tail, are covered with long hair (Frontispiece). Animals in Natal are a uniform, dark brown with a characteristic lighter coloured nose, which contrasts with the rest of the face (Frontispiece).

The head differs from that of Galerella and Herpestes in that the muzzle is short and the skull massive. The dental formula is:-

$$\frac{3\ 1\ 3\ 2}{3\ 1\ 3\ 2} = 36$$

The carnassials show little ability to slice but show an adaptation for crushing which reveals an evolutionary trend away from a meat diet and associated slicing carnassials (Petter 1969). This species had the highest EQ of 0,8, among

the Cape viverrids, approaching the hypothetical value of unity (Sheppey & Bernard 1984) while Radinsky (1975) has associated a larger brain size with increased tactile sensitivity and muscular control of the forepaws.

Atilax is widely distributed in Africa south of the Sahara but is influenced by the distribution of well-watered terrain and cover (Rosevear 1974; Smithers 1983). It occurs from Senegal, across West to East Africa and thence south along the east coast to the Cape (Smithers 1983). It is absent from much of South West Africa/Namibia, Botswana and the drier parts of Zimbabwe (Smithers 1983).

In South Africa, Atilax is evenly distributed in the Transvaal being absent only from the arid northwest and southwest (Rautenbach 1982; Fig. 3.6). They are common in the Orange Free State, especially along large rivers but are absent from the dry central and western areas (Lynch 1983; Fig. 3.6). In Natal they are widespread (Pringle 1977; Rowe-Rowe 1978) and occur wherever there are streams, vleis or rivers as well as along the coast (Stuart 1981; Smithers 1983; Fig. 3.6).

Mungos mungo (Gmelin 1788)

Mungos is monospecific in Southern Africa and two subspecies are recognised; M. m. grisonax (Thomas 1926) in northwestern Transvaal, Botswana and South West Africa/Namibia while M. m. taenianotus (A. Smith 1834) is found along the northeastern Cape and Natal coasts, Eastern Transvaal, Mozambique and Zimbabwe (Meester et al 1986). Mungos mungo, is distributed throughout Africa south of the Sahara whereas the second species, gambianus, is restricted to West Africa (Rosevear 1974).

Mungos mungo taenianotus (hereafter Mungos) is small (Smithers 1983) with hunched appearance, short tail (Table 3.1) and transverse, black bands across the back which show clearly against the reddish-brown fur (Frontispiece). The pelage is long and slightly rough and there is an almost complete lack of underfur. Long claws on the front paws facilitate digging (Taylor 1974, 1979).

The head is broad and the muzzle fairly blunt. The dental formula is:-

$$\frac{3\ 1\ 3\ 2}{3\ 1\ 3\ 2} = 36$$

The carnassials have no marked cutting adaptations but have high cusps, suited to an insectivorous diet. This, with the animal's small size, sociality and diurnal habits, is typical of an advanced viverrid (Petter 1969; Baker 1987c) but Sheppey & Bernard (1984) found Mungos to have a low EQ of 0,3.

Mungos occurs south of the Sahara but is rare in West and North Africa (Rosevear 1974; Smithers 1983). They are patchily distributed in East Africa but common in Mozambique, Zambia, Angola, northeast South West Africa/Namibia, northeast Botswana and across to Wankie National Park in Zimbabwe (Smithers & Wilson 1979; Smithers 1983).

In South Africa they are found throughout the Transvaal, excluding montane forests and the escarpment sourgrass areas (Rautenbach 1982; Fig. 3.7). In Natal, Mungos are mainly limited to the coastal or low-lying eastern areas (Rowe-Rowe

1978) occurring as far south as Oribi Gorge Nature Reserve (Bourquin & Mathias 1984) but are absent from the Free State and Cape Province (Lynch 1983; Stuart 1981; Fig. 3.7).

General.

Observations of the social organisation of the viverrids at VCNR are presented in Table 3.4. Genetta, Herpestes, Galerella and Atilax are considered solitary as many of sightings of two or more individuals were of breeding pairs (Table 3.4). Mungos was clearly social (Table 3.4; Neal 1970; Rood 1975; Rautenbach 1982; Sadie 1983; Smithers 1983).

TABLE 3.4. Social organisation of viverrids at VCNR based on observations.

Species	Group size								
	1	2	3	4	5	6	7	8	9
G. tigrina	15								
G. sanguinea	49	2	1						
H. ichneumon	56	4							
A. paludinosus	3								
M. mungo	2		6	8	3	3	2		1

The general evolutionary trend in carnivores (see above; (Petter 1969; Rautenbach & Nel 1978; Waser & Waser 1985; Baker 1987c), is shown in this assemblage of viverrids. Thus, Genetta, Galerella and Herpestes are seen as plesiomorphic, although both Galerella and Herpestes are diurnal (Petter 1969; Baker 1987c). Atilax, with its advanced crushing dentition, is intermediate while the small, social, insectivorous, diurnal Mungos is highly apomorphic (Petter 1969; Baker 1987c).

CHAPTER 4

DIETS OF THE VIVERRIDAE

INTRODUCTION

The feeding biology of animals is a vital part of their ecology and much effort has been spent trying to quantify diet selection (Scott 1941; Lockie 1959; Korschgen 1971; Melton 1978; Hyslop 1980; Putman 1984; and associated references). Although theory predicts that habitat, not diet, is the most common way by which sympatric animals segregate (MacArthur & Wilson 1967; Schoener 1974a), dietary segregation in carnivores is well documented (Erlinge 1969, 1972; Wise et al. 1981; Powell & Zielinski 1983; Sadie 1983; Bothma et al. 1984; Macdonald & Nel 1986). This chapter describes the diets of the five species of viverrid to establish whether segregation can be achieved along the trophic niche (Chap. 1). These data, and the prey availability data (Chap. 5), are used to calculate dietary niche breadth and overlap indices which are presented in Chapter 5.

Few accounts of the diets of the five viverrids studied have been published and many of these are European (Delibes 1976; Alcover 1984; Delibes, Aymerich & Cuesta 1984), Israeli (Ben-Yaacov & Yom-Tov 1983) or East African studies (Neal 1970; Rood 1975; Vaughan 1976; Rood & Waser 1978). Most work in Southern African has dealt with Atilax (Rowe-Rowe 1978; Whitfield & Blaber 1980; Macdonald & Nel 1986; Louw & Nel 1986; Baker 1987c, 1988a). Analyses of Herpestes scats (Stuart

1983) and those of Galerella and Genetta during a decline in rodent numbers have been completed (Bowland 1985) while the feeding ecology of Mungos was the subject of an M.Sc. thesis (Sadie 1983). Large, general texts by Smithers (1971, 1983), Stuart (1981) and Rautenbach (1982) provide data on all five species.

Scat (faecal) analysis was used to determine the diet of the viverrids in this study. Advantages of this technique include the continuous determination of feeding habits, relatively simple methodology, limited interference with study animals and, once middens are found, a continuous source of material is available, (Scott 1941; Lockie 1960; Putman 1984). It may also be the only material available (Putman 1984) and avoids ethical problems of killing animals for gut analysis.

However, because prey have different digestibilities and/or leave different proportions of undigested parts in the faeces (Putman 1984) it is often difficult to accurately determine diet once food has passed through the digestive tract. Recently, new methods of scat analysis and data presentation have been developed (Wise et al. 1981; Kruuk & Parish 1981) which are more accurate than the older methods (Lockie 1959; Rowe-Rowe 1977; Appendix 1). These techniques were used to analyse the scats of captive viverrids (Lockie 1959; Wise et al. 1981; Kruuk & Parish 1981). Based on these results the most accurate method was selected to analyse scats collected in the field (Appendix 1). Despite the problems associated with scat analysis, it can be reliable (Day 1966; Erlinge 1969; Dickman & Huang 1988), and as the advantages far outweighed the disadvantages, it was used in this study.

MATERIALS & METHODS.

Scat collection.

Scats were collected monthly from middens or wherever encountered between April 1984 and October 1986. Occasionally the surrounding farmland was searched and scats were found in sugar cane but not in Eucalyptus spp. plantations.

A number of features enabled the field identification of scats. Size, diameter, shape (Grobler, Hall-Martin & Walker 1984) and deposition site (Table 4.1) were often diagnostic. In all cases, field identification was confirmed in the laboratory by the presence of "own" hair (ingested while grooming) and scats that could not be positively identified were discarded.

Determining the age of scats was achieved by noting their weathering along a route that was walked daily. It was possible to age scats to within a month of them being deposited and errors were reduced by frequent collection along the route and by collecting on the first and last days of each monthly field trip.

Single scats were placed in paper packets and labelled with the date, locality/habitat, initial identification and age. Samples were oven-dried at 65-70^{o}C to constant mass, weighed and stored dry in cardboard boxes.

Due to small sample sizes during 1984 and 1985, the scats of Genetta and Galerella were analysed bimonthly, not monthly as were the Atilax and Herpestes samples. During 1986 sufficient Genetta and Galerella scats were collected to allow monthly

TABLE 4.1. Location of the middens (A) of five species of viverrid at VCNR and their characteristic sites (B).

A. Frequency of occurrence of middens.

	Genetta	Herpestes	Galerella	Atilax	Mungos
Forest		2,2			32,1
Under rocks	34,9		6,3		10,7
Rock near water		0,5		20,9	
Road	12,3	10,2	7,1	22,7	
In trees	19,8				
Forest margin			15,2	9,1	10,7
Open					
Grassland	2,8	61,8	16,1	20,6	17,9
Bushclump			45,5		
Vlei			0,9		
Cane	2,8	16,1	6,3	12,1	14,3
Road	1,9				
Rocks near dam	1,9	9,1	2,7	14,6	14,3
Rocks in scrub	23,6				
Totals	106	186	112	330	28

B. Characteristics of middens.

Genetta. In middens in the forest. Either in large trees or under overhanging rocks.

Herpestes On pathways or roads through grassland. Scats were not found in groups but spread along the paths.

Galerella. In middens, usually on large flat rocks away from water but under some cover.

Atilax In middens, on large flat rocks near rivers, streams and dams. On rocks or prominent places away from water.

Mungos. In middens, near burrows where the animals slept.

analyses. Few Mungos scats were found, hence seasonal diet analysis could not be made and results were presented as a single analysis of overall feeding trends.

Analysis.

Scat analysis was carried out using percentage of mass at time of ingestion and frequency of occurrence, as described in Appendix 1. Results based on these two methods were plotted on a pair of axes (Kruuk & Parish 1981) to indicate (a) the mass contribution of prey categories[1] to the diet - Y axis, (b) how often the prey categories were eaten - X axis and (c) the overall importance of the various categories.

The term, overall importance, is used frequently in this chapter and, therefore, requires a brief explanation. A prey category with great overall importance would have a high frequency of occurrence - i.e. it would be eaten regularly, and it would be eaten in large amounts, thereby contributing much to the mass of food eaten. This would result in a plot in the top right of the graph. At the other extreme, prey with a low overall importance would contribute little to the diet (infrequently eaten and in small amounts) and would plot near the origin.

Overall importance (overall abundance or overall diet) was estimated by multiplying the mass contribution (Y axis) by the frequency of occurrence/100 (X axis) (Kruuk & Parish 1981). Points with equal X and Y values were connected by a set of

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1. Prey category represents the best classification possible of prey in the diet. It may be at the Order or Familial level but the meaning will be clear each time.

isopleths facilitating comparison among prey categories (Kruuk & Parish 1981). Primary prey categories were arbitrarily considered to lie above the 25% isopleth, secondary prey between the 25 and 5% and supplementary prey below the 5% isopleths. Prey below the 1% isopleth was termed trace food. The importance of various prey categories in the diet are shown visually while the frequency with which prey was eaten and the quantitative bulk of that item were combined. Thus, equal weight is given to two crucial aspects of feeding biology, overcoming some of the problems of scat analysis (Appendix 1) and presenting the results in an easily interpreted form (Kruuk & Parish 1981). Throughout this chapter it is necessary to note the important distinction among frequency of occurrence, mass contribution to diet and overall importance (overall abundance or overall diet).

Seasonality.

Statistical analyses relied on non-parametric methods because the largest number of prey categories found in a single scat was eight (Atilax, Genetta and Galerella) but a mean of between 4,2 (Genetta) and 2,8 (Mungos) categories per scat was found. As there were 16 possible prey categories, most received a value of zero for each sample, thus, the data were not normally distributed.

Monthly (or bimonthly) grouping of scat samples enabled examination of seasonal fluctuations in the diet. A general indication of seasonality was obtained by comparing the monthly mass contribution of each dietary category with the mean value, while the coefficient of variation (CV) gave an

indication of resource utilisation variability (Bothma et al. 1984). Further information on the extent of temporal variation was provided by calculating the relative variance of each prey category (percentage occurrence or percentage mass divided by mean percentage occurrence or mean percentage mass; Kruuk & Parish 1981).

Monthly results of the scat analyses were pooled and a separate mean prey mass determined for each month. Tests for independence (Chap. 1; Zar 1974) were used to detect significant differences between observed and uniform selection of each prey category. Categories were then subjected to Bonferroni's z statistic (Neu et al. 1974; Byers et al. 1984; Alldredge & Ratti 1986). This test compares observed with expected values and, by computing confidence intervals, goes beyond the chi-square analysis by identifying those groups (months) responsible for the significant difference (Neu et al. 1974; Byers et al. 1984; Alldrdge & Ratti 1986). Assumptions of this model are provided in Appendix 3.

It was considered better to analyse the pooled data for seasonal patterns, i.e. three years data pooled into a 12 month period. If seasonality was present it should be evident each year whereas analysis of unpooled monthly samples (data from each month of the study) might detect differences resulting from small sample sizes or atypical environmental conditions.

The original monthly scat analysis data (unpooled) were analysed for between-month differences using the Categorical Modelling programme (CATMOD; SAS package). This procedure

tested the hypothesis that, if seasonal predation occurred, significant differences in diet would be detected only between seasons or as the animal changed from one seasonal diet to the other. Differences within each season would not be expected.

Finally, diversity indices, which included both nominal and quantitative values, were needed to determine whether viverrids had a wider/narrower diet selection during certain months, testing the hypothesis that, as food becomes scarce, diet diversity increases (MacArthur & Wilson 1967; Schoener 1974a, 1986). The Shannon-Wiener function (H) fitted this requirement (Southwood 1978) and was used to calculate monthly diet diversity. Temporal variation in these indices was tested using the Kolmogorov-Smirnov goodness-of-fit test (Zar 1974).

Prey size selectivity.

Except for Atilax and Genetta, the viverrids differed in size (Table 3.2) and I checked if prey size selectivity by these carnivores reflected these size differences. Prey were grouped into five mass divisions (<5 g; 5-24,9 g; 25-79,9 g; 80-200 g and >200 g) and the total number of prey in each class was summed for each viverrid species. This unequal class interval was necessary to prevent dominance by the relatively numerous prey of low mass. Such subdivisions are acceptable if frequencies vary rapidly over certain intervals (Rayner 1967) and have been used for prey size classes (Rosenzweig 1966). These data were arranged into a contingency table and tests for independance among the five species were made.

A comparison between prey mass and predator mass was made using Spearman's rank correlation coefficient (Jaksic et al. 1981). This tested the hypothesis that large predators feed on larger prey than do smaller predators (Jaksic et al. 1981).

RESULTS.

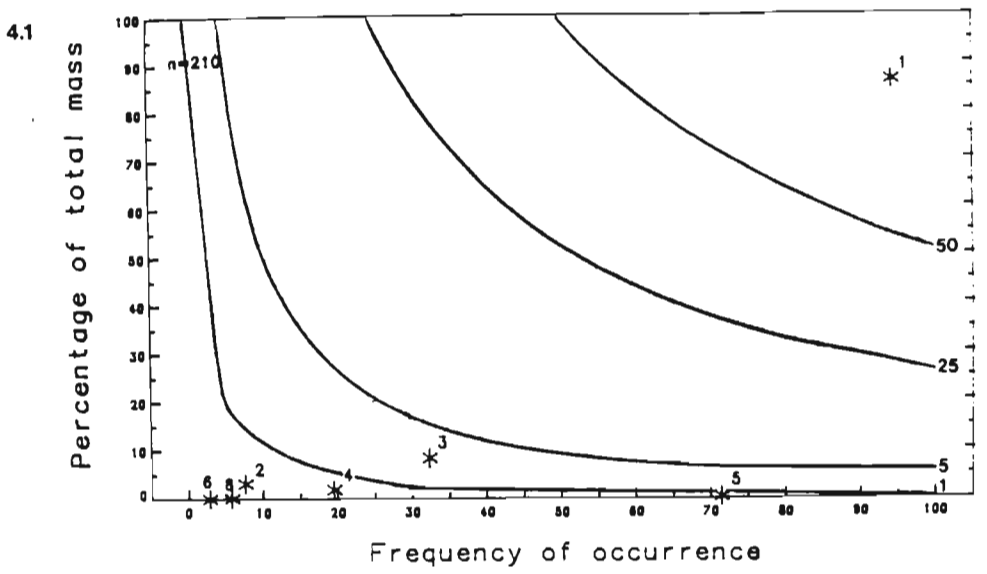
The detailed diets of the five species of viverrid are presented in Table 4.2 and shown graphically in Figures 4.1 to 4.5. A preview of Figures 4.1 to 4.5 gives an idea of the food profiles of the five viverrids. Clumping of categories in the lower left corner revealed that birds, frogs, reptiles, Arachnids and other arthropods represented trace items (<1% overall importance) for most predators (Figs. 4.1 - 4.5). Similarly, with the exception of Mungos (Fig. 4.5), insects had high frequency of occurrence but low mass contribution, indicating that, although frequently eaten, they contributed little to the diet (Figs. 4.1 - 4.5). Prey categories extending away from both axes had increasing overall importance in the diet which could be determined by noting their position relative to the closest isopleth and using the arbitrary scale indicating primary (>25%), secondary (5-25%), supplementary (1-5%) or trace (<1%) prey, as devised in the Materials and Methods.

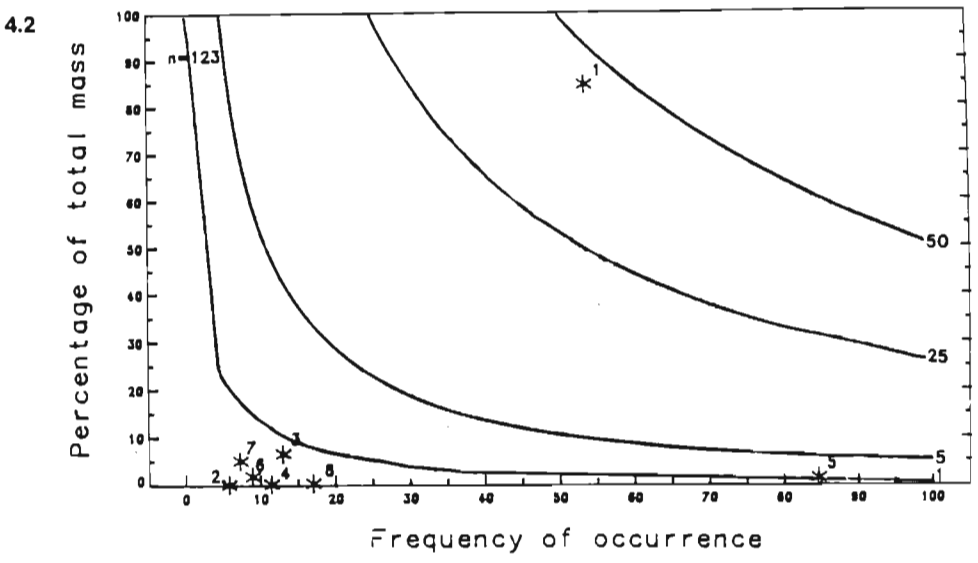
Mammals.

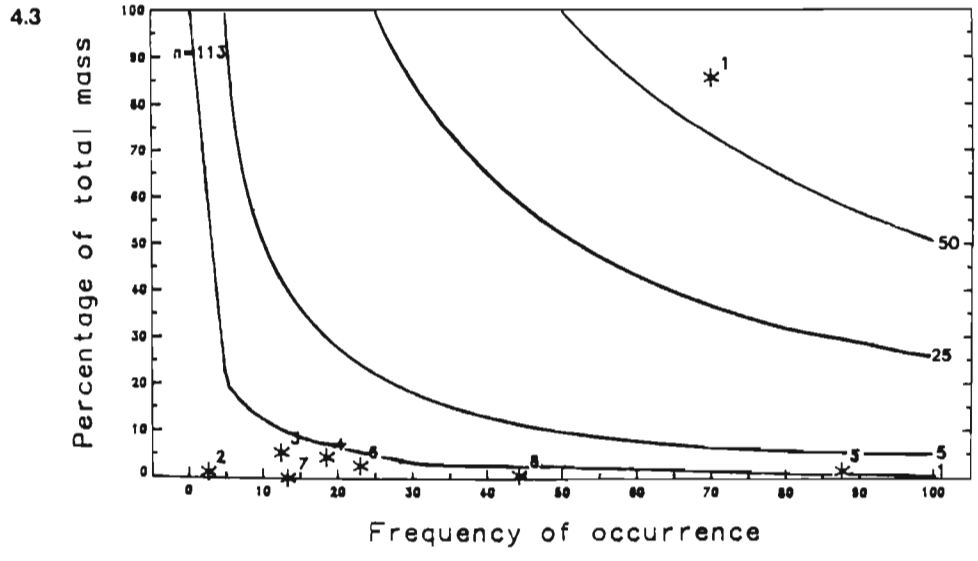
Mammals were the primary food of Herpestes, Galerella, Genetta and Atilax. Predation on mammals by the first three species is considered first as they showed many similarities. Atilax is considered later.

TABLE 4.2. Foods eaten by the five species of viverrid during the period February 1984 to October 1986. The results of the two analyses are shown: 1 = frequency of occurrence and 2 = percentage of total mass. 3 = coefficient of variation (CV). T(Trace) <0,1%. * = Plants expressed as relative bulk.

	G. tigrina n=113			H. ichneumon n=210			G. sanguinea n=123			A. paludinosus n=349			M. mungo n=33	
	1.	2.	3.	1.	2.	3.	1.	2.	3.	1.	2.	3.	1.	2.
Mammalia (total)	69,9	85,7	27,6	94,3	86,1	11,1	53,7	84,5	27,7	49,6	54,3	22,5	6,1	27,1
Rodentia	50,4	47,5	68,2	85,2	73,9	25,4	46,3	64,6	47,1	23,2	23,8	68,4	6,1	27,1
Insectivora	19,5	5,2	106,7	18,6	2,0	170,1	10,6	2,6	125,6	8,0	2,0	139,0		
Lagomorpha	0,9	1,9	332,0	3,3	5,3	-	1,6	3,1	-	2,6	4,5	258,5		
Artiodactyla (Bovidae)	8,0	14,9	169,8	1,4	2,0	-				8,3	7,8	134,5		
Hyracoidea	3,5	7,4	216,9	1,9	2,6	269,8	3,3	6,2	201,2	6,0	8,6	119,7		
Unidentified Mammalia	4,4	8,6	219,6	1,4	1,5	-	4,1	8,6	166,1	6,3	7,7	117,4		
Aves (total)	2,6	1,2	-	7,6	3,2	157,5	7,3	5,0	184,2	5,7	5,1	170,3	3,0	6,8
Passiformes	0,9	T												
Unidentified Aves	1,8	T												
Reptilia	1,2	5,6	168,1	32,3	8,3	91,0	13,0	6,5	127,3	8,0	2,6	167,1	3,0	3,0
Serpentes	1,2	5,6		26,7	7,3		10,6	6,4		2,9	2,5			
Sauria				1,0	0,2		0,8	T		2,0	T			
Unidentified Reptilia				4,8	0,8		1,6	T		3,1	T			
Amphibia (total)	18,5	4,6	211,6	19,5	1,9	123,0	8,9	1,8	170,8	57,8	13,7	61,0	6,1	17,9
Crustacea										69,9	22,6	43,0		
Insecta (total)	87,6	1,7	110,2	71,4	0,4	124,6	84,6	1,4	208,7	66,5	0,5	52,8	93,9	38,3
Coleoptera (total)	62,8	0,8	176,0	40,5	0,1	242,1	75,5	0,8	243,8	52,7	0,3	61,3	87,9	27,0
Carabidae	6,2	T		1,0	T		18,7	T			T		6,1	T
Tenebrionidae	1,8	T		1,9	T		0,8	T			T		3,0	T
Curculionidae	9,7	T		4,8	T		2,4	T			T		3,0	T
Cerambycidae							0,8	T			T			
Scarabaeidae				0,5	T		0,8	T			T			
Unidentified Coleoptera	53,1	T					52,0				T		81,8	
Orthoptera (total)	75,2	0,7	128,9	48,1	0,2	162,2	65,9	0,4	117,9	30,1	0,2	103,6	48,5	9,3
Ensifera	5,3	T		1,9	T									
Gryllidae	3,5	T					1,6	T			T			
Caelifera	6,2	T		6,2	T		2,4	T			T			
Unidentified Orthoptera				45,2	T									
Blattodea	27,4	0,2		1,9	T		6,5	T		4,6	T		6,1	0,3
Isoptera	1,8	T		1,9	T		4,1	T		-	T		9,1	1,1
Mantodea				0,5	T									
Diptera	0,9	T												
Lepidoptera													6,1	T
Unidentified larvae	1,8	T		1,4	T		0,8	T		4,9	T		6,1	0,9
Unidentified Insecta	2,7	T		4,3	T		3,3	T		5,7	T		3,0	0,1
Arachnida (total)	23,0	2,7	120,2	2,8	T	237,1	11,4	0,2	115,9	21,5	0,1	105,7	12,1	0,5
Amblypygidi							0,1	T		9,5	T		3,0	T
Scorpiones	23,0	2,7		1,4	T		8,9	0,1		12,3	0,1		9,1	T
Araneae				1,4	T						T			
Myriapoda (total)	44,2	0,7	173,1	5,8	0,1	220,1	17,0	0,4	237,6	25,8	1,2	105,3	36,3	9,1
Diplopoda Juliformia	0,8	T		1,0	T		0,8	T		1,7	T		33,3	8,9
Oniscomorpha	6,2	0,4		3,8	0,1		2,6	0,3		22,1	1,1			
Chilopoda Scolopendromorpha	41,6	0,3		1,0	T		13,8	0,1		5,7	T		3,0	0,2
Unidentified Arthropoda	13,3	0,1					5,7	0,1		5,7	0,1		12,1	1,0
Plantae	44,3	14,6*		18,6	2,0*		31,7	11,3*		30,7	7,5*		24,2	5,6*

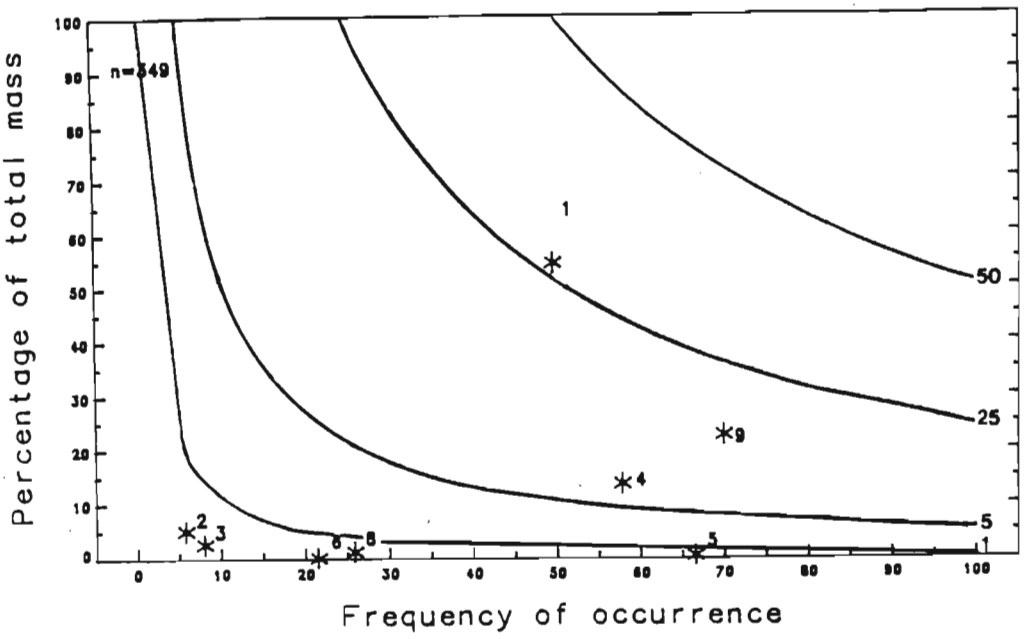




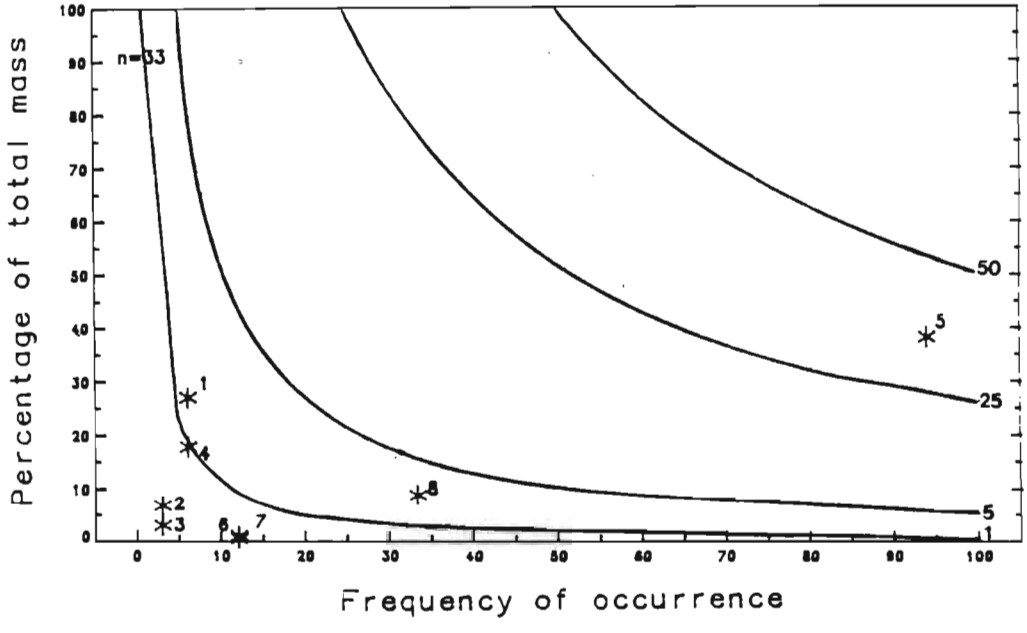


FIGURES 4.1 to 4.3. Graphical representation of the overall importance of the major prey categories in the diets of H. ichneumon (Fig. 4.1), G. sanguinea (Fig. 4.2) and G. tigrina (Fig. 4.3). Percentage of the total mass of food at time of ingestion is plotted against its frequency of occurrence. Isopleths connect points of equal overall importance. 1=Mammalia, 2=Aves, 3=Reptilia, 4=Amphibia, 5=Insecta.

4.4



4.5



FIGURES 4.4 to 4.5. Graphical representation of the overall importance of the major prey categories in the diets of A. paludinosus (Fig. 4.4) and M. mungo (Fig. 4.5). Legend as for Figure 4.1. 9=Crustacea.

The mass of mammals consumed by Genetta, Herpestes and Galerella was similar (more than 84% of the total mass; Table 4.2), but the relative importance of this prey was determined by the frequency with which mammals were eaten. Herpestes often took mammals (94% occurrence) and this, combined with their large mass contribution, gave an overall abundance of 81% (Table 4.2), with the mammal plot occurring well above the 50% isopleth (Fig. 4.1). This illustrates the importance of this food for Herpestes and it was by far the largest contribution of any prey to the five predator species (Fig. 4.6a).

Genetta ate mammalian prey more frequently than did Galerella (70% against 54%; Table 4.2) consequently the overall contribution of this prey was greater for Genetta (60% against 45%) and is clearly shown in Figures 4.3 and 4.2 and 4.8a and 4.7a.

The mass of mammals in the diet of Herpestes showed no significant seasonal variation when the pooled data were analysed ($P>0,05$; CV=30,7%; Fig. 4.6a). However, Galerella ate fewer mammals than expected in May, June and September while Genetta ate less in March but more than expected in August (pooled data; $P<0,05$; CV=54,5% and 58,9% respectively; Figs. 4.8a & 4.7a).

Herpestes, Galerella and Genetta showed similar trends of predation on mammals but these were most clearly seen in Herpestes (possibly the small sample sizes and bimonthly grouping of data obscured the pattern in Galerella and Genetta). The importance of rodents in the diet of these three

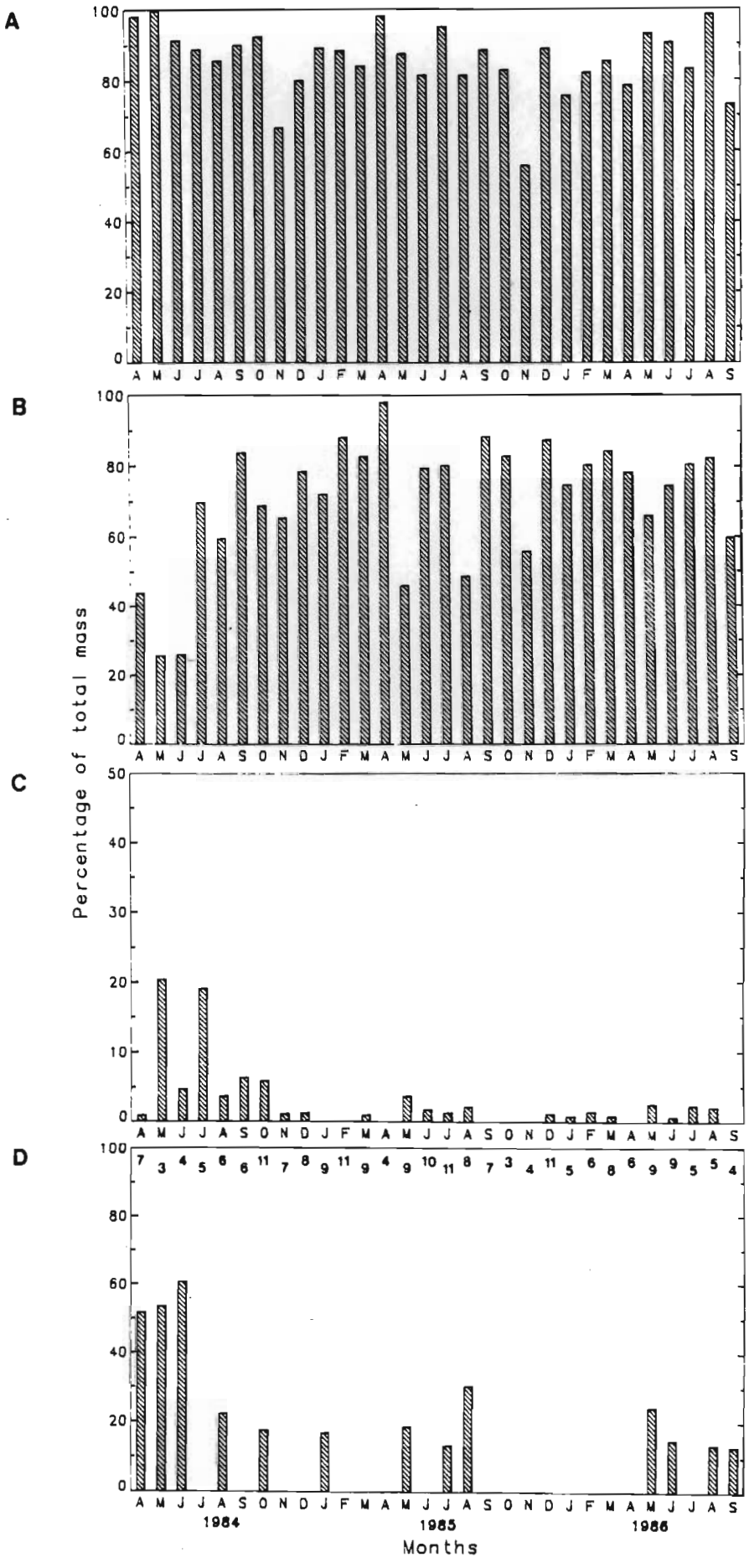


FIGURE 4.6. Monthly percentages of total mass of mammals eaten by H. ichneumon. A=Mammalia, B=Rodentia, C=Insectivora, D=Other Mammalia. Sample sizes are shown in the bottom figure.

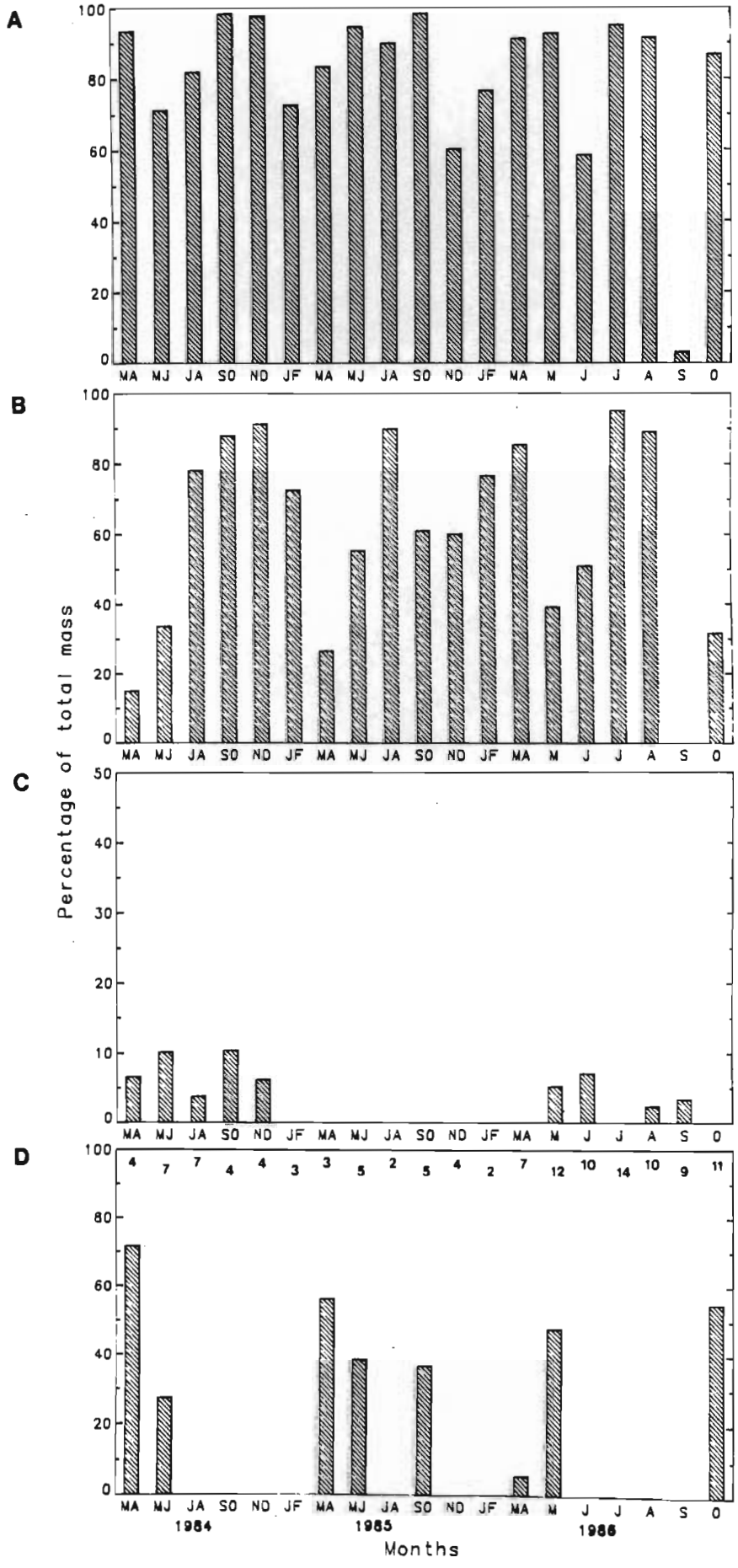


FIGURE 4.7. Monthly percentages of total mass of mammals eaten by G. sanguinea. Legend as for Figure 4.6.

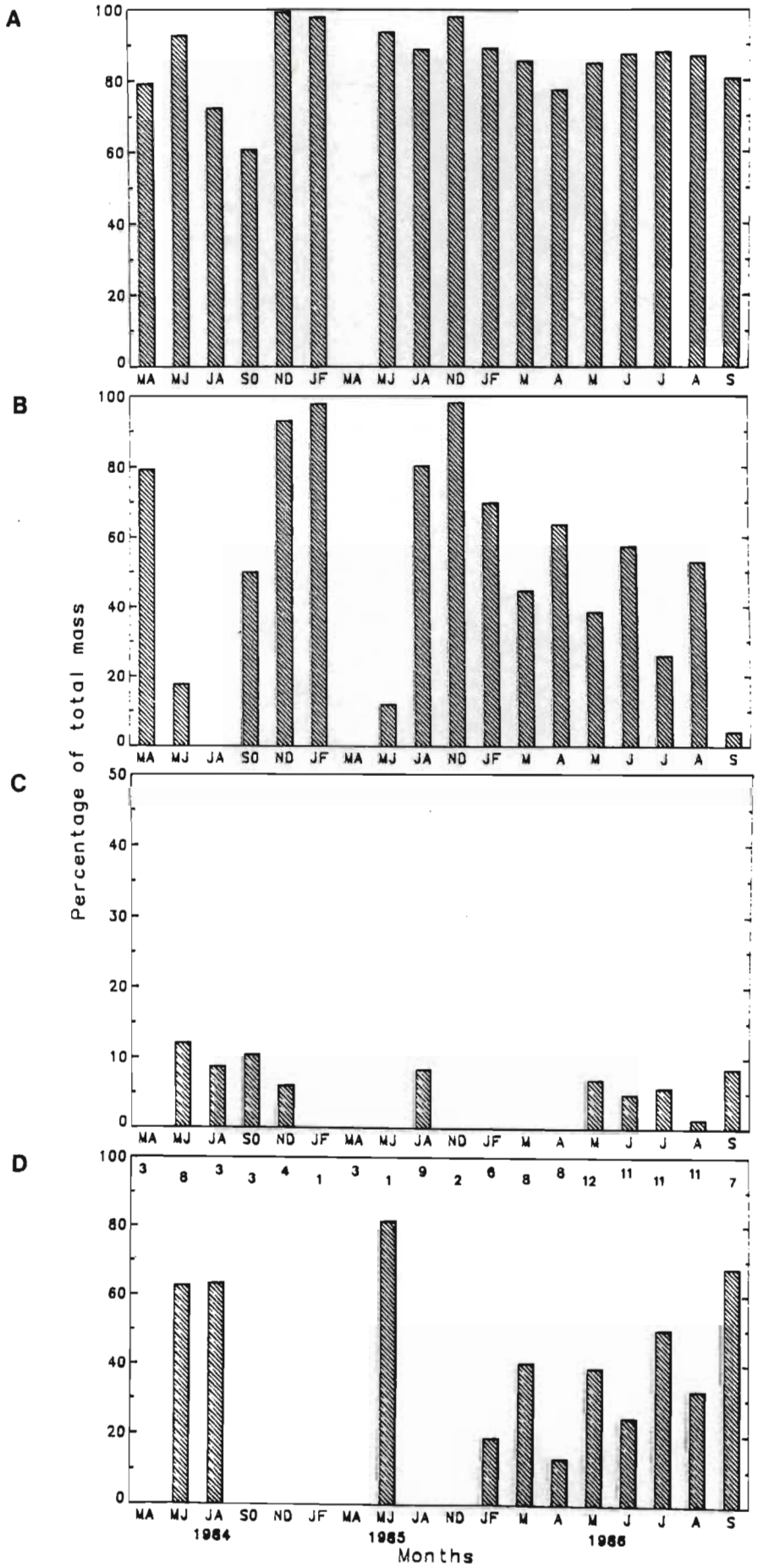


FIGURE 4.8. Monthly percentages of total mass of mammals eaten by G. tigrina. Legend as for Figure 4.6.

carnivores was obvious (Figs. 4.6b - 4.8b) as was the smaller amount of rodents eaten during 1984, especially by Herpestes (Fig. 4.6b) and Galerella (Fig. 4.7b).

A second important trend was the decrease in the number of rats and mice eaten during autumn and winter (Figs. 4.6b - 4.8b). A significant decrease in the amount of rodents eaten by Herpestes in May of all years, was noted ($P<0,05$; Fig. 4.6b). For the rest of the year, no significant increase or decrease in the monthly number of rodents eaten by Herpestes was noted ($P<0,05$; Fig 4.6b).

A similar pattern existed for Galerella and Genetta. Rodents were less common in the diet of Galerella in March, May and June (pooled data; $P<0,05$; Fig. 4.7b). More mice were eaten at the end of winter (August) but there was an unexpected decrease in rodents in the diet during September ($P<0,05$; Fig. 4.7b). Genetta ate fewer rodents in March and May and more during August (pooled data; $P<0,05$; Fig. 4.8b). For all three species, the CV values were quite high (range 25% to 68%; Table 4.2) indicating a degree of fluctuation in exploitation of this resource. However, these values were low relative to the CV values for the rest of the dietary categories (Table 4.2).

During 1984 and in autumn and winter 1985 and 1986, when few rodents were eaten (Figs. 4.6b - 4.8b), large mammals (hares, dassies and blue duikers) and, to a lesser extent, shrews[1]

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1. Because of difficulty in identifying these insectivores, Crocidura and Myosorex spp. are referred to as shrews throughout the thesis.

(more important to Galerella and Genetta), supplemented the diets of these predators (Figs. 4.6c&d - 4.8c&d). An increase in the mass of larger mammals and shrews occurred in the diet of Herpestes during April and May, a time when fewer rodents were eaten (pooled data; $P<0,05$; Fig. 4.6c&d). But the amount of non-rodent prey taken by Herpestes decreased in 1985 and 1986 (Fig. 4.6c&d).

Further analysis of the mammalian prey of these predators showed that the vlei rat (Otomys irroratus and/or O. angoniensis hereafter Otomys spp.) was the most important prey of Herpestes ($P<0,001$; Table 4.3). A total of 196 (48%) individuals were identified in the scats of this species against 43 (11%) for Rhabdomys pumilio and 40 (10%) for shrews (Table 4.3). Besides Otomys spp. more Rhabdomys pumilio together with Lemniscomys rosalia, and more shrews were eaten than expected ($P<0,05$).

For Herpestes there was a clear pattern; Otomys spp. appeared infrequently in the diet during 1984 and peaked in January and February 1985 and 1986. During autumn and winter, Otomys spp. were again taken infrequently (May, June and July 1984; April and May 1985 and May 1986; Fig. 4.9a). A slight decline in the other important prey species, R. pumilio and L. rosalia, occurred during winter (Fig. 4.9a). R. pumilio also decreased in the diet between January and March 1985 and 1986 when most Otomys were being eaten (Fig. 4.9a). Fluctuations in the numbers of these three prey species in the diet of Herpestes underlay the overall variation in the number of rodents eaten (Figs. 4.6b & 4.9a).

TABLE 4.3. Frequency of occurrence of mammals identified in the scats of four species of viverrid at VCNR.

Number in sample	Galerella 102	Genetta 122	Herpestes 410	Atilax 207
Insectivora				
Large shrews	11,8	18,9	9,8	14,0
Suncus infinitesimus	1,0	0,8	0,2	1,4
Amblysomus hottentotus	1,0	0,8		1,4
Hyracoidea (Procaviidae)				
Procavia capensis	3,9	3,3	1,2	10,1
Artiodactyla (Bovidae)				
Philantomba monticola		6,6	0,5	8,2
Rodentia				
(Bathyergidae)				
Cryptomys hottentotus			0,5	0,5
(Muridae)				
Otomys spp.	28,4	14,8	47,8	11,6
Dendromys spp.	4,9	10,7	3,6	4,4
Dasymys incomtus		0,8		1,5
Rhabdomys pumilio	9,8	4,1	10,5	1,9
Lemniscomys rosalia	3,9	9,0	6,8	2,4
Mastomys natalensis	9,8	10,7	5,9	2,9
Mus minutoides	3,9	7,4	2,2	4,4
Aethomys chrysophilus	2,0		1,0	
Thryonomys swinderianus	1,0	1,6	2,7	14,0
(Gliridae)				
Graphiurus murinus		2,5		
Unidentified Rodentia	10,8	2,5	4,4	5,8
Lagomorpha				
(Leporidae)				
Lepus saxatilus	2,0	0,8	1,7	4,4
Pronolagus crassicaudatus				
Unidentified Mammalia	5,9	4,9	0,7	10,6

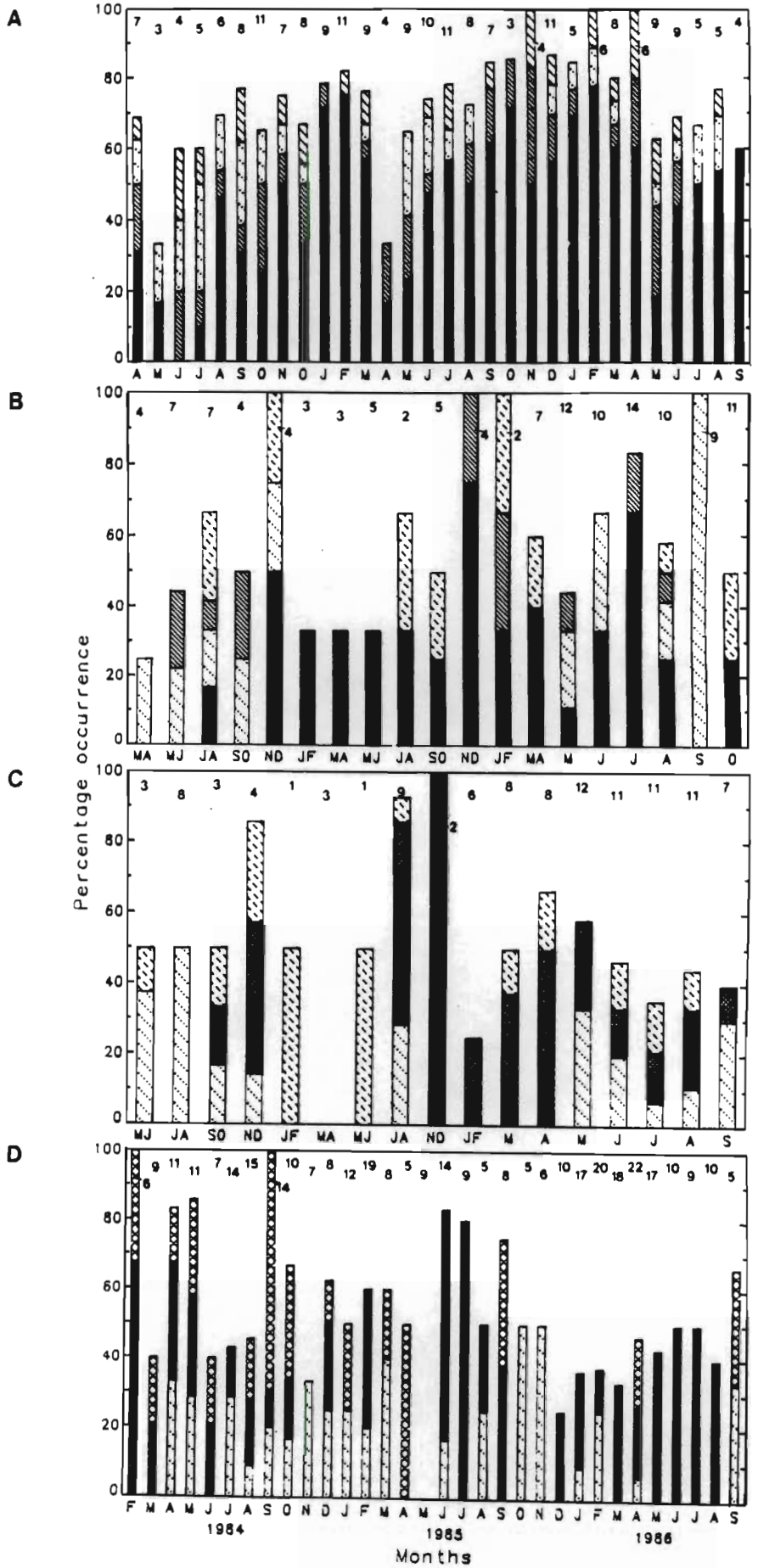

FIGURE 4.9. Monthly frequency of occurrence of the four major mammalian prey species in the diets of H. ichneumon (A), G. sanguinea (B), G. tigrina (C) and A. paludinosus (D). ■ =Otomys spp., ▨ =R. pumilio, ▩ =Large shrews, ▨ =L. rosalia, ▩ =M. natalensis, ■ =Dendromys spp., ■ =T. swinderianus and ▩ =P. capensis. Dendromys spp. in the diet of Genetta only and T. swinderianus in the diet of Atilax only.

Otomys spp. were also the main mammalian prey of Galerella ($P<0,05$) and an important food item for Genetta, contributing 28% and 15% respectively to the mass of mammals eaten by these carnivores (Table 4.3). However, in contrast to Herpestes, which ate Otomys spp. throughout 1984 (albeit in small quantities; Fig. 4.9a), these rats appeared in the scats of Galerella only in July/August 1984 and in the diet of Genetta in September/October 1984 (Fig. 4.9b & 4.9c). Otomys declined in the diet of Galerella during early spring (September/October of all three years; Fig. 4.9b) but not during winter as shown for Herpestes. No clear trend of predation by Genetta on Otomys spp. was evident, apart from a peak in November/December 1985 and rather low numbers throughout 1986 (Fig. 4.9c).

Shrews were also an important dietary item for Galerella (despite not appearing in the scats during 1985, possibly as a result of the small sample size; Fig. 4.9b) and were the major prey of Genetta (Table 4.3) although not significant at the 5% level. As with Herpestes, shrews were mainly taken by Genetta and Galerella during the cool, dry months (May/June to September/October; Fig. 4.9b and 4.9c). Because of the importance of small mammals in the diets of Herpestes, Galerella and Genetta, these species are hereafter referred to as the small mammal guild.

Atilax was the fourth viverrid to feed extensively on mammals (albeit less frequently and in smaller quantities than the small mammal guild) which provided an overall abundance of 33% and were regarded as primary prey (Fig. 4.4; Table 4.2). The mass of mammals eaten by this mongoose was significantly less

than expected in summer and late autumn ($P<0,05$; Fig. 4.10a). Overall, the mammals eaten by Atilax showed a similar monthly variation (CV= 22,5%) to those eaten by Galerella and Genetta (Table 4.2).

The finding that, in 1984, fewer rodents were eaten by Genetta, Galerella and Herpestes than in 1985 and 1986 (above) was also true for Atilax (Fig. 4.10b). But Atilax showed a significant increase in the number of rodents eaten in July (pooled data; $P<0,05$) while the other three species ate fewer rodents in winter (compare Figs. 4.6b - 4.8b with 4.10b). The increase of rodents in the winter diet was due to cane rats, Thryonomys swinderianus, being eaten by Atilax during this period (Fig. 4.9d). This large rodent (about 4 kg; Smithers 1983) was eaten mainly from April to August - the months when rodents increased in the diet (Fig. 4.10b). The seasonal nature of rodent food is reflected in Figure 4.10b. The CV value was rather high (68%; Table 4.2), again indicating that rodents were not taken regularly (Fig. 4.10b).

