

T AN
INTEGRATED APPROACH
TO THE
MANAGEMENT OF COMMON REEDBUCK
ON
FARMLAND IN NATAL /

by

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PREFACE

The experimental work described in this thesis was carried out from the Institute of Natural Resources, University of Natal, Pietermaritzburg, under the joint supervision of Dr J. Grimsdell and Professor J. Hanks, over the period December 1980 to December 1983.

This thesis, unless specifically indicated to the contrary in the text, is my own original work. It has not been submitted for a degree to any other university.

Peter C. Howard

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ABSTRACT

This study was motivated by the Natal Parks Board which has been receiving a growing number of complaints from farmers concerning reedbuck grazing of commercial crops. The reedbuck is an important conservation species, which has recently disappeared from 80 % of its previous range in South Africa, and has become extinct in the Cape Province and the Orange Free State. The study was intended to look objectively at the crop damage problem and conservation status of reedbuck on private land in Natal, and make recommendations for management.

A postal questionnaire was used in assessing the species' present distribution in Natal, and an intensive study was undertaken in the Underberg district of the Natal highlands. The study area comprised approximately 10 500 ha of semi-intensive agricultural land, divided into 23 farm properties, and was considered representative of farmland throughout the highland and midland regions of the province, where nutritious food in the form of irrigated pasture grasses is available throughout the year.

Four animal census techniques were critically evaluated, and reedbuck numbers assessed throughout the study area. The study area was divided into no-cull, low-cull and high-cull blocks, and population trend examined over two years in each. Population stability was demonstrated in all blocks. Post mortem examination of nearly 200 reedbuck showed that the animals were in excellent physiological condition throughout the year, and the population appeared to be at, or close to its genetic potential as regards productivity. A 20 % annual 'surplus' of animals appeared to be produced. Eighty four reedbuck were marked, and resightings of some of these far from their place of capture confirmed that emigration of young animals is an important population regulatory process.

A multiple regression analysis of reedbuck-habitat relations, based on observed reedbuck numbers on the 23 farm properties, demonstrated that population size appeared to be limited by the availability of cover. An examination of social organisation and behaviour led to the belief that cover is limiting because it is a resource that is monopolised by dominant territorial males at the time when females are attracted to it to give birth. Within two months these females, nursing their newborn lambs, become oestrous again, and are mated by the territorial males.

Because of the relatively low densities at which stability is achieved, crop damage only becomes a problem in exceptional circumstances. A best estimate of 0,2 t of pasture grass lost per reedbuck per winter was made

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from a series of exclusion experiments on winter pastures, and it was calculated that to recover costs a farmer would have to shoot 20 % of his reedbuck population annually. However, in an agricultural perspective, prevention of the losses attributed to reedbuck would yield negligible benefits under most circumstances when compared with alternative methods of improved agricultural productivity.

Recommendations were made for improving the conservation status of the species throughout the province, through the establishment of 'reintroduction centres' in parts of northern Natal, and the active encouragement of utilisation in other (specified) areas. Some methods of control were recommended for those situations in which genuine crop damage problems exist.

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CHAPTER ONE

INTRODUCTION

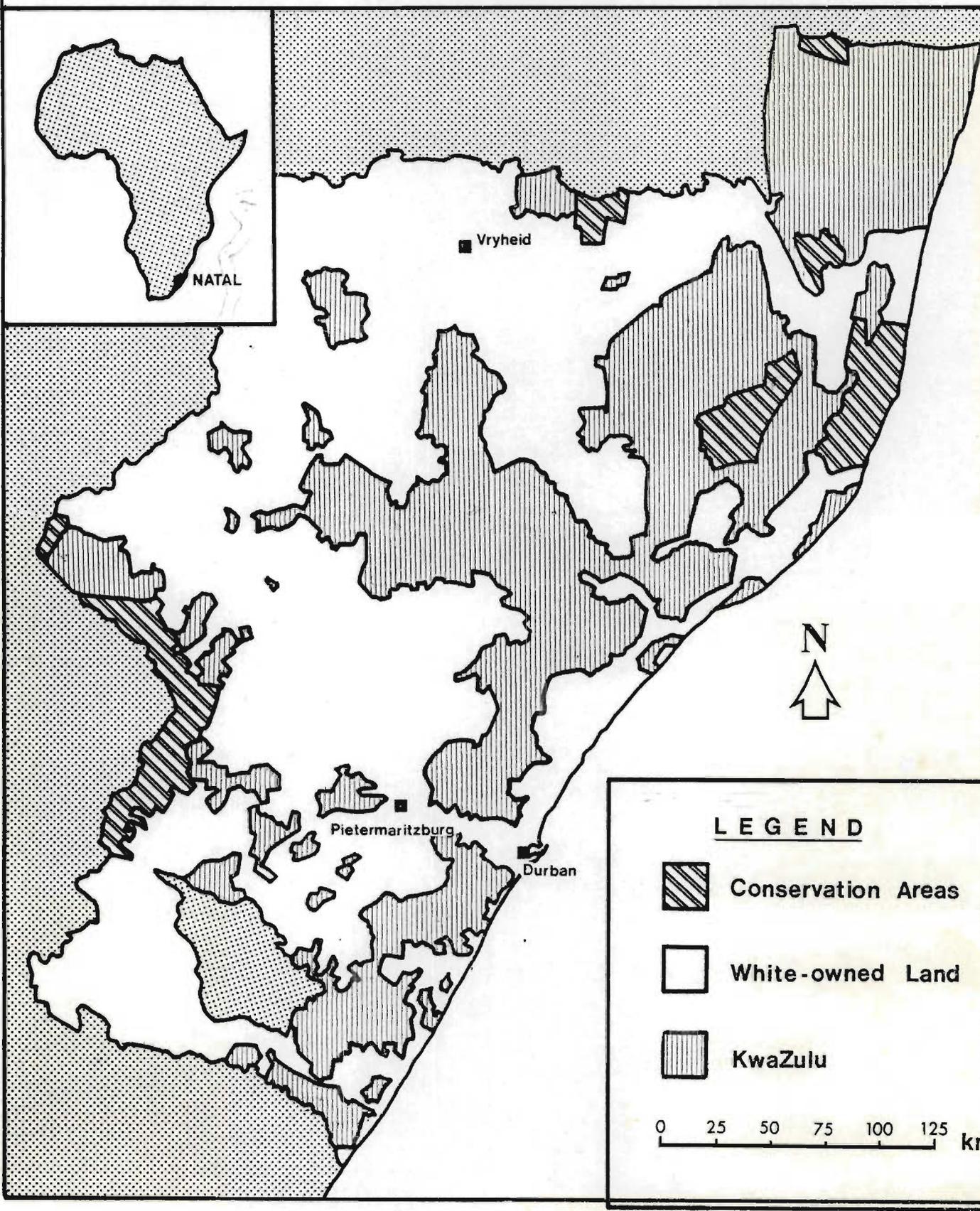
1.1 FARM GAME IN NATAL: AN OVERVIEW

1.1.1 The place of wildlife on farmland

In the World Conservation Strategy (IUCN, 1980) conservation is defined as 'the management of human use of the biosphere so that it may yield the greatest sustainable benefit to present generations while maintaining its potential to meet the needs and aspirations of future generations'. The emphasis is clearly on human use, but also on controlling that use in a world where escalating human populations and aspirations for improved living standards threaten wildlife, and all the other components of natural ecosystems as never before. The sentiments expressed in the World Conservation Strategy are not new ones, and many far-sighted ecologists (Nicholson, 1970; Curry-Lindahl, 1972; Meadows et al., 1972; Owen, 1973; Allen, 1980) have foreseen the limits to growth and warned against over-exploitation of natural resources in a proliferation of earlier literature. The need for conservation is clearly very real. If we accept as inevitable the predicted increase in human numbers from the present 4,7 to 10,5 billion (Barney, 1980), we must also accept that this will necessitate increased agricultural productivity that can only be achieved at the expense of the world's wild places, and the flora and fauna they support. As more land comes under cultivation, farmers, as the managers and guardians of that land, have an increasingly important role to play in conservation.

In Natal almost 60 % of the land is under private ownership (White-owned land; FIG. 1.1) compared with about 6 % under the management of 'conservation' bodies. Of the remainder, the vast majority (34 % of the province) is designated 'KwaZulu', which is the 'homeland' of the Zulu people, held communally and destined to become an 'independent' state under present government policy (FIG. 1.1). The conservation areas are managed to preserve representative areas of natural ecosystems on a sub-economic basis with little or no material exploitation. Privately-owned land, on the other hand, is managed to maximise profit, and all too often short-term exploitation leads to irreparable environmental degradation. Just as there are strong arguments in favour of controlled utilisation of resources within conservation areas, so there are for the maintenance of wildlife on

FIG.1.1 : Land Use in Natal-KwaZulu



farmland. Certainly, some wildlife species are incompatible with man's agricultural activities (for example, lion (Panthera leo) and elephant (Loxodonta africana)) and specially designated 'conservation' areas are necessary to preserve them. Others, however, are compatible with modern farming practice, and might even become a secondary form of land use (Collinson, 1979). Natal farmers are becoming increasingly conscious of the aesthetic, sporting and carcass value of wildlife on their farms.

1.1.2 Natal Parks Board operations on farmland

Indeed it was in response to requests by Natal landowners that the Natal Parks Board (NPB) established its Farm Game (extension) Section in 1965. Today, the section comprises four professional officers, a technician and two rangers whose job it is to advise on veld and game management on private land. Further, the Natal Parks Board employs fourteen extension officers (zone officers) based at inland field stations throughout the province. Although this, together with office support staff in the field, represents only about 6% of the Board's complement of European staff, it is seen as a significant stimulus to conservation on farmland. The importance of this service can be judged by the fact that, of the nineteen naturally occurring species of antelope in Natal, all occur on privately-owned land, and eleven of them (bushbuck (Tragelaphus scriptus), blue duiker (Cephalophus monticola), grey duiker (Sylvicapra grimmia), grey rhebuck (Pelea capreolus), common reedbuck (Redunca arundinum), mountain reedbuck (Redunca fulvorufula), blesbok (Damaliscus dorcas), impala (Aepyceros melampus), oribi (Ourebia ourebia), steenbok (Raphicerus campestris) and suni (Neotragus moschatus)) are considered to be more abundant there than they are within designated wildlife reserves (Collinson, pers. comm.).