Insectivores which, together with cane rats, comprised numerically the most important mammal prey for Atilax, were eaten infrequently during winter - in contrast to Herpestes, Galerella and Genetta (Figs. 4.9a-d). Shrews appeared in the diet significantly more often in October and November; the period when rodents declined in the diet (pooled data; $P<0,05$; Fig. 4.9d).

The amount of larger mammals (mainly blue duikers and dassies) in the diet varied during the year, perhaps reflecting opportunism in finding carrion (Fig. 4.10d). However, it is

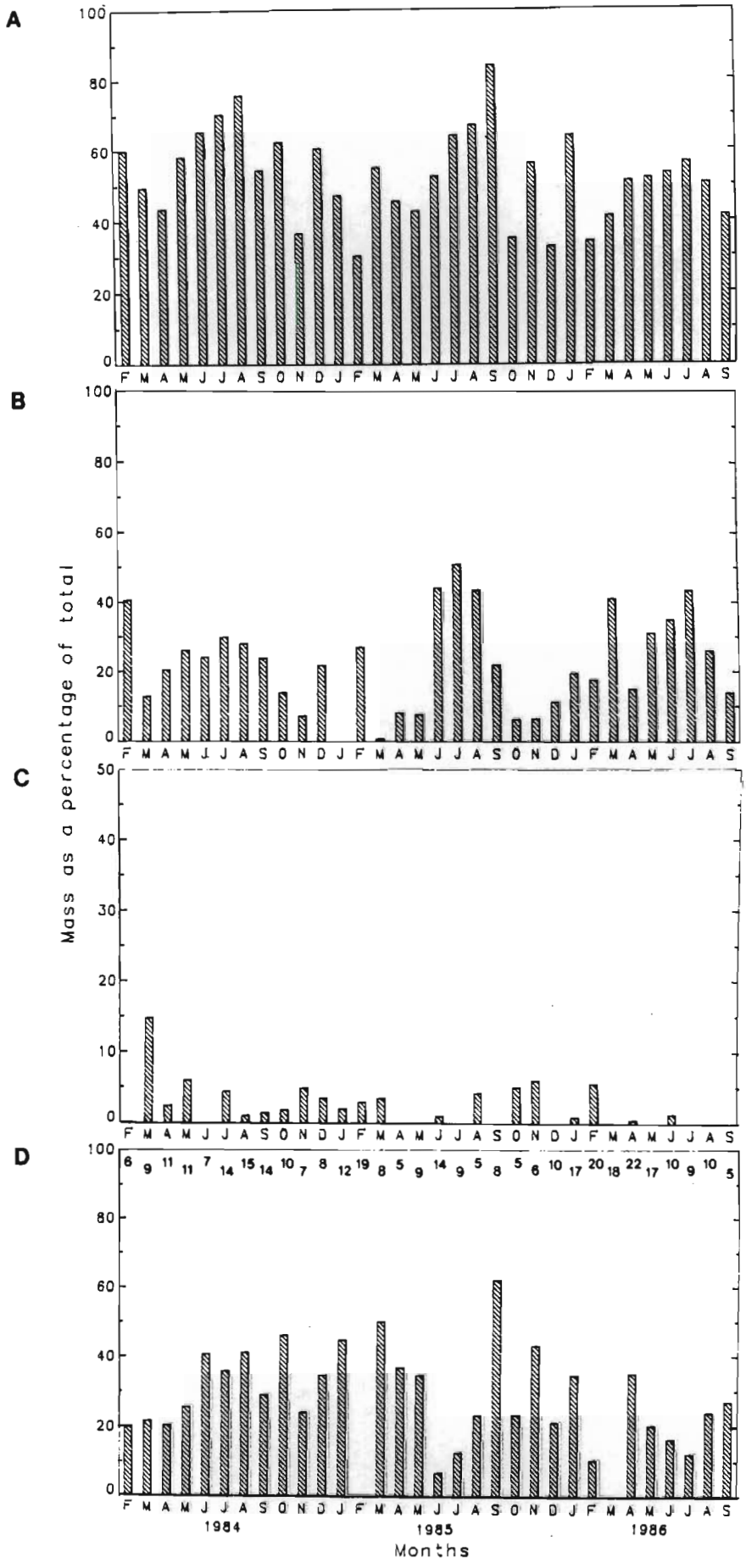

FIGURE 4.10. Monthly percentages of total mass of mammals eaten by A. paludinosus. Legend as for Figure 4.6.

A= Mammals, B= Rodents, C= Insectivora, D= Other Mammals

not certain whether these larger prey were scavenged or killed by Atilax. Notwithstanding, a characteristic of the diet of this species was that, of the five most important mammalian prey, three (dassies, cane rats; Fig. 4.9d; and duikers) had a mass greater than that of the predator ($P<0,05$). This is unlike the predation on mammals by the small mammal guild, none of which frequently selected prey larger than themselves (Figs. 4.9a-c).

In contrast to the other viverrids, mammals were recorded in the diet of Mungos only twice (Table 4.2) and, as a result, their overall abundance in the diet was small (<2%; Fig. 4.5).

Insecta.

Insects were the primary prey of Mungos, contributing 36% to overall food abundance and appearing in 94% of the scats (Table 4.2; Fig. 4.5). Unfortunately, the small number of Mungos scats prevented seasonal analysis of the data. Coleopterans were by far the most important insects eaten (23% overall importance; Fig. 4.5) and, although most remains were too finely masticated to classify to family, it appeared that Carabids were preferred; Tenebrionids and Curculionids were also frequently identified (Table 4.2).

Orthopterans contributed nearly 5% to the overall diet of Mungos (Fig. 4.5). Blattids, alate termites and larvae were recorded in low numbers (Table 4.2).

Of the remaining four viverrids, insects were the most frequently eaten prey by all except Herpestes (Table 4.2). However, because of their small size (low mass) and the small

quantities in which they were eaten, insects contributed less than 1% to the overall diets (Figs. 4.1 - 4.4) suggesting that these trace prey, were taken opportunistically. The high CV values support this (range 53 - 209%; Table 4.2).

Generally, fewer insects were taken by Herpestes, Galerella, Genetta and Atilax in the cooler months, particularly May and July but Galerella and Herpestes also ate fewer in the summer ($P<0,05$). Increases were noted in the diet of Genetta in April and August, and in November for Atilax ($P<0,05$). The lack of clear seasonal trends further suggests opportunistic feeding on insects.

Coleoptera and Orthoptera comprised the bulk of the insects in the diet of the these four species and the former were eaten in greater amounts by all except Herpestes (Table 4.2). Generally, Coleoptera were taken more in the warmer months (September to February) and Orthoptera more during the cooler part of the year (March to July). Cockroaches and alate termites appeared in the diet irregularly (Table 4.2).

Amphibia.

Amphibians occurred as important secondary prey of Atilax (Table 4.2) with 361 individuals being counted (an order of magnitude greater than the amount eaten by the remaining viverrids; Table 4.4). Amphibians had an overall abundance of 8% (Fig. 4.4), were commonly eaten and comprised nearly 14% of the total mass of Atilax's diet (Table 4.2).

No clear seasonal pattern of predation on frogs by Atilax was evident (Fig. 4.11) and a CV of 61% suggests more constant use

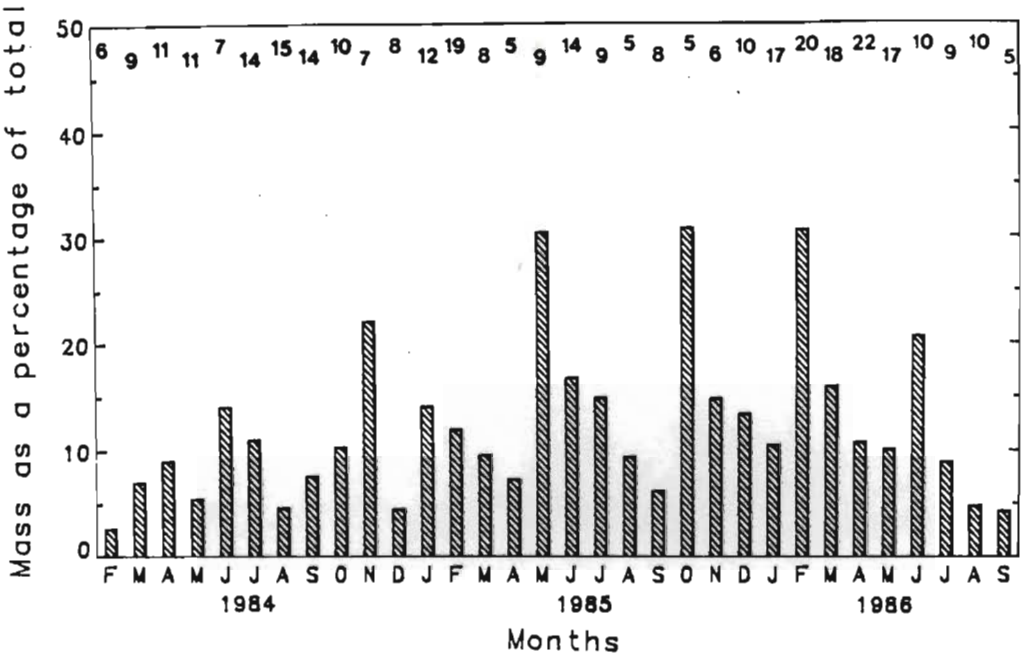

FIGURE 4.11. Amphibia as a percentage of the total mass of food ingested by A. paludinosus each month.

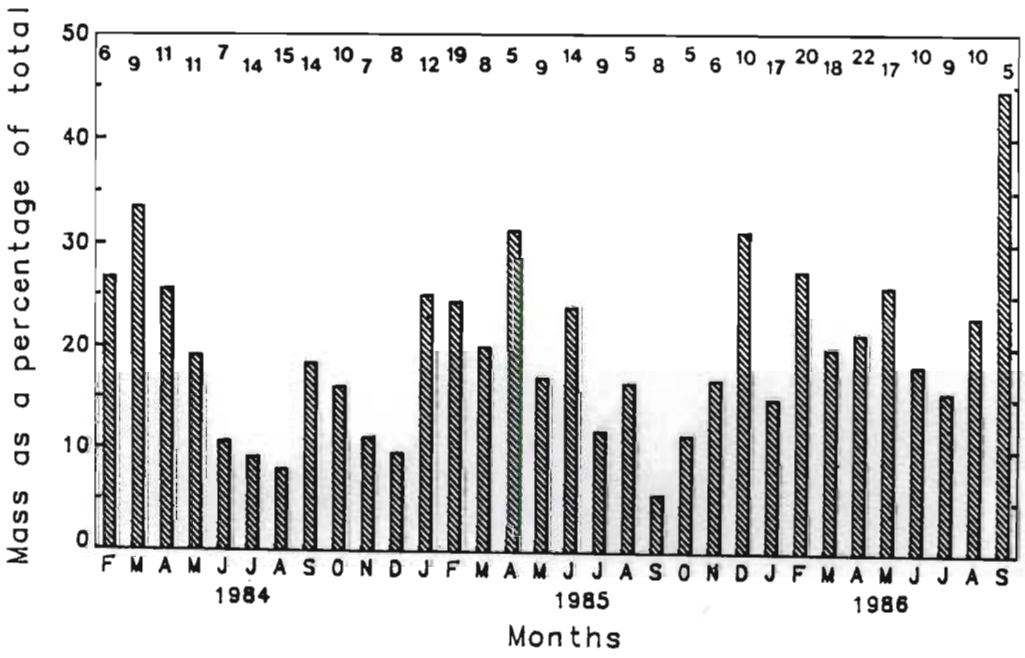

FIGURE 4.12. Crustacea as a percentage of the total mass of food ingested by A. paludinosus each month.

throughout the year compared with the other viverrids (Table 4.2). Nevertheless a CV of 61% does suggest some seasonality (Table 4.2) and, although the mass of frogs eaten in early winter increased, it was not significant (Fig. 4.11). These peaks decreased rapidly and fewer anurans were taken in late winter (August) but increased in the diet apparently after spring rains (October and November; pooled data; $P<0,05$; Figs. 4.11 & 2.5).

Anurans occurred as minor prey for the other viverrids, (Figs. 4.1 - 4.4 & Table 4.2). Mungos ate them infrequently (6% occurrence) but because of their large mass relative to other Mungos prey, amphibians contributed 1% to the overall diet of this carnivore (Table 4.2). Genetta and Herpestes ate amphibians relatively frequently (18,5 & 19,5% occurrence respectively) and they contributed 0,9 and 0,4% respectively to the overall diet of each species (Table 4.2). Frogs and toads were eaten most infrequently by Galerella and, like Herpestes, made up a small portion of the diet (Table 4.2).

No frogs were identified from the scats of Galerella and it was possible to identify only between 30 and 50 percent of the amphibians from Genetta (seven species), Herpestes (two species), Mungos (one species) and Atilax scats (10 species; Table 4.4). Of these Bufo was taken most often (Table 4.4). Ranids were heavily preyed on by Atilax with 5,3% of their amphibian prey belonging to this family (Table 4.4). No other family or species appeared to be preferred by the viverrids but this may have been because relatively few frogs were but this may have been because relatively few frogs were identified.

TABLE 4.4. Frequency of occurrence of Amphibia eaten by the viverrids at VCNR. None were identified from the scats of *Galerella*.

	Atilax	*Herpestes*	*Genetta*	*Mungos*
	n=361	n=44	n=30	n=2
Pipidae				
Xenopus l. laevis	0,8		6,7	
Heleophrynidae				
Heleophryne natalensis	1,1			
Microhylidae	0,6			
Breviceps v. verrucosus	1,1		6,7	
Bufo spp.	16,1	18,2	3,3	50,0
Ranidae	5,3		6,7	
Strongylopus spp.	0,3			
Tomopterna natalensis	0,8		6,7	
Rana spp.	1,9		3,3	
Natalobatrachus bonebergi	0,3			
Hyperolidae				
Afrixalis f. fornasinii	0,3			
Hyperolius spp.	1,4	2,3	6,7	
Unidentified Anura	70,1	79,05	60,0	50,0

Crustacea.

Freshwater crabs (*Potamonautes sidneyi*) were an important secondary prey of *Atilax*, occurring in 70% of the scats and contributing nearly 23% to the total prey mass consumed (Table 4.2). The overall contribution was 16% (Fig. 4.5) making crabs the second most important prey item of *Atilax* (Table 4.2). Crabs were rarely eaten by *Herpestes* and *Genetta* (twice each), only once by *Galerella* and were never recorded in the scats of *Mungos*.

Fewer crabs were eaten by *Atilax* during the cool, dry months (June - August) and most were taken in summer and spring (January - April and December 1985 and September 1986; Fig. 4.12) when temperatures and rainfall were high. However, these differences were not significant (pooled data; $P<0,05$; Fig. 4.12) and the CV was 43% (Table 4.2). Large crabs (>38 g)

were eaten mainly during late summer and early autumn. Crabs contributed little to the winter diet in 1984 possibly reflecting the influences of the recent drought (Fig. 4.12).

Reptilia.

Apart from Herpestes, the overall abundance of reptiles in the diet of the viverrids was less than 1% which was due to a low frequency of occurrence rather than a low mass percent in the diet (Table 4.2; Figs. 4.1 - 4.5).

Reptiles were the second most important prey of Herpestes but, with an overall abundance of about 3% (Fig. 4.1), were considered supplementary prey. Signficantly more reptiles were eaten in November while fewer were taken in April, May, June and September (pooled data; $P<0,05$) and the CV of 91% confirms the irregularity of use of this prey (Table 4.2).

Although unimportant to the overall diet of Galerella, reptiles were also the second most important prey based on mass (Table 4.2; Fig. 4.2). The mass contribution of reptiles to the diet was irregular; more individuals were consumed during January and fewer in May, September and November (pooled data; $P<0,05$). Both Genetta and Atilax showed an increase in reptiles in the diet at the end of winter and early spring and Atilax showed an increase in early autumn ($P<0,05$). Fewer reptiles were taken in July by both species ($P<0,05$). This seasonal utilisation was also indicated by the high CV values (range 127 to 168; Table 4.2). Mungos ate one unidentified reptile.

Viverrids preyed more on snakes than on lizards and five

species of Serpentes were noted in the diet of Herpestes, four in the diet of Galerella and two each for Atilax and Genetta (Table 4.5). Herpestes and Atilax ate brown house snakes (Lamprophis fuliginosus) most frequently while Galerella and Genetta ate southern slug eaters (Duberria l. lutrix) more often than other snake species (Table 4.5).

Genetta, Galerella and Herpestes consumed few lizards but 22% of reptiles eaten by Atilax were lizards including a juvenile water leguaan (V. niloticus; Table 4.5) taken in July 1986. Lizards were captured during late autumn and winter (May - August).

Aves.

The insignificance of birds in the diet of the predators is shown in Figures 4.1 to 4.5 where all plots occurred below the 1% isopleth. Like reptiles, birds were taken infrequently (maximum of 7,6% occurrence for Herpestes; Table 4.2), and contributed little to the diet (maximum of 5% of total mass for Galerella and Atilax (Table 4.2). Birds appeared in the diet of Herpestes and Atilax mainly in the warm months, October to December, compared with the cooler months (May and May to July respectively; $P<0,05$). A similar trend was seen in Galerella and only one bird was recorded in the diet of Mungos, in December. The high coefficients of variation indicated that these prey were taken sporadically(Table 4.2).

Although appearing infrequenty in the diet, a range of bird species was eaten, particularly Passiformes (Table 4.6). Five species being taken by Atilax, four by Herpestes, three were noted in the scats of Galerella and only one in (Genetta)'s

TABLE 4.5 Frequency of occurrence of Reptilia identified in the scats of four species of viverrid at VCNR.

	Herpestes	Galerella	Genetta	Atilax
Number in sample	66	17	14	32
Sauria (Total)	3,0	5,9	7,1	22,1
Scincidae				3,1
Mabuya varia				3,1
Varanidae				
Varanus n. niloticus				3,1
Unidentified Sauria	3,0	5,9	7,1	12,8
Serpentes (Total)	93,8	88,3	92,7	87,5
Colubridae				
Lamprophis fuliginosus	18,2	5,9		12,5
Duberria l. lutrix	6,1	29,4	14,3	
Tribe Aparallactini	1,5	11,8	7,1	
Crotaphopeltis hotamboeia	4,5			6,3
Dasypeltis inornata	4,5			
Viperidae				
Bitis a. arietans		5,9		
Unidentified Serpentes	59,0	35,3	71,3	56,3

TABLE 4.6. Frequency of occurrence of Aves identified in the scats of four species of viverrid at VCNR.

	Herpestes	Galerella	Genetta	Atilax
Number in sample	15	10	3	19
Galliformes				
Phasianidae	13,4	10,0		15,8
Columbiformes				
Columbidae		10,0		5,3
Passeriformes				
Dicruridae				10,5
Oriolidae	6,7			5,3
Corvidae				5,3
Sylviidae	6,7	10,0		
Motacillidae			33,3	
Ploceidae	6,7			
Estrildidae				
Unidentified Aves	66,7	70,0	66,7	57,9

scats (Table 4.6). However, the most consistently eaten birds belonged to the family Phasianidae (francolins and quail; Table 4.6) which are more terrestrial than many other families.

Myriapoda.

Myriapods were an important supplementary prey category for Mungos, occurring in about a third of the scats and contributing nearly 10% to the total mass eaten (Table 4.2). This mongoose did not eat pill millipedes, (Sphaerotherium spp.) while centipedes, (Cormocephalus pseudopunctatus) were taken infrequently and in small quantities; the bulk of the myriapods eaten being Juliform millipedes (Table 4.2). As a result of the low mass of millipedes, myriapods formed a small overall abundance (less than 3,5 %; Fig. 4.5). It was, however, interesting that, for all predators except Mungos, myriapods represented trace prey (Figs. 4.1 - 4.5).

Myriapods were frequently eaten by Atilax but contributed just over 1% to the ingested mass (Table 4.2). In contrast to Mungos, Sphaerotherium spp. accounted for most myriapods eaten by Atilax (Table 4.2) which increased in the diet during November and December and decreased between May and September (pooled data; $P<0,05$; Fig. 4.13). These seasonal trends were confirmed by comparing the CV value (Table 4.2), the mean mass eaten and the monthly distribution of myriapods recorded in the diet (Fig. 4.13). More myriapods were eaten by Atilax in 1986 compared with the previous two years (Fig. 4.13).

Herpestes, Galerella and Genetta (Table 4.2) did not rely on myriapods; the first two predators consuming very few

millipedes (Juliformia) and centipedes (Table 4.2). The small myriapod contribution came from pill millipedes although they occurred irregularly and with low frequency (Table 4.2). This is shown by the very large CV percentages (Table 4.2). In contrast, Genetta ate many centipedes (42% frequency of occurrence) and their mass contribution to the diet nearly equalled that of the much heavier, but infrequently eaten, pill millipedes (Table 4.2).

Arachnida.

Arachnids were trace prey in the diet of all predators, illustrated by an overall importance of less than 0,5% (Figs 4.1 - 4.5; Table 4.2). Scorpions (Opisthocanthus validus) were the most frequently eaten arachnids having a maximum frequency of occurrence of 23% for Genetta, 12% for Atilax, 9% for Galerella and Mungos but only 1,4% for Herpestes (Table 4.2). They contributed 2,7% to the diet mass of Genetta and were the only arachnids eaten by this predator.

The amblypygid, Damon variegatus, occurred in 10% of the scats of Atilax and 3% of Mungos' scats but, due to their low mass, made little contribution to these diets (Table 4.2; Figs. 4.4 - 4.5). Spiders were infrequently eaten (Table 4.2).

Plants.

Plants (including grasses, leaves, bark and fruits) could not be analysed according to mass for obvious reasons. Therefore all plants recovered from scats were expressed as relative bulk percentage (Appendix 1) and not mass percentage. These values are thus not comparable.

Plants appeared in the scats regularly, being most frequently eaten by Genetta (44% occurrence and a relative bulk of 15%; Table 4.2) and occurring in about a third of the scats of Galerella and Atilax (relative bulk of 11 & 7,5% respectively; Table 4.2). Plant material was less important in the diets of Mungos and Herpestes and, although eaten regularly (24% & 19% occurrence respectively), had small relative bulk values (6% & 2% respectively; Table 4.2).

Fruits were the most important plant food for all predators, being eaten from summer through to winter (Table 4.7) as they ripened. Bridelia micrantha was the most important dietary fruit between December and April and was taken by all five viverrids, particularly Genetta and Atilax (Tables 4.7, 4.2), between December and April. Fruits of Phoenix reclinata (wild date palm) and Ficus spp. were eaten in smaller quantities between March and June by all viverrids while Antidesma venosa fruits appeared in the diet of Genetta during winter 1986 (June and July; Table 4.7). A number of unidentified fruits were also recovered from the scats during the period January to July.

Other plants included grass, leaves and bark. The scats of Genetta contained relatively large quantities of undigested green grass (Table 4.7). This differed from the dry, dead grass in the scats of Herpestes and Atilax, which, with dead leaves, were probably ingested accidently during prey capture. Sugar cane was occasionally eaten by Atilax and Herpestes while bark periodically occurred in the diet of the former species.

TABLE 4.7. Plants eaten by four species of viverrid at VCNR. B= *Bridelia micrantha*, P= *Phoenix reclinata*, F= *Ficus* spp., A= *Antidesma venosa*, S= *Solanum*, G= grass, C= cane, R= Rubiaceae and ?= unidentified fruit.

		Herpestes	Galerella	Genetta	Atilax
1984	Mar				B G
	Apr	G			G
	May	G			G
	Jun	G	?	G	PCG
	Jul	G			P
	Aug	G			C G
	Sep	G			G
	Oct	G			
	Nov	G			
	Dec		?		B
1985	Jan				R
	Feb	B G	B		BR?G
	Mar	G			BPFG
	Apr	G		B	B G
	May	P G			G ?
	Jun	G	?		PRCG
	Jul				C G
	Aug	C		B G	G
	Sep	G			G ?
	Oct				G ?
	Nov				
	Dec				
1986	Jan				B
	Feb			B G	B C
	Mar			BG?	B G
	Apr		F ?	BGP?	
	May			GP?	F ?
	Jun	SG?	?	A G	G ?
	Jul		?	A G	
	Aug			G	
	Sep		F ?		G ?

Seasonality

Seasonal variation in prey selectivity has been mentioned in the previous section and indicated in Figures 4.6 to 4.13. Further quantification of monthly differences of primary and secondary prey in the viverrid diets were tested using the relative variance of the percentage mass of prey eaten (Fig. 4.14). Because of the small sample, monthly diet analysis could not be calculated for Mungos. Mammals and insects showed least variation in the diet of Herpestes and Atilax (Fig. 4.14).

Overall, relative variance values were low for Atilax (Fig. 4.14) suggesting minimal seasonal feeding behaviour and fairly constant exploitation of major prey throughout the year. Values were also low for Herpestes except for reptiles, indirectly supporting the claim that they were eaten irregularly. Relative variance was higher for Galerella and highest for Genetta (Fig. 4.14) suggesting either less selective feeding behaviour or opportunistic exploitation of prey.

Examination of the monthly diet diversity indices revealed no significant differences between observed values and those expected if feeding were totally uniform. Thus, the viverrids did not appear to become more or less selective during different months of the year suggesting that food may not have been a limiting resource in the reserve (see Appendix 4). Herpestes, which preferred mainly rodents, had the lowest overall diet diversity followed by Genetta, Galerella and lastly Atilax.

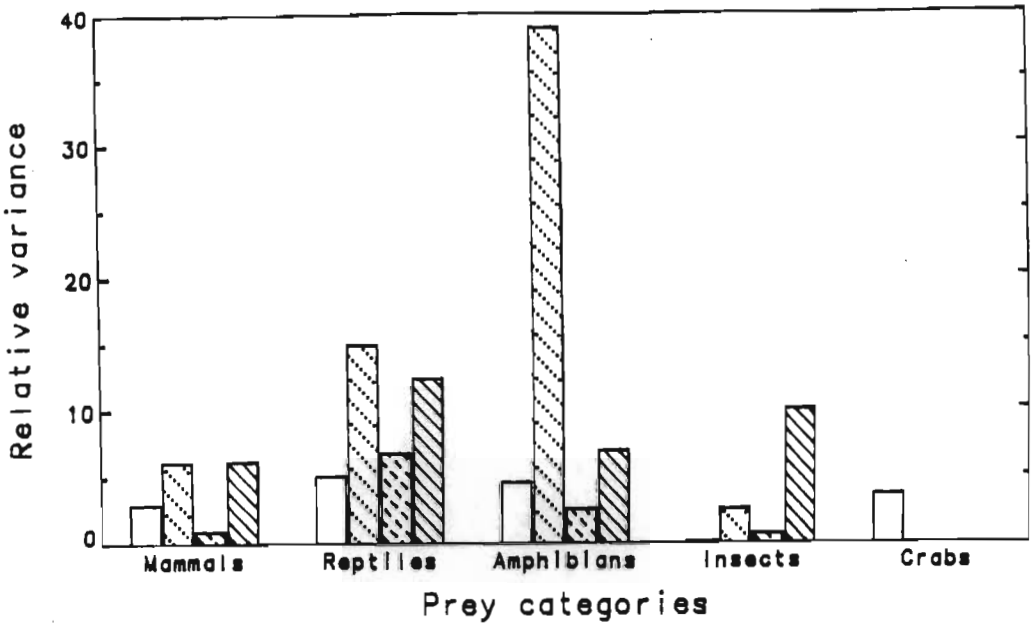

FIGURE 4.14. Relative variance in the monthly (bimonthly) mass of the main prey categories in the diet of four species of viverrid at VCNR. See text for details. Because of the small sample Mungos was omitted. =Atilax, =Genetta, =Herpestes and =Galerella.

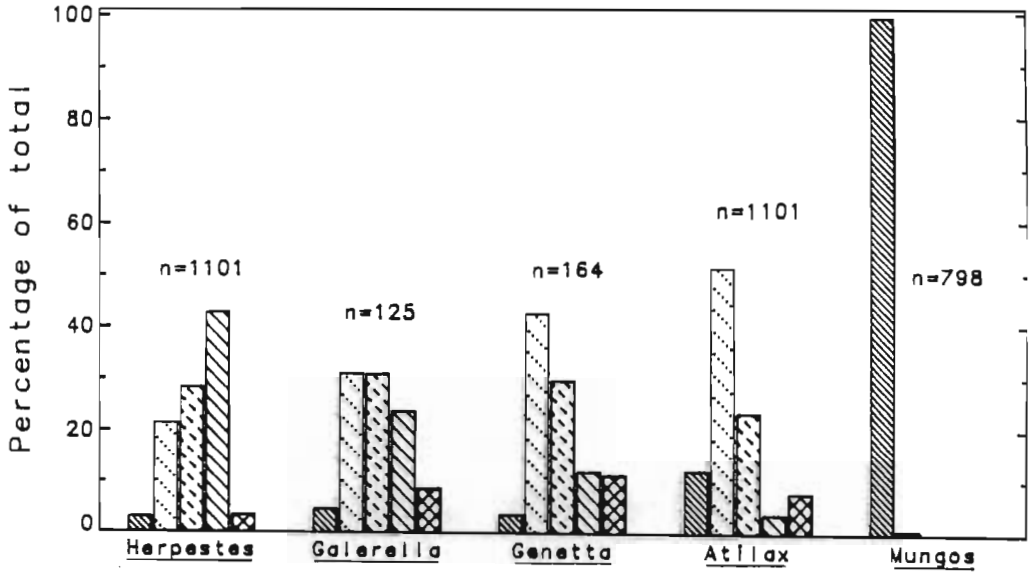

FIGURE 4.15. The size distribution of prey in the diets of five species of viverrid at VCNR. =<5g, =5-24,9g, =25-79,9g, =80-200g and = >200g.

Results of the monthly, intraspecific dietary comparisons (CATMOD), were not clear. Herpestes showed some evidence of seasonal feeding in that no differences were noted among the April, May, June and July 1984 diets; the March, April and May 1985 diets and the May and June, and July and August 1986 diets (autumn and winter; chi-square range 0,67 to 3,95; P<0,33). No differences were seen in the January and Febuary 1985 diets (chi-square=3,2; P<0,67). All other differences were significant (P<0,001). Comparison of Atilax diet, for all months, was also significantly different (P<0,001); possibly a result of the wider dietary selectivity exhibited by this species (Table 4.2).

The results for Genetta and Galerella appeared to be influenced by the 1984 and 1985 bimonthly groupings. No significant differences between bimonthly diets were found for either species (P<0,04) but differences were significant when the monthly data were compared (P<0,001). It was difficult to draw conclusions from these data.

Prey size selectivity

There was no significant correlation between the mass of the viverrids and the mass of their primary and secondary prey (n=4; rs=0,75; P>0,2). This result was influenced by the small sample size (which required perfect correlation to show significance), selection of large prey by the smallest viverrid (Galerella) and selection of small prey by the second largest viverrid (Atilax Fig. 4.15). In addition, viverrids ate a range of different prey sizes making it difficult to estimate the mean prey size eaten. Nevertheless, the

viverrids selected significantly different sized prey (below).

The frequency distribution of different sized prey in the diets of the five species of viverrid is shown in Figure 4.15. Comparisons revealed that nine of the possible ten species pairs preyed on significantly different sized prey from each other (chi-square between 35,2 and 1 321,2;, P<0,001). Only Galerella and Genetta ate similar size prey (chi-square 8,9; P>0,05). Both predators selected small items (5-79,9 g) but ate few prey weighing less than 5 grams (Fig. 4.15). Surprisingly, the smaller Galerella ate more prey in the 80 to 200 g division (mainly Otomys spp.) than did Genetta (Fig. 4.15). Genetta selected mainly small mammals although the numbers of the largest (>200 g) and second largest prey eaten were equal (Fig. 4.15). Galerella, on the other hand, although eating small mammals, showed a slight preference for intermediate sized prey (Fig. 4.15). However, these differences were not significant.

Herpestes concentrated on prey weighing between 80 and 200 g, taking decreasing amounts of smaller prey (Fig. 4.15). Otomys accounted for 90% of the prey in the 80-200 g class and small mammals also accounted for much of the lighter prey (Fig. 4.15). Few prey less than 5 g or greater than 200 g featured in the diet of Herpestes (Fig. 4.15). Thus, in contrast to Galerella, which had a more uniform prey size distribution, Herpestes selected prey in the 80 to 200 g range (Fig. 4.15b).

Atilax ate mainly small prey (5-24,9 g; Fig. 4.15) reflecting selection for crabs and frogs, which fell in this size

category. Differences in prey size selection were noted between this species and the similarly sized Genetta (Fig. 3.2; chi-square=98,0; P<0,001).

DISCUSSION

In this discussion two main points are made. First, seasonal occurrence of prey in the diet is evaluated to facilitate comparison with prey availability (Chap. 5) and calculation of overlap indices (Hurlbert 1978; Petraitis 1979; Abrams 1980; Feinsinger et al. 1981). Second, dietary differences and similarities among the viverrids are examined to determine if niche segregation could be achieved by differences along the trophic resource axis (Schoener 1974a) i.e. Hypothesis I (Chap. 1). This hypothesis will be reappraised in Chapter 5.

Seasonality

Seasonality in prey utilisation was divided into three groups: irregular, markedly seasonal and weakly seasonal. "Irregular" referred to categories taken in such low quantities that seasonal trends were not apparent and included trace items like birds and reptiles, which were probably taken opportunistically. "Markedly seasonal" referred to prey that were absent from the diet during certain months and served as additional, supplementary food when available, for example, pill millipedes which were not eaten by Atilax during autumn or winter. "Weakly seasonal" were those prey that were eaten year round but declined slightly in the diet during some months (usually the cooler months - April to September). This group represented the important categories; rodents, crabs and frogs.

Seasonal differences in prey selection were therefore evident, usually in the form of a decline during winter and increase in summer but these were not always statistically obvious. Obvious changes were perhaps the autumnal/winter decrease in rodents and concurrent increase in larger mammals and shrews in the diets of Herpestes, Galerella and Genetta and the decrease of frogs and crabs in the diet of Atilax. Atilax preyed more on rodents during winter but ate shrews in summer suggesting a different feeding strategy to the small mammal guild. These changes in the primary prey were however, small, sometimes not significant and never altered the status of the prey. An investigation of prey abundance is necessary to further elucidate the feeding strategies of the viverrid assemblage (see Chap. 5).

Trophic segregation

Since food is important to satisfy daily energy requirements and, ultimately, to convert into offspring, feeding can be maximised by natural selection (Schoener 1971). Hence, strong selective pressure to forage efficiently can be envisaged. Perhaps because efficient feeding is adaptive (Schoener 1971), a variety of different feeding strategies have evolved (Rosenzweig 1966; Schoener 1971; Gorman 1979). Coexistence may be achieved because different prey are available to carnivores using different hunting strategies or hunting sets (Canids that run down their prey or Felids that stalk it, are examples of different hunting sets; Rosenzweig 1966).

Despite regional differences in viverrid diets, due to different prey availability (Rautenbach 1982; Smithers 1983;

MacDonald & Nel 1986), certain trends are typical (Chap. 5; Stuart 1981; Sadie 1983; Smithers 1983; Baker 1987c, 1988a) implying basic, species-specific feeding strategies. When different species with the same hunting set are sympatric, other factors such as body size or more subtle differences, may facilitate coexistence (Rosenzweig 1966; Simms 1979). The extent to which viverrids at VCNR segregate along the trophic niche will now be examined.

Diets are compared by reviewing the feeding biology of each predator separately. Factors which affect overlap, such as prey taxon, prey size, viverrid social structure and foraging behaviour (Rosenzweig 1966; Rautenbach & Nel 1978; Simms 1979) are used to stress differences and similarities. Two of the five species, Mungos and Atilax, have unique diets and it is unlikely that there is much overlap between these two and any other sympatric viverrid. However, striking similarities were noted in the diets of Genetta, Galerella and Herpestes which formed the small mammal guild (see Root 1967). As suggested by Rosenzweig (1966), more subtle differences must be sought in order to separate these three species (Rautenbach & Nel 1978; Simms 1979). Interspecific differences are always present (Pianka 1983) but ecologically meaningless differences must be distinguished from the meaningful ones.

If predator mass and prey mass are positively correlated, differences in the size of sympatric predators facilitates coexistence (Rosenzweig 1966; Wilson 1975; Jaksic et al. 1981; Bekoff et al. 1984). The lack of a significant correlation between viverrids and their prey probably resulted from the relatively small size range of the viverrid

assemblage. These viverrids would fit into the smallest size class of above-mentioned studies (Tables 3.1 & 3.2). It therefore appears, that to find correlations, large size differences among the predators are required (Schoener 1986).

In any case, it appears that influences other than morphology affected prey size selectivity. Most prey in the 80 to 200 g class were Otomys spp. suggesting that these rodents were selected. Predation on small animals by Mungos may be because there were insufficient small vertebrates to support a social species (Waser 1981; Sadie 1983). Nevertheless, although there was no size related correlations between the predators and their prey, significant differences in prey size selected by the predators were noted and may aid resource partitioning and facilitate coexistence (Chap. 7).

1. Mungos.

Mungos, in contrast to the other viverrids, specialise in the capture of slow-moving, terrestrial, semi-fossorial or fossorial (invertebrate) prey (Neal 1970; Rood 1975; Sadie 1983) for which their dentition (Petter 1969; Smithers 1983) and limb structure (Taylor 1974, 1979) are well adapted. This selectivity has been attributed to social groups not finding enough vertebrates to feed all members (Rood 1975; Waser 1981) and/or group life interfering with predation (Ewer 1973; Baker 1987c). Similar interference has been reported for waders feeding on invertebrates (Goss-Custard 1970) and planktonivorous fish (Leong & O´Connell 1969).

Groups of Mungos alleviate this problem by spreading out and moving slowly, individuals hunting alone by digging, scraping

and turning over stones, logs and other debris (Rood 1975; Rautenbach 1982; Sadie 1983) particularly droppings of large herbivores which attract various insects (Neal 1970). This unique foraging technique facilitates the capture of small invertebrate prey (Rasa pers. comm.[1]) and is suited to the social structure of this species (Sadie 1983). Thus, foraging strategy and diet selection, including soft-bodied, unpalatable and fossorial prey (Sadie 1983), which results from the social structure of this viverrid, effectively separates Mungos from other sympatric viverrids.

2. Atilax.

Trophic niche separation was achieved by the water mongoose because of its preference for aquatic prey (Rowe-Rowe 1977; Whitfield & Blaber 1980; Smithers 1983; Louw & Nel 1986; MacDonald & Nel 1986; Baker 1987c, 1988a), a resource not exploited by the other viverrids. Selection for aquatic prey was reflected in the size of prey which differed from other viverrids. Differences were also apparent in the pattern of predation on mammals - the primary viverrid food. For example, Atilax ate many dassies, cane rats and duikers but few intermediate-sized mammals, which were preferred by other predators. Further, Atilax took shrews in summer and rodents in winter, while the reverse situation applied to the other viverrids.

These differences indicated that the water mongoose also, had a unique foraging strategy (Rowe-Rowe 1977). Unlike other

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1. Rasa, A. MRI, University of Pretoria

viverrids, Atilax hunts in shallow water (Chap. 6) "feeling" under stones and in burrows for prey (Rowe-Rowe 1977; Smithers 1983; Baker 1988a; Maddock unpubl. data). The specialised adaptations for this strategy have been indicated by Radinsky (1975) who suggests that tactile sensitivity and muscular control are well developed in this species. Atilax also possesses the broad skull and crushing dentition (Chap. 2), necessary for dealing with hard bodied prey and Baker (1987c, 1988a) states that these prey are more easily caught by a solitary, rather than a social, species. The importance of mammals and birds in the diet indicate terrestrial habits as well (Rowe-Rowe 1977; Smithers 1983; MacDonald & Nel 1986; Baker 1987; present study).

That the unique diet of Atilax reduces interspecific competition has been recorded: MacDonald & Nel (1986) found little dietary overlap with three sympatric carnivores in the Cape while Rowe-Rowe (1977) showed that this mongoose had different food preferences from two species of sympatric lutrines in Natal. Thus, the broad diet, including a number of prey unique to this species, separates this carnivore from other sympatric viverrids at VCNR.

3. Herpestes.

Foraging behaviour of Herpestes is well suited to capturing fast-moving, terrestrial, vertebrate prey and this species differs from the two previously mentioned by moving rapidly (Taylor 1970), pouncing and chasing prey (Rasa pers. comm.). Many researchers have found that vertebrates, mainly mammals, were the major prey of Herpestes (Delibes 1976; Stuart 1983;

Smithers 1983; Delibes *et al.* 1984), the last authors suggesting that *Herpestes* always took its preferred prey when available - a conclusion supported by this study.

But the data are not consistent with the statement by Delibes and co-workers (1984) that *Herpestes* is opportunistic. Rodents, particularly *Otomys* spp., had far greater overall importance in the diet of *Herpestes* than any prey in the diet of the other viverrids and the finding that over 90% of the scats had mammal remains, demonstrates selection reminiscent of a specialist. This species differed from other sympatric viverrids, including those of the small mammal guild, by its selection for rodents, predominantly *Otomys* spp. It appears that *Herpestes* exhibits more selector than opportunist traits. I develop this idea in Chapter 5 and propose a new feeding strategy that may also be characteristic of *Atilax* and *Mungos* and perhaps other small carnivores.

4. *Galerella*.

Nearly 98% of the diet biomass of *Galerella* comprised vertebrates; a finding consistent with many other workers (Roberts 1951; Smithers 1971; Rood & Waser 1978; Stuart 1981; Rautenbach 1982; Sadie 1983; Appendix 1). However, feeding behaviour differed from *Herpestes* in that selection for rodent prey was less marked and a wider range of mammals was taken, although both preferred *Otomys* spp. The mass contribution of mammals was similar in the diet of both species but mammals were eaten far more frequently by *Herpestes* and prey size selectivity differences were also apparent (Rosenzweig 1966). *Galerella* appeared less selective than *Herpestes*.

5. Genetta.

In many ways, the diet of Genetta reflected its occurrence in forest habitats (Chap. 6; Smithers 1983) and although similar to that of Galerella, some differences were apparent. These include greater dependence on invertebrates (Orthoptera, Arachnida and Myriapoda) and amphibians. Invertebrates accounted for more than 5% of the diet biomass, a figure exceeded only by Mungos. Surprisingly, few birds were eaten by Genetta but its ability to hunt arboreal prey is shown by the presence of Graphiuris murinus in the diet. No other viverrid ate this rodent which rarely comes down to the ground (Chap. 5).

Dietary differences between Genetta and Herpestes include selection of different sized prey with Genetta relying less on mammals and eating fewer Otomys spp. and reptiles. Like Galerella, Genetta appears to have a more opportunistic diet than the other three viverrids.

Although dietary differences were apparent among Genetta, Galerella and Herpestes, these species ate similar foods, particularly Genetta and Galerella, and Galerella and Herpestes. Even so, extensive trophic overlap can be tolerated if food is not limiting and the similar diversity indices for each month suggest that food was not a limiting resource. Genetta and Galerella had the least specialised diet and it is possible that, as a result, they could tolerate greater overlap, particularly if food was abundant (Chap. 5). This is certainly a different strategy to that exhibited by the other three carnivores which had unique diets. Nevertheless, a

simple quantification of dietary differences may not necessarily translate into realistic ecological differences. Segregation of these species is not clear-cut and will be reconsidered in Chapters 5, 6 and 7.

These dietary profiles invite more detailed examination of the idea that viverrids are opportunistic (Ewer 1983; Smithers 1983; Delibes et al. 1984). But it is inappropriate to attribute selector or opportunistic habits until an idea of prey availability is obtained and this is the subject of the next chapter.

Summary and Conclusion.

The compression hypothesis predicts that, if food abundance decreases, so should food selectivity (MacArthur & Wilson 1967; Schoener 1974b, 1986). This was true for Herpestes which ate a broader range of prey during 1984 when Otomys spp. numbers were low compared with 1985 and 1986 (Chap. 5). Similarly, but for different reasons, when a competitor reduces prey populations, diet should remain the same or include more items although habitats should diverge (MacArthur & Wilson 1967; Schoener 1974b, 1986; Chap. 5). Although extremely difficult to determine and fraught with problems, a possibility is that the highly predacious Galerella (Ewer 1973; Rautenbach & Nel 1978) increased its diet breadth due to overlap with Herpestes.

In general, the initial data support Hypothesis I that these species segregated along the trophic niche. Segregation resulted from the unique diets of Atilax and Mungos while prey size selectivity differences and selection of different prey

species appeared important in partially segregating the diets of the small mammal guild. Other differences (temporal and spatial) are considered in Chapters 6 and 7. Further, the contrast between the insectivorous diet of the social Mungos and the vertebrate diet of the solitary species was marked (Gorman 1979; Waser 1981).

But the monthly diversity indices suggest that food is not limiting (see Appendix 4) and, therefore, partitioning along the trophic niche may not be important in segregating these species. However, this may be a result of resource partitioning. (During 1984, there was evidence of Otomys spp. being scarce and perhaps then trophic segregation was important; Wiens 1977). These factors and that of dietary segregation resulting from the different diel activities of the viverrids and their prey are examined in Chapter 7.

CHAPTER 5

PREY ABUNDANCE

INTRODUCTION

In a detailed examination of feeding ecology, it is insufficient merely to quantify foods eaten. Much greater understanding of the factors governing feeding ecology can be obtained if there is some quantification of prey availability (King 1980a; Wise et al. 1981; Swift, Racey & Avery 1985). To detect prey abundance and whether the foods eaten by viverrids underwent temporal fluctuations, either seasonally or over longer periods, regular sampling of the prey populations in various habitats was carried out. Prey habitat associations, derived from these data, are considered together with the predator habitat preferences in Chapter 6.

Information on prey abundance, when compared with the results of the scat analysis (Chap. 4), aids interpretation of the feeding strategies of viverrids and enables the calculation of trophic overlap and niche breadth values which take prey availability into account (Petraitis 1979; Johnson 1980; Feinsinger et al. 1981). Further, selector or opportunist feeding behaviour (see Rosenzweig 1986) can be determined only if there is some idea of prey abundance. As a more realistic idea of the ecology of an animal should be realised if there is an understanding of resource use and resource availability, the primary aim of this chapter is to quantify seasonal abundance of viverrid prey as revealed by trapping.

Relative methods were particularly suited to the aims of this study (Appendix 2) and were used to produce indices of population abundance. The reasons for this decision and justification of the methods used are detailed in Appendix 2. To give a more realistic understanding of prey abundance and to verify the indices, absolute estimations were carried out once the major viverrid prey were known (Chap. 4). Assumptions of the absolute abundance models are also tested in Appendix 2.

Abundance and seasonal fluctuations of viverrid prey were estimated between July 1984 and September 1986. General array trapping was conducted at six sites on a monthly basis while small mammal trapping at six sites was conducted every three months. Other areas were sampled to indicate spatial variability in prey numbers in the reserve. This trapping programme and the results are described in this chapter.

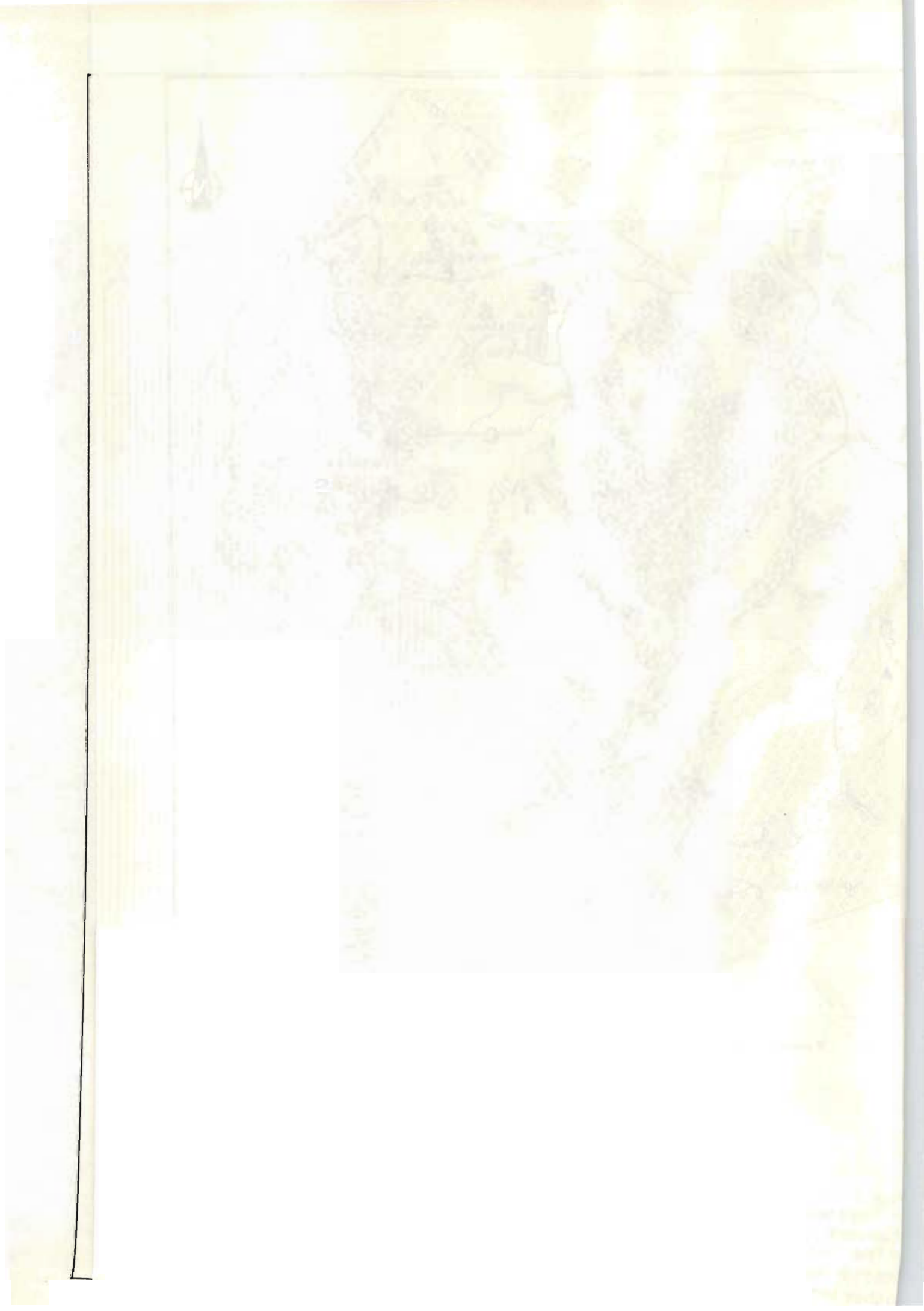
MATERIALS AND METHODS.

Trap site locations were selected by identifying, a priori, those areas within the major habitat types most likely to be used by viverrids. The viverrid spatial analyses were also largely based on these habitat types which comprised a mosaic of small units (Fig 5.1; Sandwith & Brown 1981).

Relative estimations.

1. Pitfall and array traps

Bucket pitfall traps (PFTs) were used in this study between July and October 1984. Three buckets (7,5 l capacity; 74,4 cm



circumference), set 15 m apart, with their rims 1 cm below ground level, were set in four different habitats (secondary grassland, grassland, riverine forest and riverine forest/grassland margin; Fig. 5.1).

Between October 1984 and February 1985 bucket PFTs were replaced by more efficient array traps, comprising PFTs, drift fences and funnel traps (Campbell & Christman 1982). Array traps caught a wide range of animals and were easy to maintain and use. Four 5,4 m X 60 cm 26-gauge galvanised iron drift fences were arranged in a cross with a 5,4 X 5,4 m open area in the centre (Fig. 5.2). Cylindrical, aluminium mosquito netting funnel traps (90 X 10 cm) were placed flush against either side and in the middle of the four drift fences (Fig. 5.2) with soil, leaves and grass placed in their entrances to allow easy access for small animals. Buckets (7,5 l capacity; 74,4 cm circumference), buried at each of the eight ends of the drift fences, formed the PFTs (Fig. 5.2). Johnson (1987; p 91) has provided details of trap construction.

Array traps were set in Idiphini and Nkwashizela grasslands and along two streams that passed through these habitats (Fig. 5.1). Arrays were also set in Idiphini forest/grassland margin and Mtakathati forest clearing (Fig. 5.1).

Both the bucket PFTs and the array traps were operational for 8-10 trap-nights each month and were checked daily (throughout this study one trap-night (TN) represents the continuous 24 hr period when a trap was operational; Rowe-Rowe & Meester 1982). Animals were identified, counted and their size determined as described in Appendix 1, prior to their release at the point

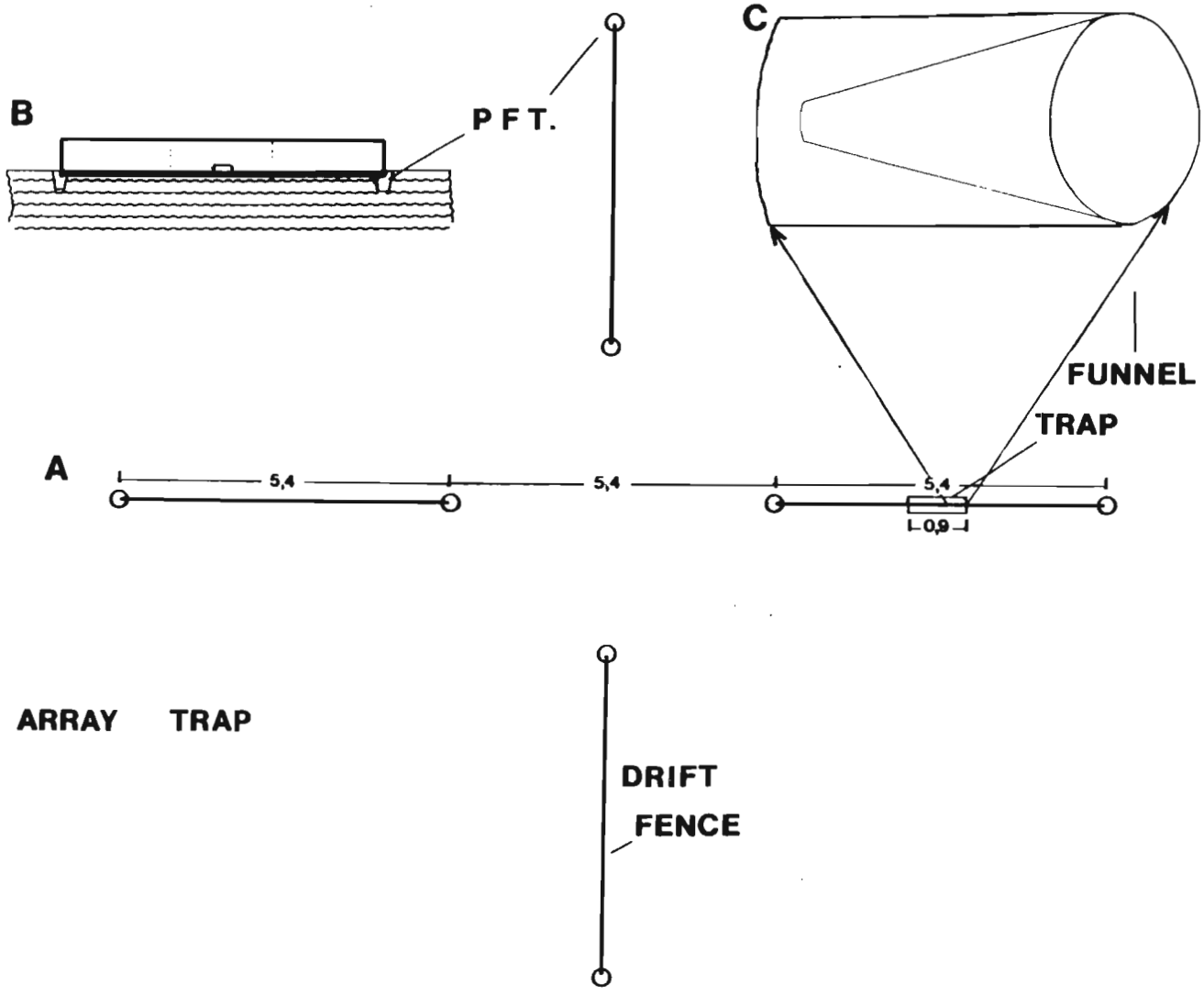


FIGURE 5.2. Views of the general array trap. A. Plan view showing distances in metres. B. Side view showing bucket Pitfall Traps (PFT), drift fence and funnel trap. C. End view of a funnel trap.