The most significant recent development in Natal's conservation programme on farmland was the establishment of the Balgowan Conservancy in 1978, and the birth of the conservancy concept. Briefly, a conservancy comprises a group of adjacent farms whose owners collectively employ NPB trained game guards to patrol the area and provide communal security. Between 1978 and the end of 1982 eighty three conservancies were formed, involving 1016 landowners and covering nearly 7 000 000 hectares (13,2 % of privately owned rural land in the province).

1.2 STUDY MOTIVATION

This study was originally motivated from the Farm Game Section of the Natal Parks Board, under the broad heading 'Problem Animals on Farmland'. There are numerous mammals and birds that cause damage to farmer's crops in Natal, and these include both legally protected and unprotected species. Eland (Taurotragus oryx), common reedbuck, bushbuck, francolin (Francolinus sp.), cranes (family Gruidae) and geese (family Anatidae) are the most

commonly encountered members of the first group, while unprotected 'pests' include grey duiker, porcupine (Hystrix africae-australis), vervet monkey (Cercopethicus pygerythrus) and bushpig (Potamochoerus porcus). As the work was to be undertaken under the aegis and financial support of the University of Natal/Natal Parks Board Research Fund, it was decided that it should make at least some contribution to the conservation of 'endangered' wildlife in the province. The field was thus narrowed down to consideration of protected species, even though some unprotected species were believed to be more serious pests in terms of economic damage to crops. It was felt that where unprotected wildlife species cause problems, the onus could remain with the farmer to implement whatever appropriate control method he deemed necessary, and that the Natal Parks Board had a responsibility to ensure wise management of those species that fell into its custody. Of the protected game species that are most commonly implicated in crop damage, it was decided for various reasons not to make a study of any of the birds, and since a study of bushbuck had recently been initiated in Natal, and the decision had been taken to control the eland problem by the construction of a high fence along the Drakensberg stateland/farmland boundary, the reason for opting to study reedbuck is self-evident.

The following aspects of the 'reedbuck problem' were identified at an early stage:

1.2.1 Conservation status

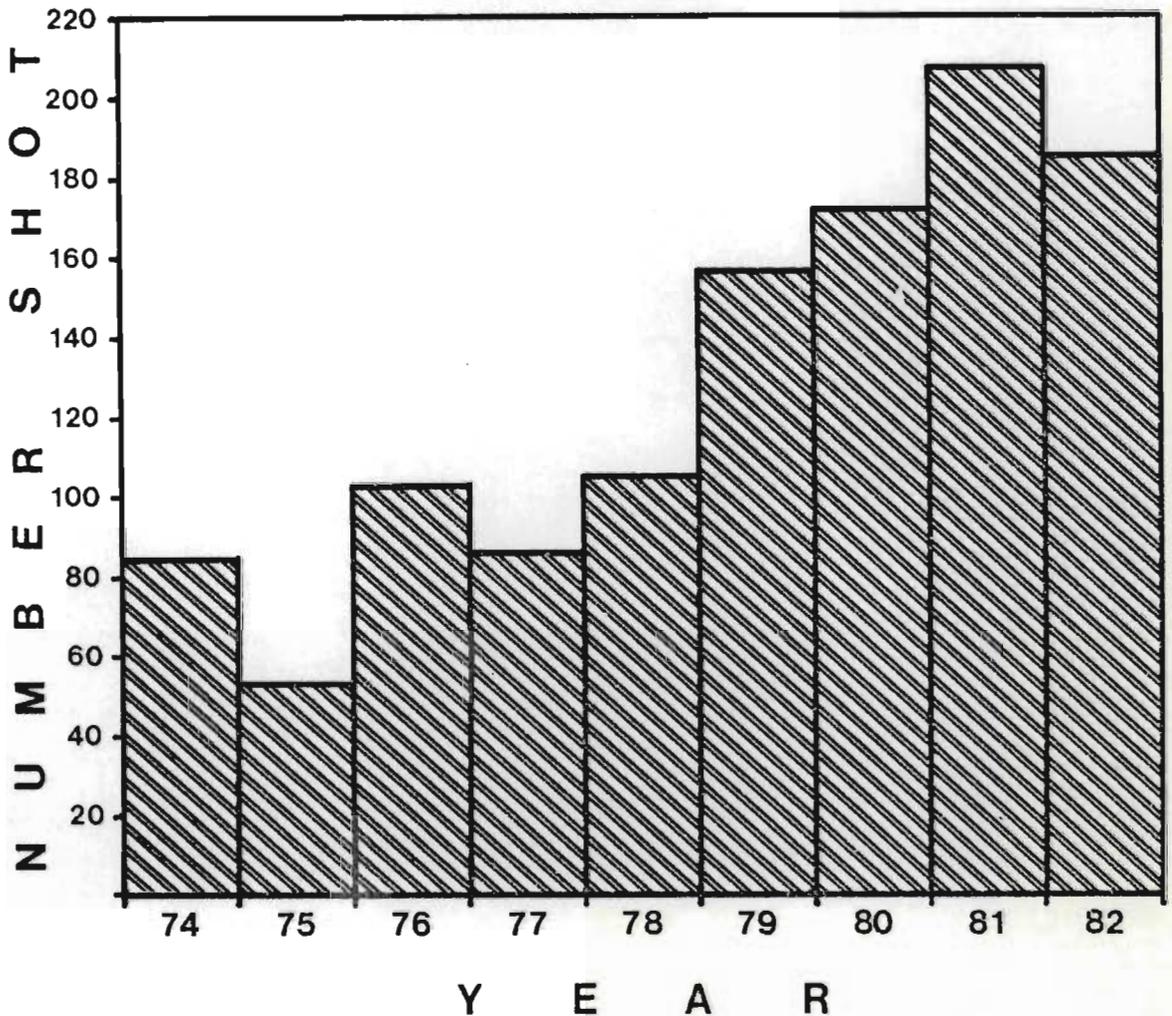
The common reedbuck is included in the list of endangered large mammals compiled for the South African Red Data Book, where its status is described as 'rare, common locally in parts of Zululand'(Skinner et al., 1978). Though 'secure' throughout much of its range in central and southern Africa (Bothma, 1975), it has disappeared from 80 % of its former range in South Africa (Zaloumis and Cross, 1974). An assessment of its present distribution, and the likely factors governing this, was considered to be a prerequisite to sound conservation policy.