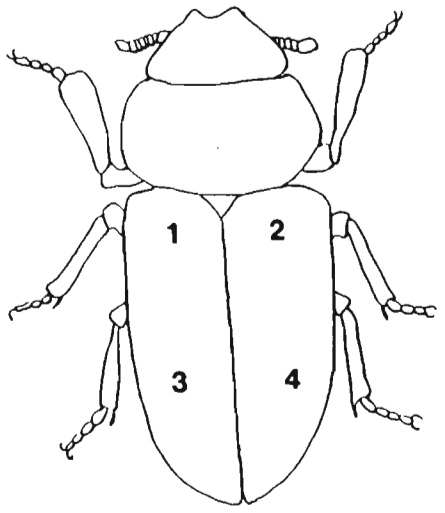
of capture. Dead animals were used in the reference collection (Chap. 4). Raw data were corrected for differences in the number of traps set per month and log transformed to reduce stochastic variation and to facilitate data presentation (Thomas & Sleeper 1977).

During 1986 trapped animals were marked with typists' correcting fluid or nail varnish (Hanrahan & Yeaton in press; Fig. 5.3) and subjected to Capture-Mark-Recapture (CMR) analysis. Since recaptures were few, all prey categories were pooled and data analysed by the weighted mean model (Begon 1979).

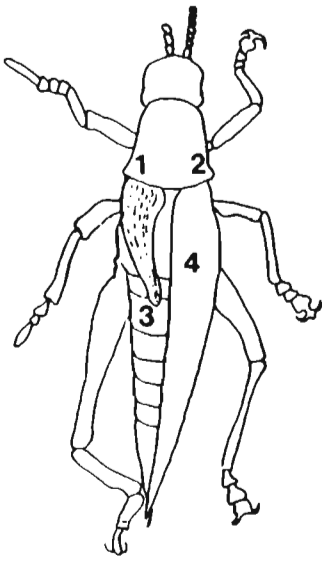
2. Small mammal live traps

Array traps were inefficient at capturing certain small mammal species and, since small mammals formed a major part of the diet of viverrids (Chap. 4), more accurate censusing was required. Consequently, Linn's trapline method (1963) with a number of modifications, was employed. Much controversy exists over the best methods for small mammal trapping therefore the reasons for using Linn's method (1963) and the modifications are explained in Appendix 2.

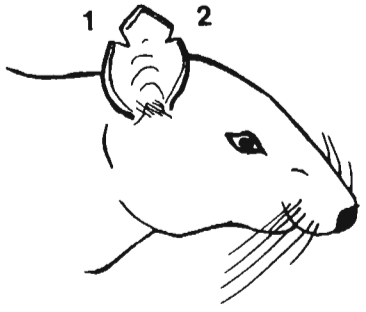
Trapping methodology was standardised as far as possible (Southern 1973): PVC live traps (280 X 60 X 60 mm; Willan 1979), baited with rolled oats and peanut butter or raisins and oats,were used (Appendix 2). Two days prebaiting preceded CMR which was continued for three days. Twenty trap stations, spaced linearly at 15 m intervals, with three traps per station, yielded 180 TN during each three-day session. Three traps per station (i.e. 180 TN) were adequate (see Appendix 2)



A/ COLEOPTERA

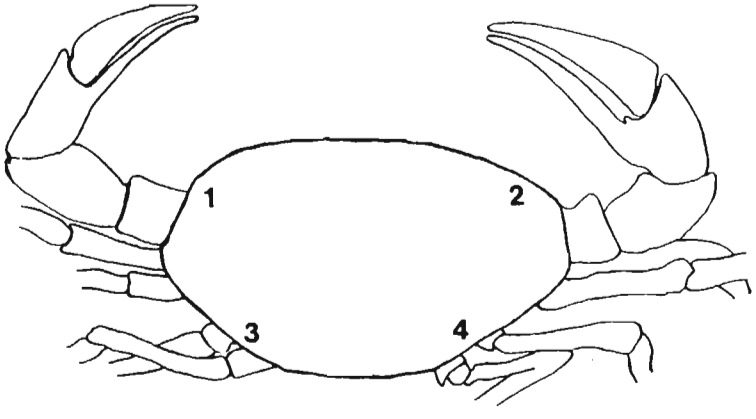


B/ ORTHOPTERA



C/ SMALL MAMMALS

D/ AMPHIBIA



E/ CRUSTACEA

FIGURE 5.3. Marking of the different prey. Numbers represent the day on which the animal was caught. When trapping was continued for more than four days, different colours were used to distinguish days one to four, five to eight or nine to twelve.

except for the forest habitats. Captures in the forest were consistently low so, after one year, the number of traps per station was reduced from three to one (i.e. 60 TN not 180).

Traps were checked each morning and animals released at the point of capture after being identified, weighed, sexed and their reproductive condition noted (Twigg 1975). Earnotching was used to mark animals (Fig. 5.3; Southern 1973) as individual marks were not required.

At least every three months, straight traplines, except in the vlei where the habitat prevented this, were set in six habitats; grassland, secondary grassland, riverine forest, riverine forest/grassland margin, vlei and a sugar cane plantation bordering the reserve (Fig. 5.1). These habitats were considered homogeneous and represented the major trap sites. During each trapping session an additional area was sampled to provide information from different habitats or to duplicate one of the major trap sites.

Absolute estimations.

Once it was ascertained that small mammals, crabs, frogs, Orthoptera and Coleoptera were important prey (Chap. 4), their absolute abundance was assessed. Selection of absolute abundance models is detailed in Appendix 2.

1. Small mammals.

Absolute numbers were estimated on an 8 X 8 grid, with two PVC traps per station and 10 m between stations. A small grid was necessary to ensure it remained a sufficient distance from adjoining habitats. Grids were set in Mthakathi grassland

and vlei, previously used for trap lines (Fig. 5.1) because the main rodent prey (Chap. 4), occurred in these habitats (Chap. 6). Other than trap number and spacing, methodology was identical to that of the trap lines and trapping was conducted in January, July and September 1986.

2. Crabs.

Crabs were collected along a 50 m stretch of stream within riverine or streambank forests (areas preferred by Atilax; Chap. 6; Fig. 5.1) during December 1985, January, July and September 1986. Collection attempts at the dam in Edamini Enkulu were unsuccessful. Animals were caught by dangling meat tied to string into the water (Raubenheimer 1986; 10 pieces per 50 m of stream), marked with nail varnish and released (Fig. 5.3). This method was unsuccessful at night as torchlight disturbed the crabs and trapping was conducted daily for four days between 17h00 and 18h30, one of the main activity periods of the crab (Raubenheimer 1986). In September 1986, more intensive sampling was carried out and two sites in the riverine and two in the streambank forests were sampled.

3. Orthoptera.

Sweep sampling was conducted in a 20 X 20 m grassland quadrat, set in Nkwashizela (Fig. 5.1). The quadrat was subdivided into 15 sampling strips. While traversing these strips, sampling was done with an American net (handle length 90 cm; net diameter 30 cm and net depth 52 cm) and duplicating strokes every metre. Throughout, care was taken to use the same stroke each time. After completion of each strip the net was checked and captives identified, marked (Fig. 5.3) and

released on the quadrat. The procedure was repeated four times with a five-minute break between each repetition (totalling 2 400 sweeps). As with other methods, sweep sampling was continued for four days during January, July and September 1986.

In September 1986, more intensive sampling was carried out and two quadrats at Nkwashizela and two near Edamini Enkulu were sampled simultaneously (Fig. 5.1). In addition, both Nkwashizela quadrats were sampled at night to quantify temporal distribution of prey.

4. Coleoptera.

An 8 X 8 grid of tin PFTs (23,4 cm circumference), spaced 1 m apart, was used for trapping beetles. Grids, set in Nkwashizela grassland and Mthakathi forest clearing during December 1985, July and September 1986 (Fig. 5.1), were checked daily for nine or ten days. Marking is shown in Figure 5.3.

5. Anurans.

A labour intensive, search and seize method (Vogt & Hine 1982), conducted in a 40 X 45 m quadrat along the Nkwashizela stream (Fig. 5.1), was sampled by eight people moving abreast. The stream and each bank were separately and systematically searched for frogs which were identified, marked with cotton leg ties (Fig. 5.3) and released. Sampling was conducted twice a day (beginning at 08h00 and again at 20h00) for three days. Since a large amount of manpower was required for this exercise it was conducted only during September 1986.

Analysis.

The weighted mean, Fisher-Ford, Hayne's and Moran's removal methods (Southwood 1978; Begon 1979; Appendix 2) were used to estimate absolute numbers. Small mammal sample sizes were larger and populations were estimated using Bailey's triple catch (Begon 1979), Jolly's stochastic (1965) and Hayne's removal methods. No Coleoptera were recaptured in the PFT grid so estimates were given as the minimum number caught i.e. an underestimate. In all cases, the calculated population sizes were compared with the number of animals caught.

Prey size and mass were determined as outlined in Appendix 1. During each trapping session, total captures of different prey categories and their sizes (see Table A1.1) were summed and multiplied by the relevant mass (Chap. 4) giving the total biomass caught. A comparison between prey abundance and biomass was made and relative data are presented as the number of prey caught per 10 trap-nights (arrays) or per 100 trap-nights (PVCs). Absolute data are presented as the abundance (or biomass) per hectare.

An attempt was made to combine the results of the array and PVC trapping using correction factors. This resulted in an unwieldy and highly subjective data set so it was decided to present the data as two separate entities to maintain objectivity.

Seasonality

The 22 months of array trap results, after being corrected for number of traps set, were pooled and a mean prey mass

determined for each of the 12 months of the year (Chap. 4). These data were checked for significant differences using chi-square or Kolmogorov-Smirnov tests, as were the scat data (Chap. 4) and, if significant, were subjected to Bonferroni's analysis (Neu et al. 1974; Appendix 3).

To facilitate comparisons, a similar level of taxonomic accuracy, as achieved in the analysis of scats (Chap. 4), was required for the prey abundance data. As occurred in the scat analysis, the level of taxonomic identification varied among the prey animals so the term "category" (Chap. 4) was maintained when referring to particular prey or group of prey. Despite its taxonomic inadequacy, this system facilitated the main aim which was to compare prey eaten and prey available. Also, trapping results are presented in the same way as for the diets (Figs. 4.1 - 4.5; Table 4.2) - indicating how often the categories were encountered and the relative contribution of that prey to overall biomass (Chap. 4; Appendix 1).

RESULTS.

The 913 array trap-nights (TN) yielded 11 209 individuals and, in 12 374 small mammal (PVC) trap-nights, 1 102 individual rodents and shrews (small mammals) were caught. (Notes on the status of the vertebrates, individual species descriptions and some of the identification problems are given in Maddock & Zaloumis 1987). These results are summarised in Table 5.1 and are presented in the same way as the feeding results (Table 4.2) and can be directly compared. There were no significant correlations between frequency of occurrence of prey in the traps and in the diet of the five viverrid species (Spearman´s rank correlation; n=11; rs range 0,46 to 0,59), nor between prey biomass and mass contribution of prey to the diet of the viverrids (n=11; rs range 0,25 to 0,58). Atilax was an exception an showed a significant correlation with respect to prey mass in the diet and in the traps (n=11; rs=0,84; P<0,002).

Of importance was the finding that all prey categories identified in the scats, except birds and large mammals, were trapped (Table 5.1). Collectors´ accumulative curves for the six array trap sites and the six major small mammal trap lines (Fig. 5.4) formed asymptotes, suggesting that representatives of each prey category, in each habitat, were collected. Some animals were, however, not easily trapped (centipedes, scorpions, amblypygids, various insects; Table 5.1) and, consequently, may have been more abundant than indicated (Appendix 2). Furthermore, the array and PVC traps clearly differed in their ability to capture small mammals; lighter mammals (< 15 g) being relatively common in the array traps

TABLE 5.1. Total relative prey abundance and biomass determined by trapping and presented as were the scat analysis results (Table 4.2) thereby facilitating direct comparisons.

	Array traps		PVC traps	
	% occurence	mass %	% occurrence	mass %
Mammalia (total)	2,6	21,3		
R. pumilio	0,1	4,2	42,5	43,7
M. natalensis	0,05	1,0	38,3	37,8
Shrews	1,3	10,6	6,7	3,2
L. rosalia	0,0		6,2	8,5
M. minutoides	0,2	1,3	3,1	0,5
Otomys spp.	0,02	1,0	1,6	4,4
A. chrysophilus	0,0		0,8	1,1
D. incomtus	0,0		0,4	0,9
Dendromys spp.	0,4	1,9	0,3	0,06
S. infinitesimus	0,5	0,8	0,1	0,01
Reptilia	1,7	23,4		
Amphibia (total)	4,2	22,7		
Crustacea	2,0	21,2		
Insecta (total)	33,6	4,2		
Coleoptera (total)	15,6	1,7		
Carabidae	5,1	0,3		
Tenebrionidae	1,3	0,1		
Curculionidae	3,0	0,5		
Cerambycidae	0,2	0,03		
Scarabaeidae	3,0	0,4		
Unidentified Coleoptera	2,0	0,3		
Orthoptera (total)	13,3	1,9		
Ensifera	5,1	1,0		
Gryllida	5,5	0,6		
Caelifera	2,7	0,3		
Blattodea	1,3	0,1		
Mantodea	0,4	0,05		
Phasmatodea	0,5	0,05		
Hemiptera	0,9	0,1		
Unidentified larvae	1,3	0,2		
Unidentified Insecta	0,3	0,06		
Arachnida (total)	38,4	1,6		
Amblypygi	0,9	0,01		
Scorpiones	0,2	0,2		
Myriapoda (total)	17,5	5,6		
Diplopoda Juliformia	3,3	2,0		
Oniscomorpha	1,4	2,6		
Chilopoda	0,2	0,1		
n =	12 374		1 102	

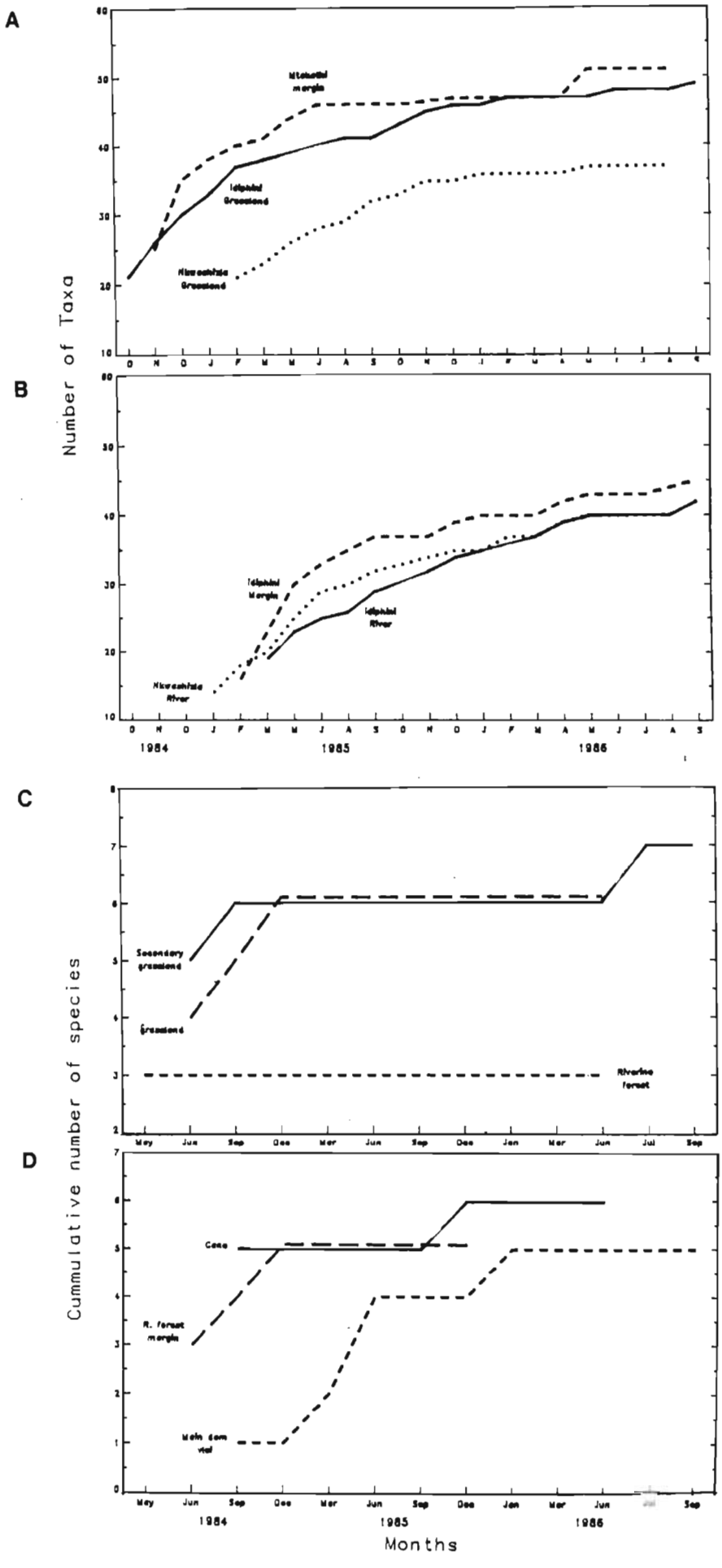


FIGURE 5.4. Collectors accumulative curves for the six array traps (A and B) and six PVC traps (C and D). The origin of the curves indicates when trapping began.

whereas slightly larger species were more often caught in the PVC traps (Table 5.1). Although these two techniques complement each other they also exemplify the problem of differential trappability which is well known (Southwood 1978) but poorly understood (Appendix 2). Therefore, it is stressed that these results should be interpreted carefully.

To test if the six array trap sites could be treated as paired replicates of three broad habitats (grassland, stream and forest margin), showing less variation than that among the unpaired sites (for example, grassland and river or river and forest margin etc.), all possible twosome trap site combinations were compared using chi-square analysis. All 15 combinations showed similar, highly significant differences in the number and biomass of prey categories caught ($n=9$; $P<0,001$).

Despite this quantitative difference, categories in the paired sites had significantly similar rankings ($n=40$; stream $P<0,02$; grassland $P<0,05$; margin $P<0,01$) whereas other combinations were dissimilar ($n=40$; $P>0,1$). These statistical comparisons revealed that, although the paired sites caught significantly different numbers of prey, prey categories had similar status in the paired array traps. Similar status among prey categories was not found in the unpaired sites.

The chi-square results raised the question of whether to treat the data as six separate habitats or group them. Since VCNR comprises numerous streams and a mosaic of small habitat blocks (Fig. 5.1), a viverrid would likely enter a range of different habitats during its normal daily activities (see

Chap. 6). For this reason, and to simplify data presentation, results from the six different array trap sites were initially pooled. Similarly, the data obtained from all small mammal trap lines were pooled for initial analyses. However, to present a more detailed analysis than was possible with the grouped data, the results were further examined as paired habitats (i.e. grassland, stream and forest margin each comprising two array traps). This treatment was also used to determine prey habitat associations (Chap. 6).

Dominance.

The pooled trap results should indicate the broad range of prey available in the reserve (Tables 5.1 - 5.2). Although the relative data may not represent true abundances of the various categories, the trends are probably realistic.

Total numbers of small mammals, caught in all PVC trap lines, are shown in Table 5.2 (column a). Clearly, R. pumilio and M. natalensis were dominant, comprising more than 80% of small mammals trapped (Table 5.2a). Of particular interest was the capture of only 17 Otomys spp. which were important prey (Chap. 4; Table 5.2a).

If biomass is considered, R. pumilio and M. natalensis still remain dominant (Table 5.2a). But the larger Otomys spp., D. incomtus, A. chrysophilus and L. rosalia, move to a higher ranking relative to the more numerous shrews and Mus minutoides which had a low individual mass (Table 5.2b). This illustrates the important contribution to overall biomass made by the larger species. More specifically, R. pumilio and M. natalensis were respectively 26 and 24 times more numerous

than Otomys spp. but had only 10 and 9 times as great a biomass (Table 5.2).

TABLE 5.2. Dominance ranking, based on number and biomass, of all small mammals caught in the PVC trap lines. Pooled data from all sites.

A. Total number caught.		B. Total biomass (g) of animals.	
R. pumilio	450	R. pumilio	18 990
M. natalensis	406	M. natalensis	16 402
Shrew	71	L. rosalia	3 696
L. rosalia	66	Otomys spp.	1 900
M. minutoides	25	Shrew	1 406
Otomys spp.	17	A. chrysophilus	490
A. chrysophilus	8	D. incomtus	400
D. incomtus	4	M. minutoides	220
Dendromys spp.	3	Dendromys	24
S. infinitesimus	1	S. infinitesimus	4

A similar trend was evident in the array trap data in which biomass was plotted against abundance (Fig. 5.5; see also Figs. 4.1 - 4.5). Elton's pyramid of numbers was evident as small invertebrates were numerically dominant while the remaining categories, mainly larger animals, were considerably fewer (Fig. 5.5; X axis).

When dominance was determined by mass, less numerous but larger animals dominated (particularly large snakes of which few were caught; Fig. 5.5; Y axis). Animals in the top left of the graph (Fig. 5.5) were large but few. Equitability (evenness) was therefore low with a clearly defined, but different, group of dominant categories when either abundance or biomass was considered (Fig. 5.5). Similarly, low equitability was noted for the mammals (Table 5.2). No categories had an overall importance (Chap. 4) of more than 1% (Fig. 5.5) although, if mammals were caught more efficiently by the array traps they probably would plot above the 1%

isopleth (Fig. 5.5). Nevertheless, this figure is very different to Figures 4.1 t to 4.5 which represent the diets of the viverrids.

Of further interest was that three of the five most abundant categories (Araneae, Opiliones and Polydesmoidea) had low biomass and were not eaten by viverrids (Fig. 5.5; Table 4.2). Consequently, they have been excluded from further analyses. Coleoptera (mainly Carabidae) and Orthoptera (mainly Stenopelmatidae, Tettigoniidae and Gryllidae), (and Juliformia) were also abundant and had low biomass (Fig. 5.5). These animals represented major prey for Mungos only (Table 4.2) possibly because of their rapid renewal rate (see Waser 1981). In contrast, categories with a large biomass, but low abundance (reptiles, anurans, mammals and crabs), were important food for the other four viverrids (Fig. 5.5; 4.1 - 4.5).

Seasonality

Differential trappability (Appendix 2) precludes direct interpretation of the abundance estimates derived from the array traps but, as explained above, the relative temporal changes in abundance should reflect real fluctuations. These results indicate periods of prey abundance and relative scarcity (Figs. 5.6 - 5.21).

1. PFT and array traps

Considered in isolation, the four months of bucket pitfall trapping (Fig. 5.6) are uninformative, and are best compared with the array trap results. When seen together, both showed

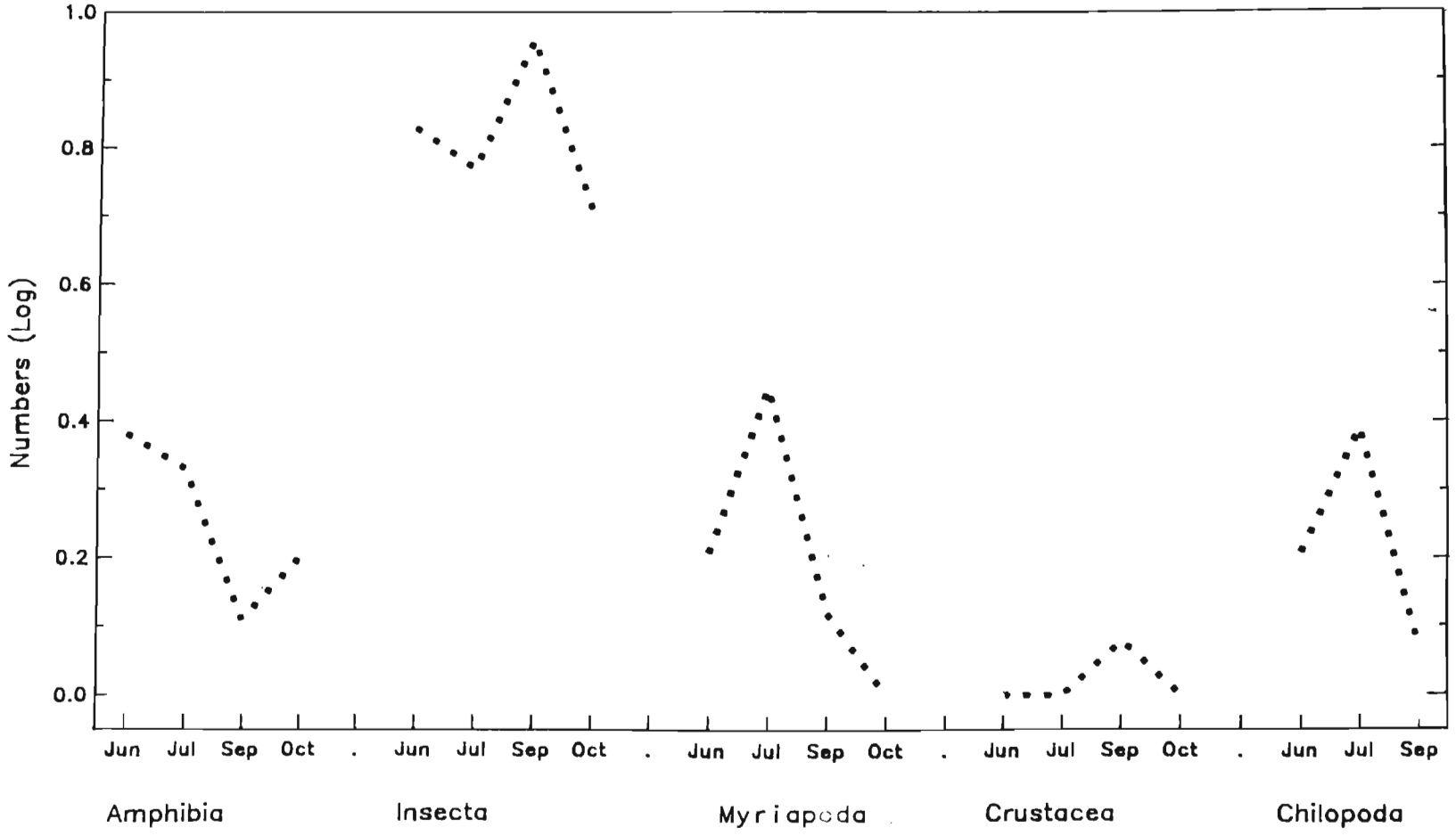


FIGURE 5.6. Total number of prey caught in the bucket Pitfall Traps from June to October 1984. Traps were set in riverine forest, riverine forest margin, grassland and secondary grassland. A shortened trapping session in October may account for few captures in that month.

similar trends which are outlined below. A shortened bucket pitfall trapping period during October 1984 resulted in a low catch and consequent apparent decline in numbers (Fig. 5.6) which should be borne in mind.

The pooled data showed that crabs (P. sidneyi were caught more often than expected in November and January and less often between May and September ($P<0,05$; Fig. 5.7). Crabs were particularly common during the warm, rainy season, occurring a distance from water, but, during winter, were never caught and could not be lured from their burrows (Fig. 5.7). Pill millipedes (S. dorsale, S. punctulatum) were scarce between June and October but abundant in December ($P<0,05$; Fig. 5.8) and Juliform millipedes (probably Doratogonus setosus uncinatus, Chersastus annulatus and unidentified genera of the Odontopydidae) were common in spring but occurred in the traps less often than expected from January to August (pooled data; $P<0,05$; Fig. 5.9). All three prey categories (crabs, pill millipedes and millipedes) were considered markedly seasonal (see Chap. 4; Figs. 5.7 - 5.9). The paired habitat analyses confirmed those made on the pooled data (Figs. 5.7 - 5.9).

Amphibia and Coleoptera, were present throughout the year but the pooled and paired site data sets both showed that fewer than expected were caught in winter and more were caught in summer ($P<0,05$; Figs. 5.10 - 5.11). Most striking was the decline in numbers during autumn and dramatic increase during spring, particularly of the Amphibia (Figs. 5.10 - 5.11). Similar trends among the frogs were seen in the bucket traps (Fig. 5.6).

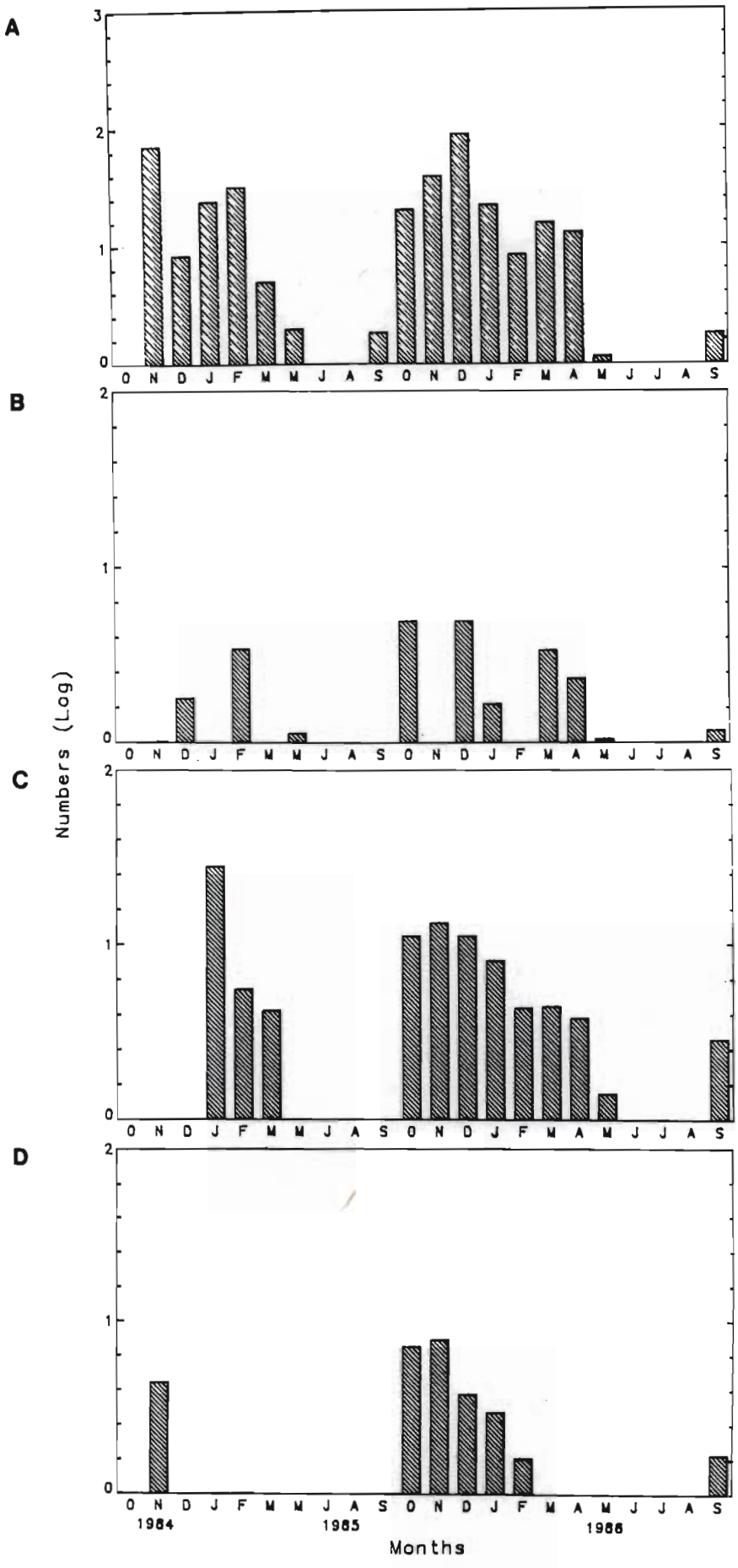


FIGURE 5.7. Total number of crabs caught each month in the array traps between October 1984 and September 1986. A=pooled results, B=forest margin traps, C=stream traps and D=grassland traps. Note stream trapping began in January 1985.

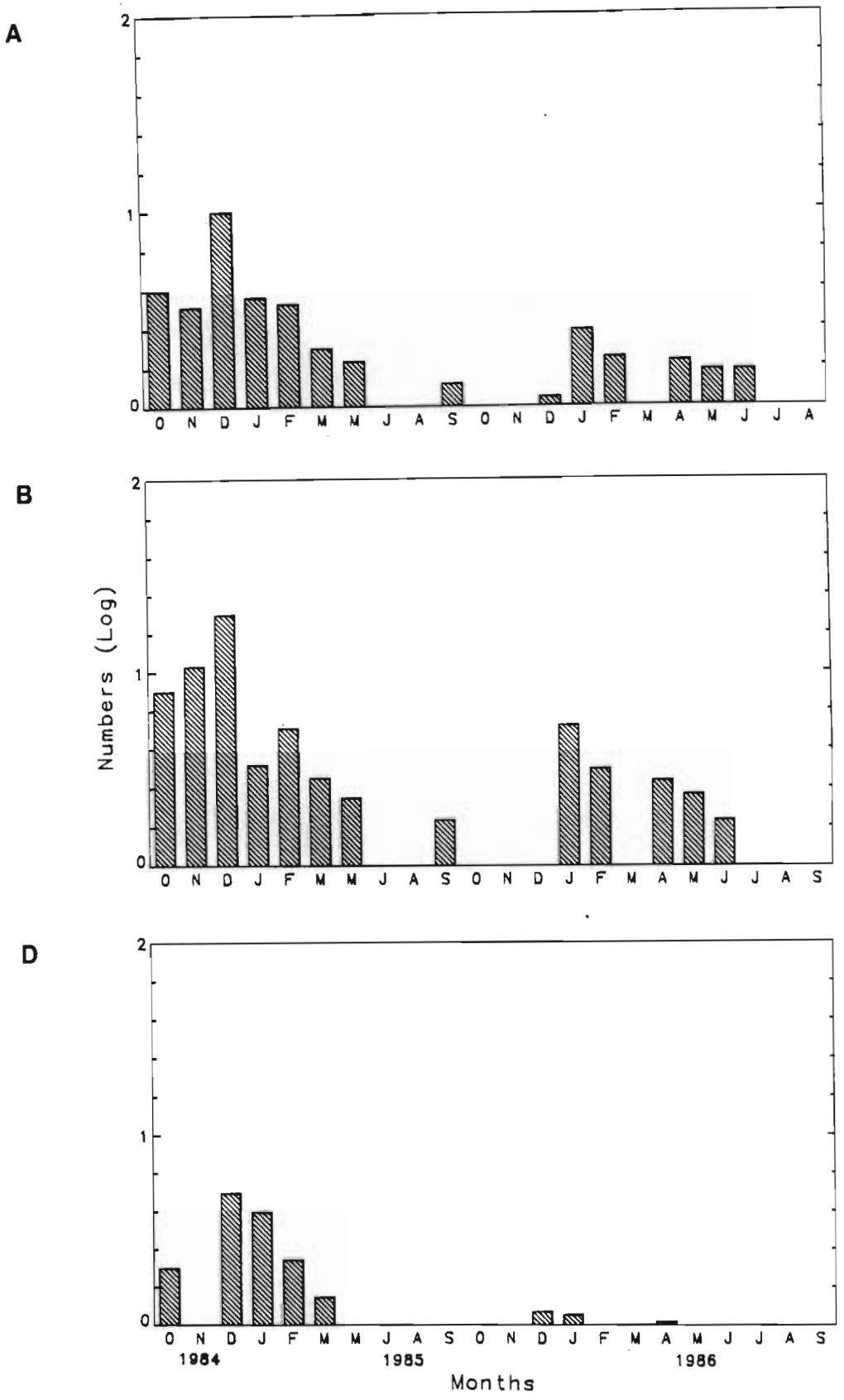


FIGURE 5.8. Total number of pill millipedes (Sphaerotherium spp.) caught each month in the array traps. No pill millipedes were caught in the stream traps. Otherwise legend as for Figure 5.7.

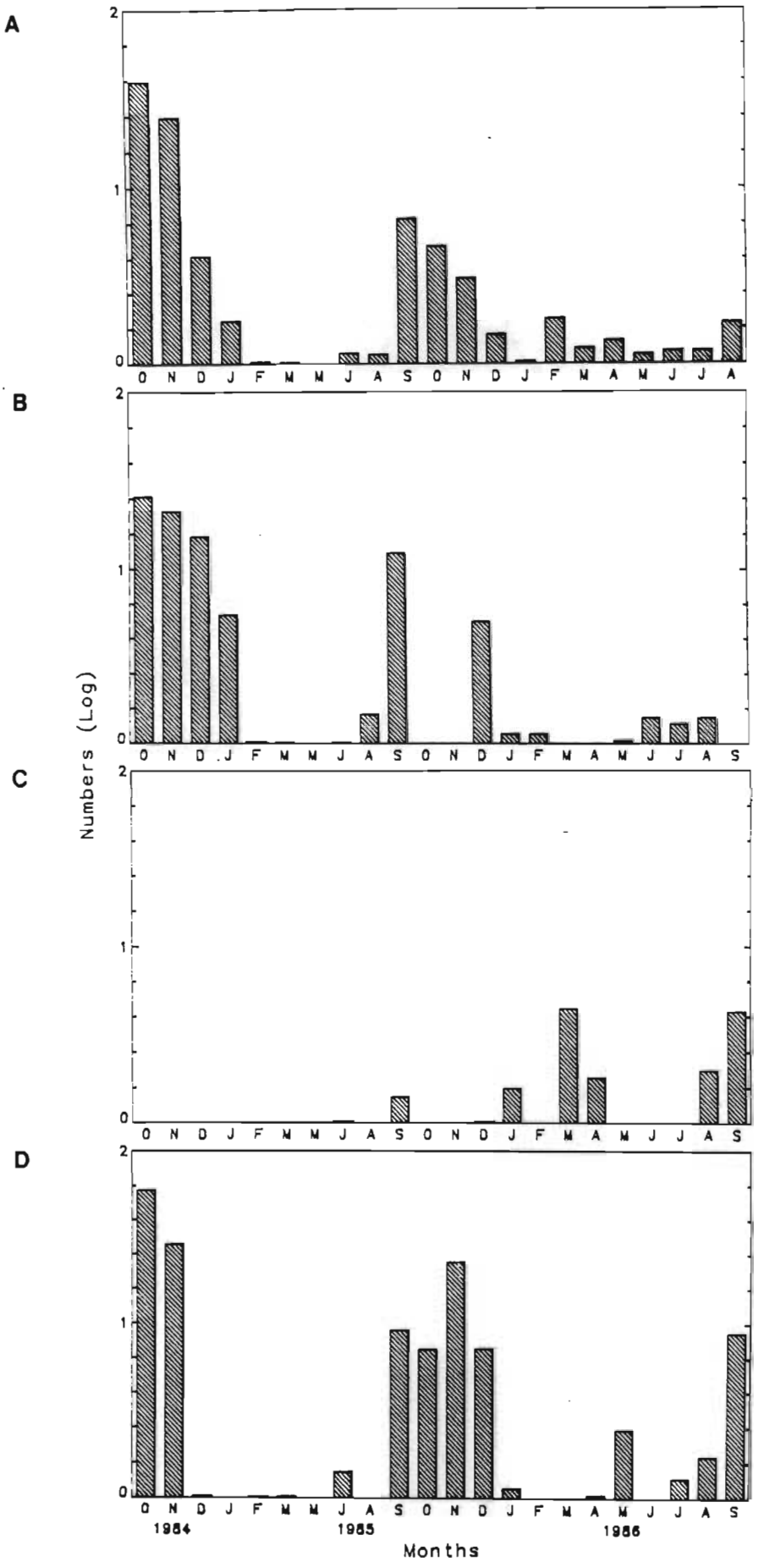


FIGURE 5.9. Total number of Juliform millipedes caught each month in the array traps. Otherwise legend as for Figure 5.7.

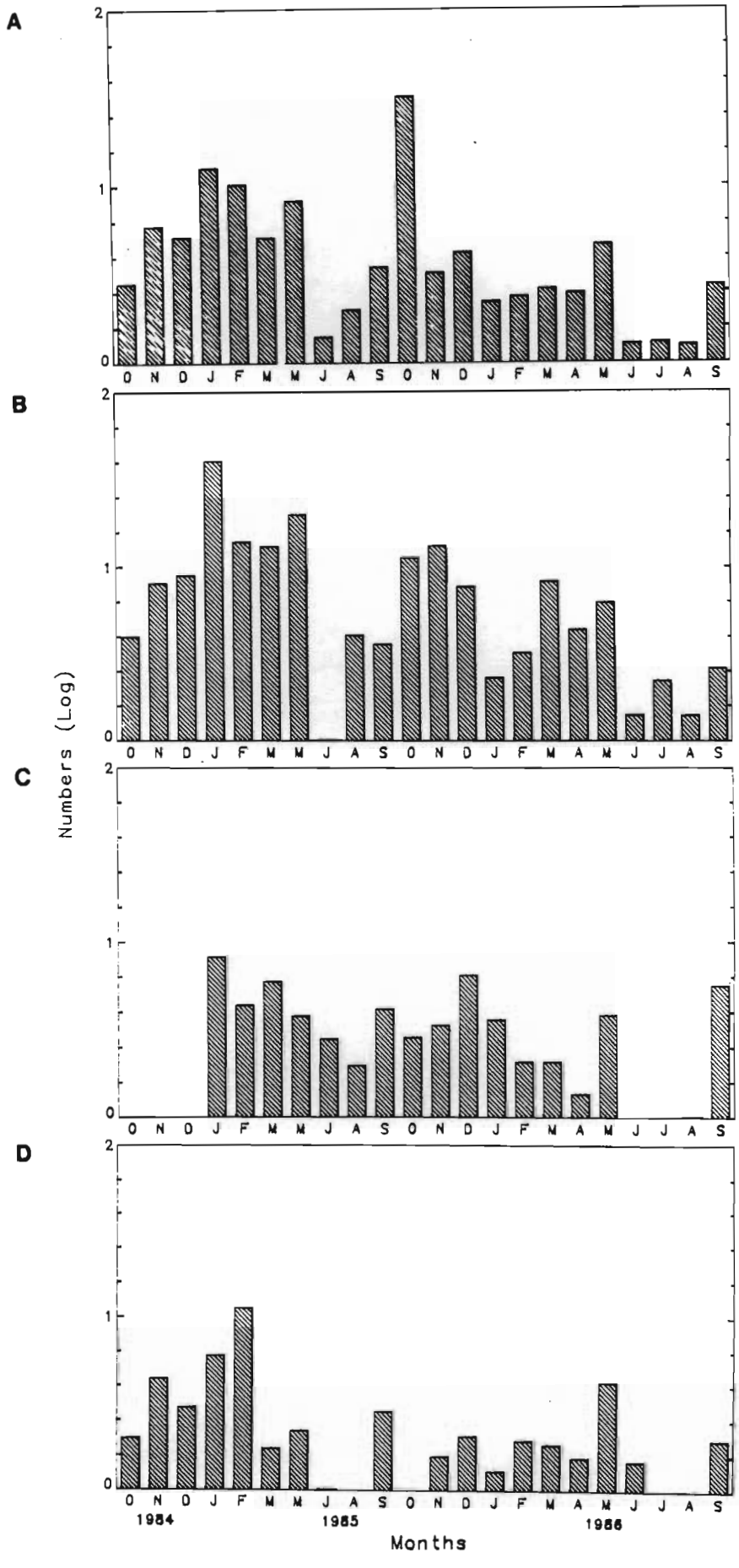


FIGURE 5.10. Total number of Amphibia caught each month in the array traps. Otherwise legend as for Figure 5.7.

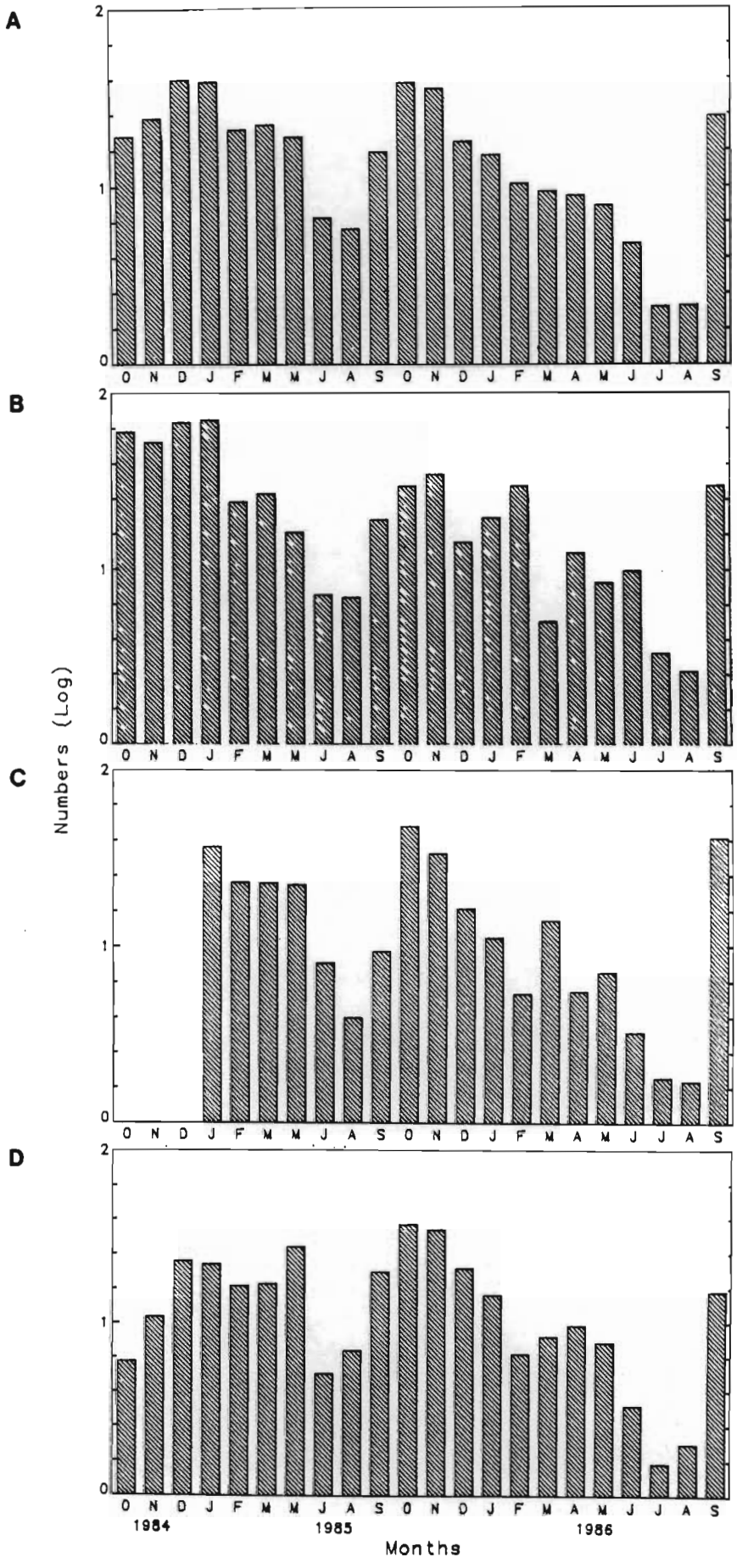


FIGURE 5.11. Total number of Coleoptera caught each month in the array traps. Otherwise legend as for Figure 5.7.

Reptile captures, reflected in the pooled and paired habitat analyses (Fig. 5.12) were infrequent and irregular (Fig. 5.2) particularly snakes. Lizards were caught more often. Reptiles were caught in proportion to the numbers expected at the 5% probability level, except in June when fewer were caught (Fig. 5.12). However, snakes were most frequently seen in the field during April and May which may be attributed to increased activity prior to winter.

From December 1984 until March/May 1985, Orthoptera were numerous but decreased as winter approached (Fig. 5.13). A slight increase followed in September 1985 but thereafter fluctuations in abundance were small (Fig. 5.13). Pooled results showed Orthoptera to be caught more often in summer and in May and less often in winter and October ($P<0,05$; Fig. 5.13a).

Insects, excluding Coleoptera and Orthoptera, were weakly seasonal although fewer than expected were caught in March and June ($P<0,01$; Fig. 5.14). Insects from the forest margin showed little seasonal variation (Figs. 5.14b). In contrast, a decrease in winter and rapid increase in spring, resembling that of the Coleoptera (Fig. 5.11), was evident in both the stream and grassland array traps during 1985 and 1986 (Fig. 5.14c&d). The pooled insect data showed regular, non-seasonal, fluctuations in numbers (Fig. 5.14). Insects caught in bucket PFTs showed a spring (September) increase before declining in October (Fig. 5.6). However, this decline may have resulted from the short October sampling period (Fig. 5.6).

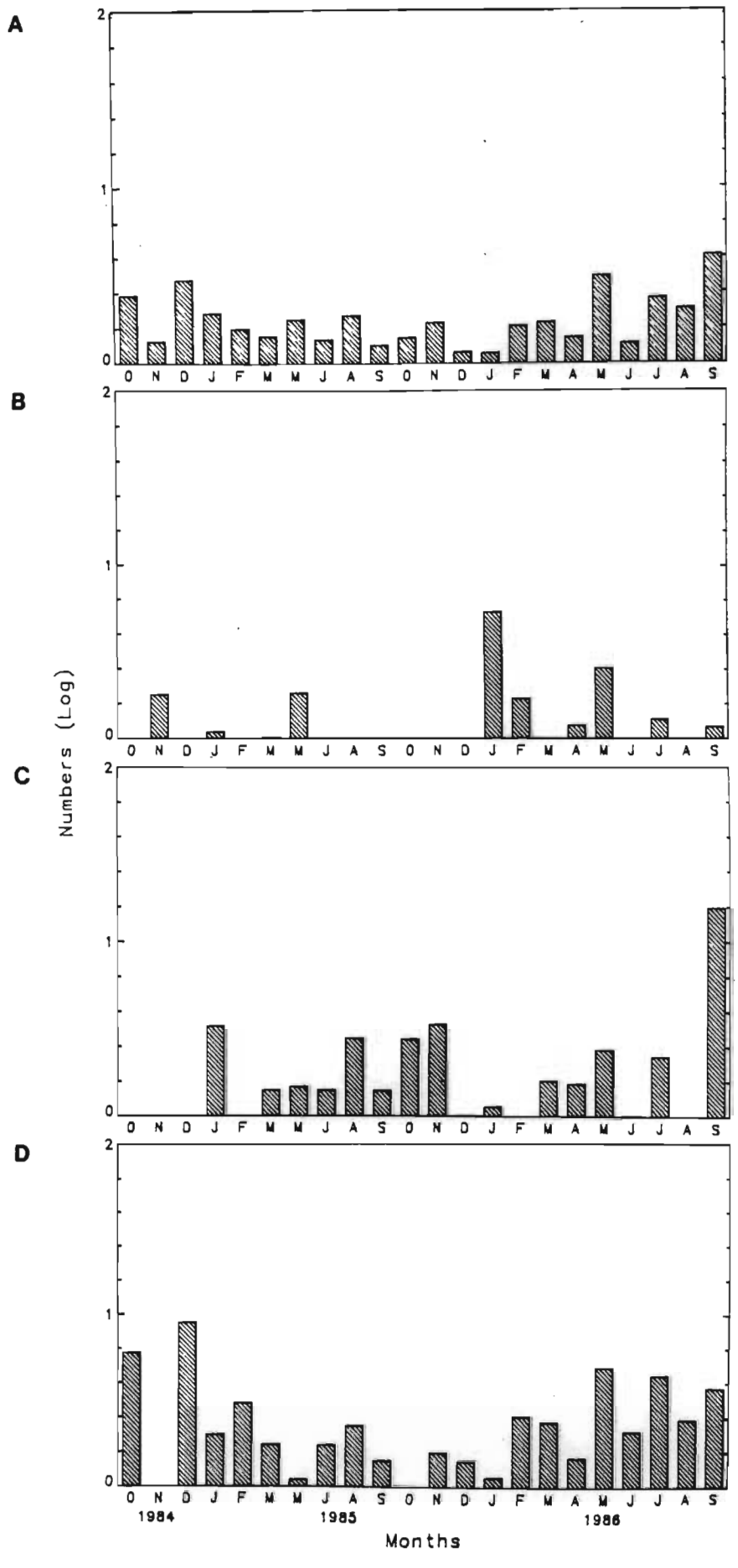


FIGURE 5.12. Total number of Reptilia caught each month in the array traps. Otherwise legend as for Figure 5.7.

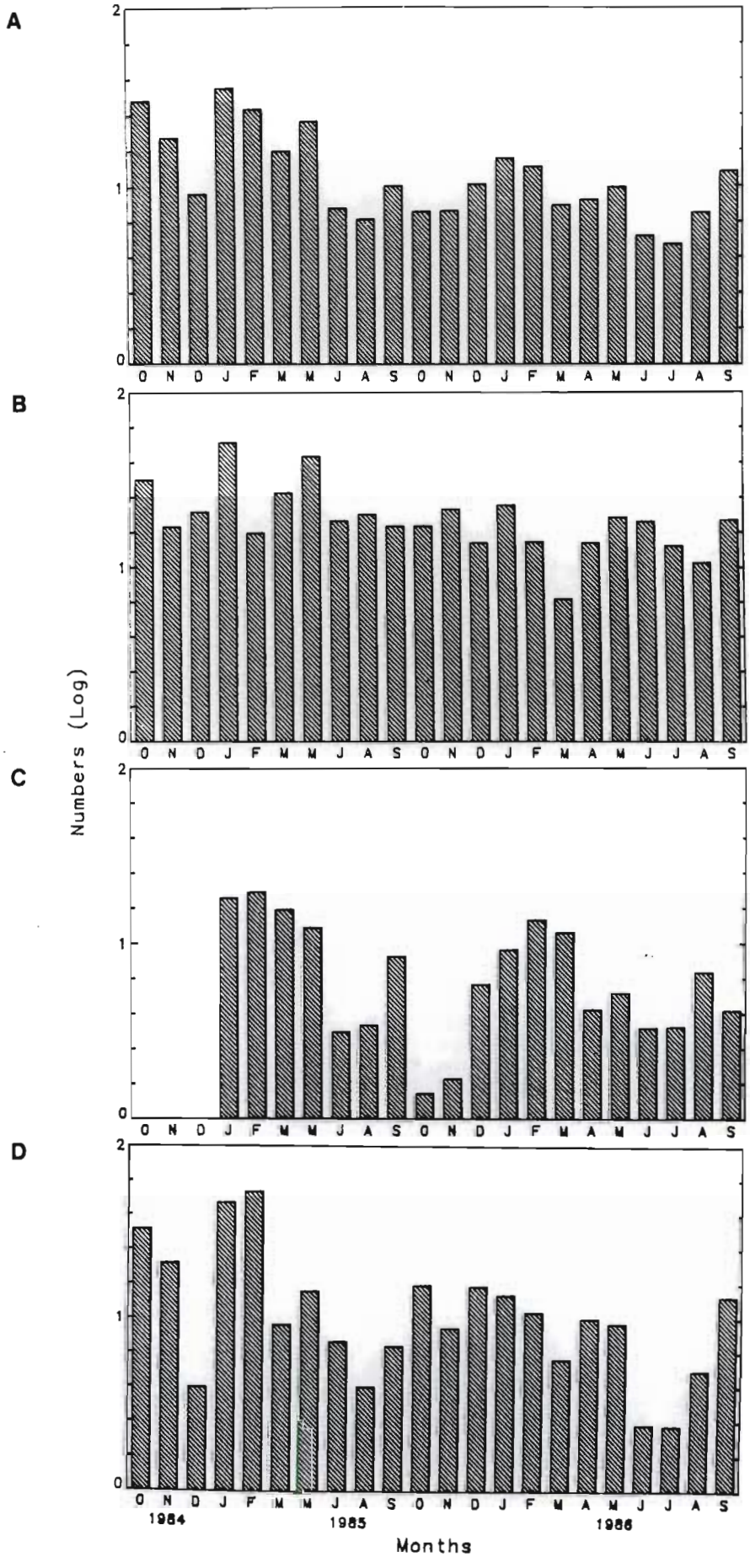


FIGURE 5.13. Total number of Orthoptera caught each month in the array traps. Otherwise legend as for Figure 5.7.

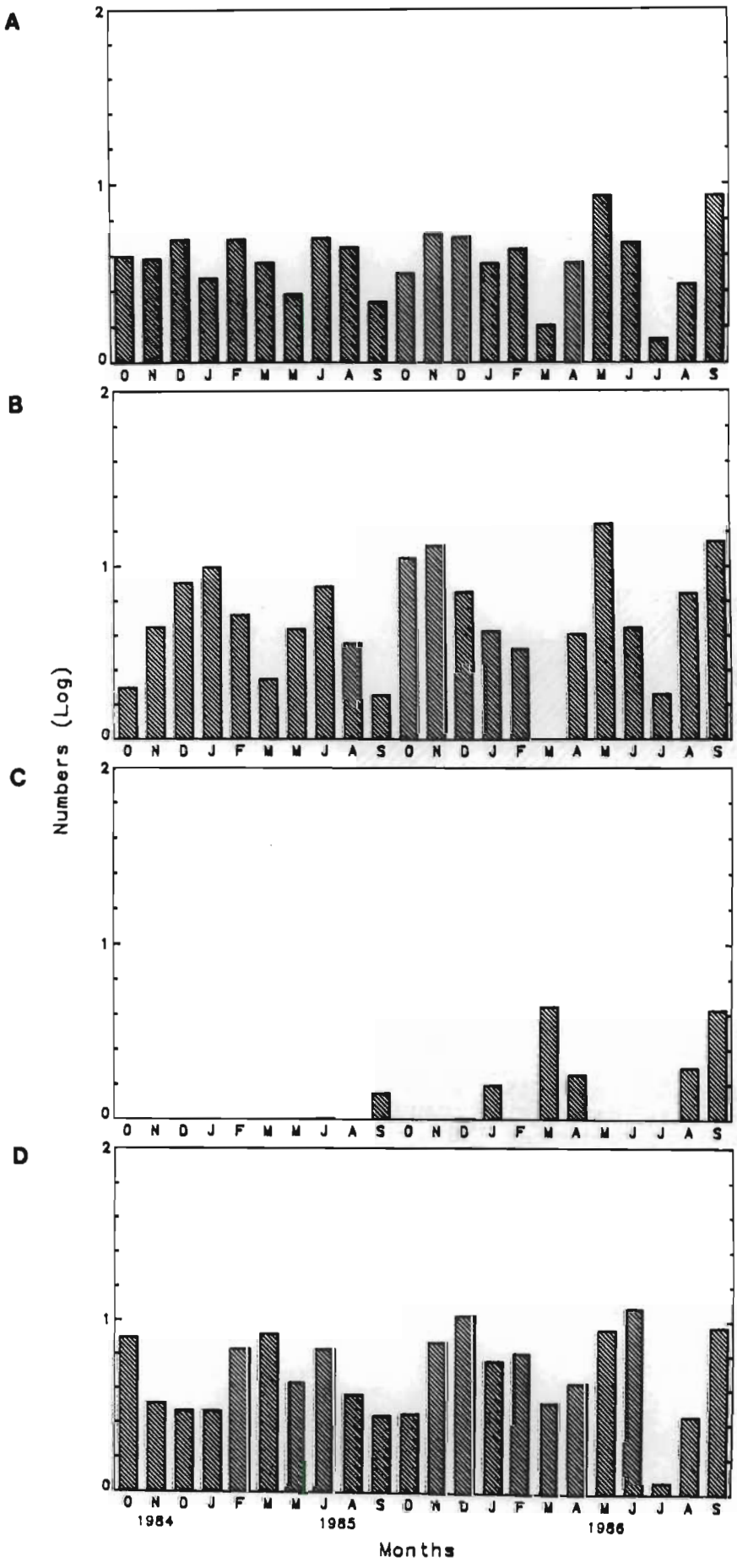


FIGURE 5.14. Total number of Insecta excluding, Orthoptera and Coleoptera, caught each month in the array traps. Otherwise legend as for Figure 5.7.

Centipedes (C. psuedopunctatus, Scutigera coleoptrata natalensis and Paralamyctes spenceri), scorpions (O. validus) and amblypygids (D. variegatus) were caught infrequently and in low numbers, making identification of trends difficult, but a decline in winter was noted. Centipedes were absent in July only, while scorpions and amblypygids were never caught in June or July but were present in May and August.

Array trap: Capture-Mark-Recapture (CMR)

Results of the CMR study on the array-caught (Fig. 5.15) animals, showed trends similar to those seen above (Figs. 5.6 - 5.14) and a consistent pattern emerged from consideration of all the data (Figs. 5.6 - 5.15). A gradual decline in numbers of most prey categories occurred between February and June followed by a period of low abundance in winter and an abrupt increase between August and October. Usually the increase in spring occurred over a shorter period than the autumnal decline (Figs. 5.6 - 5.14). During 1985, the spring rains fell in late September with heavy rain in October while, in 1986, the rains fell slightly earlier in August/September (Fig. 2.5). The spring increase in most prey categories was slightly delayed in 1985 compared with 1986 suggesting that rainfall influenced population dynamics (see below).

2. PVC small mammal trapping

A different situation was seen in the trap line-caught mammals (Figs. 5.16 - 5.18). Small mammals were most numerous during winter (June and July) and least numerous in summer (December) or early autumn (March; Figs. 5.16 - 5.18). However, seasonal changes in biomass (Figs. 5.16 - 5.18) were noted and M.

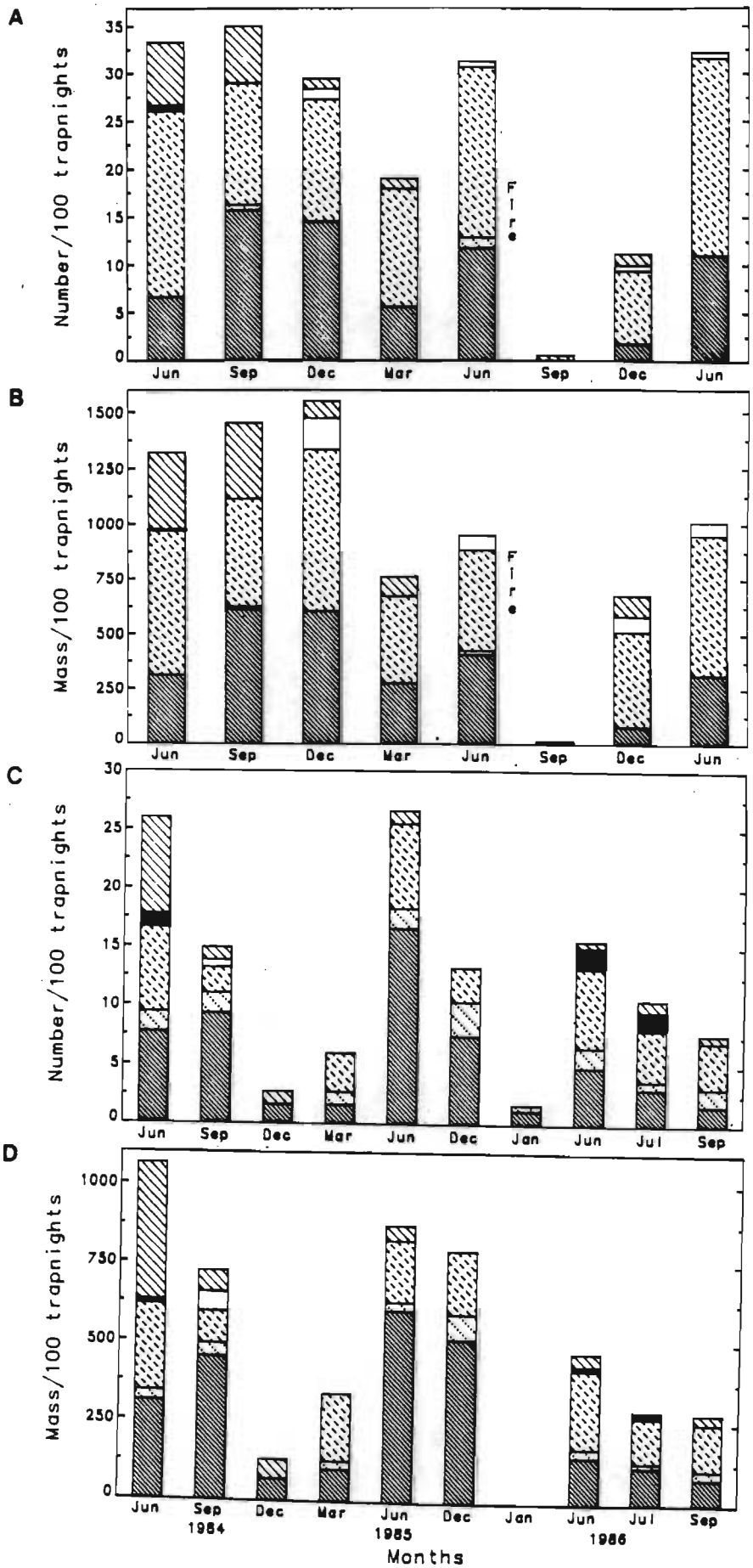


FIGURE 5.16. Total numbers (A and C) and biomass (B and D) of mammals caught in secondary grassland and grassland PVC traplines respectively. =R. pumilio, =large shrews, =M. natalensis, =Otomys spp. =L. rosalia, =Dendromys spp. =M. minutoides

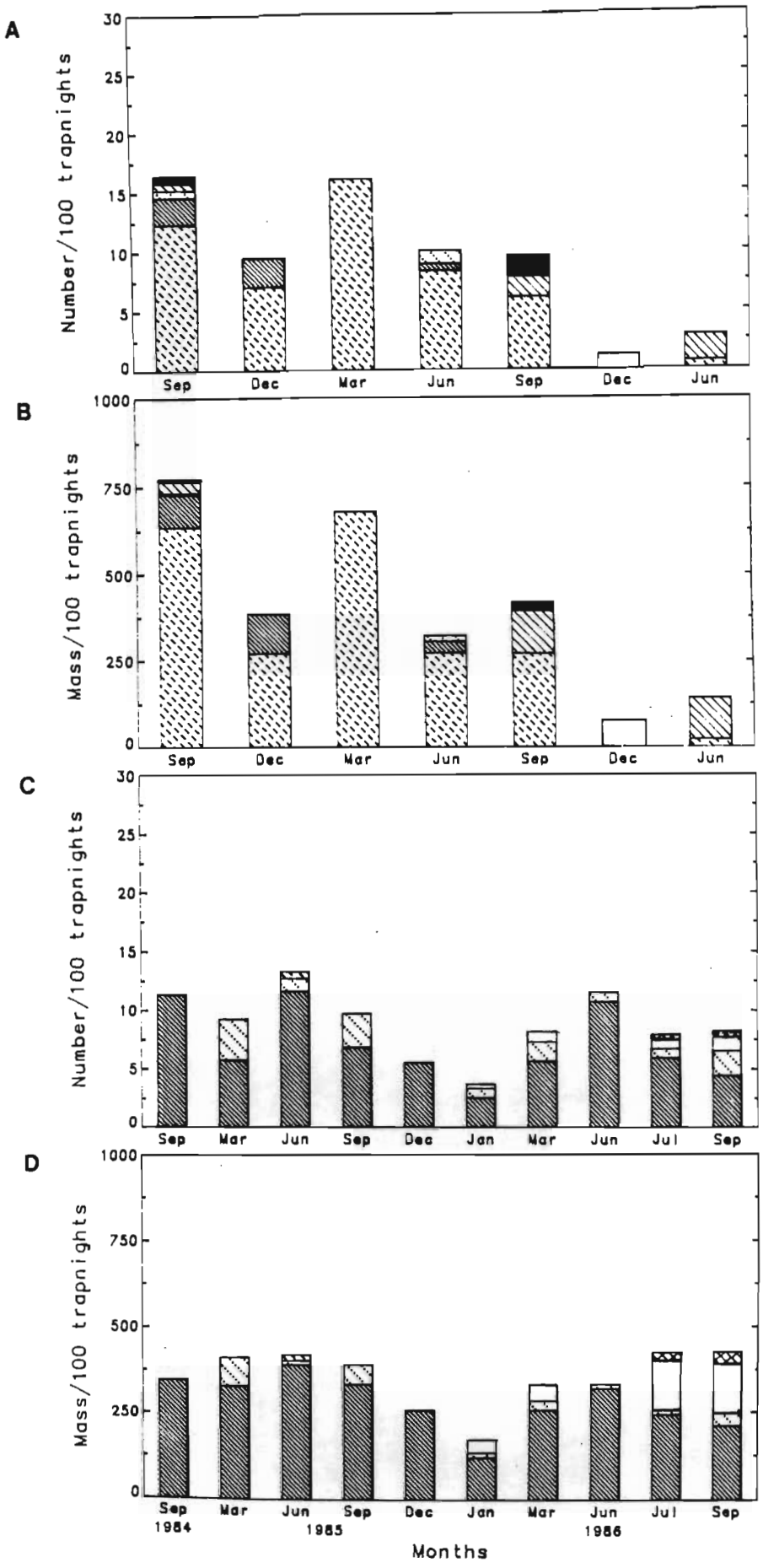


FIGURE 5.17. Total numbers (A and C) and biomass (B and D) of mammals caught in cane and vlei PVC traplines respectively. ⊠ =D. incomtus. Otherwise legend as for Figure 5.16.

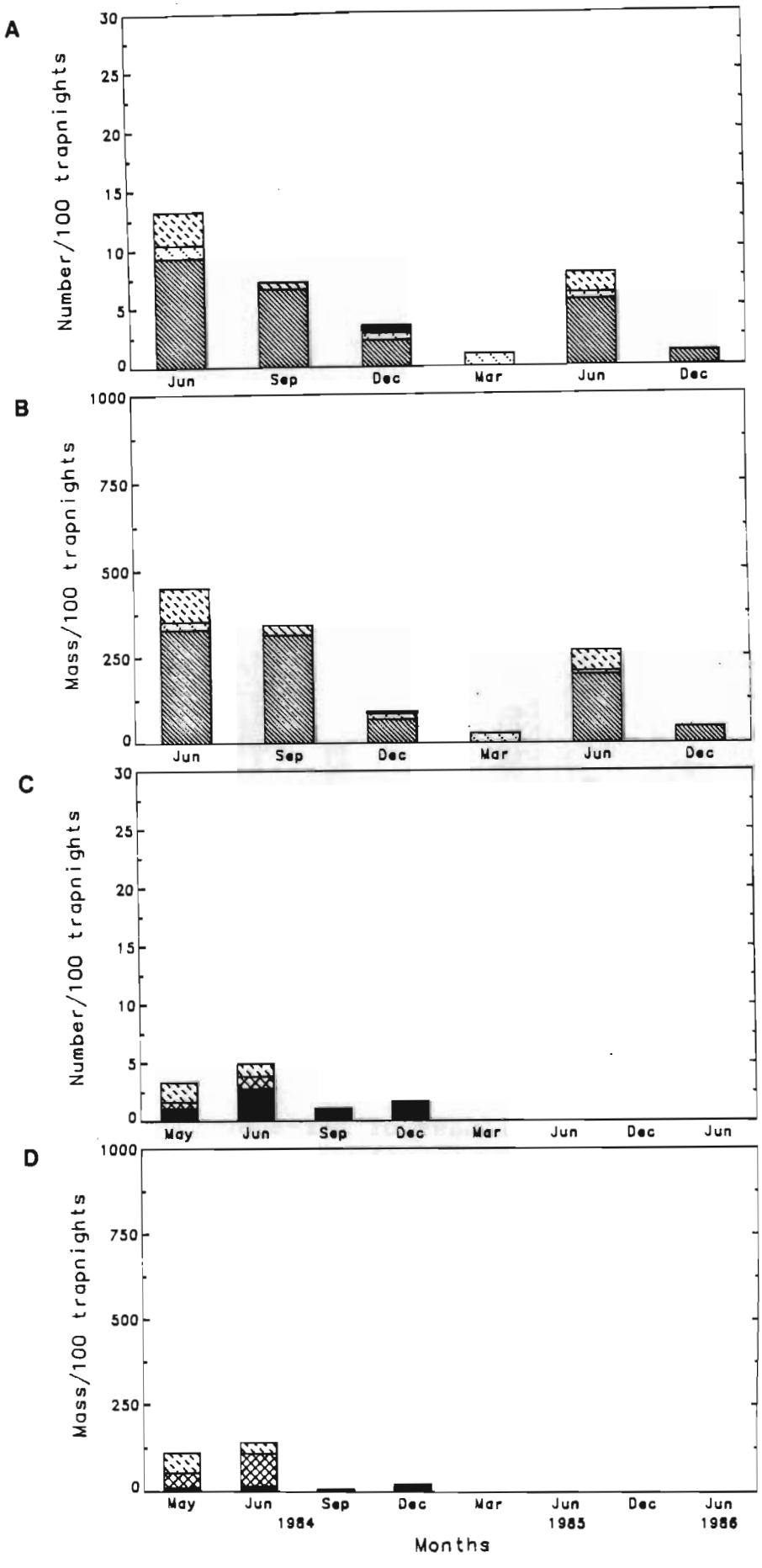


FIGURE 5.18. Total numbers (A and C) and biomass (B and D) of mammals caught in riverine forest margin and riverine forest PVC traplines respectively. ▨ =A. chrysophilus. Otherwise legend as for Figure 5.16.

natalensis, R. pumilio and L. rosalia all had a mean winter mass consistently lower than either the spring or summer mean masses (Fig. 5.19). Thus, the trappable rodent population at least, comprised mainly juveniles and sub-adults in winter while adults dominated between September and March (Fig. 5.19).

Absolute prey abundance.

Tests of the assumptions of each model used in the absolute abundance calculations are provided in Appendix 2.

1. Small mammals

Results of the three models used to determine population estimates of small mammals inhabiting the vlei and secondary grassland are shown in Table 5.3, as is the overall mean of these three estimates. The same trends noted in the PVC trap lines were apparent, i.e. an increase in numbers during mid-winter combined with a decline in overall biomass (although this biomass pattern is obscured by the presence of small and large species; Table 5.3).

Greater fluctuations in both numbers and species composition, as well as greater species richness were found in the grassland compared to the vlei. Four species occurred regularly in the vlei (R. pumilio, D. incomtus, Otomys spp. and shrews) while six species were recorded in the grassland (R. pumilio, M. natalensis, L. rosalia, shrews, M. minutoides and Dendromys spp.). The last two species and L. rosalia appeared infrequently but R. pumilio, M. natalensis and shrews were permanent inhabitants.

TABLE 5.3. Absolute population estimates for small mammals inhabiting vlei (A) and secondary grassland (B) at VCNR. The mean estimate derived from three different models is presented. The standard deviation given with the overall mean reflects the variation obtained from the three methods but does not consider variation within each method. Given in numbers and grams (g) per hectare. X =estimate less than number caught.

	Bailey's	Hayne's	Jolly's	Overall mean
January 1986				
A.	26,5±25,0	24,3	37,4	29,4±7,0
	1282,6±1207,1	1131,7	1810,8	1408,4±356,6g
B.	12,5	12,5	12,5	12,5±0,0
	571,5	571,5	571,5	571,5±0,0g
July 1986				
A.	X	50,0	X	50,0±0,0
		2709,9		2708,9±0,0g
B.	59,2±22,0	89,8	63,2	70,7±16,6
	1620,5±602,2	2458,8	1732,3	1937,2±455,2g
September 1986				
A.	X	43,7	X	43,7±0,0
		1986,9		1986,9±0,0g
B.	X	75,7	X	75,7±0,0
		2389,1		2389,1±0,0g

Based on catch per unit effort, trap lines caught consistently more small mammals than did the grids. For example, in June 1986, the secondary grassland and vlei trap lines achieved successes of 15,7 and 11,6 animals per 100 TN (Figs. 5.16a & 5.17c respectively) while grid trapping one month later caught 8,0 and 10,7 animals per 100 TN respectively. This was probably due to overemphasis of the edge effect and larger trap spacing in the trap lines resulting in greater catch per unit effort.

2. Coleoptera and Orthoptera

As suggested by the array trapping (Figs. 5.11 & 5.13), Coleoptera and Orthoptera declined in winter and increased rapidly in September (Tables 5.5 & 5.4). (Only Moran's removal method showed orthopterans declining from winter to spring; Table 5.4). Noticeable was the great diversity in population estimates both among different sites and within the same site using different models (Table 5.4). Similar variation was noted for crabs (Fig. 5.6).

A feature of the sweep sampling was that mainly small (<15 mm) and few medium-sized (15-19,9 mm) animals were caught. Large grasshoppers, although seen, were never caught, resulting in underestimation of total numbers and, particularly, biomass. Nevertheless, Orthoptera were abundant in the grassland achieving high densities in both July and September (Table 5.4).

In contrast, coleopterans were caught in low numbers, therefore, population estimates were based on the minimum

number of beetles caught. Consequently, density estimates were low (Table 5.5). The discrepancy between Coleoptera and Orthoptera may well have resulted from the greater efficiency of sweep sampling relative to the PFTs but the possibility that Orthoptera were more numerous must not be dismissed. Certainly, field indications support the latter view.

3. Crabs

The absence of crabs during winter and their sudden appearance in September was conspicuous (Table 5.6) but agreed with the array trap findings (Fig. 5.7). Of further interest was that crab biomass exceeded that of the other four categories. Although this can be related to the fact that sampling was conducted in an area of prime crab habitat, the results are still impressive (Table 5.6).

As with the Orthoptera (Table 5.4), crabs also exhibited among-site population variability; compare the values for the two riverine forest and streambank forest sites in September 1986 (Table 5.6). Habitat differences were also apparent with the streambank forest revealing a consistently lower crab density than the riverine forest sites (Table 5.6).

Most crabs caught with bait were large (>30 mm carapace width) but many small crabs could be collected by hand under the rocks. In two hours one large and one medium sized crab were caught on string while 26 small ones were collected from under the rocks. The difference in crab biomass, as a result of not including these small animals, is not known but may be large.

TABLE 5.5. Absolute abundance estimates for Coleoptera in Nkwashizela grassland (A) and Mtakathi forest clearing (B). Due to absence of recaptures population estimates were derived from the minimum number of animals caught.

	grams/hectare	number/hectare
December 1985 A.	392	1562
July 1986 A.	No animals caught	
September 1986 B	127	781

TABLE 5.6. Absolute population estimates for crabs inhabiting streams in riverine Forest and Streambank Forest at VCNR. The mean estimate derived from three different models is presented. The standard deviation given with the overall mean reflects the variation obtained from the three methods while variation within each method is shown by CV%. No CV% is shown for Hayne's removal method because SD were not calculated. Given in numbers and grams (g) per hectare. A=Streambank forest, B=Riverine forest.

	Weighted mean CV%	Moran's Removal CV%	Overall mean ± SD	CV%
December 1985 A.	133,3	6,7	1466±231 27918±4396g	15,8
January 1986 B.	57,9	48,5	3022±1210 54840±21953	40,0
July 1986 B.	No animals caught			
September 1986 Site 1 A.	128,6	6,0	755±154 21749±4432	20,4
Site 2 A.		9,9	533±0,0 12880±0,0	0,0
Site 1 B.	58,3	38,5	1555±204 46741±28796	13,1
Site 2 B.	67,2		5688±2118 55851±20794	37,2

In a separate analysis, the number of crab burrows per 20 m of stream in riverine forest was counted. The results confirmed that crabs were numerous in this habitat and a mean of 43,8±12,5 burrows was counted per 20 m of stream (n=8).

4. Frogs

Because of the large amount of manpower required, frog sampling was conducted only during September 1986. Consequently seasonal population changes could not be made and must, therefore, be inferred by comparison with the array trap data (Fig. 5.10), in particular Figure 5.10c.

Frog densities were high in September 1986 (Table 5.7). Figure 5.10 shows this to be the period when frog numbers increased after winter, therefore, this density of 450 animals per hectare was considered maximal. Lower numbers would be expected during winter (Table 5.7; Fig. 5.10c).

Causes of variation

Results of the absolute population estimates support and extend those derived from the relative methods. Similar trends were observed and a more detailed idea of animal abundance obtained by viewing both data sets in concert. Both methods showed most prey categories exhibiting quite distinct seasonal changes, with June to August emerging as the period when fewest prey were available (Figs. 5.6 - 5.15). Small mammals, although numerous during winter (Figs. 5.16 - 5.18), had a low individual mass during this period (Fig. 5.19).

The finding that most prey categories showed seasonal patterns of abundance is important. If the variables governing these

seasonal patterns are obvious, these cues may be identified by predators. Although factors responsible for such patterns are likely to be complex and varied, meteorological changes often influence animal abundance (Gentry, Golley & McGinnis 1966; Thomas 1979; Bowland in prep.). More specifically, rainfall and temperature, which show definite seasonal variations (Figs. 2.4 & 2.5), are the most obvious factors that may influence changes in the abundance of viverrid prey and have been implicated above.

Rainfall and temperature.

The only prey category to show a statistical, linear correlation between monthly rainfall and abundance was crabs ($n=22$; $P<0,001$). However, a number of categories correlated positively with temperature including frogs ($n=19$; $P<0,05$), crabs ($n=19$; $P<0,01$) and Coleoptera ($n=19$; $P<0,01$). Of course, many environmental variables (relative humidity, evaporation, wind etc.), other than biotic effects, may also have a profound influence on these communities.

Fire

Veld burning, usually during July and August, is used annually as a management tool; thus fire is probably an important factor influencing viverrids and their prey.

Figure 5.16a shows small mammal abundance in the secondary grassland (Fig. 5.1) between June 1984 and June 1986. This area was burnt in late July 1985 and, when the PVC traps were set in early September 1985, ground cover was absent. During 180 TN, only one M. natalensis was caught, emphasising the

drastic effect of fire on small mammal populations (Fig. 5.16a). (Compare numbers caught prior to September 1985, especially September 1984 and June 1985; Fig. 5.16a).

Trapping in three surrounding habitats (Fig. 5.1) revealed low numbers in the riverine forest margin (1,1 animal/100 TN) but a capture rate of 8,5 animals/100 TN was achieved in the scrub forest and highest numbers were caught in the exotic bush (18,9 animals/100 TN). These captures possibly included some animals from the burnt grassland - A. chrysophilus were not typical grassland inhabitants but some multimammate mice may have emigrated to the exotics. None of the rodents caught in the three habitats bore marks from previous trapping.

Despite this drastic crash in small mammal numbers, the burns were recolonised rapidly (Fig. 5.16a). In December 1985 a capture rate of 11 animals/100 trap-nights was achieved, mainly M. natalensis but including one L. rosalia marked the previous June (Fig. 5.16a). By June 1986, the population had recovered and was comparable with previous June results (Fig. 5.16a).

In a second example, during September 1984, 13 animals/100 TN were caught in grassland. A year later and three weeks after a fire, no captures were made in 108 TN.

The effect of cover removal on small mammals was seen in the sugar cane plantations bordering the reserve (Fig. 5.1). In September 1984 numerous small mammals were caught in mature cane and in December 1984, three weeks after harvesting, fewer were caught (Fig. 5.17a). In December 1985, again three weeks after harvesting, only one animal was caught (Fig. 5.17a).

This low value, compared with that of the previous December, was attributed to absence of trash (cover) on the ground in 1985 - whereas, in 1984, a thick layer provided cover.

Determining population responses to fire in the array-caught animals (particularly the invertebrates) was difficult. Generally, diversity decreased immediately following fire although total captures declined only slightly. Lizards (Tropidosaura motana and Mabuya varia), spiders and Carabid beetles were trapped soon after the burn while frogs, Orthoptera and many Myriapods only returned about two months later when new grass shoots had begun to grow. Diversity and numbers increased during this time (September) when numbers of animals throughout the study area were increasing.

The overall effect of fire and cover removal on animals was a dramatic decrease in numbers (although certain pioneer species survived on burnt land) and alteration of species composition. Although recovery was rapid, the effect of a decrease in viverrid prey numbers, at a time when food might be limiting, is unknown.

Trophic niche breadth and overlap

In the previous chapter it was not possible to calculate niche breadth and overlap values because the prey availability data had not been presented (see Chap. 1). These values, which were based on the broad prey categories listed in Table 5.1, are now presented in Tables 5.8 and 5.9. Mungos clearly had a very narrow niche breadth because it did not select mammals which made up an important part of the prey biomass. Also evident is the relatively wide niche breadth of Atilax which had three

prey categories above the 5% isopleth (Fig. 4.4). The other three species, Herpestes, Galerella and Genetta had rather narrow niche breadths but they were very similar to each other (Table 5.8). These viverrids belonged to the small mammal guild and ate similar proportions of the major prey categories (Table 4.2). It must be noted that, because these calculations are based on broad prey categories, some of the important differences (prey species and prey size) discussed in Chapter 4 are not evident.

TABLE 5.8. Trophic niche breadth for the viverrids at VCNR. Calculations were done using the Proportional Similarity Index (Feinsinger et al. 1981) which includes the mass of prey eaten and the biomass of prey available. Values range from 1,0 (use of resources in proportion to their availability to 0,0 (selection for the rarest resource).

Species	Niche breadth
Mungos	0,1445
Herpestes	0,2737
Galerella	0,2835
Genetta	0,3021
Atilax	0,6567

Trophic overlaps are presented in Table 5.9 but because not all differences in the diets can be included in these overlap values (see above), overlap between some species are higher than they should be. Nevertheless, the important trends are apparent.

The unique diets of Mungos and Atilax result in low overlap between these two species and other viverrids (both are at the top of the list in Table 5.9). Second, the small mammal guild, Herpestes, Galerella and Genetta have high overlaps with each other but not with the other species (Table 5.9). Thus, the segregation of the viverrid community into a small mammal

TABLE 5.9. Trophic niche overlap between the ten viverrid species pairs at VCNR. Calculations were done using Hurlbert's (1978) index which includes the mass of prey eaten and the biomass of prey available. Values range from 0,0 (no shared resources) to >1,0 when certain resources are used more than others. A value of 1,0 indicates both species use the same resources in proportion to their availability.

Species pairs	Niche overlap
Herpestes/Mungos	0,2374
Atilax/Mungos	0,3051
Atilax/Galerella	0,7991
Atilax/Genetta	0,7999
Atilax/Herpestes	0,8063
Mungos/Galerella	1,0114
Mungos/Genetta	1,0631
Galerella/Genetta	3,7806
Herpestes/Genetta	3,7952
Herpestes/Galerella	3,9756

guild (three species) and two species with unique diets is clearly shown (Chap. 4; Fig. 5.9).

DISCUSSION.

My intention in this discussion is to elaborate those factors associated with the prey populations that may influence viverrid feeding ecology. First, the accuracy of the population estimates are assessed. Then the extent of seasonal availability of food and its effects on prey selectivity are examined. The finding that most prey are seasonal, yet major prey of the viverrids do not mimic these fluctuations, is investigated. This is anomalous as small carnivores have long been considered opportunistic feeders (Rowe-Rowe 1971, 1978; Ewer 1973; Delibes 1976; Kingdon 1977; Rood & Waser 1978; Smithers 1983 Lynch 1983; Ben-Yaacov & Yom-Tov 1983; Delibes *et al*. 1984; Alcover 1984; Louw & Nel 1986) although recent work has questioned these findings (Kruuk & Parish 1981; Sadie 1983).

Important points and hypotheses will be raised to prepare the reader for the final discussion in Chapter 7. In particular, much attention will be given to the small mammals which represent the bulk of viverrid prey (Chap. 4).

Accuracy.

A central issue of any estimate of animal abundance is its degree of accuracy and precision (Southwood 1978). Since precision refers to deviation about the estimate, high precision need not imply accuracy (Begon 1979). Variability is more the rule than the exception in natural systems and a certain loss of precision must be accepted. Although difficult to determine, accuracy indicates the reliability of the results and an attempt must therefore be made to interpret

1. Small mammals

Large captures of R. pumilio, M. natalensis and L. rosalia (Appendix 2) were expected as these species are easily caught (Meester, Lloyd & Rowe-Rowe 1979; De Graaff 1981; Nel 1983; David & Jarvis 1985). Otomys spp., on the other hand, are notoriously difficult to trap (Davis 1973; Taylor & Green 1976; Bond, Ferguson & Forsyth 1980) and may be under-represented by trapping (Rowe-Rowe & Meester 1982; Mendelsohn 1982; Rowe-Rowe 1983; Appendix 2). The statements by De Graaff (1981) and Willan (1982), that Otomys spp. are often plentiful where they occur, further alludes to under-representation of this genus.

Trap size has an important influence on trap success. That M. natalensis and R. pumilio were the optimal size for the trap used in the study (Willan 1979) may further explain their high capture rate. Similarly, low captures of the difficult-to-catch M. minutoides, Dendromys spp. and S. infinitesimus may be due partly to their small mass and the coarse sensitivity of the PVC trap trigger mechanism (Rautenbach 1982; De Graaff 1981; Smithers 1983; Bowland 1985). Willan (1979) has suggested smaller traps with more sensitive triggers when catching these species. Higher captures of M. minutoides in the array traps probably resulted from their poor jumping powers (De Graaff 1981) and may have applied to other small species.

At the opposite extreme, larger traps than used in this study, may be required to trap Otomys efficiently (Willan 1979),

although other factors such as behavioural response to traps and bait preferences (Willan 1986) undoubtedly influence success rates. But, despite using preferred bait (Willan 1986) and setting traps in optimal habitat, Otomys spp. captures were still low.

Otomys spp. are key prey for many predators (Chap. 4; Vernon 1972; Dean 1973; Rowe-Rowe 1983) and their low numbers are surprising, especially if viverrids are opportunists (see references at beginning of discussion). Before 1980, at VCNR, Bourquin & Sowler (1980) considered Otomys spp. less common than R. pumilio (Bourquin & Sowler 1980; Bourquin pers. comm.[1]). It is likely that small mammal abundance declined during the severe 1982/3 drought (see Davis 1973; Brooks 1974; Meester et al. 1979; Perrin 1980b; Willan 1982; Bowland 1985; Delany 1986). Trapping results during 1984 support the idea that R. pumilio and especially M. natalensis, as a result of high reproductive capabilities (Meester et al. 1979; Perrin 1980a; Delany 1986), increased rapidly after the drought but Otomys spp. did not as they are slow to recolonise (Meester et al. 1979; Perrin 1980a).

In February 1985, floods (Fig. 2.5) may have further reduced Otomys populations (see Davis 1973; Perrin 1980a; Willan 1982) and trapping figures for 1985 were similar to those for 1984. Runways with feeding sign, an important indicator of Otomys presence (Rowe-Rowe & Meester 1982), were infrequently seen during these years. In 1986 fewer R. pumilio, M. natalensis

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and L. rosalia were caught, Otomys spp. being the only rats to increase, albeit slightly. During 1986, in contrast to previous years, Otomys sign was more abundant and they were caught each time traps were set although in low numbers.

In conclusion, consecutive density-independent factors reduced Otomys spp. populations in the early 1980's but signs of recovery were evident by 1986. But because Otomys spp. populations are difficult to estimate using trapping methods, their numbers are probably higher than indicated (Appendix 2; see Rowe-Rowe 1983). Nevertheless, the very low numbers caught, the overall scarcity of their sign and the belief that VCNR may not be optimal Otomys habitat (Willan pers. comm.[2]) suggests that this genus was not abundant. Indeed, there is no evidence that these rodents were abundant in the reserve. This has an interesting consequence; since Otomys spp. are major prey (Chap. 4) but occur in relatively low numbers, they represent a limiting resource and selection for this species is implied.

But why should these viverrids select Otomys spp. over the more abundant R. pumilio and M. natalensis? If the viverrids are to be able to distinguish among different prey species (Chap. 4), is it unreasonable to believe that they can identify a large species like Otomys, nearly three times the mass of R. pumilio and M. natalensis? Because of this mass discrepancy the energy return per unit effort would be higher for Otomys than the other rodents. Further, if this "optimal

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prey" is readily caught and highly palatable, it will compound selection for that prey. Factors such as palatability are unmeasureable, but Otomys are sluggish relative to R. pumilio and M. natalensis.

If Otomys spp. can be identified, then more effort should be put into pursuing this species because it is energetically valuable. But, if another rodent is encountered, it is unlikely that the predator will not chase it although the giving up time (GUT) (Charnov 1976) may well be shorter for the non-preferred prey. The combination of factors, high energy value for Otomys and its ease of capture, may account for selective predation on Otomys spp. when compared with the lower energy value and relative difficulty in capture for other small rodents. However, the abundance of these other rodents may explain why they occur in the diet of viverrids and especially Herpestes.

2. Other prey

Less information is available on differential trappability of prey other than small mammals (Appendix 2), therefore this section is limited to general comments. Similar population estimates, derived from different methods, enhance the reliability of those estimates (Southwood 1978). Comparison of Orthoptera numbers, determined from absolute and relative methods, indicat s a degree of congruency, certainly within the limits of the estimates. A similar comparison for Amphibia also shows agreement and these prey categories were considered adequately represented. But beetles and small mammals were under-represented in the absolute estimates

compared with the relative techniques. Rood (1975) found that invertebrates had a greater biomass than vertebrates in East Africa and the absolute estimates in this study similarly revealed Coleoptera and Orthoptera having greater biomass than small mammals.

The array traps were biased towards epigeic species and this was reflected in the large number of beetles (particularly Carabidae) caught in the traps. Numerous Orthoptera were also captured but few other insect Orders. Few scorpions, Scolopendromorph centipedes and amblypygids were trapped although eaten regularly by viverrids (Table 4.2). Their preference for cover (under rocks, logs and decaying material; Lawrence 1953) and the relative openness and lack of rocks surrounding the array traps, may partly explain these low captures. Nevertheless, it is likely that these invertebrate predators were less abundant than other invertebrate groups.

The array traps were designed to capture reptiles (Campbell & Christman 1982) but their effectiveness is probably limited by the size of the reptile. Although most snakes are wide-ranging, active predators and unlikely to occur at very high densities, infrequent capture and recapture suggests they were scarce. This contrasts with the reptile species diversity in which 32 reptilian species have been listed (Maddock & Zaloumis 1987) and it is possible that reptiles were more common than revealed by trapping.

With respect to crabs, Turnbull-Kemp (1960) indicated higher biomass estimates for Potamonautes sp. than found here. However, the difference between Turnbull-Kemp's (1960) results

and mine may be attributed to the inclusion of numerous small crabs in his estimate. Consequently, densities at VCNR may accurately represent the stream populations of adult crabs, since the sampling method is effective (Raubenheimer 1986; L. Alexander pers. comm.[3]) and the impression was that most large crabs were collected. However, because small crabs were excluded total biomass was under-estimated but still revealed an abundance of this prey.

Seasonality.

Seasonality in many prey categories was shown. In particular, anuran ecology and behaviour are closely associated with temperature extremes and rainfall (Duellman & Trueb 1986) resulting in hibernation (Poynton & Bass 1970) or, at least, inactivity during winter.

The markedly seasonal fluctuations in crab numbers (P. sidneyi), also noted by other workers (Raubenheimer 1986 and references therein), have been explained by inactivity and/or cessation of feeding associated with cold water, ecdysis or periods of berry (Passano 1960; Raubenheimer 1986). P. sidneyi also exhibits sexual differences in moulting times (Raubenheimer 1986), when crabs may remain in their burrows (Vannini & Gheradi 1981). Crab abundance in this study correlated well with these variables; fewest animals were collected when water temperatures were low, or both sexes were in ecdysis or females in berry (March to June). Most animals were collected between October and December when both sexes

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were active and intermediate numbers were collected when only one of the sexes was moulting. Thus, although abundant during the rest of the year, crabs are seen as a limiting resource during the cooler months and Atilax requires special hunting strategies to locate these prey (Baker 1987c, 1988a).

Climatic factors considered responsible for low captures of both crabs and frogs during winter may well affect S. punctulatum and Juliform millipedes, Coleoptera and Orthoptera which all show distinct seasonal patterns of abundance. Climatic influences may also be indirect, mediated through vegetation growth, hormonal stimulation of breeding behaviour etc. (Perrin 1980b). Whatever the causal agents, most prey categories decrease in number during winter and increase dramatically in spring when temperatures rise and rains fall (Figs. 2.4 & 2.5). Thus, although prey populations do not disappear during winter, Carabid beetles may be present year round (Miller pers comm.[5]), fewer prey are available between May and August. Similar findings were recorded by Sadie (1983) in the Transvaal.

Small mammals were an exception and increased in number after the summer breeding season. Most rodents have a winter non-breeding season (Davis 1973; De Graaff 1981; but see Perrin 1980a&b) when populations are composed almost entirely of individuals born in the previous breeding season (Brooks 1974; Coetzee 1965; Perrin 1980a&b; Mendelsohn 1982; Nel 1983).

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Seasonal breeding results in high density, juvenile-dominated winter populations (Mendelsohn 1982) and individuals with low mass (Coetzee 1965); adults dominate the breeding populations in summer (Perrin 1980b). Towards the end of winter, when conditions are harsh and food is of low quality (Perrin 1980a; Davis & Meester 1981), mortality may be high and predators are confronted with low-mass rodent prey (juveniles in poor condition) and increasingly smaller populations of all prey (Sadie 1983). Therefore, although rodent trapping was not conducted at the end of winter, it appears that small mammals, like other prey populations, decline during this period (Coetzee 1965; Davis 1973; Taylor 1976). The overall result is that less food is available during late winter compared with other periods.

The seasonal fluctuations of most prey was not observed in the diet of the viverrids (Chap. 4) especially the major fluctuations of the prey of Atilax. Rodents also showed a slight decline in the diets of Herpestes, Galerella and Genetta despite being more abundant in traps during mid winter although they may have declined by late winter. Increased rodent sociality during this period (Brooks 1974; Willan 1982) may result in increased vigilance against predators making these prey difficult to capture. Thus, the finding that prey eaten did not track the availability of prey in the environment and that Otomys spp. were important prey, despite being relatively rare, calls for a more detailed examination of prey selectivity by these viverrids.

Prey selectivity

Before I discuss prey selectivity, the terms generalist, opportunist and specialist must be defined. Previously, generalist and opportunist have been used interchangably but few authors have defined these or the term specialist (see Rosenzweig 1986). However, it is vital to the understanding of resource use that these terms be used in context. Rosenzweig (1986), in an attempt to clarify this problem, suggested a distinction be made between behaviour and ability. Thus, "generalist" describes the ability to use a wide range of resources and "specialist" the ability to use a small subset of those resources (Rosenzweig 1986). "Opportunist" and a new term "selector" describe the behaviour of an animal, i.e. an opportunist uses a wide range of resources roughly in proportion to their availability while a selector uses a smaller range (Rosenzweig 1986). These terms will be used below.

The diets (Chap. 4) of these five "opportunistic" viverrids (Rowe-Rowe 1971, 1978; Ewer 1973; Delibes 1976; Kingdon 1977; Rood & Waser 1978; Smithers 1983 Lynch 1983; Ben-Yaacov & Yom-Tov 1983; Delibes et al. 1984; Alcover 1984; Louw & Nel 1986) differed, sometimes markedly, did not reflect seasonal changes in prey abundance and the viverrids did not increase the range of prey taken during periods of food shortage (Chap. 4). In addition, Sadie (1983) found that Mungos showed a preference for vertebrates in feeding trials and were as capable of killing these prey as were the more predatory viverrids. However, the natural diet of Mungos is small invertebrates (Neal 1970; Rood 1975; Smithers 1983; Sadie

1983) and Sadie (1983) concluded that selection for invertebrates was a matter of necessity not choice. A similar finding was made for Atilax which showed a preference for rodents and avoidance of crabs in feeding trials but in the scats of wild animals, this was reversed (Baker 1987c, 1988a).

Clearly then, prey selection is influenced by a number of factors and not just prey abundance as is implied by opportunism. As suggested above, I consider this poor evidence of opportunism and a more detailed examination of prey selection is required. Habitat preferences of predators and prey are considered in Chapter 6 therefore the influence of habitat on prey selectivity will be deferred until Chapter 7.

In terms of supplementary prey viverrids were opportunistic, as predation on these prey tracked the seasonal fluctuations of availability (Chap. 4). For example, Sphaerotherium spp. in the diet of Atilax (Fig. 4.13) and dassies, blue duikers and cane rats, which appeared in the diet of Atilax, Genetta and Galerella from late autumn to early spring were also the main prey of Crowned, S. coronatus and Martial Eagles, P. bellicosus (Maclean 1985). These raptors breed during this period (Maclean 1985) and it is possible that, during this time of increased predation by the eagles, prey remains were scavenged from beneath eagle nests. But, unpublished results indicate that the viverrids could have killed some of these larger mammals (see Langley 1986).

With opportunistic feeding, it is predicted that as food abundance decreases, diet diversity (trophic niche breadth)

should increase (MacArthur & Wilson 1967; Schoener 1974b). No such increase in niche breadth in winter was evident (Chap. 4). Thus, a relatively constant prey preference throughout the year implies a selective mode of foraging.

If I am correct in assuming at least a degree of selectivity in viverrid feeding behaviour, then similar selectivity patterns should be in evidence throughout the range of these viverrids. For example, I suggest that Atilax separates from the other sympatric viverrids along the trophic niche by selecting aquatic, often hard-bodied, prey (Chap. 4). In St. Lucia, Natal, Atilax feeds mainly on crabs, prawns, insects, frogs and fish (Whitfield & Blaber 1980) while in the Natal midlands, crabs, frogs and mammals were important prey (Rowe-Rowe 1975). A comparative study of inland- and coastal-dwelling Atilax feeding habits revealed that amphipods (common on beached kelp), crabs and insects were main prey of the coastal animals while inland mongooses ate mainly crabs, fish and insects (Louw & Nel 1986). Finally, in the Mountain Zebra Park, crabs were again the main prey followed by birds and insects (Du Toit 1980). No other South African viverrid feeds preferentially on crabs or fish (Smithers 1983). Thus, there is a striking similarity in the diets of Atilax living in habitats as diverse as beaches, riverine thickets surrounded by arid montane grassland, and forest as well as with the results of this study.

The selection of crabs by Atilax must be examined in more detail. Feeding trials indicate that crabs ranked low in the food preference test (Baker 1987c, 1988a). Further, crabs are troublesome prey: they were difficult to locate, capture, kill

and eat compared with frogs, rodents, shrews, birds and insects, although this may, in part, have been exaggerated by captivity (unpublished data Maddock; Baker). Baker (1987c, 1988a) suggests that selection for crabs in the wild is a function of its solitary nature, manual dexterity, well developed teeth (Chap. 3) and jaw musculature and a vacant trophic niche (recall that crabs were very abundant at VCNR). The foot structure of this species enables it to walk across soft mud (Taylor 1974, 1979), places at VCNR where numerous Atilax and crab spoor were seen. But, although water mongooses are pre-adapted to dealing with crabs, opportunism does not explain why Atilax eat crabs in preference to the abundant, less seasonal and apparently preferred rodents and frogs (Baker 1987c, 1988a). It does appear that Atilax bases its prey selection on factors in addition to prey abundance.

At VCNR, the very high occurrence of Otomys spp. in the diet of Herpestes is indicative of selection for these rodents. When Otomys spp. were absent in 1984, other rodent and mammalian prey supplemented the available Otomys spp. (Chap. 4) but Otomys spp. were still taken most frequently. These rodents were never the most common prey at VCNR yet Herpestes showed overwhelming selection for them. Surely this is not an example of an opportunistic feeder, taking prey in proportion to its abundance.

Few diet analyses are available for Herpestes but these indicate a broad similarity in food preference: scats collected from the margins of exotic Acacia cyclops and indigenous forest in the Cape Province show Herpestes eating mainly rodents, (R. pumilio and O. irroratus having the

highest and equal frequency of occurrence) with smaller numbers of birds and reptiles (Stuart 1983). Insects were the only other prey item to occur frequently in this sample (Stuart 1983). Delibes et al. (1984), working in Spain, concluded that mammals, mainly rabbits (Oryctolagus cuniculus) and reptiles, formed the basis of this species' diet, both in their frequency of occurrence and as a percentage of the consumed biomass. All other prey were regarded as supplementary (Delibes et al. 1984). Delibes (1976), reached similar conclusions in an earlier study which are in essential agreement with those presented here. The larger size of this mongoose (Table 3.1) and its generalist leg structure (Taylor 1974, 1979) would enable the animal to cover large areas in search of its preferred prey (see Table 6.9) while its dentition is well suited for a predatory mode of life (Petter 1969; Ewer 1973; Chap. 3).

The other viverrid that I consider to show selector feeding behaviour is Mungos. Neal (1970), working in East Africa, found coleopterans and millipedes major prey of Mungos and this was supported by Rood (1975) in the same area. In the Transvaal, in a more detailed analysis based on biomass, Sadie (1983), found Coleoptera and millipedes as well as vertebrates were important prey and concluded that Mungos were specialists on slow-moving terrestrial, semi-fossorial and fossorial, invertebrate prey. Little variation was found among the diets of Mungos living in different habitats suggesting that prey selectivity is relatively consistent (Rood 1975; Sadie 1983).

Data presented in this thesis and those of Waser (1980) show

similar results to the above-mentioned studies. Particularly important was the selection by this viverrid for distasteful prey, like millipedes, which possess repugnatorial glands (Lawrence 1953) and should be avoided by many predators. The ability to feed on distasteful prey segregates Mungos from sympatric small carnivores (Sadie 1983).

The reasons for Mungos feeding mainly on invertebrates are probably complex, involving consideration of more than just prey abundance (Sadie 1983). Unlike large carnivores, the social groups of Mungos and H. parvula have evolved as an anti-predator strategy and not in response to food (Kruuk 1975; Rosevear 1977; Rood 1983). Being social has an important consequence for Mungos; sociality requires a food supply that occurs at relatively high densities (McNab 1983) thus, groups tend toward insectivory (Ewer 1973), concentrating on clumped prey which will not be disturbed by large numbers of hunters (Baker 1987c, 1988a). Further, social viverrids feed on rapidly renewed prey, such as invertebrates, to offset the costs of shared foraging areas (Waser 1981). Overall, the dentition of this species is well adapted to an insectivorous diet (Petter 1969) and its long claws are used to excavate fossorial prey (Chap. 3; Taylor 1974, 1979; Sadie 1983).

Thus, despite the abundance of alternative prey and despite the seasonal fluctuations of preferred prey, Atilax, Herpestes and Mungos selected prey with remarkable consistency throughout the study, a conclusion which is supported by previous studies in Africa. Further, these viverrids appear pre-adapted for this selection.

Based on this evidence, what I propose is that these viverrids have a relatively wide range or group of preferred prey and this group is species specific. Authors generally agree that Herpestes eats mainly mammals, predominantly rodents, that Atilax eats mainly aquatic prey supplemented with mammals and other terrestrial organisms while Mungos specialises on invertebrates (see references above). The diets of these three sympatric predators are therefore very different although they may well confront similar prey items.

The ability of mongooses to utilise a wide variety of prey has been well documented (Rowe-Rowe 1971, 1978; Kingdon 1977; Smithers 1983; Baker 1987c; this study) and used to support the idea of opportunistic feeding. Therefore, in the terminology of Rosenzweig (1986), they are generalists (i.e. they have the ability to exploit a wide range of food types). But each of these three species concentrates on a specific group of prey (mammals, aquatic prey and invertebrates). When possible, they feed on the preferred item (Otomys spp., crabs and Coleoptera and millipedes; Delibes et al. 1984 and references above) but are quite able to eat the broader group of prey and also non-preferred prey, i.e. prey not within the preferred group (Taylor 1986). A similar type of feeding pattern was described on theoretical grounds by Glasser & Price (1982) who consider a species that selects when resources are abundant but is opportunistic when resources are rare, a facultative strategist.

This strategy is adaptive. Numerous viverrids exist in sympatry (Chap. 1) and the ability to specialise on a particular prey group may well aid coexistence throughout

their range (Chap. 4; Taylor 1986) and it is more likely for small carnivores to act as selectors than large carnivores (Bekoff *et al.* 1984). In this regard, viverrids act as "selectors" (Rosenzweig 1986). However, prey of small carnivores are often subject to great aseasonal fluctuations in number so, the ability to exploit a range of prey when preferred food is scarce would be an advantage. Specialisation, without the ability to exploit other prey, could greatly reduce the fitness of these carnivores, therefore they maintain their ability as generalists (*sensu* Rosenzweig 1986). These three mongooses are thus generalist selectors (Rosenzweig 1986).

There is also theoretical support for this generalist/selector behaviour. Because of a small energy gain per item, it is generally not considered advantageous for a vertebrate to specialise on a food type (Schoener 1974b). A compromise between specialisation (selector behaviour) and the ability to eat a wider range of food when necessary, *i.e.* a generalist/selector, may be most advantageous.

This strategy also appeared to benefit *Herpestes* when *Otomys* spp. were scarce. During 1984 this species, in contrast to the rest of the viverrid community (Fig. 4.9), ate more *Otomys* spp. than other rodents. If there is indeed an advantage to eating these large rodents (large energy return, short handling time, palatability *etc.*; Charnov 1976), *Herpestes* certainly benefitted from its selector behaviour in 1984.

These three viverrids are thus, considered to show, not opportunistic behaviour, but selector behaviour which can be

adaptive. Perhaps part of the reason why researchers have considered small carnivores opportunistic is because semi-quantitative methods of scat analysis have been used (Sadie 1983; Appendix 1) consequently it has not always been possible to distinguish supplementary prey (which *are* taken opportunistically), from primary and secondary prey (which are often selected).