1.2.2 Crop damage

The Farm Game Section of the NPB receives numerous complaints each winter about reedbuck grazing pressure on irrigated pastures and other crops. Such complaints usually result in the issue of permits to shoot a number of the offending animals, but quotas are decided upon almost arbitrarily. During the past nine years, for which records are available, the number of reedbuck legally shot on private land has shown a three-fold increase (FIG. 1.2). As far as the farmer is concerned the aesthetic, sporting or carcass value of these animals may offset, to a variable degree, the 'cost' of their upkeep in terms of lost grazing for his stock. Clearly there was a

need to consider the value of these animals to the farmers on whose land they are maintained, the extent of the damage they cause, and the extent to which they can be 'utilised'.

FIG.1.2 : The number of reedbuck legally shot on private land in Natal, over the period 1974 to 1982



1.2.3 Management options

In recent years there has been increasing interest in the translocation of animals from areas where they are locally abundant to 'bolster' populations in other areas, reintroduce a species to an area that it formerly inhabited or introduce it to an area where it never previously existed. In conservation management the 'translocation option' is in danger of becoming an acceptable alternative to the preservation of naturally occurring populations or sub-populations. In Natal two quite distinct sub-populations of reedbuck exist: one in the highlands and midlands south and west of Pietermaritzburg; the other in the Zululand lowveld around Lake St. Lucia. These sub-populations may have been isolated from one another for some considerable time, and the process of genetic adaptation to the very different environmental conditions to which each is subject, may have

produced some significant differences between the two. The success of indiscriminate translocation of these animals to new areas throughout South Africa might be affected by their degree of genetic adaptation. It will almost certainly be affected by the suitability of the the habitat to which they are introduced. Neither of these aspects has previously been examined, despite a heavy demand by private landowners for surplus reedbuck, and substantial numbers allocated each year.

1.3 AIMS

Broadly the objectives of the study are:

- 1 To assess the distribution and status of reedbuck on privately-owned rural land in Natal, and evaluate governing environmental factors.
- 2 To assess the habitat and nutritional requirements of reedbuck on farmland, and determine how these are, or may be provided.
- 3 To evaluate the extent of any conflict between the requirements of reedbuck on farmland, and the interests of the farmers on whose land they are maintained.
- 4 To determine the present status of a representative sub-population under intensive study, and investigate the potential for sustained yield harvesting.
- 5 To provide a statement on the present and potential value of the resource on private land in Natal in relation to competing or complementary forms of land use.
- 6 To review conservation management options in recolonisation programmes and make specific recommendations on translocation.
- 7 To make recommendations for the management of reedbuck on farmland with specific reference to the control of crop damage, maintenance and expansion of viable populations, key methods of population monitoring and sustained yield harvesting.
- 8 To make recommendations on the legal protection of the species, and future research and extension priorities.

The purpose of specific aspects of the study is given more detailed consideration in the introduction to each chapter. Throughout, the aims of the study are management orientated.