The other two viverrids at VCNR, *Genetta* and *Galerella*, do not appear to exhibit a similar degree of selective behaviour; their foods include a range of important prey, they show more seasonal variation in foods eaten than *Herpestes*, *Atilax* and *Mungos* and although their niche breadths were intermediate, were third and fourth highest in the study (Table 5.8). Thus, like the above-mentioned viverrids, they would be generalist in terms of ability but would differ in being less selective in terms of behaviour (Rosenzweig 1986). Theoretically and practically, it is easier to pack three generalist selectors and two generalist opportunists into an assemblage than five generalist opportunists. Competition between a facultative strategist (*Atilax*, *Herpestes* or *Mungos*) and a obligate generalist (possibly *Genetta* or *Galerella*) results in increased niche overlap, terminating in overlap greater than observed for other strategist combinations as resources become scarce (Glasser & Price 1982). However, in the more natural situation, where resources are renewed, overlap between these two strategists may be held at a lower level than other combinations (Glasser & Price 1982) and result in increased stability.

The point I am making is not that these viverrids select

solely the rarest resource (extreme form of selector behaviour; Hurlbert 1978) but suggest that Herpestes, Atilax and Mungos pass over certain prey in favour of more preferred food. Note "passing over" may refer to hunting in a certain manner, habitat or at a specific time so that the probability of capture of a particular prey is maximised.

It may be best, or easiest, for a predator to eat the most abundant prey but other factors, together with abundance undoubtedly influence prey selection: ease of capture, search image, distribution pattern, energy return and size of prey etc. (Curio 1976; Kruuk 1975; Bekoff et al. 1984) as well as hunting strategy and social organisation (Waser 1980, 1981). It seems short sighted to believe, based on semi-quantitative analyses, that predators select prey purely on the basis of abundance. The hypothesis that these viverrids select easily captured prey when possible but maintain the ability to feed on a wider range when necessary is more realistic. In support of this, van Hensbergen (1984) working in Europe, found Genetta genetta more selective in feeding habits than three other sympatric small carnivores. According to the theory above, the adaptive behaviour of Genetta genetta enabled it to feed selectively when possible.

Throughout this discussion habitat selectivity by predators and prey, as well as their activity regimen, has been discounted. The next Chapter investigates the spatial niche and in Chapter 7 I will take up this argument and introduce the results of habitat selection.

In summary, Hypothesis I, that the viverrid assemblage

segregates along the trophic niche (Chap. 1), appears to be upheld in so far as Mungos and Atilax have unique diets. If the idea of Herpestes selecting Otomys is correct, then this species also has a unique diet. The wider, less selective, diets of Galerella and Genetta, may also facilitate coexistence within this assemblage. In addition, size of prey and their activity periods differ among the viverrids.

CHAPTER 6

USE OF TIME AND SPACE

INTRODUCTION

This chapter deals with the spatial and temporal niche dimensions of the five viverrid species and tests if viverrids partition resources along these niche dimensions (Chap. 1; Hypotheses II and III). Most animals have certain habitat requirements or are more likely to be encountered in one habitat than another (Dixon & Chapman 1980). Thus, the aim of this chapter is to determine the extent of habitat selectivity exhibited by these predators and their major prey species and to note differences among the viverrids. This is achieved by examining viverrid home range utilisation as revealed by radio-tracking and comparing habitat selectivity with habitat availability in the reserve. Traps used to capture viverrid prey (Chap. 5) were set in different habitats and analysis of these trapping results is used to determine habitat preference of the major prey categories. In Chapter 7, both data sets are used to see how closely viverrid habitat and food selectivity are associated.

The habitat configuration at VCNR makes it difficult to analyse habitat selectivity. Open habitats (grassland, vlei, bushclump) occupied more than 70% of the reserve while among the closed habitats (forest, riverine, scrub and streambank forests) there was great vegetational diversity (Fig. 2.1 & 2.3). Often these habitats formed small, isolated units with

riverine and streambank forests having a linear distribution (Fig. 2.1). This resulted in a mosaic of small habitat blocks and a large area of forest margin.

This fine-grained pattern meant that viverrids probably passed through several different habitats during their daily activities. This is even more likely for species with large home ranges. Consequently, the data were expected to contain considerable "noise" due to viverrids passing through non-preferred habitats; nevertheless, trends indicating preferred habitats should be apparent.

Consideration of the diel activity regime of the viverrids is used to formally demonstrate the partitioning of this resource among the five species. This is an important aspect of the study as it extends Schoener's (1974a) findings that predators only are most likely to partition this resource (Chap. 1).

MATERIALS AND METHODS

Viverrids caught in drop-door traps were immobilised with ketamine hydrochloride (Chap. 3; Maddock 1988) and fitted with radio transmitters (148 MHz, AVM Instrument Co., California), either as a collar or harness. Radio-marked viverrids were located with a hand-held, three element Yagi antenna and either an AVM LA 12 or Telonics (Telonics Inc., Arizona) receiver using standard triangulation methods from known points (Rolley & Warde 1985). Because of the large distances travelled by some individuals, known point triangulation was impracticable so these radio-marked viverrids were followed and their movements mapped. This technique is similar to "predictive tracking" (MacDonald 1978) but differed in that

visual sightings of the animals were rare. In all cases locations were made every 20 minutes or hourly, depending on whether the animal was moving or inactive and radio-tracking sessions continued for two to thirty-six hours at a time. In addition, spot checks were made on all animals at least six times a month and usually more frequently. All data were transcribed on to a 1:10 000 habitat map and the locations assigned to one of ten habitat types (Fig. 2.3).

The accuracy of the radio-tracking equipment was within 55,4+49,0 m of the correct location (n=7). This was determined by placing transmitters randomly in the reserve and locating them in the same manner used to find the radio-marked viverrids.

Viverrid activity regime

Data on the activity regime of the different species were gathered during radio-tracking sessions. An animal was considered "active" if its position changed between successive fixes. Further information was obtained from sightings of undisturbed viverrids in the reserve.

Viverrid habitat utilisation

1. Bonferroni **z** statistic

The radio-tracking data, supplemented with random observations of viverrids, their spoor and locations of scats collected for diet analysis (Chap. 4) were used for the habitat utilisation studies (Pietz & Tester 1983; van Hensbergen 1984; Litvaitis, Sherbourne & Bissonette 1985b). Bonferroni's confidence intervals, based on the **z** statistic and used in conjunction

with a goodness-of-fit test, were employed to determine if viverrids exhibited habitat selection (Neu et al. 1974; Byers et al. 1984; Litvaitis et al. 1985a; Rolley & Warde 1985; Alldredge & Ratti 1986). By using simultaneous confidence limits this method tested the difference between the proportional observed and expected use of specific habitats (Neu et al. 1974; Chap. 1).

Availability (area) of all habitats in the reserve, was measured from a 1:10 000 vegetation map (Sandwith & Brown 1981) using a planimeter (Figs. 2.1 & 2.3). A 50 ha sugar cane plantation was included in this analysis because it was where rodent trapping was conducted (Fig. 5.1) and where numerous scats of all five species of viverrid were collected. It also included part of the home range of a male Herpestes. The relative abundance of forest margins, vlei, stream and dam edges were determined using diagonals drawn from the NW to SE corners of a 1 km^2 grid map-overlay (Kaminski & Prince 1984). The number of times the diagonal intersected one of these habitat variables was expressed as a percentage of the total number of intersections (Kaminski & Prince 1984).

Expected values were based on the assumption that viverrids moved through the reserve at random, using each of the ten habitats in proportion to their availability (Fig. 2.3; Pietz & Tester 1983). Differences between observed and expected values were considered to indicate habitat selectivity when $P<0,05$.

The Bonferroni z statistic was also computed for each home range to test habitat selectivity within the immediate

vicinity of the home range and the extent to which viverrids selected the area in which to establish that home range (Johnson 1980). Habitat availability was determined by connecting the points of maximal peripheral viverrid movements and measuring the area of each habitat type enclosed in the minimum concave polygon (Collins & Urness 1983).

2. Stepwise multiple regression

The Bonferroni **z** statistic is a useful way of testing habitat selectivity (Litvaits et al. 1985a; Rolley & Warde 1985). However, stepwise multiple regression allowed a finer resolution of viverrid habitat utilisation by introducing additional variables considered important in explaining viverrid distribution (Table 6.1). Strength of association between the dependent variable (species) and independent variables was determined by the coefficient of multiple correlation (R) (Kaminski & Prince 1984). The relative influence of the independant variables on the dependent variable was indexed by the absolute value of the former´s standardised regression coefficient - Beta (Kaminski & Prince 1984).

Prior to statistical treatment, data were subjected to Pearson´s correlation analysis (Kaminski & Prince 1984). Table 6.1 lists the variables with correlations less than 0,75 which were included in the analyses (Table 6.1).

TABLE 6.1. The nineteen habitat variables used in the multivariate analyses. Distances were measured directly from the viverrid location to the nearest features listed below.

Computer label	Variable and meaning
HABITATA	One of the 10 habitat types in which animal was located (Fig. 2.3)
WDIST	Distance to nearest water measured in metres
CROPS	Distance to nearest crops measured in metres
ROX	Distance to boulders in streams in metres
FOR	Distance to the cover of forest in metres
OPEN	Distance to grassland, vlei, cane or disturbed grassland in metres
STREAM VLEI DAM TRCKL	Distance to nearest water type measured in metres

3. Canonical discriminant function analysis

Finally, to elucidate those habitat variables that segregated the viverrid assemblage, the data were subjected to canonical discriminant analysis (Hayward & Garton 1988). This is a predictive model, used when there are more than two a priori identified groups (Jeffers 1978). This type of multivariate analysis has been criticised as subjective because the model aims to emphasise differences among dependent variables (Rotenberry & Wiens 1980). This valid criticism was, however, rejected since the three methods used here yielded similar results. It was unlikely that the canonical analysis results were spurious, and they were considered to clarify differences.

4. Home range analyses

Throughout this study home range is defined as that area which an animal occupies during its normal daily activities (Burt 1943). The data used to determine the home range of the

viverrids were derived from radio-tracking. A 125 X 125 m grid (larger than the error in the telemetry data collection) was placed over the plotted locations of each radio-tracked individual and the number of locations in each grid square recorded. These data were then analysed by the McPaal Program, which analyses animal location data by five commonly used models: Minimum Convex Polygon (Mohr 1947); Minimum Concave Polygon (Stickel 1946); 95% Ellipse (Jenrich & Turner 1969; Koeppl, Slade & Hoffman 1975); Fourier transformation (Anderson 1982) and Harmonic Mean (Dixon & Chapman 1980).

These models vary in sophistication and realism; the minimum area methods being computationally simple and perhaps slightly subjective while the other methods have a probabilistic and, therefore, more objective, distribution (Anderson 1982; Spencer & Barrett 1984). The probabilistic distribution also confers a realistic advantage: home ranges are usually amoeboid therefore it is unrealistic to assign fixed boundaries to a home range (Burt 1943). The probabilistic models avoid this assumption. I have tabulated the results of all five models for comparative purposes (see Jenrich & Turner 1969) because there is little agreement among biologists of how to measure home range and, often, results from several models are most useful (Anderson 1982).

In all models, excluding the minimum area methods, I used 95% contours based on a bivariate probability density function (Jenrich & Turner 1969; Koeppl et al. 1975; Ford & Krumme 1979; Dixon & Chapman 1980; Anderson 1982). This indicates the probability of containing 95% of the animal's locations within that contour. Anderson (1982) suggests using the Fourier

transform 50% probability contour rather than the 95% contour because of the error involved in estimating the height of the utilisation distribution tails. Although the 50% Fourier transform values compared favourably with other models using the same contours, they are not estimates of home range size (Anderson 1982). Consequently, despite the errors and to facilitate comparisons, 95% contours were also used for the Fourier transform data. This model was limited to data with a minimum of 40 locations (Anderson 1982).

In Appendix 4, the home range data and intraspecific overlap in home ranges are used to approximate the density of viverrids at VCNR. These data are compared with the density of major prey in the reserve and the amount of prey eaten per species per day. These results give a rough indication of whether food is a limiting resource and are used in Chapter 7 (Appendix 4).

General

The Bonferroni analyses were carried out using a programme written for a HP 41CX calculator while Pearson's correlations and all multivariate analyses as well as all initial data manipulation were carried out on the University of Natal's Sperry mainframe computer using the Statistical Package for the Social Sciences (SPSS-X) (Nie 1983). Significance was considered when $P<0,05$ except where otherwise stated. Assumptions of these models are examined in Appendix 3.

Once habitat utilisation by the viverrids had been determined, a random numbers table was used to locate 50 sites at VCNR to aid verification of these results (Johnson 1981). Using the habitat analysis results, I predicted which species of

viverrid should occur at each site. I then returned to the study area and searched each site for evidence (spoor, scats, observations) of viverrid presence.

Prey habitat utilisation

To investigate the habitat associations of various prey, Bonferroni's **z** statistic, in conjunction with a goodness-of-fit test, was again employed (Neu et al. 1974). The method identified the habitat in which particular prey were likely to be found by testing the hypothesis that animals distributed themselves equally across all habitats. This was chosen as a null hypothesis rather than comparing selectivity and availability (Neu et al. 1974; Byers et al. 1984) because only a small, standardised area of each habitat was trapped.

To account for the different number of traps set in each habitat, raw data were converted to number of animals caught per 500 trap-nights for the PVC-caught animals, and number caught per 10 trap-nights for the array data (Chap. 5). Since the paired habitat array results (i.e. from traps set in similar habitats) showed a similar dominance ranking (Chap. 5), these data were pooled for examination of the habitat associations of the various prey.

RESULTS

Radio transmitters were placed on 21 viverrids. Due to transmitter failure, only four radio-marked Herpestes, two Atilax, four Genetta and two Galerella (Fig. 6.1), provided more than 20 locations each and could be used in the home range analyses. In total, 819 usable locations were obtained during the study. No radio-tracking data were obtained for Mungos because the only individual captured (Chap. 3) occurred when transmitters were not available.

Viverrid activity regimen

The viverrids were divided into two distinct groups; Genetta and Atilax being active at night while Galerella, Herpestes and Mungos were diurnal (Fig. 6.2). Results are presented as time before or after sunrise or sunset to avoid seasonal bias.

Atilax became active approximately 26 minutes after sunset (n=9; 26±29 min) and, as far as could be discerned by remote sensing, remained active until between 01h00 and 02h00 the following morning (n=4; 2h 56±45 min before sunrise; Fig. 6.2a). There was no evidence of diurnal activity (Fig. 6.2a). Genetta had a similar activity regimen and emerged from their daytime resting-sites between 17h00 and 19h00 (n=13; 53±53 min after sunset) although some were active as early as 16h00 (Fig. 6.2b) and, in two instances, radio-marked Genetta moved from one resting-site to another during the day. Observations were made until 01h00 (Fig. 6.2b).

Most Galerella were active between 08h00 and 18h00 (Fig.

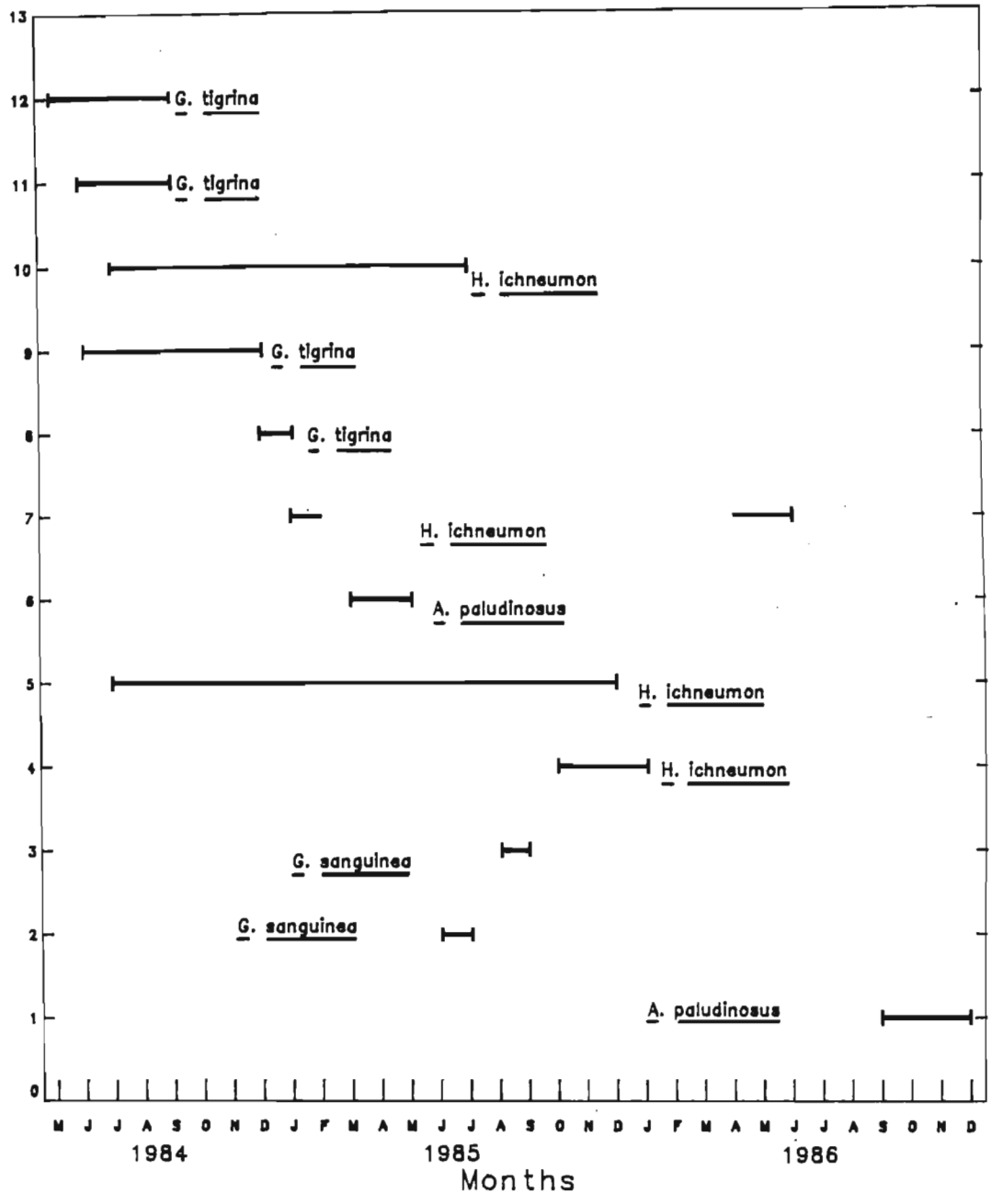

FIGURE 6.1. Duration of attachment of functional radio transmitters to four species of viverrid at VCNR between March 1984 and December 1986.

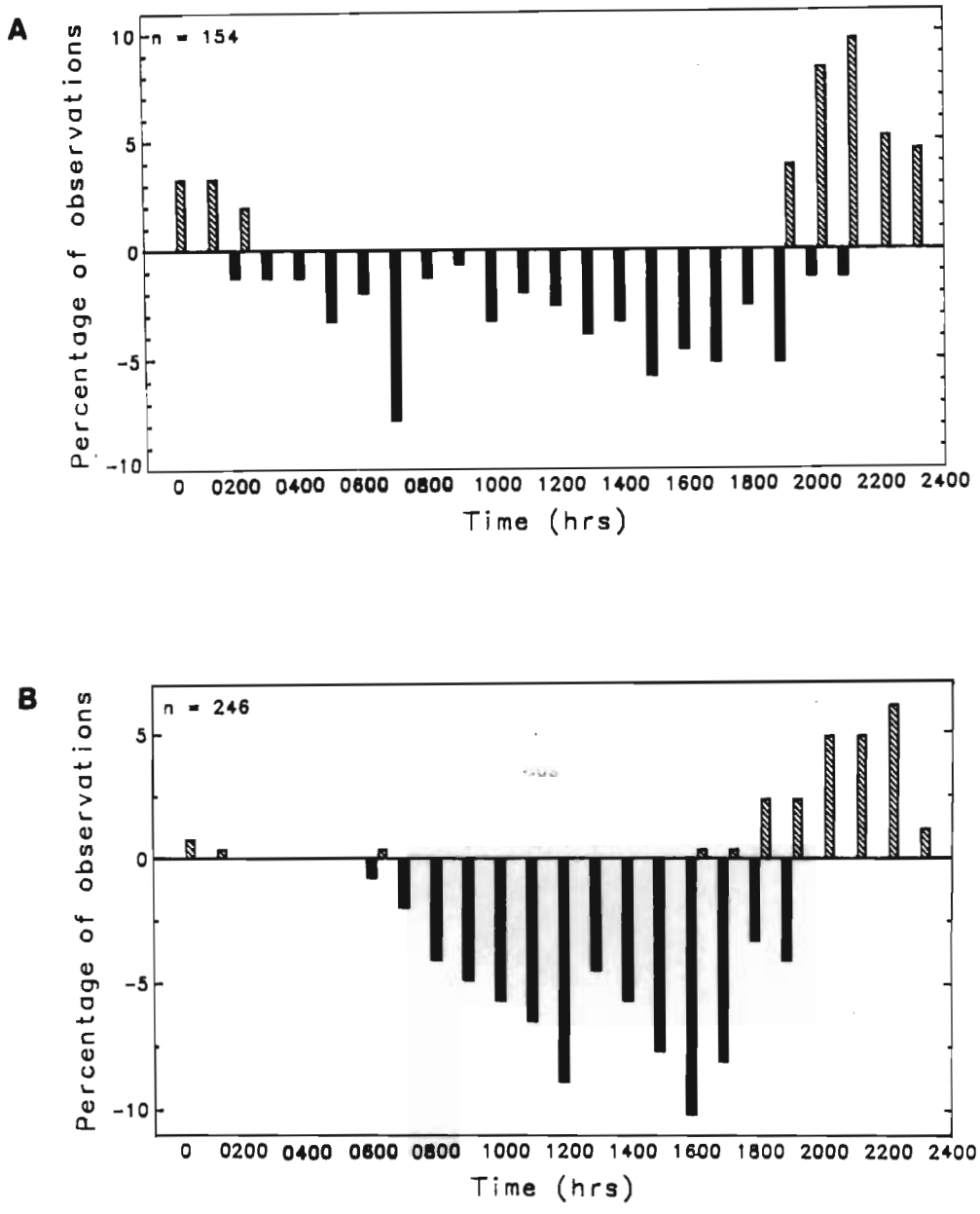

FIGURE 6.2. Proportion of time viverrids were active (hatching) or resting (shaded) during the 24 hour day. A =Atilax, B =Genetta, C =Galerella, D =Herpestes and E =Mungos.

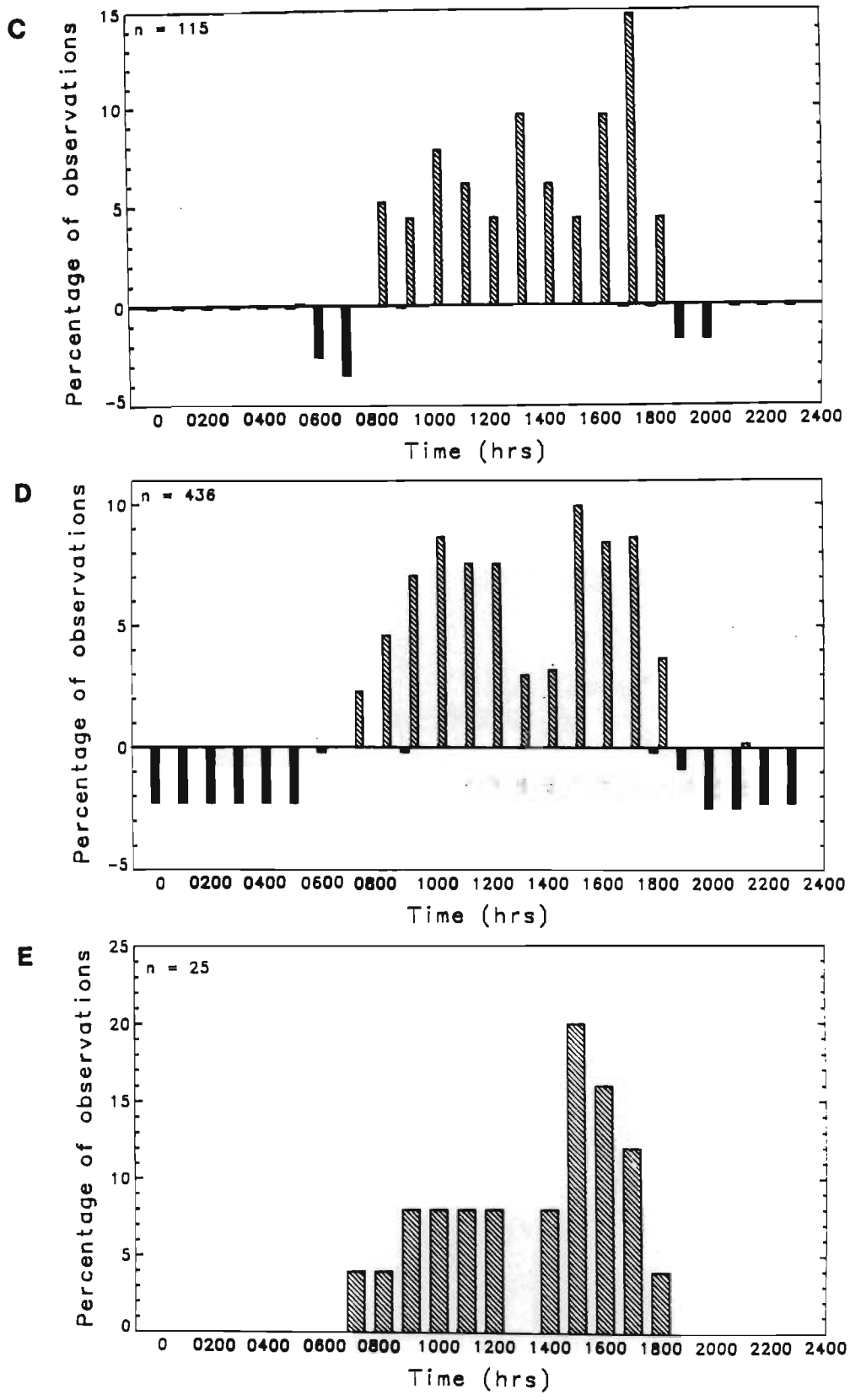

FIGURE 6.2. continued.

6.2c). Radio-marked animals moved from their resting-sites rather late in the morning (n=9; 1h 15±44 min after sunrise); but had they emerged earlier and remained in the vicinity of the den-site, their movements would not have been detected by radio tracking. Galerella showed a slight peak in activity about one hour before sunset (n=24; 52±50 min; Fig. 6.2c) and ceased activity 16±10 min after sunset. Unfortunately, the small sample prevented statistical verification of these trends.

Herpestes were first seen about 45 min after sunrise (n=8; 48±48 min; Fig. 6.2d) and were most active between 09h00 and 12h00 and again between 15h00 and 17h00 ($P<0,05$). Few were active after 18h00 (Fig. 6.2d). As no Mungos were fitted with radio transmitters, activity data were derived from direct observations and all sightings were made between 07h00 and 18h00 (Fig. 6.2e).

Predator/prey activity regimen

The nocturnal viverrids (Atilax and Genetta Fig. 6.2) showed greater selectivity for nocturnal prey (more than 70% of their prey was nocturnal) than for either diurnal (less than 12%) or polyphasic prey (Table 6.2). Such clear-cut distinctions were not apparent for the diurnal Herpestes, Galerella and Mungos (Fig. 6.2). More than 50% of the prey of Herpestes was polyphasic - most of them were Otomys spp. (Table 6.2).

Both Galerella and Mungos were enigmatic in that nocturnal prey comprised the bulk of their diets (Table 6.2). For Mungos this was due to predation on millipedes and carabid beetles (Table 4.2) but might reflect the habit of both mongooses of

searching under rocks, logs etc. where resting prey might be found. This anomaly may also have resulted from a slight overlap in activity times between the diurnal predators and nocturnal prey.

Comparison of the activity regimens of the predators and their prey reveals that most species pairs selected prey with different times of activity (chi-square ranged from 7,99 to 36,13; $P<0,05$) which may help segregate this assemblage. No significant differences were found for Atilax and Genetta or Atilax and Galerella.

TABLE 6.2. Activity periods of the major prey categories found in the diets of the five species of viverrid at VCNR. Given in percentages.

	Nocturnal	Diurnal	Polyphasic
Genetta n=343	76,7	10,5	12,8
Herpestes n=493	25,3	23,8	50,9
Galerella n=186	56,5	16,1	27,4
Atilax n=449	69,9	11,6	18,5
Mungos n=140	50,7	34,3	15,0

Habitat utilisation

1. Bonferroni analysis

The first evidence of habitat selectivity was determined by comparing the observed distribution of radio-tracking locations in each separate home range, with that of an even distribution. This measured the extent of deviation from a uniform utilisation by using Kolmogorov-Smirnov's one-tailed test (Samuel, Pierce & Garton 1985).

Results from the 12 radio-marked viverrids showed that ten deviated significantly ($P<0,001$ or $P<0,05$) from a uniform home range utilisation. Only a male and female Genetta showed no significant deviations. These results indicated that, except for Genetta, which had the smallest home range (see below), certain parts of the home range were used more than others. The highly significant values suggested the presence of core areas.

The Bonferroni tests confirmed that all five viverrids exhibited habitat selection (Fig. 6.3). Analysis of individual home range data showed the same trends that were apparent when habitat availablity of the whole reserve was compared with the mongoose locations provided by the telemetry, observational, scat and spoor data. Thus, to avoid repetition, the home range Bonferroni analyses have been omitted and only results from the larger data set are presented.

Forest types were used either in proportion to their availability by all species, or more than expected although different forest types were preferred by different species; Atilax selected riverine and streambank forest, Genetta forest, riverine and streambank forest and Galerella forest and riverine forest (Fig. 6.3a&b). Mungos stood out as the only species to select scrub forest (Fig. 6.3a). All species used grassland less than expected and generally open habitats were avoided; this was particularly true for Atilax and Genetta (Fig. 6.3b).

Herpestes was an exception and selected open habitats such as disturbed grassland, bushclump, vlei and sugar cane (Fig.

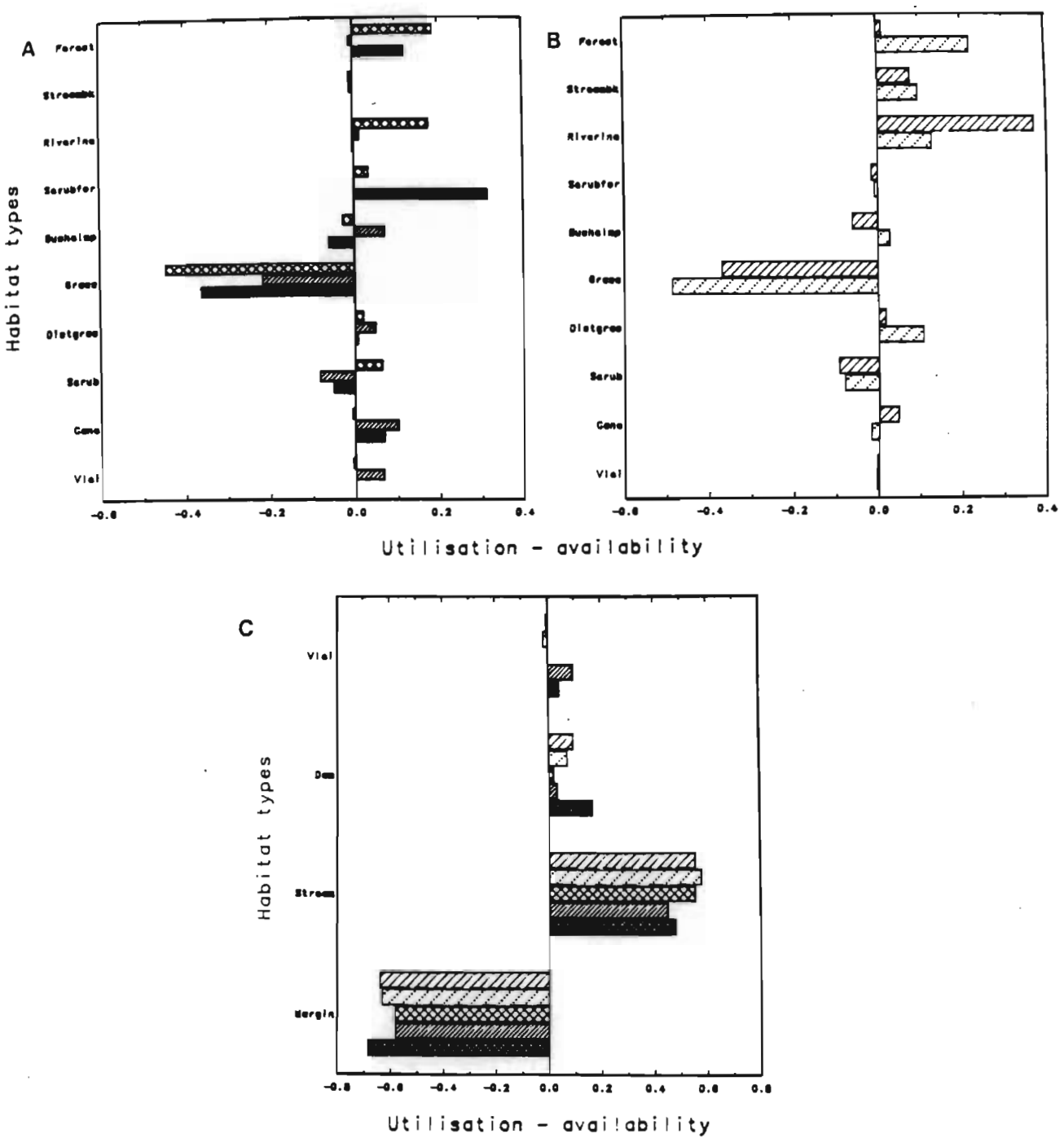

FIGURE 6.3. Macrohabitat use by the five species of viverrid at VCNR showing the difference between proportional habitat use and habitat availability. Use of the ten macrohabitats by diurnal (A) and nocturnal viverrids (B) are shown. C =use of water features and forest margins by all five species. Bonferroni´s z statistic was used to determine selection for, avoidance or use in proportion to availability of each habitat. * =P<0,05; **P<0,01; no asterisk =use in proportion to availability.

=Atilax =Genetta =Galerella =Herpestes =Mungos

6.3a). Based on the Bonferroni tests Herpestes used grassland less than expected (Fig. 6.3a). This apparent under-utilisation was due to the large area of grassland (Figs. 2.1 & 2.3) and the large expected proportional occupation of that habitat demanded by the Bonferroni test in order to show significance. The difference between used and expected was less than -0,3, suggesting that it spent much time was spent in this habitat (Fig. 6.3a) in fact, nearly 35% of observations of Herpestes were in grassland.

Proportional utilisation of streams and dams was greater than expected for most species while forest margins were used less frequently (Fig. 6.3c). This apparent avoidance of forest margins, despite numerous observations of viverrids using these areas, underscores the large area of forest margin in the reserve (Fig. 2.1). Herpestes was the only species to select vlei both as a habitat type and as the nearest source of water (Fig. 5.3a&c).

2. Stepwise multiple regression.

All regressions were highly significant ($P<0,001$) while the multiple correlation coefficients and VIF values (Appendix 3) revealed no multicollinearity among the independent variables (Table 6.3). The multiple correlation coefficients for the five viverrids were positive, indicating a moderate to moderately high association between dependent and independent variables (0,4487 to 0,6171) while 20 to 38% of the variation in species distribution was explained by these independent variables (Table 6.3).

When viewed together, the regression and Bonferroni analyses

TABLE 6.3. Variables associated with the distribution of viverrids at VCNR as revealed by stepwise multiple regression. R=multiple correlation coefficient; Beta=standardised regression coefficient.

Species	Variable	R	Beta	R^2
Atilax	WDIST *	0,4948	-0,2351	0,2448
	RIVERINE		0,1845	
	CANE		0,2015	
	ROX *		-0,1624	
	DAM		0,1564	
	OPEN *		0,1025	
	VLEI(habitat)		0,0631	
	STREAMBANK		0,0652	
Galerella	SCRUB	0,6171	0,5164	0,3809
	MARGIN		0,3558	
Genetta	FOREST	0,4487	0,3803	0,2013
	DIST. GRASSLAND		0,3187	
	RIVERINE		0,2776	
	OPEN *		-0,1409	
Herpestes	GRASSLAND	0,5320	0,5300	0,2830
	COVER *		0,2834	
	DAM		-0,2350	
	BUSHCLUMP		0,2316	
	DIST. GRASSLAND		0,1138	
	FOREST		0,1110	
Mungos	SCRUB FOREST	0,6115	0,5747	0,3740
	WDIST *		0,1356	
	DAM		0,7010	

* indicates that a negative regression coefficient represents close association between the habitat variable and viverrid distribution.

complemented each other. The Bonferroni analyses showed that Galerella selected forests (Fig. 6.3a) and, although the regression model did not do so, it demonstrated the importance of forest margins in the distribution of this species (Table 6.3). Thus, Galerella probably used the outer areas of forest and riverine forest habitats predominantly (Table 6.3; Fig. 6.3a).

The distribution of Atilax appeared to be mainly influenced by proximity to water particularly, although not exclusively, under the cover of forests (Table 6.3). The preference for water by Atilax was revealed in its avoidance of the relatively dry forest and preference for the immediately adjacent riverine forest (Figs. 2.1 & 6.3b; Table 6.3). Galerella differed by using both these adjoining habitats freely (Fig. 6.3a).

The strong positive association between sugar cane and the distribution of Atilax may have resulted from the relatively high correlation between this variable and forest cover (r=0,6473; N=1 801). Relatively few observations were made of Atilax in sugar cane compared with those made in forests and it is possible that these variables competed for entry into the regression model.

The preference for most forest types by Genetta and avoidance of open habitats is clearly shown by both analyses (Fig. 6.3b; Table 6.3). The contradictory finding that Genetta was positively influenced by open areas (Table 6.3) was a consequence of movements inside the forest near the margins, rather than frequent occurrence in the open. Selection, by

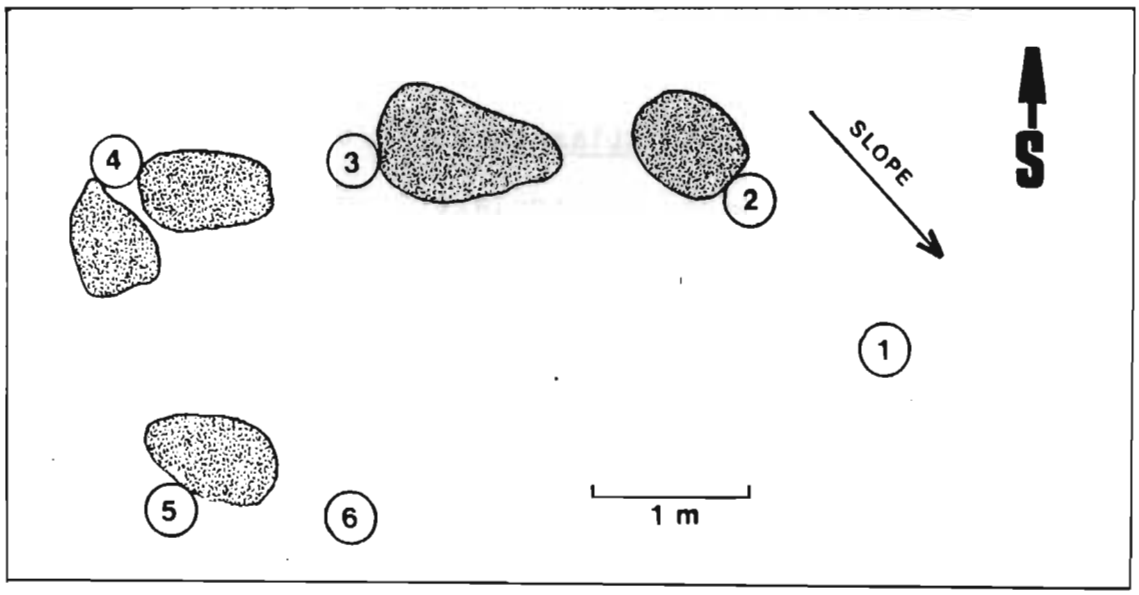

FIGURE 6.4. Plan of a Mungos burrow located in Mthakathi scrub forest. Burrow entrances are numbered and the approximate position of rocks are indicated.

Genetta, for disturbed grassland (Fig. 6.3a; Table 6.3) was due to the proximity of disturbed grassland and forest (Fig. 2.1).

Both analyses showed that Mungos selected scrub forest, which was not preferred by any other viverrid (Fig. 6.3a; Table 6.3). Finally, Herpestes was clearly influenced by open habitats and avoided forest types, although some use of forest was recorded (Fig. 6.3a; Table 6.3).

3. Resting-sites

The locations of resting-sites confirmed the Bonferroni (Fig. 6.3) and multiple regression findings (Table 6.3). Atilax frequently rested near water, particularly under large boulders in streambeds (Table 6.4). Genetta often slept in trees while only one accurate location of the resting-site of Galerella was made - in a burrow on the forest margin. The burrow was 7-8 cm across and about 700 cm deep. Herpestes preferred to sleep in the open and were found in thick tangles of grass or other vegetation (Table 6.4). Other viverrids also had resting-sites in similar areas but, in several cases, resting-sites could not be accurately located (Table 6.4).

Mungos slept in burrows. Only one currently occupied den was located (Fig. 6.4), situated about seven metres from a dry stream in scrub forest. There were six entrances, measuring 14,4±2,8 cm wide by 14,1±5,9 cm high, of which three were apparently in use (Fig. 6.4). Two other areas which had been used by Mungos in the past were located in scrub forest and consisted of slabs of overhanging rock covering an area of between 1,5 and 2 m^2.

TABLE 6.4. Viverrid resting-sites at VCNR. In cases where the resting-site could not be accurately determined, the habitat where the animal rested is given.

Species	Site and charateristics	Frequency (%)
A. paludinosus	Boulders in streambed	35,3
	Riverine forest	29,4
n=17	Reeds near stream	17,6
	Large rock in thick grass	17,6
G. tigrina	In trees (eg. Phoenix reclinata or Sclerocarya caffra	72,7
n=11	In thick grass	27,3
G. sanguinea	Forest	60,0
	Forest margin	20
n=5	Burrow in grassland 8m from forest	20
H. ichneumon	Streambank forest margin in grass	30,8
	Tangled, thick reeds	30,8
n=13	Forest margin in grass	15,4
	Cane about 10 months old	15,4
	Bushclump	7,7
M. mungos	Large burrow in scrub forest	
	Under slabs of rock in scrub forest	

4. Canonical discriminant function analysis

Statistics associated with the canonical discriminant function analysis are provided in Table 6.5. There was moderate correlation between the canonical functions and the five groups (species) and although all four canonical functions were significant ($P<0,001$), high Wilks' lambda and low eigenvalues for the fourth function indicated that it lacked discriminating power (Table 6.5). The fourth function was therefore excluded from the analysis.

TABLE 6.5. Statistics derived from the canonical discriminant functions used to segregate the five species of viverrid at VCNR. Canonical function 4 was excluded from analysis based on these statistics.

After Canonical Function	Eigen-value	Canonical Correlation	Wilks' Lambda	Chi Square	Significance
0			0,4256	1302	0,0000
1	0,3153	0,4896	0,5597	884	0,0000
2	0,2761	0,4652	0,7143	512	0,0000
3	0,2374	0,4380	0,8839	8	0,0000
4	0,1314	0,3408			

TABLE 6.6. Continua derived from the first three canonical functions used to segregate the habitat preferences of the five species of viverrid at VCNR. Variables are specified in order of importance and the percentage contribution of each function to among-species variance, is shown.

Canonical Function	Percentage Contribution	Interpretation
1.	32,8	Proximity to water and large rocks near streams. Positive association with riverine forest.
2.	28,8	Positive association with grassland, vlei, forest margin, sugar cane and bushclump.
3.	24,7	Positive association with scrub forest.

These statistics, interpreted in Table 6.6, implied that the first three canonical functions, accounting for 86% of the among-species variance, realistically discriminated among the five species of viverrid (Table 6.6). Because the results of this analysis were similar to those of the Bonferroni and multiple regression analyses, canonical correlation was not used to describe viverrid habitat associations. Rather, emphasis was placed on the differences among the viverrids.

The three canonical functions clearly segregated the centroids of the five viverrid species: particularly Mungos which was separated from the other viverrids along the third axis; Herpestes along the second and Atilax along the first canonical function (Fig. 6.5).

Atilax, Galerella, Genetta and Mungos again formed a group that was mainly associated with forest types (Fig. 6.3; Table 6.3). However, Atilax frequented forests near water, particularly those with large boulders in the streambed while Galerella occurred in "dry" forests and forest margins (Fig. 6.5). The distributions of Genetta and Galerella were similar (Fig. 6.5). Genetta showed less association with water than either Atilax or Galerella and a stronger selection for forest (Figs. 6.3 & 6.5).

Mungos was the only viverrid to select scrub forest (Fig. 6.5) and is therefore not considered part of the forest group. In contrast to the forest group, there were few observations of Mungos in forest habitats associated with water (Fig. 6.5). Finally, Herpestes differed from the rest of the assemblage by showing strong selection for areas in the open (Fig. 6.5).

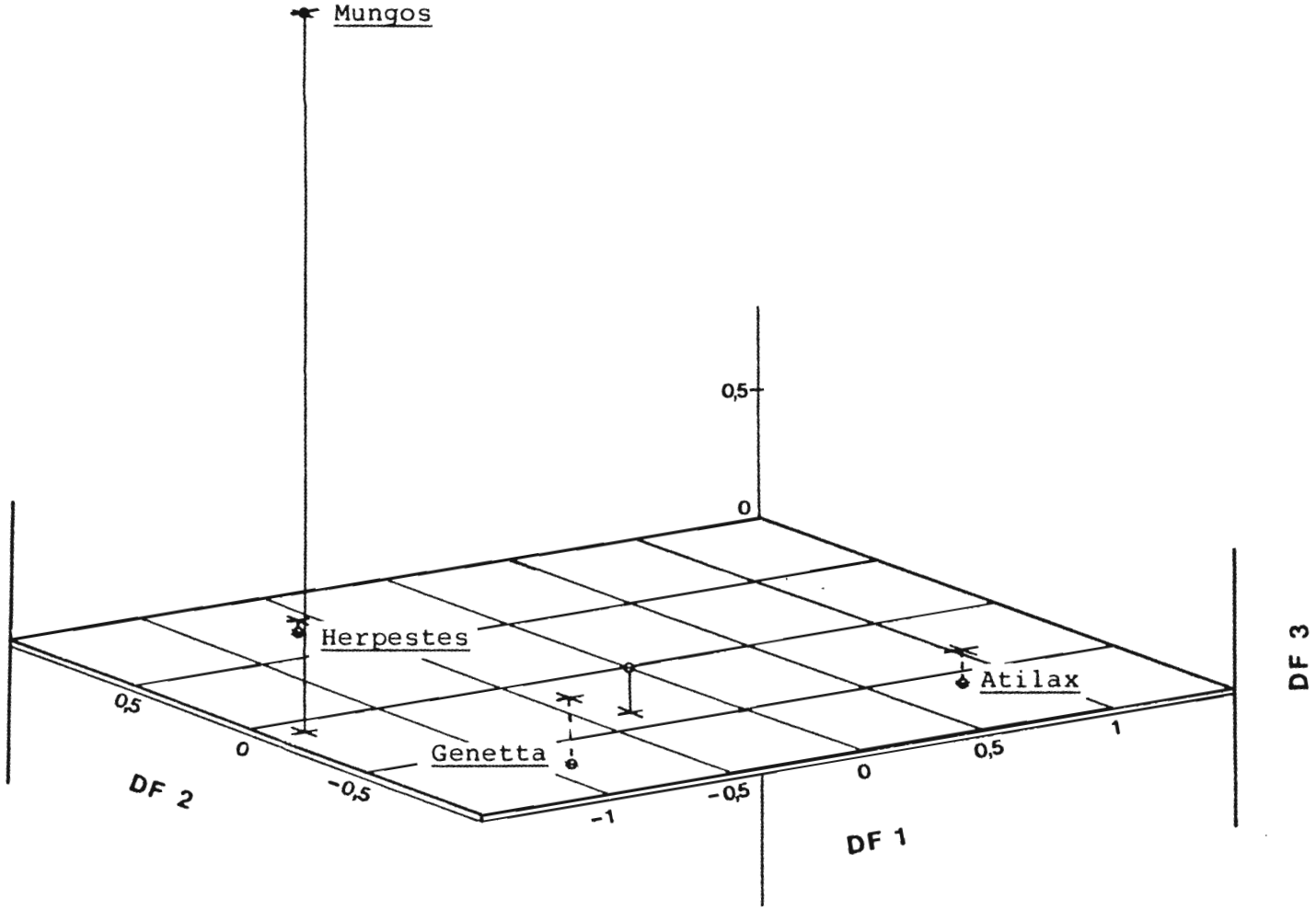

FIGURE 6.5. Three dimensional diagram showing segregation among the five viverrids at VCNR as determined by canonical discriminant function analysis. Using macro- and micro-habitat variables, the viverrids segregate along three discriminant functions.

When all the locations were considered, much habitat diversity was noted among the five viverrid species, although the 95% confidence limits about each mean (centroid) showed no overlap (Fig. 6.5). This was surprising, but narrow confidence limits are a result of large sample sizes which characterised this data set. Nevertheless, even Mungos, with only 41 observations, showed no overlap with the other viverrids (Fig. 6.5). Segregation of the centroids and narrow confidence intervals suggested that the bulk of each species' habitat locations were segregated from the other viverrids (Fig. 6.5).

5. Verification of results

The results of the field tests of the statistical habitat analyses are presented in Table 6.7. Overall, a success rate of 83% was achieved (Table 6.7) indicating that the predictions derived from the results presented in Figure 6.3 and Table 6.3 were correct.

TABLE 6.7. Results of the field test checking the habitat occupation predictions presented in Figure 6.3 and Table 6.3.

Species	No. of predictions	No. correct	No. with no sign	Overall % correct
Genetta	8	4	3	80,0
Herpestes	21	14	5	87,5
Galerella	11	4	5	66,7
Atilax	12	9	1	81,8
Mungos	3	3	0	100,0
Overall	55	34	14	82,9

6. Home range size and population density

The size of the home ranges of four species of viverrid, as determined by five models, are shown in Table 6.8. Obviously,

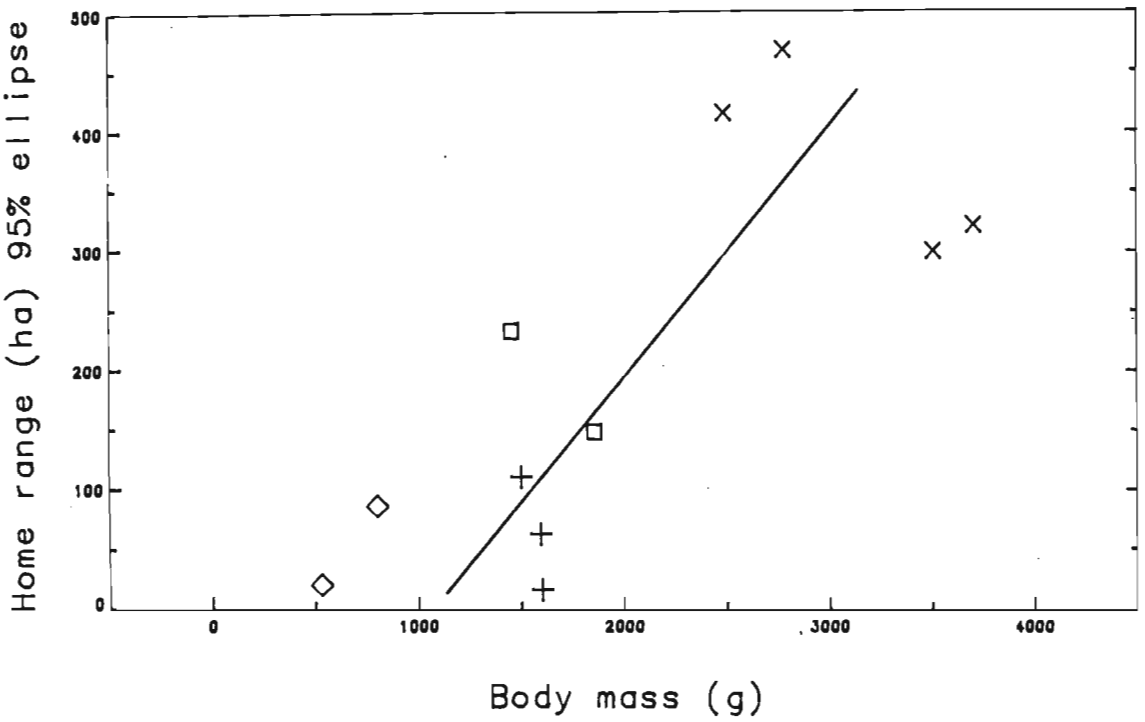

FIGURE 6.6. Body mass of individual viverrids versus the size of their home range as determined by radio-tracking. (n=11; rs=0,59). + =Genetta, × =Herpestes, □ =Atilax and ◇ =Galerella.

the longer an animal is tracked, the more likely a researcher is to determine the full extent of its movements. Galerella was followed for only 6 days while two Herpestes were followed for a year or more. Despite this disparity in sample duration, which can be seen to a lesser extent in the other two species (Table 6.8), I concluded that Herpestes, then Atilax had the largest home ranges and Genetta the smallest (Table 6.8).

This conclusion was based on the finding that viverrids frequently moved from one end of their home range to the other in a few days. Neither Genetta nor Galerella moved as far as the larger species. Despite the short time in which Galerella were followed (Table 6.8), one animal was located 60 times, indicating that many of its movements were detected. Genetta were tracked less intensively but were radio-marked for between 43 and 153 days and were located at least eight times each month (Table 6.8), suggesting that a large proportion of the home range of both species was detected.

These results conform well with theory and the positive correlation between body size and home range size (McNab 1963; Swihart, Slade & Bergstrom in press) is certainly upheld (Fig. 6.6). However, Galerella has a bigger home range than the larger Genetta which may be a consequence of arboreal utilisation of the habitat by the latter. In other words, Genetta, because it often uses the vertical component of its home range for feeding, defaecating and resting, may require a smaller horizontal area relative to terrestrial animals.

TABLE 6.8. The size of the home ranges of four species of viverrid at VCNR as revealed by radio-tracking. Home ranges are expressed in hectares and have been calculated using five different models. See text for explanation.

Species	Sex	Duration Marked (days)	No. of locations	Convex Polygon	Concave Polygon	95% Ellipse	Harmonic Mean (95%)	Fourier Transformation
				(hectares)				
A. paludinosus	F	33	121	107,0	60,9	233,0	121,0	204,8
A. paludinosus	M	67	93	85,9	51,6	148,0	96,7	131,1
G. tigrina	F	43	17	27,3	7,8	62,3	27,6	89.4
G. tigrina	F	153	44	32,8	8,6	110,6	-	-
G. tigrina	M	101	61	6,3	4,7	16,0	8,9	11,2
H. ichneumon	F	41	29	166,4	76,6	415,2	236,8	-
H. ichneumon	F	344	189	277,3	195,3	467,7	322,9	484,1
H. ichneumon	M	537	210	258,6	181,3	321,7	243,2	435,7
H. ichneumon	M	9	70	135,2	50,8	299,9	180,5	266.3
G. sanguinea	M	6	60	53,1	38,3	85,8	57,5	100,5
G. sanguinea	F	6	23	7,8	6,3	20,0	10,2	-

Prey habitat utilisation

The following array-caught prey categories were omitted from the Bonferroni analyses because they violated one or more of the model's assumptions (Appendix 3): R. pumilio, centipedes, amblypygids and scorpions. Crabs were more likely to be caught near the streams and were caught infrequently in the other two areas (Table 6.9). Lizards, millipedes and larvae preferred grassland while many insects and typical forest cryptofauna appeared in the forest margin (Table 6.9). The apparent preference for forest margins by frogs was because large numbers of small, A. wahlbergii were caught there (Table 6.9; Chap. 5).