1.4 TAXONOMIC STATUS OF REEDBUCK

The common reedbuck is a member of the sub-family Reduncinae, which includes the waterbucks, lechwe, kob, puku and the reedbucks. A description of all species and their taxonomic status is given by Dorst and Dandelot (1970), Ansell (1971), and Roberts (1951).

Within the genus Redunca there are three species: Redunca arundinum (common or southern reedbuck), Redunca redunca (bohor reedbuck), and Redunca fulvorufula (mountain reedbuck).

Ansell (op.cit.) recognises two distinct subspecies of R.arundinum:

- 1 R.a.arundinum (Boddaert, 1785), which occurs in the southern parts of the species range, possibly as far north as southern Angola and the Zambezi river.
- 2 R.a.occidentalis (Rothschild, 1907), which occurs in the northern parts of the species range, as far north as Gabon, Congo and Tanzania.

A third subspecies, R.a.thomasinae (Sclater, 1900) from Malawi and Tanzania is considered (Ansell, op.cit.) unlikely to be a valid subspecies.

This study relates to Redunca arundinum arundinum.

1.5 STUDY AREA

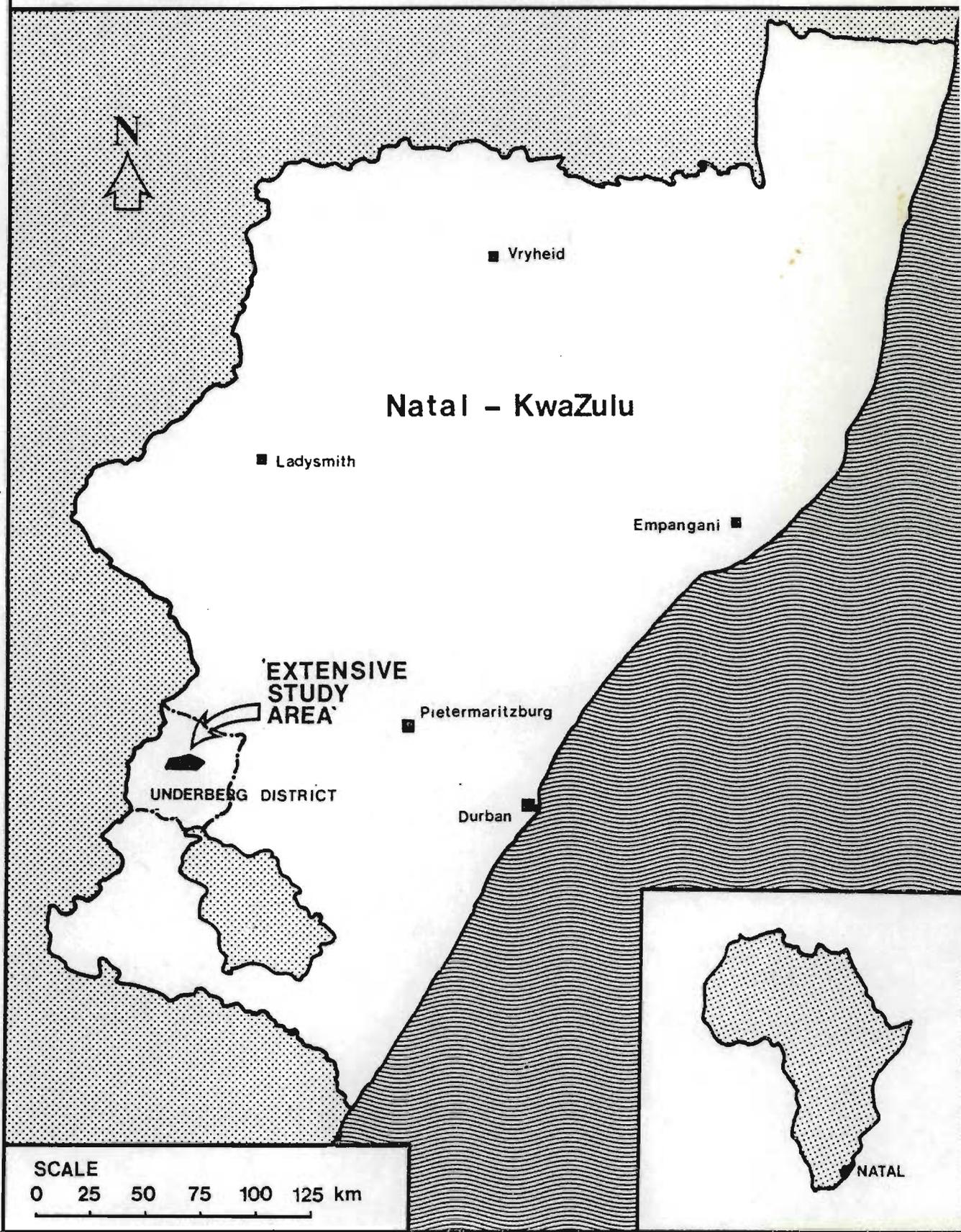
1.5.1 Introduction

The study was conducted within the provincial boundaries of Natal, South Africa. Reedbuck distribution information was collected from the entire province, considered in 7,5' x 7,5' compartments, based on latitude and longitude. Only white-owned farming land was considered, so that land administered by the state and provincial authorities, urban areas, and areas of KwaZulu did not fall within the study area.

An intensive study was undertaken on a group of about twenty mixed farms in the Polela valley, in Underberg district (FIG. 1.3). This is referred to as the extensive study area, and comprises about 10 500 hectares of semi-intensive agricultural land. The extensive study area was used in monitoring animal numbers, patterns of habitat use and distribution, and as a source of culled material.

One end of the extensive study area was designated a no-cull zone, and intensive study of social and spatial organisation, population structure, development of census techniques and year-round monitoring of pasture use

FIG.1.3 : Location of the extensive study area in Natal-KwaZulu



was undertaken in this 1 000 hectare area, referred to as the intensive study area (FIG. 1.4). A view of this area is provided by PLATE 1.

1.5.2 Land use history

Until late in the nineteenth century, Underberg district was inhabited by Bushmen, who together with a scattering of Zulu people lived off the land without exercising any significant control over it. The first white man to arrive in the district came in 1866, but he was murdered by local Zulus, and no others ventured that way until 1886. Then between 1886 (when R.W.Cockerell bought the farm Fonderling) and the turn of the century, much of the land was divided into 2 000 acre 'farms', bought at ten shillings an acre, and occupied by other settler families. The early days were not easy, and a locust plague in 1896 followed by the outbreak of rinderpest just two years later, saw many of those early settlers leaving the district. In fact only 12 of the first 92 farms still remain in the hands of descendants of the original owners.

One of those original owners, Peter MacKenzie, wrote in 1946 of early farming in the district:

'Superphosphates and other artificial fertilizers, which have made this a great potato growing district, were then unknown to us; and if they had been known we should have had to fetch them from Pietermaritzburg, our nearest railhead, a fortnight's journey by wagon. It was only on riverbanks, near vleis, and on a few highly favoured spots on some farms, that crops could be grown. Indeed the poorness of the soil was proclaimed by the small number of native kraals scattered throughout the country; for had the soil been rich enough to grow mealies the natives would not have left it so sparsely populated as Cockerell found it. There was however plenty of grass, so it followed that by stock-farming the settlers tried to make a living.'

It was not until early in the second half of this century, with the widespread adoption of mechanical farming methods, that agriculture really took off. Only then did man's activities begin to have any significant impact on the environment. The landscape was moulded by the planting of trees, the draining of vleis, and the ploughing of more extensive areas of veld. Instead of planting purely cash crops such as potatoes and mealies, large areas were put down to frost-tolerant northern hemisphere pasture grasses and dairying became popular. Yet, because of the very broken nature of the landscape, it has not been possible to cultivate extensive areas to monoculture, as has happened in many other parts of South Africa, and the resultant patchy mosaic of cultivated lands, farm dams, vleis, rugged hillsides and open hilltops characterises the region, and has done much not only for the prosperity of man, but for the reedbeek.