TABLE 6.9. Results of the Bonferroni tests on array trap data indicating which prey categories were more, or less, likely to be caught in one of three habitat types. Significance was considered when P<0,05. Categories that appear in Table 5.1 but not here used the habitats in proportion to their availability.

	River	Grassland	Forest margin
Caught more often	Crabs	Lizards Juliformia Larvae	Amphibia Pill millipedes Blattodea Coleoptera Orthoptera
Caught less often	Blattodea Juliformia Coleoptera Orthoptera Larvae	Pill millipedes Crabs Coleoptera	Lizards Crabs Snakes Juliformia

Pill millipedes also preferred the forest margin and occurred less often than expected in the grassland or stream habitats (Table 6.9). Amblypygids, centipedes and scorpions, although present in small numbers, occurred mainly in the margin traps.

Overall, more prey selected forest margins and fewer avoided these traps than either of the other two habitats and prey was most abundant in the forest margin habitat (Table 6.9).

For the PVC-caught small mammals, the following violated the assumptions of the model and were omitted from statistical treatment; Otomys spp., A. chrysophilus and M. minutoides. In contrast to the array-caught prey, results indicated that small mammals were caught less often than expected in forest margins and, in general, were absent from forest habitats (Table 6.10). M. minutoides was the exception and, although not subjected to Bonferroni analysis, was frequently caught in streambank forests. Small mammals were also under-represented in bushclump and exotics (Table 6.10). Clearly, small mammals were most abundant in grassland (no species was caught less frequently than expected and at least one representative of each species was caught in this habitat) and least common in the riverine forests (Table 6.10).

TABLE 6.10. Results of the Bonferroni tests on PVC trap data indicating which prey categories were more, or less, likely to be caught in one of nine habitat types. Significance was considered when $P<0,05$. Categories that appear in Table 5.1 but not here, used the habitats in proportion to their availability.

	Riverine	Streambank	Riverine margin	Scrub	Bushclump	Grassland	Vlei	Exotics	Cane
Caught more often						M.natalensis R.pumilio L.rosalia	Shrews		M.natalensis
Caught less often	M.natalensis		M.natalensis R.pumilio L.rosalia	R.pumilio	M.natalensis L.rosalia R.pumilio		M.natalensis		Shrews L.rosalia R.pumilio
Never caught	L.rosalia Shrew R.pumilio	L.rosalia Shrew R.pumilio M.natalensis		L.rosalia Shrew			L.rosalia	R.pumilio L.rosalia Shrew	

DISCUSSION.

The spatial niche is considered the major dimension by which taxonomically diverse, terrestrial animals partition resources (Schoener 1974a). This concept has both theoretical (MacArthur & Wilson 1967; Schoener 1974b) and empirical support (Jaksic 1982; review in Schoener 1986; but see Jaksic *et al.* 1981). Data for viverrids are lacking but some small carnivore studies, mainly on mustelids, support this view (Rautenbach & Nel 1978; Delibes 1983) although most small carnivores appear to separate along both the trophic and spatial dimensions (Erlinge 1972; Rowe-Rowe 1977; Rautenbach & Nel 1978; Waser 1980; Powell & Zielinski 1983; Bothma *et al.* 1984). Habitat heterogeneity at VCNR suggests that segregation along the spatial niche may be effective (see Schoener 1974a).

Many data indicate that the five species of viverrid overlap along the macrohabitat (Schoener 1986) level at VCNR but segregation is achieved after finer resolution within the macrohabitat, *i.e.* at the microhabitat level. In the MVA, the first canonical function approached the micro-, rather than macro-, habitat level, suggesting that segregation among the VCNR viverrids tended away from mere vegetation type differences.

However, care must be taken to avoid confusing statistical and ecological significance (Schroder 1987) and one must be aware that differences will be found if one searches hard enough (Schoener 1974a, 1986). Significant differences in the spatial requirements of the viverrids at VCNR has been shown, now the ecological support for this is investigated. More

specifically, I examine Schoener's (1974a) contention that separation along the spatial niche is an important means by which species segregate (Hypothesis II; Chap. 1). This is necessary as several factors not considered in his general review (Schoener 1974a), are important here. First, carnivores are widely considered to differ and, presumably, segregate, with regard to diet (see references above). Second, predators are more likely to partition time than other trophic classes (Schoener 1974a).

If resources are not limiting, partitioning may not be important (Pontin 1982). So identification of limiting spatial resources is attempted beginning with Mungos which are scarce in the reserve (Maddock & Zaloumis 1987). Why should this be so when they are common on the Natal South Coast and in sugar cane surrounding the reserve (Maddock & Zaloumis 1987)?

Mungos tend to avoid open areas, requiring the cover of woodland or savanna where invertebrate prey are abundant (Neal 1970; Rood 1975; Rowe-Rowe 1978; Sadie 1983; Smithers 1983) but have also been recorded in riverine (Rautenbach 1982; Smithers 1983) and dune forests (Rowe-Rowe 1978). Smithers (1983) suggests that underbrush, fallen logs and substrate detritus, as well as termitaria, are essential requirements. Mungos use dens in large termite mounds, erosion gullies or abandoned aardvark holes (Taylor 1970; Neal 1970; Rood 1975; Smithers & Wilson 1979; Sadie 1983), which are uncommon or absent from VCNR. The lack of dens may limit small carnivore numbers (Waser 1980; Taylor 1986; Rasa pers. comm.[1]) and

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1. Rasa, A. Mammal Research Institute, University of Pretoria.

this, combined with the absence of their preferred woodland or savanna habitat, may be responsible for their low numbers.

Atilax has a wide habitat variability in Southern Africa and, as long as water is available, occurs in open grassland within the cover of dense waterside vegetation (Roberts 1951; Kingdon 1977; Rowe-Rowe 1978; Du Toit 1980; Waser 1980; Stuart 1981; Rautenbach 1982; Smithers 1983). Two habitat requirements appear essential - water and dense cover to provide refuge for this shy animal. Habitat selection of Atilax at VCNR clearly showed these requirements - although these resources were limiting in the open areas, they could be obtained in the more secluded forest streams where this species commonly occurred. Riverine forests were most preferred, perhaps because of greater crab abundance there (Table 5.6) while the scarcity of dense waterside vegetation prevented Atilax from using streams in the open.

Galerella also, has a wide habitat tolerance (Kingdon 1977; Stuart 1981; Smithers 1983), but an important requirement is adequate cover, usually in the form of rocky outcrops with associated trees (Smithers 1968, 1983; Rood & Waser 1978; Jacobsen 1982; Rautenbach 1982; Taylor 1986; pers. obs.). Their presence in forests at VCNR may be due to the absence of woodland and the cover they afford. Although Galerella does occur in forests (Kingdon 1977; Stuart 1981), Taylor (1970) and Smithers (1983) dispute this and forest does not appear to be its optimum habitat (Rasa pers. comm.; Baker pers.comm.[2]).

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2. Baker, C. Department of Zoology, University of Durban Westville.

Finally, selection by four of the five viverrid species for forests which occupy only 20% of the reserve (Figs. 2.1 & 2.3), is suggestive of limiting resources. Overall, the fact that Mungos is common in surrounding areas but not in VCNR, that Atilax occurs in open habitats but not at VCNR, that Galerella appears to occur in a suboptimal habitat and, possibly, that four species select a small resource, indirectly suggests that at least some viverrids are limited in their spatial requirements. If this assumption is true, then partitioning along the spatial niche is important.

Niche breadth and overlap measurements have been included here because they facilitate discussion of spatial niche segregation. Mungos and Atilax, by virtue of their selection for relatively scarce habitats, are selectors (Rosenzweig 1985; see Chap. 5) having low niche breadths (Table 6.11) - a conclusion in agreement with Taylor (1986). The other three viverrids had intermediate values, tending towards selectors rather than opportunists (Table 6.11; Rosenzweig 1985). The highest value of 0,4 for Herpestes was due to its selection for grassland, the most abundant habitat (Table 6.11).

TABLE 6.11. Spatial niche breadth values for the five species of viverrid at VCNR. Values, computed using Hurlbert's (1978), range from 0 (selection for least abundant resource) to 1 (taking resources in proportion to their availability).

Species	Niche breadth
Atilax	0,1447
Mungos	0,1631
Genetta	0,2662
Galerella	0,3257
Herpestes	0,4013

Spatial niche overlap values were all greater than 1 (Table 6.12), indicating that resources were not taken in proportion to their availability and that habitat selection was similar among the five species (Hurlbert 1978). This is a consequence of the mosaic habitat structure so the extent of overlap is best viewed as the proportional distance from zero (Table 6.12). Thus, Atilax showed much spatial overlap with Galerella (3,7) and Genetta (3,5) but little overlap with Mungos (1,2; Table 6.12). Least spatial overlap occurred between Galerella and Herpestes (Table 6.12).

TABLE 6.12. Spatial niche overlap values for the five species of viverrid at VCNR. Values greater than 1 indicate resource selection (Hurlbert 1978).

Species pairs	Overlap value
Atilax and Galerella	3,7
Atilax and Genetta	3,5
Galerella and Genetta	2,7
Galerella and Mungos	2,0
Genetta and Herpestes	1,6
Atilax and Herpestes	1,6
Mungos and Herpestes	1,5
Mungos and Genetta	1,4
Mungos and Atilax	1,2
Galerella and Herpestes	1,1

As suggested by the niche breadth values (Table 6.11), Mungos had specific habitat requirements which resulted in low overlap values between this species and the other viverrids (Table 6.12). Spatial separation was also shown for Herpestes, although its niche breadth was relatively broad (Tables 6.11 & 6.12). This was because Herpestes selected the abundant, open habitats, in contrast to the other viverrids. Preference for these habitats is supported by previous studies (Roberts 1951;

Rosevear 1974; Kingdon 1977; Rowe-Rowe 1978; Rautenbach 1982; Smithers 1983) and the finding that rodents, the main prey of Herpestes, also preferred open areas. The occurrence of Herpestes in vleis has been recorded in Southern Africa (Smithers 1968, 1983; Rautenbach 1982) and the presence of this species near swamps, in Spain, was associated with the occurrence of rabbits, the main food, in the swamp (Beltran, Delibes & Ibanez 1985). Otomys, the main prey of Herpestes at VCNR (Chap. 4), also occur near vleis (De Graaff 1981) and it is tempting to draw a causal relationship.

The next three species (Genetta, Atilax and Galerella) comprised the forest group and showed high spatial overlap values (Table 6.12). The spatial differences involving these species therefore requires finer resolution (microhabitat) than used in the computation of the overlap indices. The selection by Atilax for forests with streams and its occurrence near water, both for food and resting sites (and possibly travel routes), would probably partially separate this species from others using the same macrohabitat (i.e. Genetta and Galerella. The home ranges of Atilax were linear, essentially following streams and rivers where crabs were abundant (Chap. 5).

Although, these two species shared the same macrohabitat with Atilax, their detailed distribution differed. Genetta is partly arboreal (Bearder 1972; Taylor 1974, 1979; Lack 1977; Stuart 1981; Rautenbach 1982) and use of the spatial niche in the vertical dimension may separate this species from the other forest group species. Genetta is also dependent on water (Kingdon 1977; Rautenbach 1982; Smithers 1983) and,

although not shown in the multiple regression analysis, occur fairly close to streams in forests - similar to the habitat occupied by Atilax. Use of a different part of that habitat would help divide this resource between the two nocturnal species. Further, Genetta appear to use a wide area within the forests and their home ranges are often circular, defined by the forest limits, whereas Atilax tend to have home ranges which follow streams and are often linear. Thus, Genetta have a more general forest utilisation than do Atilax - factors that may aid their spatial separation.

Although these factors contribute to segregating these species, the small size of many of the forests relative to home range size suggests that overlap and interactions may be high. The canonical discriminant functions used to segregate the viverrids were only exploratory and not confirmatory (Appendix 3). Thus, it appears that while this analysis reflected realistic segregation among the other viverrids, separation between Atilax and Genetta, both nocturnal, may be less clearly achieved. Galerella, being diurnal, may interact with the other two species infrequently (Chap. 7).

Before leaving the subject of the spatial niche, further examination of selection of forests in preference to the more abundant open areas is considered. A common requirement of viverrids is cover (see references above) which has been cited as an anti-aerial predator strategy (Smithers 1971; Rosevear 1977; Sadie 1983; Rood 1983; Taylor 1975, 1986) and avoidance of aerial predators by Helogale parvula influences much of their social behaviour (Rasa 1985; in press). Of 32 mammalian skulls found under the nests of Crowned Eagles (S. coronatus

at VCNR, 6,3% (2) belonged to viverrids. In the Eastern Cape, 6,6% (3) of Crowned Eagle prey were viverrids, two of which were G. tigrina skulls (Ranger unpubl. data), indicating predation on viverrids.

Even Herpestes, the only open habitat selector, patrolled their home ranges while moving in the grassland along forest margins. Other factors, such as the presence of paths which facilitate movement through thick grass, may be responsible for this behaviour but it is possible that predator avoidance also plays a role. Although Herpestes is a large viverrid (Chap. 3), Crowned and Martial Eagles (P. bellicosus), both common at VCNR, can kill animals heavier than Herpestes (Maclean 1985) particularly if predation was mainly orientated against juveniles (Rasa pers. comm.).

Thus, evidence of predation on viverrids by a very common raptor at VCNR and indications that much viverrid vigilance behaviour is directed towards raptors (Rasa 1985) strongly suggests that selection for areas giving protection against aerial predation is likely. This may be of particular importance for solitary species which may be more vulnerable to predation.

It would be naive to believe that predator avoidance is the only reason why viverrids occur in forests at VCNR. Many factors are probably responsible and among these, food availability could be very important (Chaps. 4 & 5). However, the presence of Herpestes in the open, and absence of Galerella and Atilax from these habitats, which they occupy elsewhere (Rowe-Rowe 1978; Waser 1980; Stuart 1981; Rautenbach

1982; Smithers 1983), is interesting and suggestive of habitat shift.

Habitat shift, or at least a tendency to avoid open habitats, is demonstrated by Galerella. Habitat shift is likely if two species are similar, and smaller forms are more likely to shift in response to larger ones than vice versa (Schoener 1986). Both this species and Herpestes are diurnal, belong to the small mammal guild (Chap. 4) and Galerella is smaller (Chap. 3). Although Galerella have a wide habitat tolerance, they are usually associated with woodland or savanna (Smithers 1968; Rood & Waser 1978; Stuart 1981; Rautenbach 1982). At VCNR similar open areas are occupied by Herpestes. The smaller Galerella may have moved from the more open habitats at VCNR into forest, where diurnal viverrids are absent, to avoid interactions with Herpestes. The ability to exhibit wide habitat tolerance may result from Galerella's more opportunistic diet (Chap. 5). Interestingly, this species also occupies forest at Umtamvuna Nature Reserve in southern Natal where it is sympatric with Herpestes.

A similar interpretation may apply to Atilax. Herpestes uses grassland near streambank forests and occurs near all types of water i.e. similar habitats proposed for Atilax (above). Although these two mongooses are active at different times, the shy Atilax may avoid interactions with the larger Herpestes by using forest streams where cover and its main prey are abundant.

These interpretations, for which there is no direct evidence, are in accord with the theory that, when confronted with

competition, spatial separation, rather than trophic separation, should result (MacArthur & Wilson 1967; Schoener 1974a&b, 1986). However, competition is, at the best of times, difficult to prove (Connell 1980; Bender, Case & Gilpin 1984) but, with these data, it is impossible to show. Nevertheless, the evidence is certainly worth further investigation and may have an important influence on viverrid distribution patterns.

Overall, these findings, together with field tests of the results, provide evidence that the habitat utilisation results were realistic. Thus, ecological evidence supports the statistical findings that, perhaps with the exception of the forest group, this viverrid assemblage segregates by habitat differences, in part (Hypothesis II; Chap. 1). The assemblage segregates into a species preferring open habitats, one preferring scrub forest and three that occur in forest (the forest group). But spatial differences alone may not clearly segregate this last group.

Temporal separation

The clear-cut separation of viverrids at VCNR into diurnal and nocturnal groups greatly facilitated interpretation of temporal partitioning. Rather obviously, high overlap was experienced between species active at the same time while low values were calculated for those active at different times (Table 6.13). Genetta overlapped with the diurnal species because of its habit of becoming active in the evening when the diurnal species were still active (Table 6.13).

TABLE 6.13. Temporal niche overlap for the five species of viverrid at VCNR. Feinsinger *et al.* (1981) proportional similarity index was used. Values range from 0 (no overlap) to 1 (total overlap).

Mungos and *Herpestes*	0,8327
Galerella and *Herpestes*	0,7689
Galerella and *Mungos*	0,7296
Atilax and *Genetta*	0,7210
Mungos and *Genetta*	0,1746
Galerella and *Genetta*	0,0907
Genetta and *Herpestes*	0,0881
Atilax and *Herpestes*	0,0046
Atilax and *Galerella*	0,0000
Atilax and *Mungos*	0,0000

In general, the findings in this study were similar to previously published results (Roberts 1951; Taylor 1970; Neal 1970; Rowe-Rowe 1971, 1978; Bearder 1972; Rood 1975; Lack 1977; Kingdon 1977; Rood & Waser 1978; Waser 1980; Du Toit 1980; Jacobsen 1981; Stuart 1981; Rautenbach 1982; Sadie 1983; Smithers 1983; Delibes *et al.* 1984; Delibes & Beltran 1985; Baker 1987c).

Delibes & Beltran (1985) reported peaks of activity in *Herpestes* between 08h00 and 11h00 and again between 15h00 and 18h00, as found at VCNR. However, in contrast to this study, Shortridge (1934), Roberts (1951) and Dorst & Dandelot (1976) found *Herpestes* to show nocturnal activity while Ben-Yaacov & Yom-Tov (1983) and Smithers (1983) believed them crepuscular.

Smithers (1983) comments that *Galerella* are not active until well after sunrise and take shelter before sunset. This was also observed at VCNR and only two authors suggest that these mongooses are nocturnal (Ducker 1960; Hendricks 1971 both in Jacobsen 1982) while Rosevear (1974) indicated activity on moonlight nights.

Kingdon (1977) and Rowe-Rowe (1978) report diurnal activity for Atilax and Lombard (1958) and Smithers (1983) consider them crepuscular. Rowe-Rowe (1978), recorded some daylight activity by Genetta and Smithers (1983) noted that they moved an hour or two after sunset and ended activity at about 02h00; findings that were confirmed in this study.

Taylor (1986) has suggested that, as viverrids exhibit different activity regimens, spatial and trophic overlap may be reduced by animals foraging at different times and this will be considered in the next chapter. Species do not necessarily compete for the temporal niche but it may effectively segregate them (but see Schoener 1974b; Jaksic 1982).

Hypothesis III (Chap. 1), that the viverrids segregate along the temporal dimension, clearly divides the assemblage into two groups. Further segregation is not achieved along this niche but differences in the activity of the prey eaten by the viverrids were noted which may facilitate coexistence. Significant differences in the activity regimen of the prey of Herpestes and Galerella is anomalous but may be a result of different hunting strategies (Bekoff et al. 1984) or each hunting at different times during daylight (Jaksic 1982). Similar reasons, particularly the former (Sadie 1983), may explain why Mungos eats many nocturnal prey.

CHAPTER 7

RESOURCE PARTITIONING AND COEXISTENCE

INTRODUCTION

So far each niche dimension has been been condidered in isolation. This final chapter synthesises these results into a more biologically meaningful entity using multidimensional niche overlap (May 1974; Pianka 1974). Hypotheses I, II and III are evaluated and an attempt is made to identify which niche dimension(s) is important in segregating the viverrid assemblage (Chap. 1; Schoener 1974a; Jaksic et al. 1981; Hayward & Garton 1988). The overall effectiveness of resource partitioning is also assessed.

Multidimensional overlap was measured as the product of the unidimensional niche overlaps (May 1974; Pianka 1974) which assumes that each dimension is orthogonal or independant (see Jaksic et al. 1981). In nature, niches usually vary in their degree of interdependence and orthogonality is difficult to quantify. In this discussion an unavoidable assumption is made that time, habitat and food are orthogonal. If they are not multidimensional overlap will overestimate segregation (Jaksic et al. 1981; Pianka 1983) therefore care is taken to interpret these values in the light of an understanding of the biology of the viverrids.

Throughout the chapter I continue the assumption that ecological differences among coexisting species are necessary

to avoid competitive exclusion (Chap. 1; Gause 1934; Hardin 1960). I conclude by questioning this assumption and suggest ways in which the role of competition can be evaluated in future studies.

The only new technique in this chapter involves the use of neighbours in niche space (Inger & Colwell 1977; Pianka 1980) which refers to species pairs showing greatest overlap through to those showing least overlap (Tables 5.9; 6.12 & 6.13). By plotting overlap values against neighbours in niche space, similar species plot together and dissimilar species segregate (Inger & Colwell 1977; Pianka 1980).

RESULTS AND DISCUSSION

TEMPORAL SEGREGATION

The activity regimens of the five viverrids are summarised in Figure 7.1. The diurnal Herpestes, Galerella and Mungos plot together showing high overlap with the first and second neighbours (Table 6.13; Fig. 7.1). The two nocturnal species Atilax and Genetta fall together but differ from the diurnal group having high overlap with the first neighbour only (Table 6.13; Figs. 6.2 & 7.1). From this it can be seen that high overlap with the first neighbour only, indicates a two species group while high overlap with the first and second nearest neighbours indicates a three species group (Fig. 7.1).

1. Temporal and trophic niches

Predators are more likely to partition time than other trophic groups (Schoener 1974a). This is true if resources differ qualitatively at different times (Jaksic 1982; Pianka 1983;

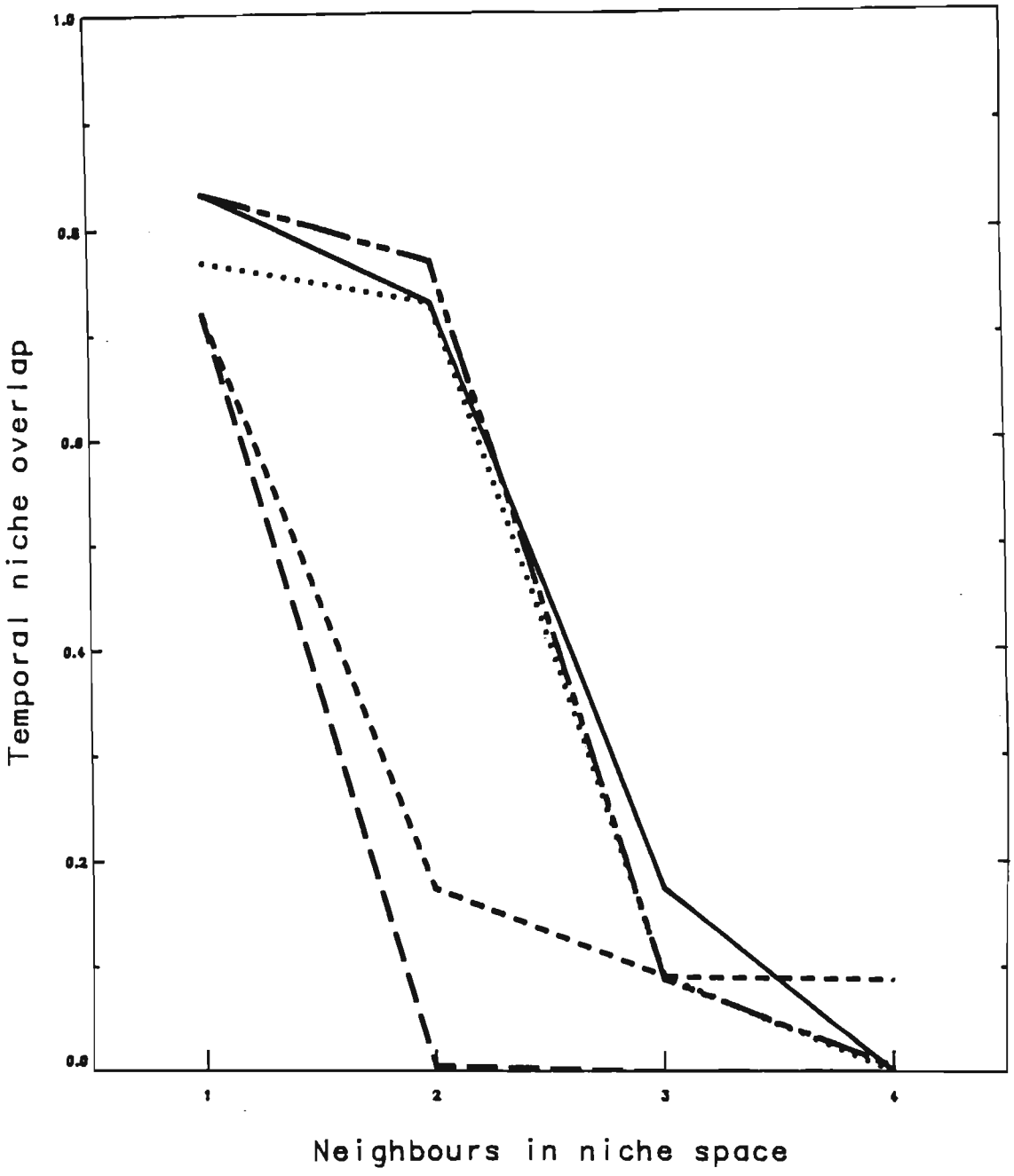

FIGURE 7.1. Temporal overlap versus nearness rank of neighbours in niche space among five species of viverrid at VCNR. A nocturnal and diurnal group of viverrids can be distinguished. Because plots in the lower part of the figure have little overlap, distances between these lines and those in the upper figure are not comparable. - - - - - =Genetta, ——— =Herpestes, ... =Galerella, — — — =Atilax and ——— =Mungos.

Huey & Pianka 1983) and was supported by the discovery that small carnivore activity is governed by the activity of their prey (Gerrell 1969; Bothma et al. 1984). To test if asynchronous viverrids at VCNR confront different prey (Jaksic et al. 1981; Jaksic 1982 Huey & Pianka 1983; Schoener 1986), new trophic overlaps, which included only those prey whose activity periods could be accurately determined, were calculated using the Shannon-Weiner niche breadth measure (Southwood 1978). If viverrids confronted different prey by being active at different times, overlap among synchronous species should be higher than among asynchronous species (Huey & Pianka 1983).

The comparison is presented in Table 7.1 but is not conclusive. Seventy five percent of the nearest neighbours were synchronous and 75% of the most distant neighbours in trophic niche space were asynchronous (Table 7.1). This result supports the hypothesis that different prey were available to asynchronous viverrids but because of the small sample size it cannot be statistically verified.

TABLE 7.1. Trophic overlap among synchronous and asynchronous viverrids arranged according to nearest neighbour in niche space. Synchronous neighbours are marked with an asterisk. See text for explanation.

	Neighbours		
Species	1	2	3
Genetta	Galerella	Herpestes	*Atilax
Atilax	*Genetta	Galerella	Herpestes
Herpestes	*Galerella	Genetta	Atilax
Galerella	*Herpestes	Genetta	Atilax
Percentage of synchronous spp. as 1st neighbour	75	Percentage of asynchronous spp. as last neighbour	75

Consideration of interspecific dietary differences based on predator-prey activity regimens is ecologically useful only if predators eat similar food (Jaksic 1982; Pianka 1983). For example, one asynchronous species might reduce overlap within the small mammal guild (Table 5.9; Cody 1974). Indeed, Genetta was nocturnal while the other two species were diurnal (Figs. 6.2, 7.1 & 7.2). As a result and, because the viverrids tended to prey on synchronous species (Chap. 6; Table 6.2), these viverrids took prey with significantly different times of activity ($P<0,05$; Table 6.2) thereby reducing bidimensional overlap (Fig. 7.2). The finding of temporal differences where most expected is not conclusive but does suggest a pattern of community organisation.

Temporal segregation, acting on the trophic niche, is often rejected by theoretical arguments (Schoener 1974a&b, 1986) and many empirical studies. Although authors have suggested that time plays a role in segregating the diet of small carnivores, quantitative data are often lacking (Sadie 1983; Bothma et al. 1984; (Delibes et al. 1984). Huey & Pianka (1983) found dietary differences resulting from different activity patterns among desert lizards but their analysis of water snakes and of raptors did not. Jaksic (1982) found no significant differences in overlap among Falconiform and Strigiform raptors and concluded that temporal segregation between these birds did not preclude exploitation of most prey resources by both nocturnal and diurnal predators. In both studies, high overlap values were found between asynchronous predators (Jaksic 1982; Huey & Pianka 1983).

Reasons for asynchronous predators having high trophic

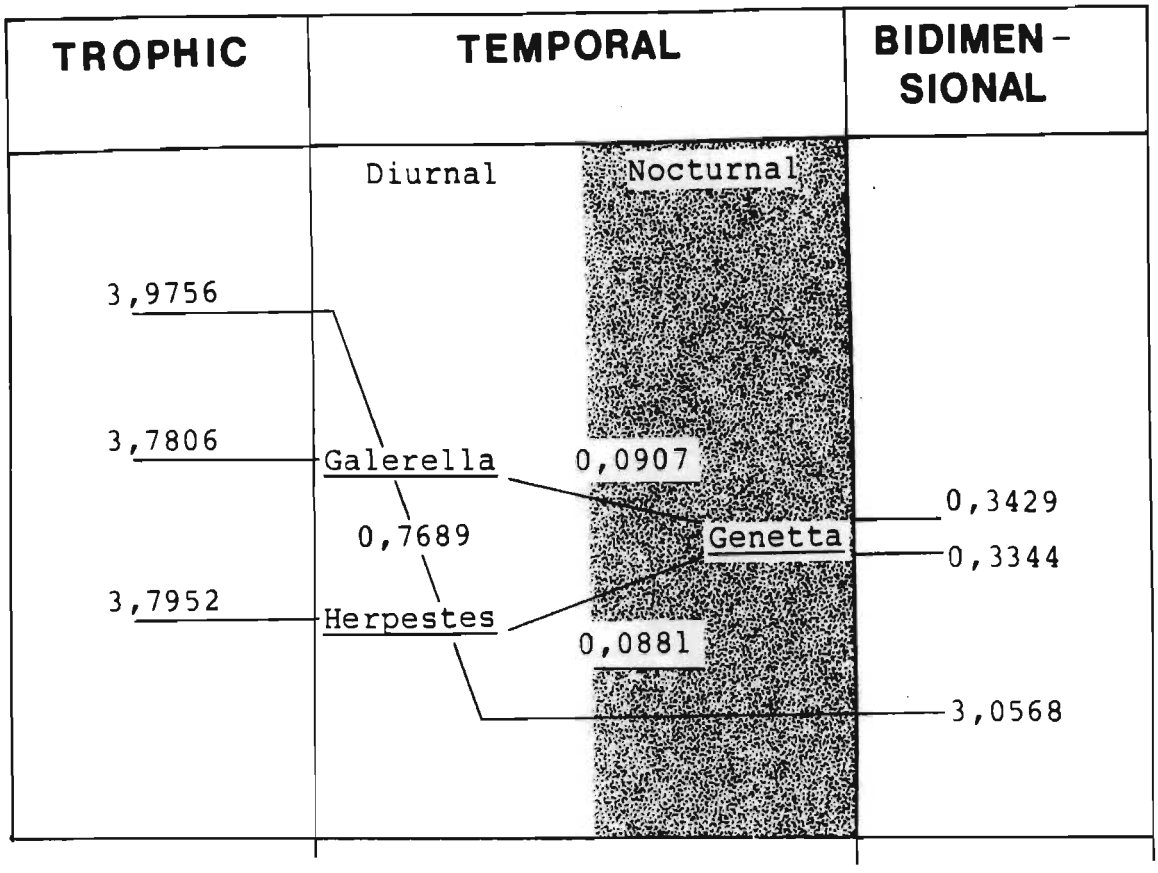

FIGURE 7.2. Trophic, temporal and bidimensional niche overlap among the small mammal guild at VCNR. High trophic overlap is reduced because of low temporal overlap between Genetta and the two diurnal viverrids (Herpestes and Galerella). Compare bidimensional overlap between the synchronous and asynchronous species.

overlaps include predators and/or prey being active outside their normal periods of activity (Jaksic et al. 1981; Huey & Pianka 1983). Viverrids in this study appeared consistent in their times of activity (Fig. 6.2) but some nocturnal prey were active during daylight including crabs, frogs and M. natalensis (pers. obs.).

However, activity outside normal periods may not be an important reason for high trophic overlap between asynchronous predators. If prey are occasionally active outside their normal periods predators would have to select them if these prey were to be registered in the scats. In the face of this strong selective pressure, prey would tend to be active only during their normal activity periods when they are presumably most able to detect and avoid predators.

Alternatively, and more likely, is that predators and prey have overlapping periods of activity (Jaksic et al. 1981). Perrin (1981) showed that the nocturnal M. natalensis (and A. chrysophilus) were also active at dusk and dawn while R. pumilio exhibited primarily crepuscular activity. Thus, nocturnal and diurnal viverrids may be partly exposed to similar prey populations. Scat analysis confirms that both nocturnal and diurnal viverrids ate M. natalensis and R. pumilio (Fig. 4.9).

A further complicating factor is that inactive prey are not invulnerable to predation (Huey & Pianka 1983). Certainly, the foraging method of Mungos, examining nooks and crannies and turning over rocks (Sadie 1983; Smithers 1983), would expose a number of resting invertebrates and explain the high number of

nocturnal prey in this mongooses diet. On the other hand, viverrid prey are sufficiently small to occupy burrows or resting sites where they are unavailable to predators. Because certain prey may be able to remove themselves from the potential prey population when inactive, temporal partitioning among small carnivores may be more important in aiding diet segregation than among large carnivores whose prey cannot occupy refuges.

Thus, the effect of temporal partitioning on diet segregation is clearly complex but it is effective in certain situations (Sadie 1983; Huey & Pianka 1983; this study).

2. Temporal and spatial niches

Given the wide spatial niche breadths and overlap among viverrids (Tables 6.11 & 6.12), temporal partitioning may be important in allowing close species packing along the spatial niche (May & MacArthur 1972). Habitat preferences of the viverrids are summarised in Figure 7.3. The forest group had high overlaps with the first and second neighbours and plotted together with Atilax differing slightly from the very similar Galerella and Genetta (Fig. 7.3). Lower overlaps were associated with Mungos and Herpestes which differed from the forest group and each other in their use of macrohabitat (Table 6.3; Figs. 6.3, 6.5 & 7.3). Because of these habitat differences Mungos and Herpestes need not be considered further.

Macrohabitat overlap among Atilax, Galerella and Genetta (the forest group) was highest in the study (Table 6.12) although some segregation was achieved at the microhabitat level (Table

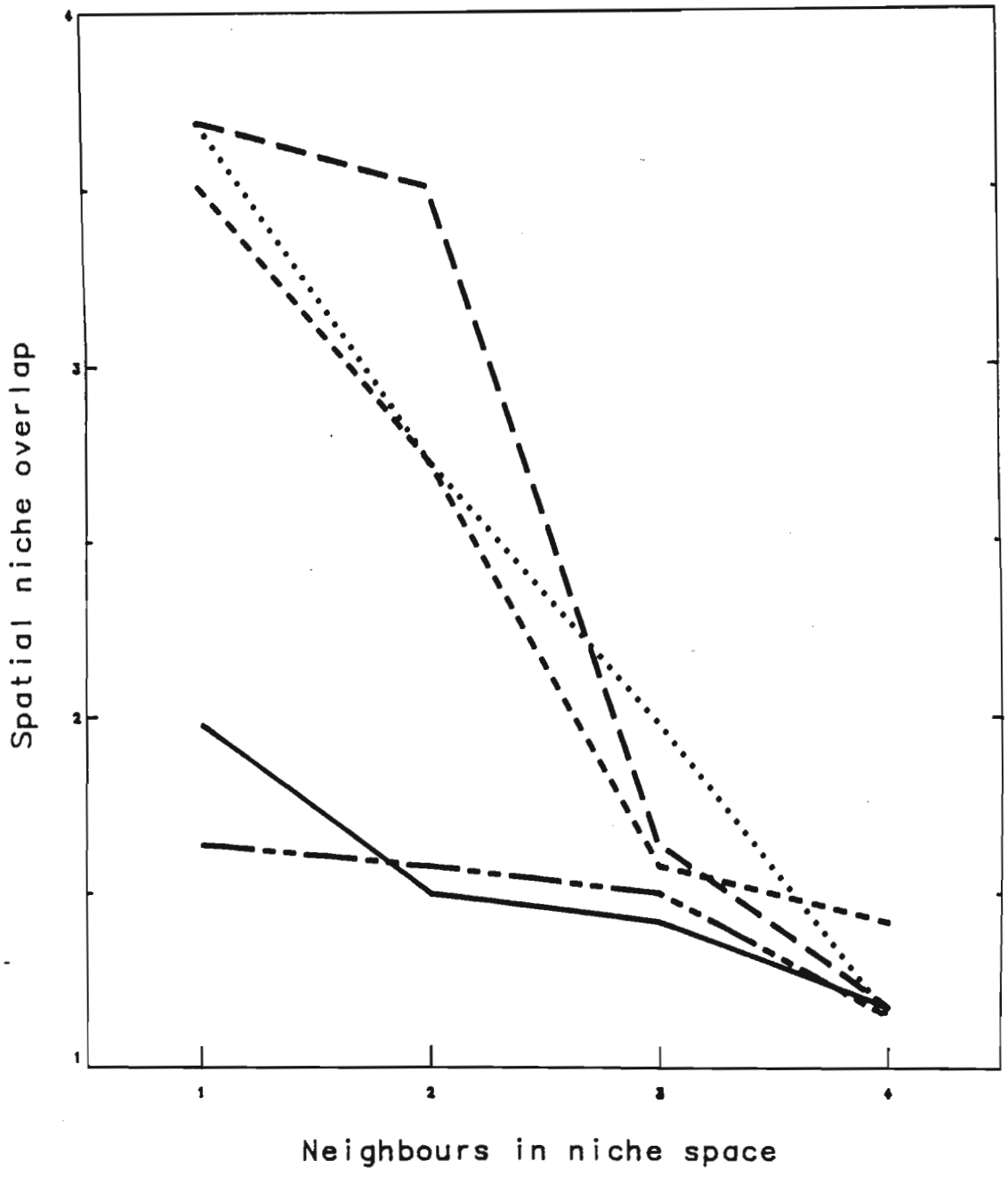

FIGURE 7.3. Spatial overlap versus nearness rank of neighbours in niche space among five species of viverrid at VCNR. The forest group is distinct from Herpestes and Mungos. Otherwise legend as for Figure 7.1.

6.3; Fig. 6.5). But microhabitat differences may not totally segregate this forest group and frequent interspecific encounters are likely (Chap. 6). However, the presence of the diurnal Galerella in this otherwise nocturnal group (Figs. 7.1 & 7.3) reduces overlap (Fig. 7.4), may well facilitate coexistence and indicates a pattern of community organisation (Fig. 7.4).

In conclusion, temporal partitioning aids coexistence among the small mammal guild at VCNR and spatial segregation is increased by differences in time of activity among the forest group (Figs. 7.2 & 7.4). These data are summmarised pictorially in Figures 7.5 and 7.6. Different times of activity may further segregate species whose trophic or spatial overlaps are low (Figs. 7.1 & 7.3). The importance of segregation by temporal partitioning relative to that of the habitat and trophic niches is examined in the final part of this chapter.

SPATIAL NICHE

Comparison of the habitat preferences of both viverrids (Table 6.3; Fig. 6.3) and their prey (Tables 6.9 & 6.10) reveals more about the foraging behaviour of these predators and aids interpretation of their habitat utilisation and segregation (Chap. 6; Jaksic et al. 1981). The relative biomass of viverrid prey in three habitats (Chap. 5) and more specifically, mammal prey in six habitats, are listed in Table 7.2 together with the overall importance of these food categories in the diet of the five viverrids (Table 4.2).

Comparison of prey eaten and prey abundance in different

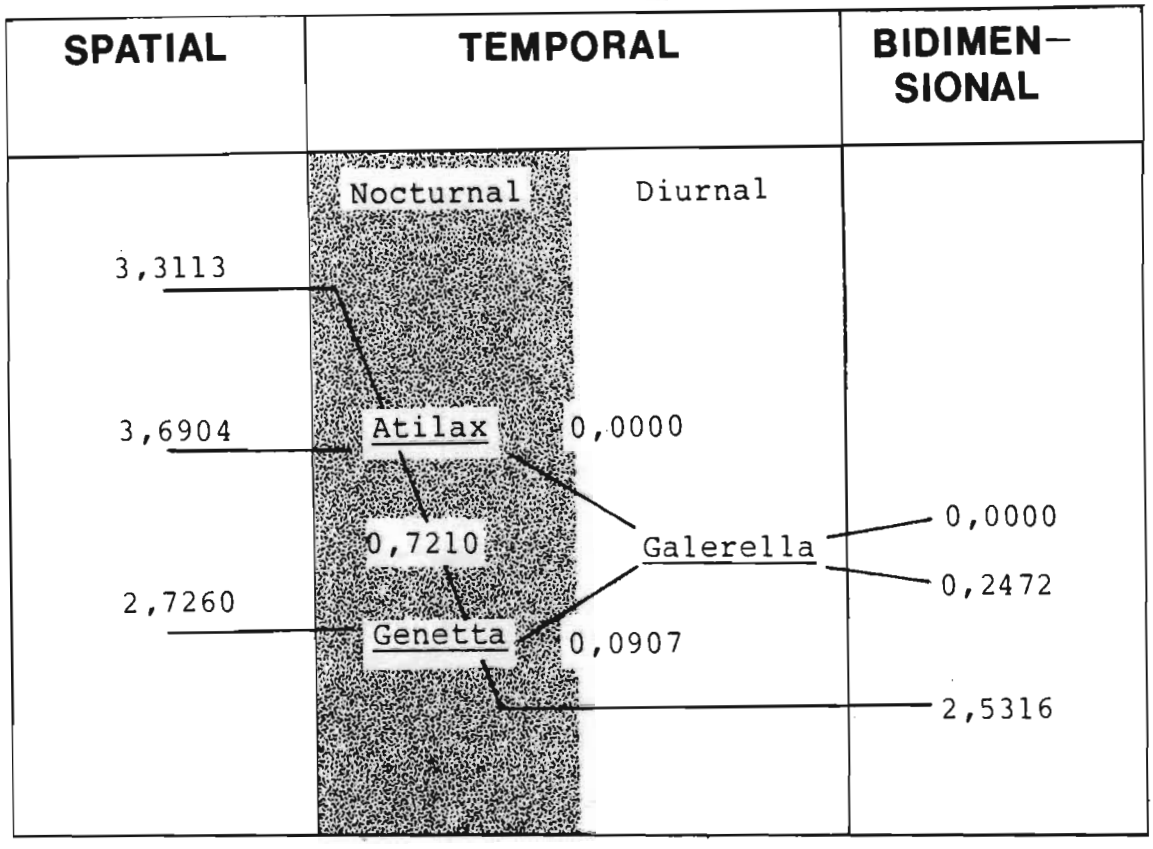

FIGURE 7.4. Spatial, temporal and bidimensional niche overlap among the forest group at VCNR. High spatial overlap is reduced because of low temporal overlap between Galerella and the two nocturnal viverrids (Atilax and Genetta). Compare bidimensional overlap between the synchronous and asynchronous species.

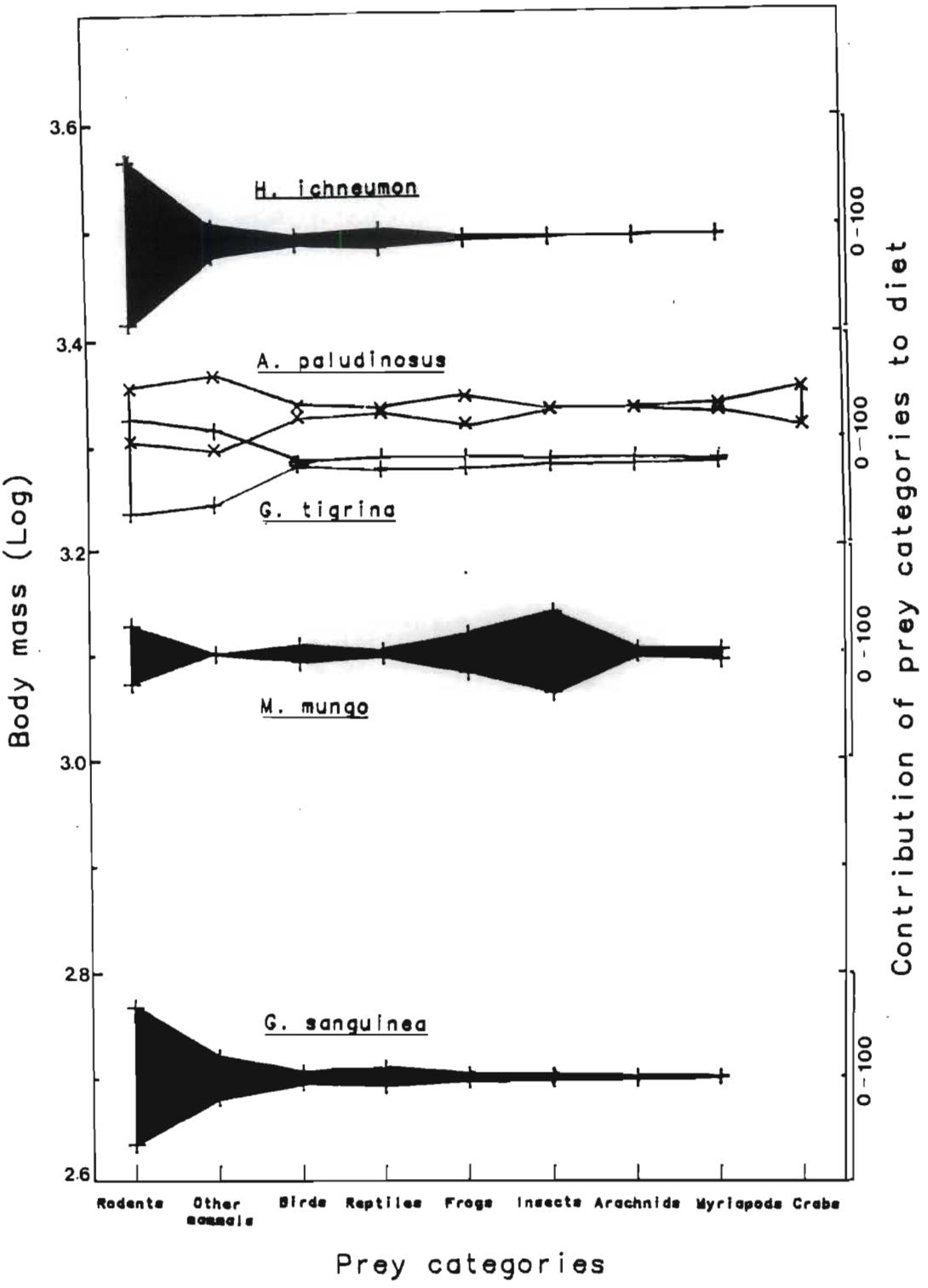

FIGURE 7.5. Pictogram showing the trophic, temporal and predator size relationships among the five species of viverrid at VCNR. Mean viverrid mass is shown on the left ordinate, mass percent contribution of prey to the diet on the right ordinate. Shaded =diurnal and unshaded =nocturnal. Note the dietary differences between the nocturnal, and similarly sized, Atilax and Genetta. The diurnal species are evenly spaced according to size as is the small mammal guild - Herpestes, Genetta and Galerella. See Table 7.5.

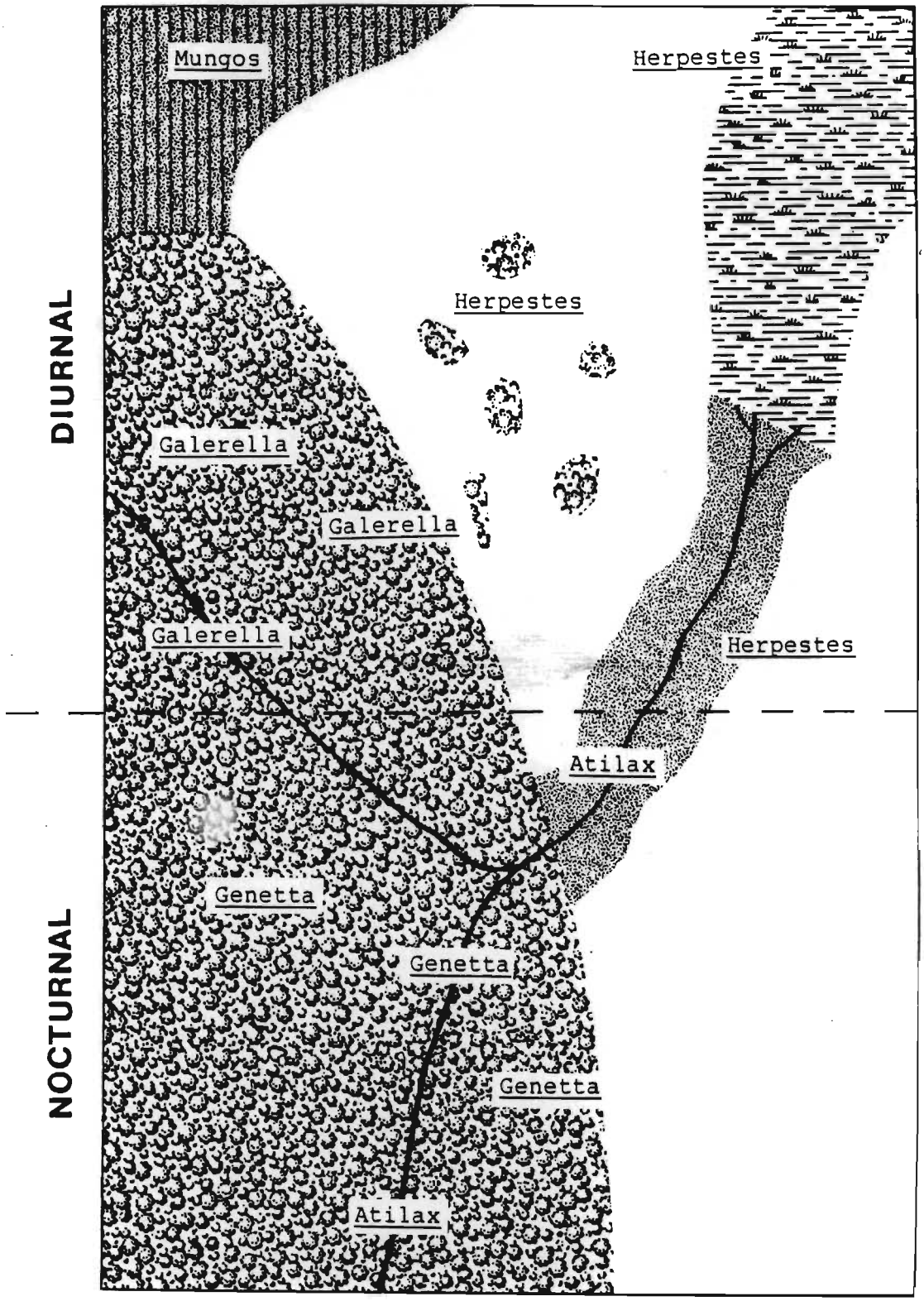

FIGURE 7.6. Diagrammatic representation of the segregation of five species of viverrid at VCNR along the spatial and temporal niches. See Table 7.5. Key as for Figure 2.1.

habitats was made using Spearman's rank correlation coefficient (Jaksic et al. 1981) therefore absolute values were not important and prey availability data were expressed by the pooled PVC and array trap results as a percentage of total mass (Chap. 5).

As trapping was conducted in relatively few habitats (Chap. 5; Table 7.2), this analysis provided only a general indication of the hunting habitats of the viverrids. Results were, however, consistent with the general habitat preference analyses (Chap. 6; Table 7.2). Herpestes was the only species to show a positive correlation between prey in the diet and in the grassland (Table 7.2). Grassland contributed significantly to the distribution of this species at VCNR (Table 6.3) suggesting that, with respect to broad prey categories, Herpestes concentrated its hunting activities in the area where its main prey, small mammals and reptiles (Tables 6.9 & 6.10), were most abundant (Table 7.2).

The positive correlation between prey on the forest margin (Table 7.2) and in the diet of Genetta and Atilax was anticipated since both species used forests extensively (Table 6.3; Figs. 6.3 & 6.5). Radio-collared Atilax spent much time near forest streams where crabs and frogs were common (Table 6.9) and both viverrids ate many "typical forest cryptofauna" - amblypygids, scorpions, centipedes and pill millipedes (Chaps. 4 & 5).

TABLE 7.2. Hunting habitat of the five species of viverrid. Differences between the overall importance of prey in the diet (primary and secondary prey) and prey biomass in three habitats were evaluated with Spearman's rank correlation coefficient (rs).

Species	Habitat types					
	Grassland		Forest margin		Stream	
	rs	P	rs	P	rs	P
G. tigrina	0,11	NS	0,63	<0,05	-0,06	NS
H. ichneumon	0,70	<0,05	0,59	NS	0,45	NS
G. sanguinea	0,56	NS	0,54	NS	0,38	NS
A. paludinosus	0,35	NS	0,70	<0,05	0,54	NS
M. mungo	-0,58	NS	-0,82	<0,05	-0,36	NS

No significant correlations were found for Galerella implying that this species did not concentrate its foraging activity in one habitat type (Jaksic et al. 1981; Table 7.2). This is not unreasonable as Galerella occurs in a wide range of habitats (Kingdon 1977; Stuart 1981; Smithers 1983) and, its intermediate spatial niche breadth of 0,4912, was second highest in the study (Table 6.11). The abundance of small mammals in the diet of Galerella (Fig. 4.7) suggests that some hunting was conducted at the forest margins (below) or in grassland (Table 6.10) while numerous forest cryptofauna in its diet suggests occurrence in forest.

Correlations shown by Mungos are difficult to explain. In particular, the significant negative correlation with forest margin (Table 7.2), where prey was probably similar to that in scrub forest, the preferred habitat of Mungos (Table 6.3; Fig. 6.3). Negative correlations are unlikely to be the result of Mungos hunting in a wide range of habitats (Chap. 6) and perhaps the analysis was affected by the small sample sizes or by Mungos selecting food according to criteria other than just prey availability.

More specific analyses were made of the mammalian prey of the viverrids excluding Mungos (Table 7.3). Significant correlations were found between the overall importance of mammals in the diets of Genetta and Galerella and prey availability on forest margins (Table 7.3). Capture of small mammals on the forest margins explains the problem of finding numerous grassland rodents (Fig. 6.10) in the diet of these forest species (Fig. 4.9).

Note that no significant correlations were found for Herpestes or Atilax in this analysis, nor for Mungos in the previous analysis (Tables 7.2 & 7.3). However, significant correlations will not result if prey are eaten under criteria other than relative abundance (Jaksic et al. 1981). These viverrids act as selectors (Chap. 5) and these results (Tables 7.2 & 7.3) support the claim that Herpestes, Mungos and Atilax took prey other than in proportion to availability (Chap. 5).

In summary, an association exists between the habitats occupied by the viverrids and their prey. Because of this, and the spatial segregation within the viverrid assemblage (Figs. 6.3; 6.5 & 7.3), spatial segregation may well represent dietary differences among the viverrids i.e. these niches are not completely orthogonal. Important findings are the spatial separation achieved between the diurnal members of the small mammal guild, Galerella and Herpestes and the similarity between the nocturnal Atilax and Genetta of the forest group (Figs 7.1, 7.3 & 7.6; Chap. 6).

TABLE 7.3. Hunting habitat of the five species of viverrid. Differences between the overall importance of mammalian prey in the diet and prey biomass in six habitats were evaluated with Spearman's rank correlation coefficient (rs).

Species	Habitat types: Grassland		Vlei		Forest margin	
	rs	P	rs	P	rs	P
G. tigrina	0,22	NS	-0,60	NS	0,74	<0,05
H. ichneumon	0,39	NS	0,25	NS	0,13	NS
G. sanguinea	0,57	NS	-0,20	NS	0,82	<0,02
A. paludinosus	0,36	NS	-0,90	NS	0,38	NS

Species	Habitat types: Forest		Stream		Cane	
G. tigrina	0,40	NS	-0,13	NS	0,26	NS
H. ichneumon	-0,50	NS	-0,11	NS	0,45	NS
G. sanguinea	0,60	NS	0,14	NS	-0,05	NS
A. paludinosus	0,40	NS	0,70	NS	0,33	NS

TROPHIC NICHE

The plot of trophic overlap and neighbours in niche space summarises the dietary differences presented in Chapters 4 and 5 (Fig. 7.7). The diets of Atilax and Mungos were unique with lowest overlaps between these two species and the other viverrids (Fig. 7.7; Table 5.9). Rather obviously, the diets of the small mammal guild were similar when presented at this broad category level. However, segregation of the viverrid assemblage was manifest by temporal (Figs. 7.1 & 7.2), habitat (Figs. 6.5 & 7.4) and prey size differences (see also Figs. 7.5 & 7.6).

Selector feeding behaviour

In Chapter 5, I proposed that Herpestes, Atilax and Mungos were selectors (see Rosenzweig 1986) but did not consider the

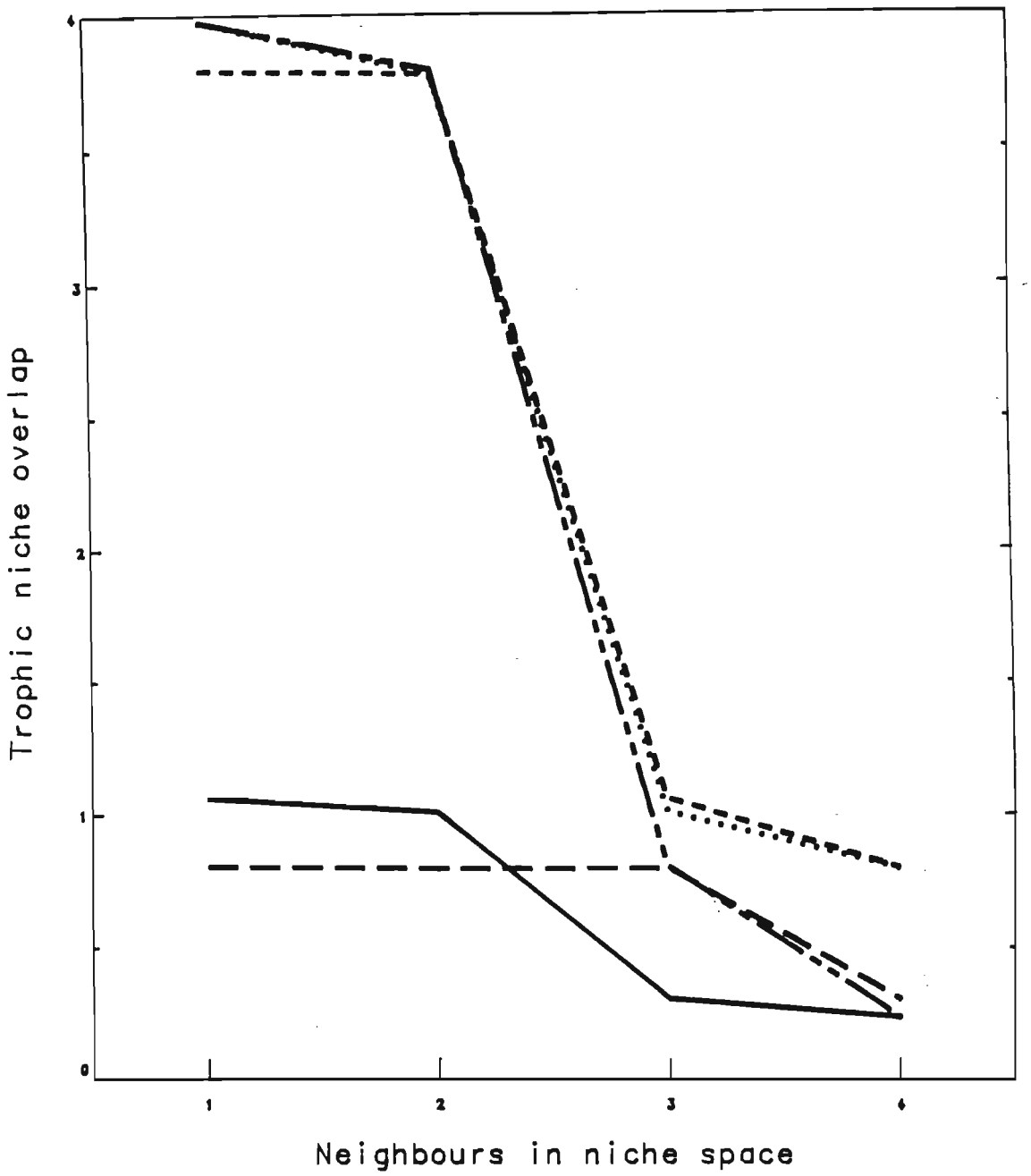

FIGURE 7.7. Trophic overlap versus nearness rank of neighbours in niche space among five species of viverrid at VCNR. The small mammal guild can clearly be seen. Otherwise legend as for Figure 7.1.

influence of habitat on prey selectivity. Use of the habitat by the viverrids can now be incorporated into the model.

An important objection to the model (Chap. 5) centres around the compression hypothesis (MacArthur & Wilson 1967) and suggests that the viverrids may be acting as habitat specialists but as trophic opportunists i.e. eating what is available within a preferred habitat. This is the basis of Schoener's (1974a&b, 1986) argument proposing that habitat is most important in segregating species. Habitat plays an important role in determining prey availability (Chap. 6, Tables 6.9 & 6.10) but the overall importance of the prey of Herpestes, Atilax or Mungos did not correlate significantly with prey abundance (Tables 7.2 & 7.3) when considered at the species level suggesting that abundance was not the sole criterion for prey selection.

To clarify the influence of habitat on the prey selector model comparisons are made between the habitat occupied by the viverrids and the range of potential prey in those habitats. Feeding trials with Atilax (Baker 1987c, 1988a), Mungos (Sadie 1983), Galerella (Baker 1980; Jacobsen 1982) and Genetta (Rowe-Rowe 1971; Maddock unpubl. data) show that a wide range of prey are acceptable to these viverrids and rodents are preferred prey. It is therefore assumed that all prey discussed below are acceptable to the viverrids and can be efficiently handled by them.

Mungos inhabits woodland or savanna where there are numerous invertebrates (Neal 1970; Rood 1975; Rowe-Rowe 1978; Rautenbach 1982; Sadie 1983; Smithers 1983) and small mammals

(De Graaff 1981; Smithers 1983). Galerella occurs in similar habitats (Smithers 1968, 1983; Rood & Waser 1978; Jacobsen 1982; Rautenbach 1982; Taylor 1986) yet both species have different diets (Smithers 1983). These two species and Herpestes and the dwarf mongoose, H. parvula, have slightly different habitat preferences in East Africa (Kruuk 1975) yet despite different species living in similar habitats, interspecific dietary differences remain fairly consistent (Chap. 5; Sadie 1983; Smithers 1983). Mungos, inhabiting different areas, shows only minor differences in food selection (Sadie 1983; Chap. 5).

Compare Mungos with the forest group, Atilax, Genetta and Galerella at VCNR (Chap. 6) which eats a large proportion of mammals (Chap. 4). Mungos prefers scrub forest (Table 6.3; Fig. 6.3) where small mammal trapping revealed twice as many rodents compared with the other forest types (Chap. 5). Also, 20% of the observations of Mungos were in grassland, second only to Herpestes. Despite inhabiting areas where small mammals were common, no selection for these prey were made. Thus, the broad similarity in diet over a wide range of habitats (Chap. 5) and the occurrence of Mungos in habitats where alternative prey are available supports, rather than rejects, the hypothesis that Mungos acts as a selector (Chap. 5).

Herpestes concentrates on small mammals abundant in its preferred habitats (Table 6.10) apparently supporting the idea of a trophic opportunist and habitat specialist. But among the prey within these habitats, R. pumilio is ten times more common than Otomys spp. (Table 5.2; Chaps. 5 & 6). Yet Otomys

spp. appeared 4,5 times more frequently in the diet of Herpestes than did R. pumilio (Table 4.3). Invertebrates are also abundant in these habitats (Waser 1980; Chap. 5) but, although forming the primary prey of the similarly sized I. albicauda (Taylor 1972) and Mungos (Sadie 1983), were insignificant in the diet of Herpestes (Fig. 4.1). Therefore, despite the diversity of prey available to Herpestes in its preferred habitats, this viverrid mainly selects Otomys spp. Similar behaviour has been reported for Herpestes in Europe; although a wide range of prey were taken, this species concentrated on rabbits O. cuniculus which comprised more than 70% of the total mass eaten (Delibes et al. 1984).

That the diet of Atilax, differed from the other viverrids was clearly shown in Table 4.2. But because this species hunts mainly near water (Rowe-Rowe 1977; Smithers 1983; Baker 1987c, 1988a), the criticism that Atilax is a habitat but not a trophic selector, is pertinent. Certainly, crabs and frogs were abundant in its preferred habitats. But Galerella and Genetta occupy similar macrohabitats to Atilax but Atilax spends more time in vlei, grassland, cane and along watercourses (Smithers 1983; Baker 1987c) where rodents are numerous (Chap. 5; De Graaff 1981; Smithers 1983). Despite this, fewer small mammals are eaten by Atilax than by Galerella or Genetta (Table 4.2). Thus, although small mammals, and especially Otomys spp., are present in Atilax's habitats, crabs and frogs are selected. Results from other studies are similar and small mammals have never exceeded crabs in the diet of this species (Rowe-Rowe 1975; Whitfield & Blaber 1980; Du Toit 1980; Smithers 1983; Louw & Nel 1986;

Baker 1987c, 1988a). However, Louw and Nel (1986) consider the diet of Atilax to vary with habitat.

Thus, consideration of the prey available to Mungos, Herpestes and Atilax, both at VCNR and elsewhere, illustrates that these species do not take prey on the basis of prey abundance only - a requirement of opportunistic feeding. A plethora of complex ecological (Ewer 1973; Waser 1981), behavioural (Baker 1987c, 1988a), morphological (Petter 1969; Taylor 1974, 1979) and genetic factors are probably responsible for these selector traits. The highly evolved and complex vigilence behaviour patterns exhibited by H. parvula (Rasa 1984) illustrate that viverrids are certainly capable of complex behaviour patterns. What I propose is not that certain viverrids are highly specialised predators but that they are well adapted to fluctuating food supplies and to surviving in sympatry with other small carnivores (Chap. 1). This is achieved by selecting specific prey whenever possible but being able to eat a much wider range of prey when necessary (Delibes et al. 1984; Chap. 5). Whatever the reasons, the end result is that dietary overlap among all five viverrids is reduced and coexistence facilitated (see below).

OVERVIEW

Schoener (1974a) found that animals partitioned habitat more often than food which was partitioned more often than time. More recent literature suggests that great variation exists in the relative importance of these three dimensions in segregating species (review in Schoener 1986). Since predators are more likely to partition time than are other trophic

groups (Schoener 1974a) and predators frequently differ in foods eaten (Rosenzweig 1966; reviews in Kruuk 1975; Bekoff et al. 1984), an examination of the importance of these dimensions in segregating the viverrid community should yield interesting results.

To determine which niche dimension is most important in segregating the viverrids, consider the degree of niche separation achieved along each dimension (Table 7.4). Clearly, the six asynchronous pairs are separated with respect to time and all but the three species in the forest group are segregated by macrohabitat differences (Table 7.4). Seven species pairs also clearly separate by dietary differences (Fig. 7.4). Among the small mammal guild more subtle dietary differences are evident and only Genetta and Galerella do not clearly separate (Table 7.4; Fig. 7.7; Chap. 5).

TABLE 7.4. Overlap for the three niche dimensions and their products (the multidimensional overlap) between all possible viverrid species pairs.

Species pairs	Time	Spatial	Trophic	Multidimensional
Genetta/Herpestes	0,0881	1,5750	3,7952	0,5266
Genetta/Galerella	0,0907	2,7260	3,7806	0,9347
Genetta/Atilax	0,7210	3,5113	0,7999	2,0251
Genetta/Mungos	0,1746	1,4150	1,0631	0,2626
Herpestes/Galerella	0,7689	1,1490	3,9756	3,5123
Herpestes/Atilax	0,0046	1,6363	0,8063	0,0061
Herpestes/Mungos	0,8327	1,4970	0,2374	0,2959
Galerella/Atilax	0,0	3,6904	0,7991	0,0
Galerella/Mungos	0,7296	1,9800	1,0114	1,4611
Atilax/Mungos	0,0	1,1750	0,3051	0,0
Number of species pairs separated	6	7	9	

The trophic niche, therefore, may separate more species pairs than the habitat niche (9 vs 7; Table 7.4), although this is not clear-cut. Time separates the least number of pairs but

all niches play important roles. This finding is not surprising as trophic segregation among coexisting carnivores is well documented (Rosenzweig 1966; Erlinge 1969, 1972; Rowe-Rowe 1977; Wise et al. 1981; Powell & Zielinski 1983; Sadie 1983; Bothma et al. 1984; Bekoff et al. 1984; Macdonald & Nel 1986) but see Kruuk (1975) and Delibes (1983). Jaksic et al. (1981) have even suggested that consideration of the trophic niche alone is sufficient to segregate predators since habitat and temporal variation are thereby implied.

The range of prey available to small carnivores is immense and includes an abundance of invertebrates (this study; Waser 1980; Sadie 1983) reptiles, frogs (Johnson 1987), birds (Maclean 1985) small mammals (this study) in most habitats. Thus, it is not surprising that segregation can be achieved by differential exploitation of this wide range of prey - an advantage probably not available to larger carnivores which mainly concentrate on large prey (Ewer 1973; Kruuk 1975). Schoener (1986) stated that the spatial niche was infinitely partitionable, so is the trophic niche of small carnivores (Chaps. 4 & 5).

However, it is pertinent to question the validity of identifying a single important dimension. A degree of subjectiveness was involved in identifying food as the primary segregating niche (Table 7.4) and it is clearly not easy to distinguish the importance of these three dimensions, especially food and habitat. Natural systems are characterised by variation (seasonal, aseasonal, genotypic etc.), inherent stochasticity and dynamic nature. In the

past, interest in univariate explanations in biology has dominated thinking but such simplistic approaches must soon be replaced with more realistic multivariate explanations (Schoener 1986). In fact, Hutchinson's n-dimensional hypervolume model (1957) was probably the first trend toward multivariate realism but because of its abstract nature was unmanagable. A compromise between the simplistic and abstract or multivariate explanations should be attempted as these extreme forms represent a continuum from the unrealistic to realistic worlds.

The idea that viverrids coexist by partitioning food resources was derived from data from which spatial and temporal effects were not excluded. Thus, the influence of habitat and time are inherent in the trophic dimension (see Jaksic et al. 1981). Habitat and time, mediated through trophic effects, may greatly aid coexistence within this community but can only be shown by a multivariate, not univariate, approach.

The combined effect of the three niche dimensions in segregating the viverrid community is summarised in Table 7.5. Two broad macrohabitat types can be distinguised; forest and open areas (Table 7.5; see also Fig. 7.6). The temporal niche divides the forest viverrids into two equal groups, both of which can be segregated by diet preferences (Table 7.5; see also Fig. 7.5). Thus, all three dimensions are required to segregate the five species. In terms of coexistence it is irrelevant which dimension segregates more species; each is important in facilitating coexistence.

CONCLUDING COMMENTS ON COEXISTENCE

Sympatric viverrids have greater species richness than either canids, felids or mustelids (Tables 1.1 & 1.2; Taylor 1986). While a wide range of factors (see Schoener 1986; Table 7.5) are likely to contribute toward coexistence among the viverrids, one point stands out - these generalist viverrids may behave as selectors (sensu Rosenzweig 1985). I have applied this hypothesis to feeding behaviour (Chap. 5) and suggested that it is adaptive under conditions of fluctuating prey populations and high species richness - conditions that characterise viverrid assemblages (Taylor 1986; Table 1.1; Chap. 5).

The great diversity of prey available to small carnivores allows considerable trophic differences within the viverrid assemblage (see above; Table 4.2). Dietary differences will be reinforced if the viverrids can act as selectors (Chap. 5). In addition, the wide distribution of these prey may extend the range of habitats available to the viverrids.

Indeed, viverrids do have wide habitat tolerances (Kingdon 1977; Rowe-Rowe 1978; Stuart 1981; Rautenbach 1982; Smithers 1983) but they require specific aspects of the habitat rather than a particular habitat type (Rautenbach 1982; Smithers 1983; this study; pers. obs.). These aspects (cover and prey abundance; Sadie 1983; Smithers 1983; Taylor 1986; Chap. 6; or proximity to water among the Southern Africa east coast viverrids; Smithers 1983) are fulfiled by a range of different habitats.

The generalist/selector feeding behaviour (Chap. 5) and wide

habitat tolerances (above) together may facilitate coexistence. At VCNR Atilax and Galerella are definite forest species (Chap. 6) whereas most data indicate they have a much wider habitat tolerance including open areas and forests (Roberts 1951; Rowe-Rowe 1978; Rood & Waser 1978; Waser 1980; Stuart 1981; Jacobsen 1982; Rautenbach 1982; Lynch 1983; Smithers 1983). Direct evidence is not available but I suggested that the presence of Atilax and Galerella in the forests was a result of interactions with Herpestes (Chap. 6). This requires further studies.

But from the data presented in Appendix 4, it could be assumed that viverrids do not need to partition resources. However, the alternative explanation is that competition or niche overlap is reduced by resource partitioning. This tautology cannot be resolved unless removal or enclosure experiments are performed. Such experimentation is impracticable because viverrid capture rates are too low, their home ranges too large and, at VCNR, removal of indigenous fauna conflicts with the aims of conservation. More rewarding may be exclosure experiments with prey animals.

One thing is clear, using the three main niche dimensions in combination, clear differences among the viverrid community are present (Table 7.5). Differences were found among the most similar species pairs, Herpestes and Galerella, and Atilax and Genetta. Whether these differences are in response to competition or other factor(s) cannot be determined from these data and requres more intensive (allotopic or syntopic) studies on one or both of these pairs and their major prey.

Viverrids are ecologically diverse (Hinton & Dunn 1967; Ewer 1973): their different activity periods (Chap. 6; Taylor 1986), differences in social organisation which translate into dietary differences (Waser 1981; Gorman 1979; Baker 1987c, 1988a) and a range of semi-aquatic, semi-arboreal or terrestrial habits (Chap. 3), together with the other ecological differences (above), further enhance coexistence at VCNR and may do so in other parts of the range of viverrids (Taylor 1986). To this I add that the ability of viverrids to occupy a range of habitats and eat a wide range of prey but also to select prey from a preferred group of items, are primary factors enabling them to reduce interactions with other viverrids and achieve high species richness.

APPENDIX 1

SCAT ANALYSIS

INTRODUCTION

Accurate quantification of diet based on scats or gut contents has long hindered biologists. Early workers found frequency of occurrence an accurate method (Scott 1941) and it, or a modified derivative, relative percentage occurrence, is widely used (Smithers 1971, 1983; Stuart 1977, 1981; Rowe-Rowe 1977; King 1980a; Alcover 1984 and many others). A major drawback is that small prey (insects) or prey with many indigestible parts (crabs) are overestimated relative to large animals (usually vertebrates) or those with few indigestible parts (frogs) (Erlinge 1968; Wise et al. 1981; Putman 1984). This method is also inaccurate when prey includes both large animals (most vertebrates which also have few indigestible parts) and small animals (for example, insects, myriapods, arachnids etc.). This problem is particularly relevant to the examination of viverrid diets which often include all of the above-mentioned prey (Smithers 1983). Finally, frequency of occurrence gives scant emphasis to quantification of prey items consumed.

More refined techniques are necessary to overcome these problems but each new technique has unique drawbacks. Volumetric or bulk methods of diet quantification are becoming widely used (Pulliainen 1980, 1981; Wise et al. 1981; Van der Zee 1981; Kruuk & Parish 1981). However, a major problem with faecal analysis is that of differential digestability in which the proportion of remains in the scat often differ considerably from the proportion in which the foods were eaten (Scott 1941; Lockie 1959; Hyslop 1980; Putman 1984). Consequently, any method relying solely on the proportion of undigested remains in the faeces will be subject to considerable error despite advantages over the frequency of occurrence method (Von Schantz 1980; Wise et al. 1981). Therefore more accurate results should be obtainable by avoiding the problem of differential digestibility where possible.

There are two ways in which this may be achieved: by using correction factors (Lockie 1959; Kruuk & Parish 1981; Van der Zee 1981; Liberg 1982) or by estimating prey mass at time of ingestion (Hyslop 1980; Tilson & Le Roux 1983; Putman 1984). The former is particularly useful and, perhaps, subject to fewer errors but requires time-consuming feeding trials. Since captive representatives of all five viverrids were not available the latter method seemed more practicable. In addition, much of the data required for estimating prey mass was routinely being collected (Chap. 5).

In view of the range of different methods of scat analysis and their varying accuracies, it was considered important to examine the effectiveness of the different methods before using them in this study.

MATERIALS AND METHODS

Scats were softened and macerated in water overnight, then thoroughly rinsed through a 1 mm sieve until the water was clear. Samples were sorted into assigned prey categories in a shallow, water-filled dish with the aid of a large magnifying glass. Where necessary, subsamples were kept for more detailed identification. Ideally, the term category should include all prey that the predator sees as similar (Hespenheide 1979) but this is difficult to do, not least because of identification problems. Consequently, category refers to taxonomical classification and may include order, family or even species. However, in each case, the meaning will be made clear.

Identification of prey remains.

Mammals were identified to species using hair (Brunner & Coman 1974; Keogh 1983, 1985), tooth cusp (De Graaff 1981) and tooth alveoli patterns (Bowland in prep.) and other diagnostic remains. Hairs were soaked for a few minutes in a 50:50 mixture of diethyl ether and absolute alcohol, then rinsed in water (Perrin & Campbell 1980). Negative cuticular scale impressions (Simms 1979) were made by laying individual hairs on slides thinly covered with clear nail varnish and removing the hairs when the varnish was dry (Hiscocks & Perrin 1987). Whole mounts, for examination of hair medulla and shape, were made using DPX mountant.

Identification of guard hairs was based on three features: hair shape, cuticular scale pattern and medulla characteristics and, where possible, was confirmed using tooth cusp (De Graaff 1981) and alveoli patterns (Bowland in prep.) Hair was preferred to tooth identification as teeth were often absent from the scats. Large and small mammals were distinguished by hair length and size of bones in the scats.

A hair reference system of mammals trapped at VCNR (including carnivores), was composed and used in conjunction with Keogh's (1983, 1985) bovid and rodent reference system. Hairs from mammals not trapped at VCNR were obtained from specimens at the Natal Museum, Pietermaritzburg.

Reptiles were identified using scale characteristics and comparing them with a reference collection (Lyn Raw, Institute of Natural Resources, University of Natal) while sacral and/or ilial bones were used to distinguish Amphibia (Rowe-Rowe 1977; Baker 1987c, 1988a). Professor G.L. Maclean (University of Natal) identified the bird remains.

Invertebrates were classified using continually updated and expanded reference material collected from VCNR (Chap. 5). Limbs, elytra, mouthparts, wings and other diagnostic parts were displayed on a board so that rapid comparisons with the faecal material could be made.

Analysis.

Three methods of scat analysis were considered for use (Lockie 1959; Wise et al. 1981; Kruuk & Parish 1981). Before final processing each was checked for representativeness and accuracy by conducting feeding trials on captive Atilax. On the basis of these results the best method of analysis was decided and used to determine the viverrid diets (Chap. 4). Three separately housed animals were starved for 24 hours. Then, for five days, were given weighed food (such as they were likely to eat in the wild) and scats were collected daily prior to feeding. Diet composition was unknown to me[1] and scat analysis was carried out as described below.

A1.1. Bulk estimation (Wise et al. 1981).

The bulk contribution of each prey category was determined on a scale of 1 to 10 so that the total score for each scat was 10 (Wise et al. 1981). Scores for each group were summed and expressed as a percentage of the maximum score possible ie. 10 multiplied by the number of scats analysed (Lockie 1959).

A1.2. Mass ingested (von Schantz 1980).

The number and size of prey when ingested was determined using diagnostic remains (limbs, teeth, bones, mouthparts, elytra, wings etc.). Prey categories were divided into head and body length size classes (dactyl length for freshwater crabs Potamonautes sidneyi; scute width and snout/vent length for reptiles; Table A1.1) and the mean mass of each size of prey category determined (A1.2.1). Individual items in the scats were assigned to one of these size classes. An estimate of mass ingested was determined by multiplying the relevant size class mass by the number of prey in the scat. Percentage contribution of each prey group to the total ingested biomass was then calculated.

TABLE A1.1. Prey categories and their size classes. During scat analysis prey sizes were determined from diagnostic remains in the scats and an approximation of mass for the various categories, obtained from regressions of size against mass.

Class	Size (mm) (see text)	Categories
I	< 9,9	Arthropoda, Crustacea, Amphibia, Reptilia
II	10-19,9	Crustacea, Amphibia, Sauria
IIa	10-14,9	Arthropoda, Serpentes
IIb	15-19,9	Arthropoda, Serpentes
III	20-29,9	Arthropoda, Crustacea, Amphibia, Reptilia
IV	30-44,9	Arthropoda, Crustacea, Amphibia, Reptilia
V	> 45	Crustacea, Amphibia, Reptilia

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1. I am indebted to C. Baker for conducting these feeding trials.

This method assumes that the whole prey is eaten which is likely since most prey were relatively small and was supported by feeding observations on captive Atilax, Genetta and Galerella. With large prey (>1 kg), the maximum mass in the stomach, determined from captive animals (Atilax, Genetta) or from the literature (Herpestes, Delibes et al. 1984; Galerella, Baker 1980) was assigned.

A1.2.1 Mass estimation.

Animals caught in traps (Chap. 5) were weighed and measured in the field using a Pesola balance and vernier calipers or weighed on a Metler balance in the laboratory. Crab, P. sidneyi, carapace width, dactyl length and mass were measured whenever these animals were encountered.

The mean seasonal mass of rodents and insectivores was obtained from trapping records (Chap. 4; Von Schantz 1980). Where possible, the age of rodents in the scats was estimated using tooth wear patterns (Perrin 1979, 1982) and they were then assigned juvenile or adult weights. If the age could not be determined, animals were assigned the mean seasonal mass. The mass of infrequently caught mammals (Graphiuris murinus, Suncus infinitesimus was obtained from De Graaff (1981) or Smithers (1983).

Snakes were weighed and scute width measured, approximately one week after feeding, at the Fitzsimmons Snake Park, Durban. Mass and snout/vent length data for lizards and amphibians were obtained from Messrs. G. Alexander (University of Natal) and A. Lambiris (Natal Parks Board) respectively. Bird masses were from Maclean (1985).

Linear regressions of size and mass were calculated for each prey category. From this a mean mass for each size class in each prey category was determined (Table A1.1). Only two items were poorly represented (scorpions and centipedes). Prey that could not be identified were assigned to the closest category (for example, Insecta, Arthropoda, large or small Mammalia, Amphibia etc.) and given the mean mass of that category.

A1.3. Frequency of occurrence (Lockie 1959).

The first occurrence of a prey category in each scat was recorded and expressed as a percentage of the total number of scats analysed.

RESULTS.

Results of the three methods of analysis are presented in Table A1.2. The method estimating mass at time of ingestion was the most accurate with a total overall error of 3,2% (Table A1.2). The other techniques had large errors which were inconsistent (relative bulk - 104%, and frequency of occurrence - 1 750%; Table A1.2). Chi-square analysis comparing food given with diet estimation showed highly significant differences when frequency of occurrence and relative bulk were used ($P<0,001$; $P<0,05$ respectively; Table A1.2). The mass ingested technique was significantly different

TABLE A1.2. Results of the feeding trials conducted on three Atilax paludinosus (A, B and C). The percentage error of three methods of scat analysis which were used to determine the foods eaten over a period of five days are presented:- **bulk** estimation, Frequency of occurrence and **Mass** at time of ingestion (see text for details).

Prey		Trials			
		A	B	C	Combined
Mammals	Bulk	21,6	-11,8	25,3	8,0
	Freq.	111,2	1109,2	97,6	103,3
	Mass	-1,8	-31,4	-14,8	-15,8
Crabs	Bulk	5,1	53,1	-11,8	24,5
	Freq.	292,7	228,6	279,5	264,0
	Mass	50,7	34,3	21,0	37,7
Frogs	Bulk	-66,3	-68,6	-13,3	-56,4
	Freq.	258,4	555,0	717,7	422,1
	Mass	-49,3	3,6	-14,3	-19,6
Reptiles	Bulk	327,8	-72,9	-38,5	-27,4
	Freq.	1680,7	16,9	251,2	235,4
	Mass	107,9	16,8	15,1	23,9
Orthoptera	Bulk	172,7	1185,7	42,9	572,4
	Freq.	9990,9	3471,4	7042,9	7727,6
	Mass	-9,1	17,1	-32,1	-10,3
Overall error for the whole diet over five days					
	Bulk	92,2	217,1	9,7	104,2
	Freq.	2466,8	1076,3	1677,8	1750,5
	Mass	19,7	8,3	7,4	3,2
Chi squ.	Bulk	<0,001	<0,001	<0,05	<0,005
	Freq.	<0,001	<0,001	<0,001	<0,001
	Mass	<0,01	<0,05	NS	NS

($P<0,05$) in two out of three trials but, overall, was not significant (Table A1.2).

More detailed examination of the percentage mass technique showed underestimation of mammals, frogs and orthopterans but overestimation of crabs and reptiles (Table A1.1). Vertebrates have relatively few indigestible parts and would be expected to leave few remains in the scats and, therefore, be subject to under-representation. The mass of Orthoptera fed to the mongooses was underestimated because these animals were heavier than the mean mass used in the estimations (Table A1.1) but, usually, small orthopterans were eaten by wild animals (Chap. 4). Overestimation of crabs was anticipated as a result of a large volume of indigestible exoskeleton. However, overestimation of snakes was unexplained as these prey leave few remains and should be underestimated.

The error in this method was relatively consistent (a prey category was either over- or underestimated by a similar degree) and more closely approximated the given diet than did the other two methods.

Frequency of occurrence was inaccurate when used to estimate volume or bulk of food ingested (Table A1.2) but was tested in its ability to estimate how often a category was eaten (Table A1.3). No significant differences were found between the number of times prey items were fed to the mongooses and the number determined using this method (Table A1.3). With the combined results the estimations were identical (Table A1.3).

TABLE A1.3. Results of the feeding trials conducted on three Atilax paludinosus (A, B and C. All=combined results). The percentage frequency of occurrence was used to determine how often various prey items were eaten and are compared with the given values (see text for details). 1=percentage frequency of occurrence, 2=estimated number of times the food was given, 3=actual number of times the food was given.

Prey	Trials											
	A			B			C			All		
	1	2	3	1	2	3	1	2	3	1	2	3
Mammals	100	5	5	100	5	5	100	5	5	100	5	5
Crabs	89	4	3	100	5	4	80	3	3	91	4	4
Frogs	100	5	4	75	3	3	100	5	4	91	4	4
Reptiles	33	1	1	13	1	1	40	2	1	27	1	1
Orthoptera	22	1	1	13	1	1	20	1	1	23	1	1
chi-square		NS			NS			NS			NS	

DISCUSSION.

Great improvements have been made in the advancements of techniques used to determine predator diets during the last decade (for example, Wise et al. 1981; Kruuk & Parish 1981; Van der Zee 1981; Tilson & Le Roux 1983). Despite these advances less effective methods are still routinely employed.

Selection of a method depends on the aims of the project but as this study shows, some methods are more accurate than others. Of the methods presented here, mass estimation appeared most accurate. Exceptions were found with reptiles in trial A (a large error resulting from overestimation of the mass of a damaged 19 g snake) and with the frogs in all trials. Both mass and number of frogs eaten are difficult to estimate since few bones occur in the scats. Nevertheless, the estimation of mass more closely approximated the food given the mongooses than the other methods. Finally, it was apparent that estimation of prey mass at time of capture/ingestion was, biologically, a more meaningful concept than those arising from the other methods. These two crucial points formed the basis for the decision to use mass estimation as the principal technique of scat analysis.

However, more than one method of analysis and presentation can often realistically reflect the diet (Korschgen 1971; Wise et al. 1981; Van der Zee 1981; but see King 1980a). Comparison of the results derived from different methods may also enable the drawbacks inherent in each technique to be partially offset. Kruuk & Parish (1981) brilliantly illustrated the benefits of using two methods in their analysis of badger scats. The results of their study were clearly shown by plotting frequency of occurrence of prey items against a method of volumetric analysis (Kruuk & Parish 1981).

Therefore, mass estimation, when combined with frequency of occurrence (which gave an excellent indication of the frequency with which prey was eaten) forms a powerful tool for the quantification of carnivore diets. Consequently, for the analysis of scats in this study, prey mass estimations were plotted against the frequency of their occurrence (Kruuk & Parish 1981). This method incorporates two crucial aspects of feeding biology; the frequency with which items are eaten and the amount (mass) of that item eaten. When plotted together these values form the overall importance of each prey to the animal (see Chap. 4, Materials & Methods).

Although these methods are considered the most appropriate they include some potential sources of error. First, all prey must be identifiable. Most categories were, with the exception of Oligochaetes, insect larvae, certain molluscs and other soft-bodied prey which leave few remains. Although not feasible in this study, this problem can be overcome by combining scat analysis with direct observations of feeding (Pulliainen 1980; Sadie 1983; Hiscocks & Perrin 1987). However, the above-mentioned prey are small, have low mass and and would probably contribute little to the diet. Thus their omission from the analyses was considered not to affect the results seriously. An exception was the banded mongoose of which soft-bodied prey can contribute more than 7% of biomass eaten (Sadie 1983).

Second, accurate enumeration of individual prey is often questionable (Scott 1941; Hyslop 1980) but for some prey this was not a problem (for example, scorpions, centipedes pill millipedes, large coleopterans). However, if large numbers of small prey were present in the scat, or when prey were finely masticated, enumeration became difficult.

A related error involved enumeration when identification was based on hair, feathers or scales rather than single diagnostic parts. The amount of these remains in the scat could not be used to determine the number of prey eaten. Accurate enumeration depended on the presence of jaws, long bones etc. These remains were not always present, resulting in some underestimation of vertebrate food.

Finally, the criticism that animals may not eat all their prey (Scott 1941) must be addressed. Also, predators eat in different ways; some skin or leave the gut and liver of their prey while others do not (Lockie 1959; Rowe-Rowe 1971). These behaviours could confound diet estimation, especially in comparative studies. Feeding trials on Genetta and Atilax (and Galerella Baker pers comm.[2]) indicated that, in captivity at least, these animals ate all their food. Examination of the stomachs of road killed Herpestes revealed numerous mice and snakes - all of which appeared to have been totally consumed. The small size of prey eaten by Mungos makes it highly unlikely that prey would be partly eaten.

Therefore, the limited data at hand indicates that prey were totally consumed by these five viverrids except where the food were larger than the stomach volume of the predator.

To conclude, a list of assumptions involved in the methods of scat analysis is provided.

1. Prey must leave remains in the scats which are identifiable.

2. All identified prey represents one individual unless indications of more than one individual are present.

3. All identified prey are entirely eaten. Prey are not skinned nor are parts of the body left. Mean mass estimations therefore closely approximate ingested prey mass.

4. Prey with a mass or volume exceeding that of the filled stomach of an adult predator are assigned the mass equal to the maximum stomach capacity of each predator species.

The influence of methodology on diet determination

To indicate the importance of accurate methodology a brief comparison between the scat analysis data presented in Chapter 4 and published reports is given below.

Generally, researchers agree on the diets of the five viverrids under study; diets are diverse but rodents, other vertebrates and insects (usually Coleoptera and Orthoptera) often rank as primary prey, particularly for Herpestes, Galerella and Genetta (Rowe-Rowe 1978; Rood & Waser 1978; Smithers & Wilson 1979; Stuart 1981, 1983; Baker 1980;

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2. Baker, C. Zoology Dept, University of Durban-Westville, Durban.

Rautenbach 1982; Smithers 1983; Sadie 1983; Delibes *et al.* 1984). As found in this study, *Atilax* has a slightly different diet of aquatic prey (crabs, frogs, mussels, prawns), insects and small mammals (Rowe-Rowe 1978; Whitfield & Blaber 1980; Smithers 1983; Louw & Nel 1986; MacDonald & Nel 1986; Baker 1987c, 1988a) while *Mungos* is primarily an insectivore but also eats myriapods and few vertebrates (Neal 1970; Rood 1975; Sadie 1983; Smithers 1983).

Although preferred foods have been identified, most authors consider these viverrids to lack dietary specialisation (above). The great variety of food found in the diet of these small carnivores certainly appears to support this claim but these conclusions were based on analysis by frequency of occurrence which indicates only how often a prey category is eaten. The method can be misleading when used to indicate important prey since frequently eaten, but small prey (for example, insects) may contribute little to the diet. Frequency of occurrence, unlike the mass percentage method, would, nonetheless, rank such categories as important.

Thus, frequency of occurrence can give an incorrect idea of overall prey importance. Animals which, in addition to their main prey, regularly sample different food, irrespective of quantity, will be considered opportunists when this method is used. A clear example of this is the idea that insects were the main prey of *Gallerella* (Baker 1980; Smithers 1983). Insects are commonly eaten by small carnivores but form the main prey of only a few (Sadie 1983). As *Galerella* is considered highly predacious (Ewer 1973) and numerous authors found vertebrates dominating the diet (Roberts 1951; Smithers 1971; Rood & Waser 1978; Stuart 1981; Rautenbach 1982; Sadie 1983; this study) it is likely that the conclusion that insects form a major part of the diet of *Galerella* is an artifact of the methodology.

Such methodological differences may account for differences between my results and published data. Results of this study are in substantial agreement with published data when frequency of occurrence methods are compared (*i.e.* an indication of how often prey are eaten). However, when the diets based on mass percentage are compared, my results only agree with authors who used more detailed methods of analysis (Delibes *et al.* 1984 on *Herpestes*; Sadie 1983 on *Mungos*). It is apparent that a more accurate idea of feeding biology can be obtained by combining the frequency with which particular prey are eaten and its bulk contribution to the diet (Kruuk & Parish 1981).

APPENDIX 2

MODELS USED TO DETERMINE PREY ABUNDANCE

INTRODUCTION

Determining absolute animal abundance, although desirable, is time consuming, problematical and, often, a unique method is required for different taxa (Smith, Gardner, Gentry, Kaufman & O'Farrell 1975; Southwood 1978; Campbell & Christman 1982). It was therefore impracticable to use absolute abundance models, with their often unrealistic assumptions. Relative methods of population estimation were used instead. Once the primary prey of the five viverrids were known, absolute methods were used to give more realistic ideas of prey abundance and to verify the validity of the indices.

Relative estimates are advantageous as they are quick, not subject to restrictive assumptions (Southwood 1978) and it is often possible to convert relative indices to absolute estimates (Seber 1973; Caughley 1977; Southwood 1978). They were also suited to the aims of this study i.e. spatial comparisons of potential prey abundances as well as determining their within-habitat temporal changes (Seber 1973; Caughley 1977; Southwood 1978). For these reasons, relative estimates (indices) of prey abundance were preferable.

Several relative methods are available (Seber 1973; Flowerdew 1976; Caughley 1977; Southwood 1978). But, when dealing with small animals, trapping is probably superior to observational methods because it is less time consuming, more objective and reliable. More importantly, trapping indicates animal abundance on a 24 hour basis (Samways 1983; Johnson 1987) thereby giving a more realistic idea of prey availability. Thus, a relative trapping method that placed a broad range of potential prey at risk (vertebrates and invertebrates) was sought.

Pitfall traps (PFTs), are simple to operate, have been used successfully for mammals (Williams & Braun 1983), reptiles and amphibians (Vogt & Hine 1982; Johnson 1987) and various arthropods (Kowalski 1976; Thomas & Sleeper 1977; Thomas 1979; Samways 1983; Mispagel & Sleeper 1983) and are particularly useful when used in conjunction with drift fences (Mispagel & Sleeper 1983). PFTs were used in this study to sample a broad spectrum of prey.

Small mammals were important prey (Chap. 4) and alternative techniques for estimating relative densities of small mammals are efficient and well known. Small mammal densities were, therefore, assessed separately using trap lines.

MATERIALS AND METHODS

Pitfall trapping (relative estimates).

A brief outline of the methods used is presented here but details will be found in Chapter 5. Initially, three 7,5 l bucket PFT

replaced with more efficient array traps (Campbell & Christman 1982) duplicated in three different habitats (Chap. 5).

The use of PFTs has been criticised (Southwood 1978) but provided the disadvantages are considered (Southwood 1978; Marsh 1984), useful information can be obtained from them (Gist & Crossley 1973; Thomas & Sleeper 1977; Vogt & Hine 1982; Campbell & Christman 1982). As the same methodology was used throughout and data were used to indicate trends (not absolute numbers) and to determine the change in numbers over time, the use of these traps was believed justified. The advantages of the array traps, i.e. efficient collection of a very wide range of prey and simple operation, outweighed any disadvantages.

Small mammal trapping (relative estimates).

Small mammal censusing, using live traps set in a trap line was employed (Chap. 5). Controversy exists over the best methods of small mammal sampling (Gentry, Golley & Smith 1968; Smith et al. 1975) and it is recognised that no single method will overcome all these problems (Southwood 1978). A modification of Linn's (1963) method, strongly influenced by work done in Africa, (Chap. 5) was used. The reasons for choosing these modifications and the final method are outlined below.

A2.1) First, to reduce the variables affecting small mammal trap success - many of which are not clearly understood (Gentry, Golley & McGinnis 1966; Hansson 1967; Patric 1970; Delany 1972, 1974; Smith et al. 1975; Flowerdew 1976; Wingate & Meester 1977; Willan 1979, 1986; Bowland in press) - trapping methods were standardised (Southern 1973).

A2.2) Live trapping enables a sequential estimate of population dynamics (Smith et al. 1975) and, in contrast to snap trapping, caused minimal disturbance to the viverrid prey. PVC live traps were therefore used (Willan 1979). These have been shown to capture small mammals at least as efficiently as other traps (Wingate & Meester 1977; Willan 1979).

A2.3) Bait has an important influence on small mammal trapping and specific baits have been devised for certain species (Patric 1970; Delany 1972, 1974; Willan 1986) but here the aim was to sample all species. So, a general bait of rolled oats and peanut butter (6:4) mixture, or raisins and oats, was used (Rowe-Rowe & Meester 1982; Willan 1986).

A2.4) Capture-mark-recapture (CMR) was continued for three days (Gentry et al. 1966; Flowerdew 1976) but was preceded by two days pre-baiting. Pre-baiting was considered preferable by Flowerdew (1976) and was also used by Davis & Meester (1981) and Southern (1973), to ensure a large catch on the first day.

A2.5) The probability of a small mammal encountering a trap depends on distance between stations and size of the animal's home range (Hansson 1967). A distance of 15 m is a useful measure (Smith et al. 1975) and is widely used (Willan & Bigalke 1982; Rowe-Rowe & Meester 1982; Bronner 1986). Probability of capture was increased by placing three

per station (Hansson 1967) to ensure no animal was denied access to a trap. Trap occupancy of less than 80% is recommended (Southern 1973; Flowerdew 1976) and only rarely during the study was this exceeded.

Absolute abundance models.

For absolute population determination a number of models are available but the decision as to which should be used can be difficult (Begon 1979). As captures were often infrequent, the use of simple models was unavoidable (Thomas & Sleeper 1977). The weighted mean (Begon 1979), an improvement on the Petersen model because it uses several recaptures, was used extensively. In addition, Hayne's and Moran's removal methods and the Fisher-Ford model were used for comparison. The geometric model (Overton 1971) was tried but greatly overestimated population sizes and was rejected.

Small mammal population sizes were calculated using Hayne's removal and Bailey's triple catch methods which give reliable results and are suitable when time is limited and a number of populations are to be compared (Begon 1979). Jolly's stochastic model (1965), is more realistic and therefore preferred (Begon 1979) and was used when possible.

Assumption testing.

The most suitable method for any CMR study is best determined by checking if the assumptions are violated. Depending on these tests, a certain degree of confidence can be applied to the estimates. The assumptions associated with various CMR models have been outlined (Pielou 1974; Caughley 1977; Begon 1979; Bronner & Meester 1987) and therefore are presented in abbreviated form in Table A2.1.

TABLE A2.1. Assumptions of the Capture-Mark-Recapture models used in this study.

1. Marking - animals do not lose their marks and captures are correctly recorded.

2. Independence of mark status - capture and marking does not affect the probability of recapture.

3. Effect of marking - capture and marking does not affect the chances of dying or emigrating.

4. Differential trappability - all individuals have equal chance of being caught.

5. Random sampling - an extension of 4 is that sampling is random.

Assumption testing has been adequately explained by Begon (1979) and his tests, as well as Caughley's test for equal catchability (1977) were used to test the five assumptions (Table A2.1). Relative methods were not tested because they rely on very few assumptions and, if the assumptions held for the absolute methods, they would also be upheld for the relative ones.

RESULTS AND DISCUSSION

The assumptions listed in Table A2.1 are examined in turn. Numbers below refer to the assumptions in that Table (Table A2.1) and results are presented in Table A2.2.

1) Marking. It was unlikely that marks would be lost as trapping duration was short and marks were known to last for at least one month (paint) or were permanent (ear notches; Fig. 5.3). Incorrect reading was, of course, possible but marking was simple and the few errors that may have been made were unlikely to alter the conclusions.

2) Tests for the independence of mark status. Data sets were small and it was difficult to draw conclusions (Table A2.2). But, of all the data collected, only the Orthoptera (Nkwashizela; September) and the small mammals in the July grassland sample, showed a significant relationship between capture/marking and subsequent recapture (Table A2.2). Thus, it was concluded that this assumption was not violated.

3) Tests for the effect of marking. Data were too few for small mammals (January), crabs and frogs, and the tests indicated that more data were required for small mammals in grassland (September) and Orthoptera at Nkwashizela (September) while significant relationships were shown for small mammals in grassland (July; Table A2.2). Only the Orthoptera at Edamini Enkulu (September) and Nkwashizela (July) showed no significant effect of marking on survival or emigration (Table A2.2).

4) As differential trappability (Table A2.1) may be one of the most important assumptions of CMR models (Caughley 1977) and has important consequences in determining prey abundance, it will be dealt with in some detail. Three tests were conducted and gave similar results. Caughley's test for equal catchability revealed that during September, in grassland, Rhabdomys pumilio and Mastomys natalensis were over-represented i.e. trap-prone while Otomys spp. and Dasymys incomtus were under-represented in vlei i.e. trap-shy (Table A2.2).

Begon's (1979) test for differences among sub-groups (here, different species in the catch) supported these results but included shrews with the trap-prone species (Table A2.2). No significant results were found in four cases due to small sample sizes (Table A2.2).

Trappability (or overall ease with which species were caught) was determined using the formula of Wingate & Meester (1977). Trappability values of zero indicate no recaptures due to

TABLE A2.2. Results of tests of the assumptions for Capture-Mark-Recapture models presented in Table A2.1.

1. Marks permanent and correctly noted. see text

2. Independance of mark status (significance = trap-prone).

Orthoptera:	Nkwashizela	(July 1986)	d.f.=2, P<0,05*
	Edamini Enkulu 1	(Sept 1986)	d.f.=2, P>0,05 NS
	Edamini Enkulu 2		d.f.=2, P<0,05*
Mammals:	Grassland	(July 1986)	d.f.=2, P<0,005**
		(Sept 1986)	d.f.=2, P>0,5 NS
	Vlei	(July 1986)	d.f.=2, P>0,1 NS
		(Sept 1986)	d.f.=2, P>0,1 NS

Orthoptera Nkwashizela (Sept 1986), mammals Vlei (Jan 1986), Grassland (Jan 1986) and Crabs and frogs: All samples too small.

3. Effect of marking (significance = influence on marking).

Orthoptera:	Nkwashizela	(July 1986)	d.f.=2, P>0,5 NS
	Nkwashizela	(Sept 1986)	d.f.=2, P<0,05 * (X2)
	Edamini Enkulu 1	(Sept 1986)	d.f.=2, P>0,75 NS (X2)
Mammals:	Grassland	(July 1986)	d.f.=2, P<0,05*
		(Sept 1986)	d.f.=2, P>0,1 NS
	Vlei	(July 1986)	d.f.=2, P>0,25 NS
		(Sept 1986)	d.f.=2, P>0,9 NS

Mammals Grassland & Vlei (Jan 1986), Crabs and frogs: All samples too small.

4. Differential trappability (significance = unequal catchability among different species of mammals). See also Table A2.3

Mammals:	Grassland	(Jan 1986)	d.f.=1, P>0,25 NS
		(July 1986)	d.f.=3, P>0,1 NS
		(Sept 1986)	d.f.=2, P<0,05*
	Vlei	(Jan 1986)	d.f.=2, P>0,5 NS
		(July 1986)	d.f.=2, P>0,25 NS
		(Sept 1986)	d.f.=3, P<0,05*

5. Random sampling (significance =non random).

Orthoptera:	Nkwashizela	(Sept 1986)	d.f.=2, P>0,5 NS (X2)
	Edamini Enkulu	(Sept 1986)	d.f.=2, P>0,9 NS
Crabs:		(Jan 1986)	d.f.=2, P>0,5 NS
	1	(Sept 1986)	d.f.=2, P>0,25 NS
	2	(Sept 1986)	d.f.=2, P>0,9 NS
Frogs:		(Sept 1986)	d.f.=1, P>0,9 NS
Mammals:	Grassland	(Jan 1986)	d.f.=2, P>0,5 NS
		(July 1986)	d.f.=2, P>0,1 NS
		(Sept 1986)	d.f.=2, P>0,25 NS
	Vlei	(Jan 1986)	d.f.=2, P>0,5 NS
		(July 1986)	d.f.=2, P>0,1 NS
		(Sept 1986)	d.f.=2, P>0,75 NS

Orthoptera Nkwashizela (July 1986) (Sept 1986), crabs (Dec 1985); All samples too small. Crabs (July 1986) ...

animals being difficult to catch, present in low numbers or both. High values indicate the opposite.

Wingate & Meester's (1977) formula expanded the results of the previous two methods (Table A2.3). Among the PVC (small mammals) captures, the largest rodents, (Otomys spp. and Dasymys incomtus) and smallest species (Mus minutoides, Suncus infinitesimus, Dendromys spp. and shrews) achieved values approaching unity (Table A2.3) indicating that these species were under-represented. This is supported by the higher captures of small mammals in the array traps (Table 5.2) and Otomys spp. are known to be poorly revealed by trapping (Rowe-Rowe & Meester 1982). Higher values for Rhabdomys pumilio, Mastomys natalensis and Aethomys chrysophilus indicated that these species were easier to catch (Table A2.3) and may have been over-represented relative to the very small and larger species.

TABLE A2.3. Trappability values of small mammals caught at VCNR using PVC live traps. To calculate these values the total number of captures were divided by the number of individuals caught.

	Number caught	Index		Number caught	Index
R. pumilio	669	1,49	S. infinitesimus	1	1,00
M. natalensis	583	1,44	Dendromys spp.	3	1,00
L. rosalia	85	1,29	Shrews	54	1,00
A. chrysophilus	10	1,25	G. murinus	2	1,00
M. minutoides	26	1,04	Otomys	8	1,00
			D. incomtus	4	1,00

Trappability values were calculated for all prey categories caught in the array traps at least once during 1986. High values were recorded for reptiles (due to the large number of recaptured lizards - no snakes were recaptured), and for pill millipedes, Sphaerotherium punctulatum and S. dorsale. Other categories with high values were Scarabaeidae, Mantodea and Anura. Crabs, Carabidae, Curculionidae and Orthoptera had rather low trappability values, which together with their large numbers (Chap. 5; Table 5.2) might indicate that these animals were more common than lizards and pill millipedes.

5) Caughley's truncated poisson distribution supported the assumption of random sampling in all groups (Table A2.2). None of the tests was significant and only two (crabs in the riverine forest during September) indicated that sizes were too small (Table A2.2).

Conclusions.

Most of the five assumptions tested were upheld, suggesting that the population estimates were reliable. But, closer scrutiny shows that sample sizes were often small or statistical probability values were inconclusive. The most

optimistic conclusion therefore, is not that the estimates are valid, but that the assumptions could not be adequately tested for all population estimates.

Violation of just one assumption alters the conclusions that can be drawn from the final data. But some assumptions are more important than others (Begon 1979) with unequal catchability being the greatest source of error in mark-recapture studies (Caughley 1977). Certainly, differential trappability was shown for most prey categories in this study and the regrettable conclusion, that the models used are invalidated, must therefore be drawn. (Thus it is likely that animals have not been trapped in proportion to their abundance and this important aspect is further considered in the Discussion of Chapter 5). However, there is, a reprieve as small violations of assumptions can be accepted provided too much is not demanded of the results (Begon 1979).

Having checked the assumptions one must avoid the error of "making this ritualistic obsequiance to statistical propriety (they) then proceed to interpret the results as if no possibility of error existed" (Caughley 1977). I accept that some of the fundamental assumptions of models I have used either have been invalidated or cannot be tested but justify their inclusion by using the estimates as indications of prey abundance trends, primarily for comparative purposes. These estimates will be referred to as absolute abundance estimates; but, by this, is implied the variability associated with the violations discussed above.

APPENDIX 3

JUSTIFICATION OF METHODS USED IN CHAPTER 6

Method selection

1. Multivariate methods

Ecological work yields a mass of multidimensional variables, many of which are correlated or irrelevant (Green 1971, 1974; Johnson 1981). These data are difficult to interpret. Green (1971) lists three problems with ecological data and believes that multivariate statistical methods help to overcome them. Although bivariate methods are less complex, they may not unravel some of the problems inherent in the multivariate sample and often the relevant variable may not be one that is measured but a composite of a number of environmental parameters (Green 1971, 1974). Thus, multivariate techniques appear well suited to these cases (Diamond pers. comm.[1]).

Multiple regression analysis appeared appropriate for the examination of viverrid habitat utilisation (Johnson 1981) and segregation among these *a priori* groups (species) was best achieved using canonical discriminant function analysis (Jeffers 1978).