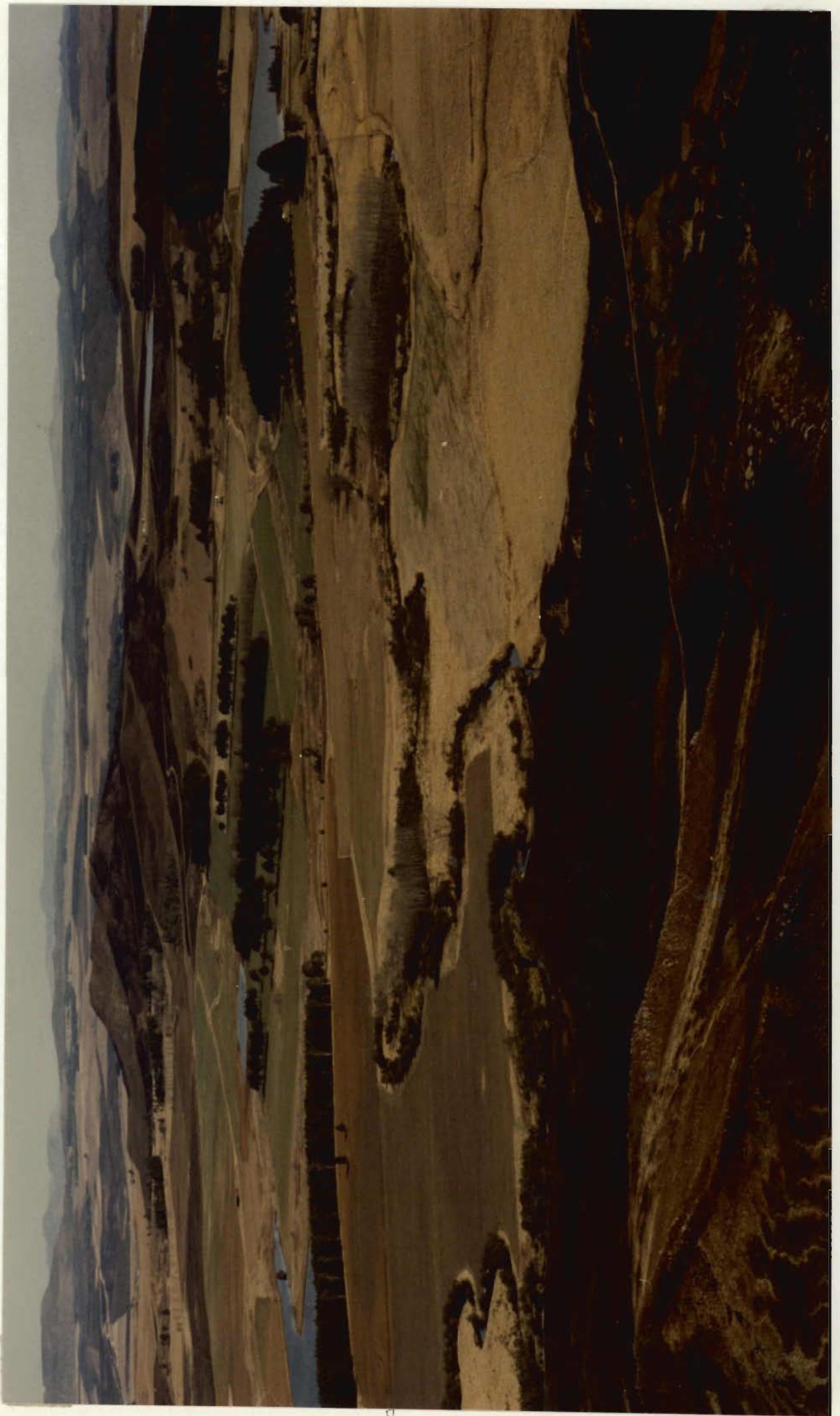
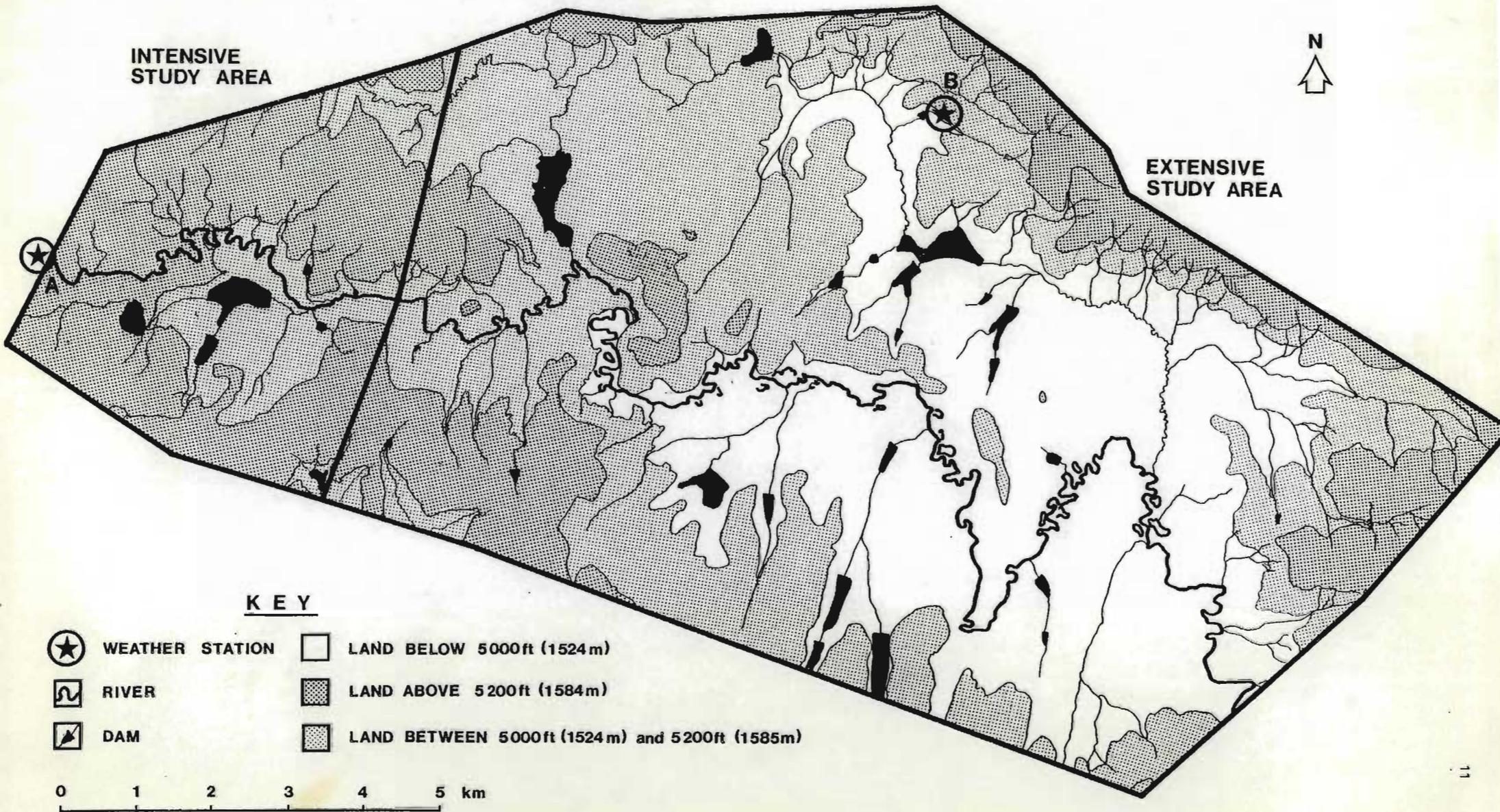