Assumptions of the models

1. Bonferroni z statistic

In an analysis of various methods used to compare resource selection, Litvaitis, Sherburne & Bissonette (1985a&b) and Alldredge & Ratti (1986), concluded that the Bonferroni statistic was a useful comparison of resource use and availability (see Chaps. 4 & 5). The assumptions associated with the method (Neu *et al.* 1974; Alldredge & Ratti 1986), which are outlined in Table A3.1, are now examined.

Assumptions 1,3 and 6 were always met and assumptions 4, 5 and 7 ensure that the sample size is large enough. Sample size was considered sufficient if two of these three assumptions were met. Using these criteria to assess valid entry into the analysis of habitat use (Chap. 6), all viverrids were included (although *Mungos* was a borderline case, with a mean observation of 5,5 and 44 observations). The prey groups excluded from the analysis were *M. minutoides*, *Otomys* spp. and *Aethomys chrysophilus* for the PVC line traps and *R. pumilio*, *M. minutoides* and the amblypygid *Damon variegatus* for the array traps.

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TABLE A3.1. Assumptions of the Bonferroni z statistic when used as a comparison of resource use and availability.

3.1.1.	The animal can select any resource.
3.1.2.	Observations are collected in a random, unbiased manner.
3.1.3.	There is at least one expected observation in each category.
3.1.4.	Averaged over all categories, the expected observation is six or more.
3.1.5.	The sample size is large enough if: np and n(1-p) > 5.
3.1.6.	The number of resources is about 10.
3.1.7.	There are at least 50 observations per animal.

Assumption 2 held for the viverrids but was violated because certain prey species did not enter traps in proportion to their abundance (Chap. 5; Appendix 2). Thus, prey numbers determined from trapping results may not reflect actual habitat associations (or, for that matter, relative abundances) but this error could not be avoided when using these trapping methods. Consequently, where data are available, results of the prey habitat preferences are compared with the literature.

All assumptions were met in the dietary analyses (Chap 4).

2. Multivariate statistics

The problem of multicollinearity is particularly relevant to multiple regression analysis (Cavallaro, Menke & Williams 1981). To test for this, Pearson correlation was run on the raw data prior to analysis to eliminate highly correlated variables (P>0,75). This appears sufficient for Discriminant Function Analysis (DFA) since thereafter correlation among variables is reduced during the definition of the new k discriminant functions (Green 1971; Johnson 1981).

However, correlation among the variables in multiple regression can lead to incorrect results but can be tested by calculating the Variance Inflation Factor (VIF) (Cavallaro *et al.* 1981). $VIF = \frac{1}{1-R^2}$ where R^2 is the multiple correlation coefficient of one independant variable with all other independant variables. As R^2 approaches 0 (orthogonality) VIF approaches 1 and as it approaches 1 VIF tends towards infinity (Cavallaro *et al.* 1981). VIF values exceeding 10 suggest that, for those variables, the regression coefficients are unstable (Cavallaro *et al.* 1981).

In all the multiple regression analyses, multicollinearity was rejected because all variables had a VIF values less than 10 (range 1,08 to 1,64).

TABLE A3.2. Assumptions implicit in the use of Discriminant Function Analysis (after Green 1971; Williams 1983).

3.2.1	Groups are defined *a priori*.
3.2.2	Variables are collected from an *m*-dimensional multivariate normal distribution.
3.2.3	Groups are chi-square distributed in kXk discriminant space.
3.2.4	Dispersions are homogenous in order that canonical transformation eliminates correlations.
3.2.5	Prior probabilities are identifiable.
3.2.6	Means and dispersions are estimated accurately and precisely.

The assumptions associated with the DFA are listed in Table A3.2 and are examined below. Numbers refer to the assumptions listed in Table A3.2.

3.2.1 This assumption was always met.

3.2.2 Although Green (1971) states that the assumption of normality is as likely to be met here as in any other set of ecological data, it is likely that this assumption is violated.

3.2.3 The assumption of a chi-square distribution enables the testing of group separation. If the overall chi-square is significant, the canonical function (CF) coefficients are ecologically interpretable and the species separation on each CF is greater than would be expected from a random sample.

In the analyses, chi-square was highly significant ($P<0,001$), for all CF.

3.2.4 and 3.2.5 Neither of these assumptions could be adequately tested and are therefore assumed to have been violated.

3.2.6 Williams (1983) suggests that when the number of parameters to be estimated approaches the number of samples, patterns may be fortuitous and therefore the estimation of means and variances erroneous.

In this study, the number of parameters estimated was 19 (Table 6.1) while the sample sizes were 494, 187, 360, 451 and 44. Thus only in the last case (*Mungos*) did the number of parameters fall within the same order of magnitude as the sample sizes. This assumption was not violated.

Although three out of the six assumptions were met by the data used in Chapter 6, simultaneous violation of assumptions

results in statistical and interpretive problems (Williams 1983). It would therefore be a violation of the scientific method to consider the results of the canonical function analysis (Chap. 6) confirmatory. I therefore consider these results exploratory (Tukey 1980) suggesting that the five species of viverrid separate along the spatial niche. The success of the verification tests (Table 6.7) is a step in the direction to confirm these results.

APPENDIX 4

VIVERRID DENSITY AND PREY AVAILABILITY

INTRODUCTION

Estimates of the population density of viverrids at VCNR is used to approximate the amount of primary prey eaten per day by the viverrid assemblage. This information is then used to indicate whether food is a limiting resource. Because the data used to obtain this information are only estimates, the results are not conclusive but merely give an indication of viverrid abundance and their daily prey consumption.

Viverrid population density

It was impracticable to use a sophisticated population estimation model to determine viverrid abundance because traps were not set in a systematic grid and capture rates were low (Chap. 3). I therefore used a simple estimate. The home ranges of each individual viverrid, of each species, were drawn on a map of VCNR and those individuals whose home ranges were not known, were assigned a mean home range size (Chap. 5). Then, a minimum area polygon was drawn around all the adjacent home ranges, of each species, and the total area measured (Collins & Urness 1983). Thus, the extent of interspecific home range overlap for each species was included. Results were converted to the number of viverrids, per km^2, in the whole of VCNR.

The density of Mungos was estimated by plotting all the observations of this species on a map of VCNR. Sadie (1983) determined a mean exclusive home range size of Mungos in the Transvaal was 2,4 km^2. I divided this mean into the area of VCNR. Mean group size at VCNR was five (Chap. 3) therefore the number of Mungos was estimated by multiplying the mean group size by the estimated number of packs that could fit into VCNR.

Although these estimates are rough approximations, they provide an indication of the density of viverrids without violating any assumptions.

Prey density and consumption

Absolute densities of the important viverrid prey were taken from Chapter 5. The average mass of these prey per scat per species was determined from the data in Chapter 4 and multiplied by a mean defaecation rate of between 3 and 4 scats per day (Baker 1980; Sadie 1983; Maddock unpubl. data). This value was next multiplied by the number of viverrids (of each species) in the reserve (above). From these data the approximate number of small mammals, frogs, coleopterans, orthopterans and crabs eaten each day, by all species, was calculated.

Prey abundance was underestimated, rather than overestimated, especially Otomys spp., crabs and

These abundance data were derived from a limited number of habitats and, therefore, further underestimate total prey numbers. In addition, only the major prey of the viverrids were considered, thus, the data were biased towards accepting the hypothesis that the viverrids were food limited.

RESULTS

The densities of some viverrids in East Africa (Waser 1980) are provided in Table A4.1 for comparison with the VCNR results. Galerella achieved the highest density (Table A4.1) because this species had small, highly overlapping, home ranges (Table 6.8). Genetta, which was frequently caught and had the smallest home range (Table 6.8), achieved the second highest density (Table A4.1). Those species with a large home range size - Herpestes and Atilax (Table 6.8) - had the lowest densities (Table A4.1).

TABLE A4.1. Estimated densities of the five species of viverrid at VCNR. Additional data from Waser (1980).

Species	Density (individuals Km^{-2})	
	Present study	Waser (1980)
G. sanguinea	7,3	
G. tigrina	4,4	
M. mungos	2,4	
A. paludinosus	1,8	<0,1
H. ichneumon	1,2	
Genetta spp.		1,5±0,4
Ichneumia albicauda		4,3±0,8

Although approximate, the comparison of prey eaten and prey available indicate that, in general, food is not a limiting resource (Table A4.2). Insects, crabs and frogs were abundant (Table A4.2), particularly insects, which have a high turnover rate (Waser 1981). However, both coleopterans and crabs occured in very low numbers in winter (Table A4.2), possibly so did frogs (Chap. 5). Small mammals appear less common than do the other prey (Table A4.2) and are heavily preyed on (Chap. 4) thus, may form a limiting resource if their numbers decline (Wiens 1977) for example, during droughts or floods (Chap. 5).

Besides the low winter populations of coleopterans and crabs, other scarce prey are Otomys spp. (Chap. 5). Although these rats are preferred by a range of predators (Chap. 5) the selector behaviour of Herpestes (Chap. 5) should give this species an advantage when resources (Otomys) became limiting. Certainly, Herpestes ate more Otomys spp. in 1984, when these rats were uncommon (Chap. 5), than did any other viverrid (Fig. 4.9).

TABLE A4.2. Number of major prey eaten by the different species of viverrid at VCNR compared with prey availability in the whole reserve.

Prey categories	Number of prey eaten	Number of prey available		Difference between prey eaten and available	
Small mammals	969	Jan.	16 376	15 407	6%
		Jul.	90 533	89 564	1%
		Sep.	96 759	95 790	1%
Frogs	517	Sep.	438 659	438 142	0,1%
Coleoptera	5 221	Dec.	1 980 304	1 975 083	0,3%
		Jul.	0	-5 221	100%
		Sep.	990 152	984 931	0,5%
Orthoptera	3 389	Jul.	6 317 447	6 314 058	0,05
		Sep.	6 351 044	6 347 655	0,05%

Throughout this thesis, the assumption that the viverrids must differ if they are to coexist, has been made (Chap. 1). I considered this useful because it facilitated data presentation and discussion (Chap. 1). It also underlies much ecological thinking (Cody 1974; Schoener 1974a; Pianka 1976; Jaksic *et al.* 1981; Pontin 1980; Hayward & Garton 1988). Nevertheless, the premise that competition is the driving force of community structure has been questioned (Wiens 1977, 1984; Connell 1980; Price 1984) and it is relevant to briefly consider the merits of this criticism.

A major problem with competition theory is that competition is assumed but rarely tested (Wiens 1977; Connell 1983). Recently this has changed slightly with the advent of purturbation experiments (DeBenedictus 1974; Bender, Gilpin & Case 1984) but infrequently is competition weighed against alternatives (Price 1984). Predation (Connell 1975), environmental variation (Wiens 1977, 1984; Rotenberry 1980) and/or parasitism (Vizoso 1969; Price 1984) are important effects that may hold populations below the carrying capacity so that competition is avoided.

At VCNR, preliminary data (Chap. 4; above) indicates that food is not a limiting resource, except possibly during winter. However, the different hunting techniques of the viverrids and their ability to act as selectors (Chap. 5) may enable them to obtain sufficient food during these periods of food scarcity. In Chapter 6 the possibility of the forests being a limited resource was discussed.

REFERENCES

ABRAMS, P. 1980. Some comments on measuring niche overlap. Ecology 61: 44-49.

ACOCKS, J.P.H. 1975. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa 1-28. Government Printer.

ALCOVER, J.A. 1984. Uber die Nahrung der Ginsterkatze Genetta genetta (Linaeus, 1758) auf den Inseln Mallorca, Ibiza und Cabrera. Saugetierkundliche Mitteilungen 31: 189-195.

ALLDREDGE, J.R. & RATTI, J.T. 1986. Comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 50: 157-165.

ALLEN, J.A. 1924. Carnivora collected by the American Museum Congo Expedition. Bulletin of the American Museum of Natural History 47: 73-281.

ANDERSON, D.J. 1982. The home range: a new nonparametric estimation technique. Ecology 63: 103-112.

ANDERSSON, M. & ERLINGE, S. 1977. Influence of predation on rodent populations. Oikos 29: 591-597.

ANDREWARTHA, H.G. & BIRCH, L.C. 1954. The Distribution and Abundance of Animals. University of Chicago Press, Chicago.

ANONYMOUS. 1986. Vernon Crookes Nature Reserve management plan part 11. Internal NPB Report. 45: 1-30.

ANSELL, W.F.H. 1965. Standardisation of field data on mammals. Zoologica Africana 1: 97-113.

BAKER, C.M. 1980. Biology and behaviour of the slender mongoose, Herpestes sanguineus (Ruppel, 1836). M.Sc. thesis, University of Natal, Pietermaritzburg.

BAKER, C.M. 1981. Agonistic behaviour patterns of the slender mongoose, Herpestes sanguineus. South African Journal of Zoology 16: 263-264.

BAKER, C.M. 1982. Methods of communication exhibited by captive slender mongooses, Herpestes sanguineus. South African Journal of Zoology 17: 143-146.

BAKER C.M. 1984. Social care behaviour of captive slender mongooses (Herpestes sanguineus). Mammalia 48: 43-52.

BAKER, C.M. 1987a. Vocalisations of captive water mongooses, Atilax paludinosus. Zeitschrift fur Saugetierkunde. (In press).

BAKER, C.M. 1987b. Scent marking behaviour in captive water mongooses, Atilax paludinosus. Zeitschrift fur Saugetierkunde. (In press).

BAKER, C.M. 1987c. The biology and behaviour of the water mongoose Atilax paludinosus. Ph.D. thesis, University of Natal, Durban.

BAKER, C.M. 1988a. Feeding habits of the water mongoose, Atilax paludinosus. Zeitschrift fur Saugetierkunde. (Submitted).

BAKER, C.M. 1988b. Mating and reproductive behaviour in captive water mongooses (Atilax paludinosus). Ethology. (Submitted).

BAKER, C.M. & MEESTER, J. 1986. Postnatal physical development of the water mongoose (Atilax paludinosus). Zeitschrift fur Saugetierkunde 51: 236-243.

BEARDER, S.K. 1972. Watching the nocturnal genet. (Animals (Wildlife) 14: 316-321.

BEGON, M. 1979. Investigating Animal Abundance: capture-recapture for biologists. Arnold, London.

BEKOFF, M., DANIELS, T.J. & GITTLEMAN, J.L. 1984. Life history patterns and the comparative social ecology of carnivores. Annual Review of Ecology and Systematics 15: 191-232.

BELTRAN, J.F., DELIBES, M. & IBANEZ, C. 1985. Immobilisation and marking of the Egyptian mongoose, Herpestes ichneumon (L.), in Spain. Zeitschrift fur Saugetierkunde 50: 243-244.

BENDER, E.A., CASE, T.J. & GILPIN, M.E. 1984. Partubation experiments in community ecology: theory and practice. Ecology 65: 1-13.

BEN-YAACOV, R. & YOM-TOV, Y. 1983. On the biology of the Egyptian mongoose, Herpestes ichneumon, in Israel. Zeitschrift fur Saugetierkunde 48: 34-45.

BOND, W., FERGUSON, M. & FORSYTH, G. 1980. Small mammals and habitat structure along altitudinal gradients in the southern Cape mountains. South African Journal of Zoology 15: 34-43.

BOTHMA, J. Du P., NEL, J.A.J. & MACDONALD, A. 1984. Food niche separation between four sympatric Namib Dessert carnivores. Journal of Zoology (London) 202: 327-340.

BOURQUIN, O. & SOWLER, S.G. 1980. The vertebrates of Vernon Crookes Nature Reserve. 1. Lammergeyer 28: 20-32.

BOURQUIN, O & MATHIAS, I. 1984. The vertebrates of Oribi Gorge Nature Reserve. Lammergeyer 33: 35-44.

BOURQUIN, O. & VAN RENSBURG, J. 1984. Vertebrates of Vernon Crookes Nature Reserve; additional and confirming records. Lammergeyer 34: 59-61.

BOWLAND, A.E. 1985. The effect of fire, overgrazing, and drought on the abundance and diversity of small mammals (Rodentia, Soricidae) in the Central Complex and the

indirect impact on predators. M.Sc. thesis, University of Natal, Pietermaritzburg.

BROADLEY, D. 1983. FitzSimons' Snakes of Southern Africa. Delta Book, Johannesburg.

BRONNER, G.N. 1986. Demography of the Multimammate Mouse Mastomys natalensis (A. Smith, 1834) on Bluff Nature Reserve, Durban. M.Sc. thesis, University of Natal, Durban.

BRONNER, G.N. & MEESTER, J. 1987. Comparison of methods for estimating rodent numbers. South African Journal of Wildlife Research 17: 59-63.

BROOKS, P.M. 1974. The ecology of the four-striped field mouse, Rhabdomys pumilio (Sparrman, 1784) with particular reference to a population on the Van Riebeeck Nature Reserve, Pretoria. D.Sc thesis, University of Pretoria, Pretoria.

BRUNNER, H. & COMAN, B. 1974. The Identification of Mammal Hair. Inkata Press, Melbourne.

BURT, W.H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24: 346-352.

BYERS, C.R., STEINHORST, R.K. & KRAUSMAN, P.R. 1984. Clarification of a technique for analysis of utilization - availability data. Journal of Wildlife Management 48: 1050-1053.

CAMPBELL, H.W. & CHRISTMAN, S.P. 1982. Field techniques for Herpetofaunal community analysis. United States Department of Interior, Fish and Wildlife Service. Wildlife Research Report 13: 193-200.

CAUGHLEY, G. 1977. Analysis of Vertebrate Populations. Wiley, Chichester.

CAVALLARO, J.I., MENKE, J.W. & WILLIAMS, W.A. 1981. Use of discriminate analysis and other statistical methods in analysing microhabitat utilization of dusky-footed woodrats. pp. 222-231. In: Capen D.E. (ed.) The Use of Multivariate Statistics in Studies of Wildlife Habitat. USDA Forest Service General Technical Report RM.87, University of Vermont.

CHARNOV, E.L. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9: 129-136.

COETZEE, C.G. 1965. The breeding season of the multimammate mouse Praomys (Mastomys) natalensis (A. Smith) in the Transvaal highveld. Zoologica Africana 1: 29-39.

COLLINS, W.B. & URNESS, D.J. 1983. Feeding behaviour and habitat selection of mule deer and elk on Northern Utah summer range. Journal of Wildlife Management 47: 646-663.

CONNELL, J.H. 1975. Producing structure in natural communities. pp. 460-490. In: Cody, M.L. & Diamond, J.M.

(eds.) Ecology and Evolution of Communities. Belknap Press, Cambridge.

CONNELL, J.H. 1980. Diversity and coevolution of competitors, or the ghost of competition past. Oikos 35: 131-138.

CONNELL, J,H. 1983. On the prevelence and relative importance of interspecific competition: evidence from field experiments. American Naturalist 122: 661-696.

CURIO, E. 1976. The Ethology of Predation. Springer- Verlag, Berlin.

DAVID J.H.M. & JARVIS, J.U.M. 1985. Population fluctuations, reproduction and survival in the striped fieldmouse Rhabdomys pumilio on the Cape Flats, South Africa. Journal of Zoology (London) 207: 251-276.

DAVIS, R.M. 1973. The ecology and life history of the vlei rat, Otomys irroratus (Brants, 1827) on the Van Riebeeck Nature Reserve, Pretoria. D.Sc. thesis, University of Pretoria, Pretoria.

DAVIS, R.M. & MEESTER, J. 1981. Reproduction and postnatal development in the vlei rat, Otomys irroratus, on the Van Riebeeck Nature Reserve, Pretoria. Mammalia 45: 99-116.

DAY, M.G. 1966. Identification of hair and feather remains in the gut and faeces of stoats and weasels. Journal of Zoology (London) 148: 201-217.

DEAN, W.R.J. 1973. Analysis of a collection of barn owl Tyto alba pellets from Warmbaths, Transvaal. Zoologica Africana 8: 75-81.

DEBENEDICTUS, P.A. 1974. Interspecific competition between tadpoles of Rana pipiens and Rana sylvatica: an experimental field study. Ecological Monographs 44: 129-151.

DE GRAAFF, G. 1981. The Rodents of Southern Africa: notes on their identificaton, distribution, ecology and taxonomy. Butterworths, Durban.

DELANY, M.J. 1972. The ecology of small rodents in tropical Africa. Mammal Review 2: 1-42.

DELANY, M.J. 1974. The Ecology of Small Mammals. The Institute of Biology's Studies in Biology. No. 51. Arnold, London.

DELANY, M.J. 1986. Ecology of small rodents in Africa. Mammal Review 16: 1-41.

DELIBES, M. 1976. Datos sobre la alimentacion del Meloncillo, Herpestes ichneumon widdringtoni Gray, 1842, en Espana. Saugetierkundliche Mitteilungun 24: 38-42.

DELIBES, M. 1983. Interspecific competition and the habitat of the stone marten Martes fiona (Erxleben 1777) in Europe. Acta Zoologica Fennica 174: 229-231.

DELIBES, M. & BELTRAN, J.F. 1985. Activity, daily movements and home range of an Ichneumon or Egyptian mongoose (Herpestes ichneumon) in southern Spain. Journal of Zoology (London) 207: 601-613.

DELIBES, M., AYMERICH, M. & CUESTA, L. 1984. Feeding habits of the Egyptian mongoose or Ichneumon in Spain. Acta Theriologica 29: 205-218.

DICKMAN, C.R. & HUANG, C. 1988. The reliability of fecal analysis as a method for determining the diet of insectivorous mammals. Journal of Mammalogy 69: 108-113.

DIXON, J.E.W. 1964. Preliminary notes on the mammal fauna of Mkuzi Game Reserve. Lammergeyer 3: 40-58.

DIXON, K.R. & CHAPMAN, J.A. 1980. Harmonic mean measure of animal activity areas. Ecology 61: 1040-1044.

DORST, J. & DANDELOT, P. 1970. A Field Guide to the Larger Mammals of Africa. Collins, London.

DUCKER, G. 1960. Beobachtungen uber das Paarungsverhalten des Ichneumons (Herpestes ichneumon L.) Zeitschrift fur Saugetierkunde 25: 47-51.

DUELLMAN, W.E. & TRUEB, L. 1986. Biology of Amphibians. McGraw-Hill, New York.

DU TOIT, C.F. 1980. The yellow mongoose Cynictis penicillata and other small carnivores in the Mountain Zebra National Park. Koedoe 23: 179-184.

ELLERMAN, J.R., MORRISON-SCOTT, T.C.S. & HAYMAN, R.W. 1953. Southern African Mammals, 1758-1951: a reclassification. Order of the trustees of the British Museum, London.

ERLINGE, S. 1968. Food studies on captive otters Lutra lutra L. Oikos 19: 259-270.

ERLINGE, S. 1969. Food habits of the otter Lutra lutra L. and the mink Mustela vison Schreber in a trout water in southern Sweden. Oikos 20: 1-7.

ERLINGE, S. 1972. Interspecific relations between otter (Lutra lutra) and mink (Mustela vison). Oikos 23: 327-335.

EWER, R.F. 1973. The Carnivores. Weidenfeld & Nicholson, London.

FEINSINGER, P., SPEARS, E.E. & POOLE, R.W. 1981. A simple measure of niche breadth. Ecology 62: 27-32.

FLOWERDEW, J.R. 1976. Techniques in mammalogy. Chapter 4. Ecological methods. Mammal Review 6: 123-159.

FORD, R.G. & KRUMME, D.W. 1979. The analysis of space use patterns. Journal of Theoretical Biology 76: 125-155.

GAUSE, G.F. 1934. The Struggle for Existence. Williams and Wilkins, Baltimore.

GENTRY, J.B., GOLLEY, F.B. & MCGINNIS, J.T. 1966. The effect of weather on captures of small mammals. American Midland Naturalist 75: 526-530.

GENTRY, J.B., GOLLEY, F.B. & SMITH, M.H. 1968. An evaluation of the proposed International Biological Program census method for estimating small mammal populations. Acta Theriologica: 13: 313-327.

GIST, C.S. & CROSSLEY, D.A. 1973. A method for quantifying pitfall trapping. Environmental Entomology 2: 951-952.

GITTLEMAN, J.L. 1986. Carnivore brain size, behavioural ecology, and phylogeny. Journal of Mammalogy 67: 23-36.

GLASSER, J.W. & PRICE, H.J. 1982. Niche theory: new insights from an old paradigm. Journal of Theoretical Biology 99: 437-460.

GORMAN, M.L. 1979. Dispersion and foraging of the small Indian mongoose, Herpestes auropunctatus (Carnivora: Viverridae) relative to the evolution of social viverrids. Journal of Zoology, (London) 187: 65-73.

GOSS-CUSTARD, J.D. 1970. Feeding dispersion in some overwintering wading birds. pp. 1-35. In: Crook J.H. (ed.) Social Behaviour in Birds and Mammals. Academic Press, New York.

GOSZCZYNSKI, J. 1974. Studies on the food of foxes. Acta Theriologica 19: 1-18.

GREEN, R.H. 1971. A multivariate statistical approach to the Hutchinsonian niche: bivalve molluscs of Central Canada. Ecology 52: 543-556.

GREEN, R.H. 1974. Multivariate niche analysis with temporally varying environmental factors. Ecology 55: 73-83.

GROBLER, H., HALL-MARTIN, A. & WALKER, C. 1984. Predators of Southern Africa. A guide to the carnivores. Macmillan, Johannesburg.

HANRAHAN, S.A. & YEATON, R.I. (in press) Population estimates of Onymacris bicolor (Coleoptera; Tenebrionidae) in the dunefields of the Skeleton Coast Park, South West Africa/Namibia.

HANSSON, L. 1967. Index line catches as a basis of population studies on small mammals. Oikos 18: 261-276.

HARDIN, G. 1960. The competitive exclusion principle. Science 131: 1292-1297.

HAYNE, D.W. 1949. Calculation of size of home range. Journal of Mammalogy 30: 1-18.

HESPENHEIDE, H.A. 1979. Prey characteristics and predator niche width. pp. 158-180. In: Cody, M.L. & Diamond, J.M. (eds.) Ecology and Evolution of Communities. Belknap Press, Cambridge.

HINTON, H.E. & DUNN, A.M.S. 1967. Mongooses, their Natural History and Behaviour. Olivier & Boyd, Edinburgh.

HISCOCKS, K. & PERRIN, M.R. 1987. Field observations and diet of black-backed jackals in an arid coastal environment. South African Journal of Wildlife Research 17: 55-58.

HUDSON, R.J. 1976. Resource division within a community of large herbivores. Le Naturaliste Canadien 103: 153-167.

HURLBERT, S.H. 1978. The measurement of niche overlap and some relatives. Ecology 59: 67-77.

HUTCHINSON, G.E. 1957. Concluding remarks. Cold Spring Harbour Symposium. Quantitative Biology 22: 415-427.

HYSLOP, E.P. 1980. Stomach content analysis - a review of methods and their application. Journal of Fisheries Biology 17: 411-429.

INGER, R. & COLWELL, R.B. 1977. Organisation of contiguous communities of amphibians and reptiles in Thailand. Ecological Monographs 47: 229-253.

JACOBSEN, N.H.G. 1982. Observations on the behaviour of slender mongooses, Herpestes sanguineus in captivity. Saugetierkundliche Mitteilungun 30: 168-183.

JAKSIC, F.M. 1982. Inadequacy of activity time as a niche difference: the case of diurnal and nocturnal raptors. Oecologia (Berlin) 52: 171-175.

JAKSIC, F.M. GREENE, H.W. & YANEZ, J.L. 1981. The guild structure of a community of predatory vertebrates in central Chile. Oecologia (Berlin) 49: 21-28.

JEFFERS, J.N.R. 1978. An Introduction to Systems Analysis: with ecological applications. Arnold, London.

JENNRICH, R.I. & TURNER, F.B. 1969. Measurement of non-circular home range. Journal of Theoretical Biology 22: 227-237.

JOHNSON, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65-71.

JOHNSON, D.H. 1981. The use and misuse of statistics in wildlife habitat studies. pp. 11-19. In: Capen, D.E., (ed.) The Use of Multivariate Statistics in Studies of Wildlife Habitat. USDA Forest Service General Technical Report RM-87, University of Vermont.

JOHNSON, P.A. 1987. An evaluation of the effects on wildlife of Carbamate Nematicides used in the sugarbelt of coastal Natal. M.Sc. thesis, University of Natal, Pietermaritzburg.

JOLLY, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration - stochastic model. Biometrika 52: 225-247.

KAMINSKI, R.M. & PRINCE, H.H. 1984. Dabbling duck - habitat associations during spring in Delta Marsh, Manitoba. Journal of Wildlife Management 48: 37-50.

KEOGH, H.J. 1983. A photographic reference system of the microstructure of the hair of southern African bovids. South African Journal of Wildlife Research 13: 89-132.

KEOGH, H.J. 1985. A photographic reference system based on the cuticular scale patterns and groove of the hair of 44 species of southern African Cricetidae and Muridae. South African Journal of Wildlife Research 15: 109-159.

KIKKAWA, J. & ANDERSON, D.J. 1986. Community Ecology: pattern and process. Blackwells, Melbourne.

KING, C.M. 1973. A system for trapping and handling live weasels in the field. Journal of Zoology, (London) 171: 458-464.

KING, C.M. 1980a. The weasel Mustela nivalis and its prey in an English woodland. Journal of Animal Ecology 49: 127-159.

KING, C.M. 1980b. Field experiments on the trapping of stoats Mustela erminea. New Zealand Journal of Zoology 7: 261-266.

KING, C.M. & EDGAR, R.L. 1977. Techniques for trapping and tracking stoats (Mustela erminea); a review, and a new system. New Zealand Journal of Zoology 4: 193-212.

KINGDON, J. 1977. East African Mammals: an atlas of evolution in Africa. Vol. III Part A. Academic Press, London.

KOEPPL, J.W., SLADE, N.A. & HOFFMANN, R.S. 1975. A bivariate home range model with possible application to ethological data. Journal of Mammalogy 56: 81-90.

KORSCHGEN, L.J. 1971. Procedures for food-habits analysis. pp. 233-250. In: Giles, J. (ed.) Wildlife Management Techniques. Wildlife Society, Washington D.C.

KOWALSKI, R. 1976. Obtaining valid population indices from pitfall trapping data. Bulletin de L´Academie Polonaise des Sciences Serie des Sciences Biologiques II 23: 799-803.

KRUUK, H. 1975. Functional aspects of social hunting by carnivores. pp. 119-141. In: Baerends, G., Beer, J. & Manning A. (eds.) Function and Evolotion in Behaviour. University Press, Oxford.

KRUUK, H. and PARISH, T. 1981. Feeding specialization of the European Badger Meles meles in Scotland. Journal of Animal Ecology 50: 773-788.

LACK, A. 1977. Genets feeding on nectar from Maranthes polyandra

in northern Ghana. East African Wildlife Journal 15: 233-234.

LANGLEY, C.H. 1986. A Cape grey mongoose attacks grysbok lambs. African Wildlife 40: 203.

LAWRENCE, R.F. 1953. The Biology of the Cryptic Fauna of Forests: with special reference to the indigenous forests of South Africa. Balkema, Cape Town.

LAWRENCE, R.F. 1984. The Centipedes and Millipedes of Southern Africa: a guide. Balkema, Cape Town.

LIBERG, O. 1982. Correction factors for important prey categories in the diet of domestic cats. Acta Theriologica 29: 115-122.

LINN, I. 1963. A theory of small mammal index trapping. Proceedings of XVI International Congress of Zoology 2: 268.

LINN, I. 1983. Home ranges and social systems in solitary mammals. Acta Zoologica, Fennica 171:

LITVAITIS, J.A., SHERBURNE, J.A. & BISSONETTE, J.A. 1985a. A comparison of methods used to examine snowshoe hare habitat use. Journal of Wildlife Management 49: 693-695.

LITVAITIS, J.A., SHERBURNE, J.A. & BISSONETTE, J.A. 1985b. Influence of understory characteristics on snowshoe hare habitat use and density. Journal of Wildlife Management 49: 866-873.

LOCKIE, J.D. 1959. The estimation of the food of foxes. Journal of Wildlife Management 23: 224-227.

LOCKIE, J.D. 1966. Territory in small carnivores. Symposium of the Zoological Society, London 18: 143-165.

LOMBAARD, G.L. 1958. The water mongoose, Atilax paludinosus. Fauna and Flora 9: 24-27.

LOUW, C.J. & NEL, J.A.J. 1986. Diets of coastal and inland-dwelling water mongoose. South African Journal of Wildlife Research 16: 153-156.

LYNCH, C.D. 1983. The mammals of the Orange Free State. Memoirs of the National Museum, Bloemfontein 18: 120-139.

MACARTHUR, R.H. & WILSON, E.O. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

MACDONALD, D.W. 1978. Radio-tracking: some applications and limitations. pp. 192-204. In: Stonehouse, B. (ed.) Animal Marking. Macmillan, London.

MACDONALD, J.T. and NEL, J.A.J. 1986. Comparative diets of sympatric small carnivores. South African Journal of Wildlife Research 16: 115-121.

MACLEAN, G.L. 1985. Roberts´ Birds of Southern Africa. The Trustees of the John Voelcker Bird Book Fund, Cape Town.

MADDOCK. A.H. 1988. Immobilisation of four species of Viverridae with ketamine. South African Journal of Wildlife Research. (Submitted).

MADDOCK, A.H. & ZALOUMIS, G. 1987. Additional and confirming records of the vertebrates at Vernon Crookes Nature Reserve with indications of rodent and ungulate abundances. Lammergeyer 38: 40-54.

MAY, R.M. & MACARTHUR, R.H. 1972. Niche overlap as a function of environmental variability. Proceedings of the National Acadamy of Science, USA 69: 1109-1113.

McNAB, B.K. 1963. Bioenergetics and the determination of home range size. American Naturalist 97: 133-140.

McNAB, B.K. 1983. Ecological and behavioural consequences of adaptation to various food resources. pp. 664-697. In: Eisenberg, J.F. & Kleiman, D. (eds.) Advances in the Study of Mammalian Behaviour. American Society of Mammalogists. Special Publication 7, Pittsburgh.

MEESTER, J.A.J., LLOYD, C.N.V. & ROWE-ROWE, D.T. 1979. A note on the ecological role of Praomys natalensis. South African Journal of Science 75: 183-184.

MEESTER, J.A.J., RAUTENBACH, I.L., DIPPENAAR, N.J. & BAKER, C.M. 1986. Classification of Southern African Mammals. Transvaal Museum Monograph 5. Transvaal Museum, Pretoria.

MELTON, D.A. 1978. Ecology of the waterbuck in the Umfolozi Game Reserve. D.Sc. thesis, University of Pretoria.

MENDELSOHN, J.M. 1982. Notes on the small mammals of the Springbok Flats, Transvaal. South African Journal of zoology 17: 197-201.

MICHAELIS, B. 1972. Die Schleichkatzen (Viverriden) Afrikas. Saugetierkundliche Mitteilungen 20: 1-110.

MILLS, M.G.L. 1981. The socio-ecology and social behaviour of the brown hyena Hyena brunnea, Thunberg, 1820 in the southern Kalahari. D.Sc. thesis, University of Pretoria.

MISPAGEL, M.E. & SLEEPER, E.L. 1983. Density and biomass of surface-dwelling macro arthropods in the northern Mojave Desert. Environmental Entomology 12: 1851-1857.

MOHR, C.O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist. 37: 233-249.

NEAL, E. 1970. The banded mongoose, Mungos mungo (Gmelin). East African Wildlife Journal 8: 63-71.

NEL, J.A.J. 1983. Changes in population structure of Kalahari rodents over a decade. Zoologische Wetenschappen Ann. 237: 173-178.

NEU, C.W., BYERS, C.R. & PEEK, J.M. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38: 541-545.

NIE, N.H. 1983. SPSS-X: USER´S GUIDE. McGraw-Hill, New York.

NIE, N.H., HULL, C.H., JENKINS, J.G., STEINBRENNER, K. & BENT, D.H. 1975. SPSS: Statistical Package for the Social Sciences. McGraw-Hill, New York.

PASSANO, L.M. 1960. Moulting and its control. pp. 473-536. In: Waterman, T.H. (ed.) The Physiology of Crustacea vol. 1. Academic Press, New York.

PATRIC, E.F. 1970. Bait preference of small mammals. Journal of Mammalogy 51: 179-182.

PERRIN M.R. 1979. Aging criteria and population age structure of co-existing populations of Rhabdomys pumilio and Otomys irroratus. South African Journal of Wildlife Research 9: 84-95.

PERRIN, M.R. 1980 (a). Ecological strategies of two co-existing rodents. South African Journal of Science 76: 487-491.

PERRIN, M.R. 1980 (b). The feeding habits of two co-existing rodents, Rhabdomys pumilio (Sparrman, 1784) and Otomys irroratus (Brants, 1827) in relation to rainfall and reproduction. Acta OEcologica, OEcologia Generalis 1: 71-89.

PERRIN, M.R. 1981. Notes on the activity patterns of 12 species of Southern African rodents and a new design of activity monitor. South African Journal of Zoology 16: 248-258.

PERRIN, M.R. 1982. Prey specificity of the barn owl, Tyto alba, in the Great Fish River Valley of the Eastern Cape Province. South African Journal of Wildlife Research 12: 14-25.

PERRIN, M.R. & CAMPBELL, B.S 1980. Key to the mammals of the Andries Vosloo Kudu Reserve (Eastern Cape), based on their hair morphology, for use in predator scat analysis. South African Journal of Wildlife Research 10: 1-14.

PETRAITIS, P.S. 1979. Likelihood measures of niche breadth and overlap. Ecology 60: 703-710.

PETTER, G. 1969. Interpretation evolutive des caracteres de la denture des Viverrides Africains. Mammalia 33: 607-626.

PIANKA, E.R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4: 53-74.

PIANKA, E.R. 1974. Niche overlap and diffuse competition. Proceedings of the National Acadamy of Science (USA) 7: 2141-2145.

PIANKA, E.R. 1980. Guild structure in lizards. Oikos 35: 194-201.

PIANKA, E.R. 1981. Competition and Niche Theory. pp. 167-196. In: May, R.M. (ed.) Theoretical Ecology: principles and applications. Blackwell Scientific Publications, Oxford.

PIANKA, E.R. 1983. Evolutionary Ecology. Harper and Row, New York.

PIELOU, E.C. 1974. Population and Community Ecology: principles and methods. Gordon & Breach, New York.

PIENAAR, U. DE V., RAUTENBACH, I.L. & DE GRAAFF, G. 1980 The Small Mammals of the Kruger National Park. National Parks Board of the Trustees of the Republic of South Africa.

PIETZ, P.J. & TESTER, J.R. 1983. Habitat selection by snowshoe hares in north central Minnesota. Journal of Wildlife Management 47: 686-696.

PONTIN, A.J. 1982. Competition and Coexistence of Species. Pitman, Boston.

POWELL, R.A. & ZIELINSKI, W.J. 1983. Competition and coexistence in mustelid communities. Acta Zoologica Fennica 174: 223-227.

POYNTON, J.C. & BASS, A.J. 1970. Environment and amphibian distribution in Zululand. Zoologica Africana 5: 41-48.

PRICE, P.W. 1984. Alternative paradigms in community ecology. pp. 353-383. In: Price, P.W. Slobodchikoff, C.N. & Gaud, W.S. (eds.) A New Ecology: novel approaches to interactive systems. Wiley & Sons, New York.

PRINGLE, J.A. 1977. The distribution of mammals in Natal. Part 2: Carnivora. Annals of the Natal Museum 23: 93-115.

PULLIAINEN, E. 1980. Food and feeding habits of the pine marten in Finnish Forest Lapland in Winter. pp. 580-598. In: Chapman, J.A. & Pursley, D. (eds.) Worldwide Furbearer Conference Proceedings Vol. 1.

PULLIAINEN, E. 1981. Winter diet of Felis lynx L. in S.E. Finland as compared with the nutrition of other northern lynxes. Zeitschrift fur Saugetierkunde 46: 249-259.

PUTMAN, R.J. 1984. Facts from faeces. Mammal Review 14: 79-97.

RADINSKY, L. 1975. Viverrid neuroanatomy: phylogenetic and

behavioural implications. Journal of Mammalogy 56: 130-150.

RASA, O.A.E. 1973. Prey capture, feeding techniques and their ontogeny in the African Dwarf Mongoose, Helogale undulata rufula. Zeitschrift fur Tierpsychologie 32: 449-488.

RASA, O.A.E. 1984. Mongoose Watch: a family observed. Murray, London.

RAUBENHEIMER, C.D. 1986. Aspects of the biology of the freshwater crab, Potamonauetes sidneyi, with particular reference to general seasonality and female aggression. M.Sc. thesis, University of Natal, Durban.

RAUTENBACH, I.L. 1982. Mammals of the Transvaal. Ecoplan, Pretoria.

RAUTENBACH, I.L. & NEL, J.A.J. 1978. Co-existence in Transvaal Carnivora. pp. 138-145. In: Schlitter, D. (ed.) Ecology and Taxonomy of African Small Mammals. Bulletin of the Carnegie Museum of Natural History 6.

RAYNER, A.A. 1967. A First Course in Biometry for Agriculture Students. University of Natal Press, Pietermaritzburg.

ROBERTS, A. 1951. The Mammals of South Africa. Trustees of 'The Mammals of South Africa' Book Fund, Central News Agency, Cape Town.

ROLLEY, R.E. & WARDE, W.D. 1985. Bobcat habitat use in southeastern Oklahoma. Journal of Wildlife Management 49: 913-920.

ROOD, J.P. 1975. Population dynamics and food habits of the banded mongoose. East African Wildlife Journal 13: 189-111.

ROOD, J.P. 1983. The social system of the dwarf mongoose. pp. 454-488. In: Eisenberg, J.F. & Kleiman, D.G. (eds.) Advances in the Study of Mammalian Behaviour. American Society of Mammalogists. Special Publication 7, Pittsburgh.

ROOD, J.P. & WASER, P.M. 1978. The slender mongoose, Herpestes sanguineus, in the Serengeti. Carnivore 1: 54-58.

ROOT, R.B. 1967. The niche exploitation pattern of the blue-gray gnatchatcher. Ecological Monographs 37: 317-350.

ROSENZWEIG, M.L. 1966. Community structure in sympatric Carnivora. Journal of Mammalogy 47: 602-612.

ROSENZWEIG, M.L. 1968. The strategy of body size in mammalian carnivores. American Midland Naturalist 80: 299-315.

ROSENSWEIG, M.L. 1985. Some theoretical aspects of habitat selection. pp. 517-540. In: Cody, M.L. (ed.) Habitat Selection in Birds. Academic Press, Orlando.

ROSEVEAR, D.R. 1974. The Carnivores of West Africa. Trustees of the British Museum (Natural History), London.

ROTENBERRY, J.T. 1980. Dietary relationships among shrub-steppe passerine birds: competition or opportunism in a variable environment. Ecological Monographs 50: 93-110.

ROTENBERRY, J.T. & WIENS, J.A. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61: 1228-1250.

ROWE-ROWE, D.T. 1971. The development and behaviour of a rusty- spotted genet, Genetta rubiginosa Pucheran. Lammergeyer 13: 29-44.

ROWE-ROWE, D.T. 1977. Food ecology of otters in Natal, South Africa. Oikos 28: 210-219.

ROWE-ROWE, D.T. 1978. The small carnivores of Natal. Lammergeyer 25: 1-48.

ROWE-ROWE, D.T. 1983. Black-backed jackal diet in relation to food availability in the Natal Drakensberg. South African Journal of Wildlife Research 13: 17-23.

ROWE-ROWE, D.T. & GREEN B. 1981. Steel-jawed traps for live capture of black-backed jackals. South African Journal of Wildlife Research 11: 63-65.

ROWE-ROWE, D.T. & MEESTER, J. 1982. Habitat preferences and abundance relations of small mammals in the Natal Drakensberg. South African Journal of Zoology 17: 202-209.

SADIE, D. 1983. The foraging behaviour and metabolic rate of the banded mongoose Mungos mungo (Gmelin). M.Sc. thesis, University of Pretoria.

SAMUEL, M.D., PIERCE, D.J. & GARTON, E.O. 1985. Identifying areas of concentrated use within the home range. Journal of Animal Ecology 54: 711-719.

SAMWAYS, M.J. 1983. Community structure of ants (Hymenoptera: Formicidae) in a series of habitats associated with citrus. Journal of Applied Ecology 20: 833-847.

SANDWITH, T.S. & BROWN, A.D.I. 1981. Reconnaissance vegetation mapping at Vernon Crookes Nature Reserve. Unpubl. N.P.B. Report.

SAVAGE, R.J.G. 1977. Evolution in carnivorous mammals. Palaeontology 20: 237-271.

SCHOENER, T.W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2: 369-404.

SCHOENER, T.W. 1974a. Resource partitioning in ecological communities. Science 185: 27-39.

SCHOENER, T.W. 1974b. The compression hypothesis and temporal

resource partitioning. Proceedings of the National Academy of Science USA 71: 4169-4172.

SCHOENER, T.W. 1986. Resource partitioning. pp.91-126. In: Kikkawa, J. & Anderson, D.J. (eds.) Community Ecology: patterns and process. Blackwell Scientific Publications, Melbourne.

SCHOLTZ, C.H. & HOLM, E. 1985. Insects of Southern Africa Butterworths, Durban.

SCHRODER, G.D. 1987. Mechanisms for coexistence among three species of Dipodomys: Habitat selection and an alternative. Ecology 68: 1071-1083.

SCOTT, T.G. 1941. Methods and computation in fecal analysis with reference to the red fox. Iowa State Journal of Research 15: 279-285.

SEBER, G.A.F. 1973. The estimation of animal abundance and related parameters. Griffen, London.

SHEPHERD, A.J., LEMAN, P.A. & HARTWIG, E.K. 1983. Analysis of viverrid scats from the northern Orange Free State. South African Journal of Zoology 18: 400-401.

SHEPPEY, K and BERNARD, R.T.F. 1984. Relative brain size in the mammalian carnivores of the Cape Province of South Africa. South African Journal of Zoology 19: 305-308.

SHORTRIDGE, G.C. 1934. The Mammals of South West Africa. Heinemann, London.

SIMMS, D.A. 1979. North American weasels: resource utilization and distribution. Canadian Journal of Zoology 57: 504-520.

SMITH, M.H. GENTRY, J.B. & GOLLEY, F.B. 1969. A preliminary report on the examination of small mammal census methods. pp. 25-29. In: Petrusewicz, K. & Ryskowski, L. (eds.) Energy Flow Through Small Mammal Populations. Polish Scientific Publishers, Warsaw.

SMITH, M.H., GARDNER, R.H., GENTRY, J.B., KAUFMAN, D.W. & O´FARRELL, M.H. 1975. Density estimations of small mammal populations. pp. 25-53. In: Golley F.B., Petrusewicz, K & Ryszkowski, L. (eds.) Small Mammals: their productivity and population dynamics. 1BP5 Cambridge University Press, Cambridge.

SMITHERS, R.H.N. 1968. A Checklist and Atlas of the Mammals of Botswana. Trustees of the National Museums of Rhodesia, Salisbury.

SMITHERS, R.H.N. 1971. The Mammals of Botswana No. 4. Trustees of National Museums of Rhodesia, Salisbury.

SMITHERS, R.H.N. 1983. The Mammals of the Southern African Subregion. University of Pretoria, Pretoria.

SMITHERS, R.H.N. & WILSON, V.J. 1979. Checklist & Atlas of the

Mammals of Zimbabwe, Rhodesia. Museum Memoirs of the National Museums and Monuments of Rhodesia. 9: 1-147

SOUTHERN, H.N. 1973. A yardstick for measuring populations of small rodents. Mammal Review 3: 1-10.

SOUTHWOOD, T.R.E. 1978. Ecological Methods: with particular reference to the study of insect populations. Chapman & Hall, London.

SPENCER, W.D. & BARRETT, R.H. 1984. An evolution of the harmonic mean measure for defining carnivore activity areas. Acta Zoologica Fennica 171: 255-259.

STICKEL, L.F. 1946. Experimental analysis of methods for measuring small mammal populations. Journal of Wildlife Management 10: 150-159.

STUART, C.T. 1977. Analysis of Felis libyca and Genetta genetta scats from the central Namib Desert, South West Africa. Zoologica Africana 12: 239-241.

STUART, C.T. 1981. Notes on the mammalian carnivores of the Cape Province, South Africa. Bontebok 1: 1-58.

STUART, C.T. 1983. Food of the large grey mongoose Herpestes ichneumon in the southwest Cape Province. South African Journal of Zoology. 18: 401-403.

SWIFT, S.M., RACEY, P.A. & AVERY, M.I. 1985. Feeding ecology of Pipistrellus pipistrellus (Chiroptera: Vespertilionidae) during pregnancy and lactation. II Diet. Journal of Animal Ecology 54: 217-225.

SWIHART, R.K., SLADE, N.A. & BERGSTROM, B.J. in press. Ecology.

TAYLOR, K.D. & GREEN, M.G. 1976. The influence of rainfall and diet on reproduction in four African rodent species. Journal of Zoology (London) 180: 367-389.

TAYLOR, M.E. 1969. Notes on the breeding of two genera of viverrids, Genetta spp. and Herpestes sanguineus, in Kenya. East African Wildlife Journal. 7: 168-169.

TAYLOR, M.E. 1970. Locomotion in some East African viverrids. Journal of Mammalogy 51: 42-51.

TAYLOR, M.E. 1972. Ichneumia albicauda. Mammal Species 12: 1-4.

TAYLOR, M.E. 1974. The functional anatomy of the forelimb of some African Viverridae (Carnivora). Journal of Morphology 143: 307-336.

TAYLOR, M.E. 1975. Herpestes sanguineus. Mammalian Species 65: 1-5.

TAYLOR, M.E. 1979. The functional anatomy of the hindlimb of some African Viverridae (Carnivora). Journal of Morphology 148: 227-254.

TAYLOR, M.E. 1986. Aspects on the biology of the four-toed mongoose, Bdeogale crassicauda. Cimbebasia (Series A) 8: 187-193.

THOMAS, D.B. 1979. Patterns in the abundance of some tenebrionid beetles in the Mojave Desert. Environmental Entomology 8: 568-574.

THOMAS, D.B. & SLEEPER, E.L. 1977. The use of pit-fall traps for estimating the abundance of Arthropods, with special reference to the Tenebrionidae (Coleoptera). Annals of the Entomological Society of America 70: 242-248.

TILSON, R.L. & LE ROUX, P. 1983. Resource partitioning in coexisting Namib Desert owls, Bubo africanus and Tyto alba. Madoqua 13: 221-227.

TUKEY, J.W. 1980. We need both exploratory and conformatory. American Statistician 34: 23-25.

TURNBULL-KEMP, P.ST.J. 1960. Quantitative estimations of populations of the river crab, Potamon (Potamonautes) perlatus (M.Edw.) in Rhodesian trout streams. Nature (London) 185: 481.

TWIGG, G.I. 1975. Techniques in mammalogy. Chapter 2. Catching mammals. Mammal Review 5: 83-100.

VAN DER ZEE, D. 1981. Prey of the Cape clawless otter Aonyx capensis in the Tsitsikama Coastal National Park, South Africa. Journal of Zoology, (London) 194: 467-483.

VAN HENSBERGEN, H.J. 1984. Ecological separation between four species of Carnivore in the Western Pyrenees, Spain. Ph.D. thesis, Cambridge.

VANNINI, M. & GHERADI, F. 1981. Dominance and individual recognition in Potamon fluviatile (Decapoda, Brachyura). Possible role of visual cues. Marine Behaviour and Physiology 8: 13-20.

VERNON, C.J. 1972. An analysis of owl pellets collected in southern Africa. Ostrich 43: 109-123.

VOGT, R.C. & HINE, R.L. 1982. Evaluation of techniques for assessment of amphibian and reptile populations in Wisconsin. United States Dept. of Interior, Fish & Wildlife Service. Wildlife Research Report 13: 201-217.

VOIGT, D.R. & TINLINE, R.R. 1980. Strategies for analysis of radio-tracking data. pp. 387-404. In: Amlaner, C.J. & MacDonald, D.W. (eds.) A Handbook on Biotelemetry and Radio-tracking. Pergamon, Oxford.

VOLTERRA, V. 1926. Variazioni e fluttuazioni del numero d´individui in specie animali conviventi. Mem R. Acad. Nay dei Lincei 2: 31-113.

VON SCHANTZ, T. 1980. Prey consumption of a red fox population in southern Sweden. The Red Fox. Zimen, E. (ed.). Biogeographica 18: 53-64.

WASER, P.M. 1980. Small nocturnal carnivores: ecological studies in the Serengeti. African Journal of Ecology 18: 167-185.

WASER, P.M. 1981. Sociality or territorial defense? The influence of resource renewal Behavioural Ecology and Sociobiology 8: 231-237.

WASER, P.M. & WASER, M.S. 1985. Ichneumia albicauda and the evolution of viverrid gregariousness. Zeitschrift Tierpsychology. 68: 134-151.

WENZEL, E. & HALTENORTH, T. 1972. System der Schleichkatzen (Viverridae). Saugetierkundliche Mitteilungen 20: 110-127.

WHATELEY, A. & BROOKS, P.M. 1985. The carnivores of the Hluhluwe and Umfolozi Game Reserves: 1973-1983. Lammergeyer 35: 1-27.

WHITFIELD, A.K. & BLABER, S.J.M. 1980. The diet of Atilax paludinosus (water mongoose) at St. Lucia, South Africa. Mammalia 44: 315-318.

WIENS, J.A. 1977. On competition and variable environments. American Scientist 65: 590-597.

WIENS, J.A. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. pp. 439-457. In: Strong, D.R., Simberloff, D., Abele, L.G. & Thistle, A.B. (eds.) Ecological Communities: conceptual issues and the evidence. Princeton University Press, Princeton.

WILLAN, K. 1979. Design and field tests of a modified small mammal livetrap. South African Journal of Zoology 14: 81-84.

WILLAN, K. 1982. Social ecology of Otomys irroratus, Rhabdomys pumilio and Praomys natalensis. Ph.D. thesis, University of Natal, Pietermaritzburg.

WILLAN, K. 1986. Bait selection in laminate-toothed rats and other Southern African small mammals. Acta Theriologica 31: 359-363.

WILLAN, K & BIGALKE, R.C. 1982. The effects of fire regime on small mammals in S.W. Cape montane fynbos (Cape Macchia). pp. 207-212. In: Conrad, C.E. & Oechel, W.C. (eds.) Dynamics and management of Mediterranean-type ecosystems. U.S. Forest Service, Berkeley.

WILLIAMS, B.K. 1983. Some observations on the use of discriminant analysis in ecology. Ecology 64: 1283-1291.

WILSON, D.S. 1975. The adequacy of body size as a niche difference. American Naturalist 109: 769-784.

WINGATE, L.R. & MEESTER, J. 1977. A field test of six types of live-trap for African rodents. Zoologica Africana 12: 215-223.

WISE, M.H., LINN, I.J. & KENNEDY, C.R. 1981. A comparison of the feeding biology of mink Mustela vison and otter Lutra lutra. Journal of Zoology (London) 195: 181-213.

ZAR, J.H. 1974. Biostatistical Analysis. Prentice-Hall, London.

Additional References

HAYWARD, G.D. & GARTON, E.O. 1988. Resource partitioning among forest owls in the River of No Return Wilderness, Idaho. Oecologia 75: 253-256.

STRONG, D.R., SIMBERLOFF, D., ABELE, L.G. & THISTLE, A.B. 1984. (eds). Ecological Communities: conceptual issues and the evidence. Princeton University Press.