PLATE 1 View of the intensive study area after wild burning in late winter 1994

FIG. 1.4: Study area topography



PLATES 2 and 3 show the extent of the changes which have been brought about on one farm in the study area during the past thirty years or so. The significance of these recent changes in land use and farming practice to the reedbuck are considered at some length in CHAPTER FIVE.

1.5.3 The physical environment

1.5.3.1 CLIMATE

The climatic conditions prevailing in Natal have been described by Schulze (1965), and those of the Drakensberg have been given more detailed consideration by Tyson et al. (1976).

The extensive study area, lying at an altitude of about 1 550 metres in the Drakensberg foothills, is within a summer rainfall area. Between October and March, prevailing moisture laden easterly winds bring orographic (relief) rain to the Drakensberg, and about 85 % of precipitation falls at this time. The days are warm to hot with 50-60 % of possible sunshine hours (Tyson et al., op.cit.), while the nights may be warm or cool.

The first frosts usually occur in April, and the winter months (April to September) are characterised by prevailing westerly winds blowing dry air off the interior plateaulands (Schulze,op.cit.). The days are warm to cool with 70-80% of possible sunshine hours, and the nights very cold.

Valleys tend to experience greater daily extremes of temperature than do hillslopes, particularly in winter when nocturnal temperature inversion is normal. At night dense cool air flowing off the slopes tends to generate a katabatic wind blowing down the valleys, and during the day warmer air rising from the valleys creates an anabatic wind blowing into the mountains (Irwin et al., 1980).

Within the extensive study area, data are available from two established weather stations at Cobham Forestry Station (Weather Station A) and at Merrifields farm (Weather Station B)(FIG.1.4). At Cobham, rainfall records date back to 1965, and daily temperature maxima and minima to 1975. Mean values for these periods are illustrated in FIG. 1.5, together with monthly rainfall totals, and temperature means during the study period January 1981 to December 1982. A summary of climate statistics is given in TABLE 1.1, and the balance between evaporation and precipitation illustrated in FIG. 1.6.

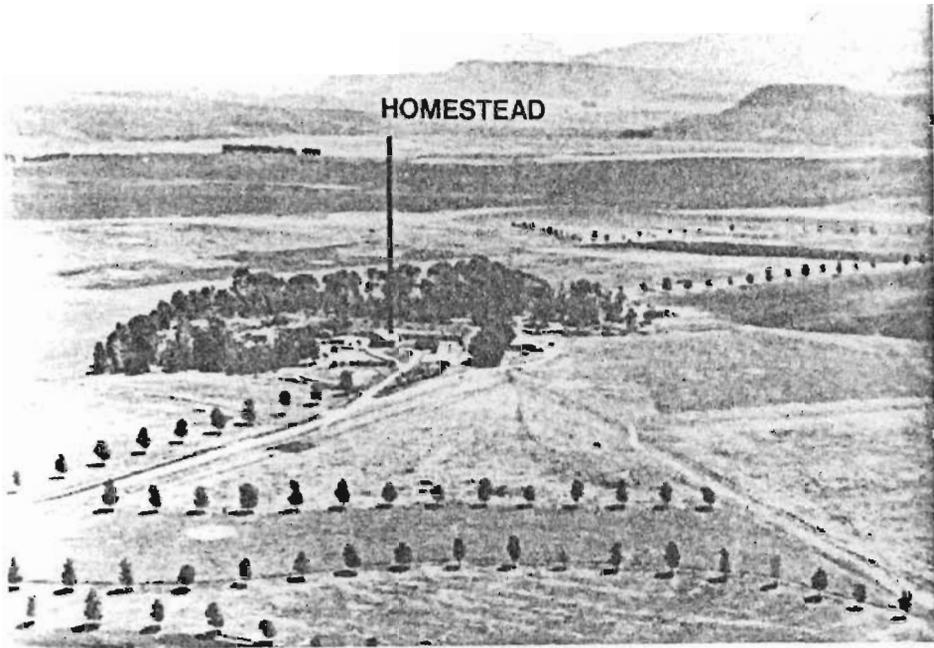


PLATE 2: Hazeldene farm; view from the north-east c.1950

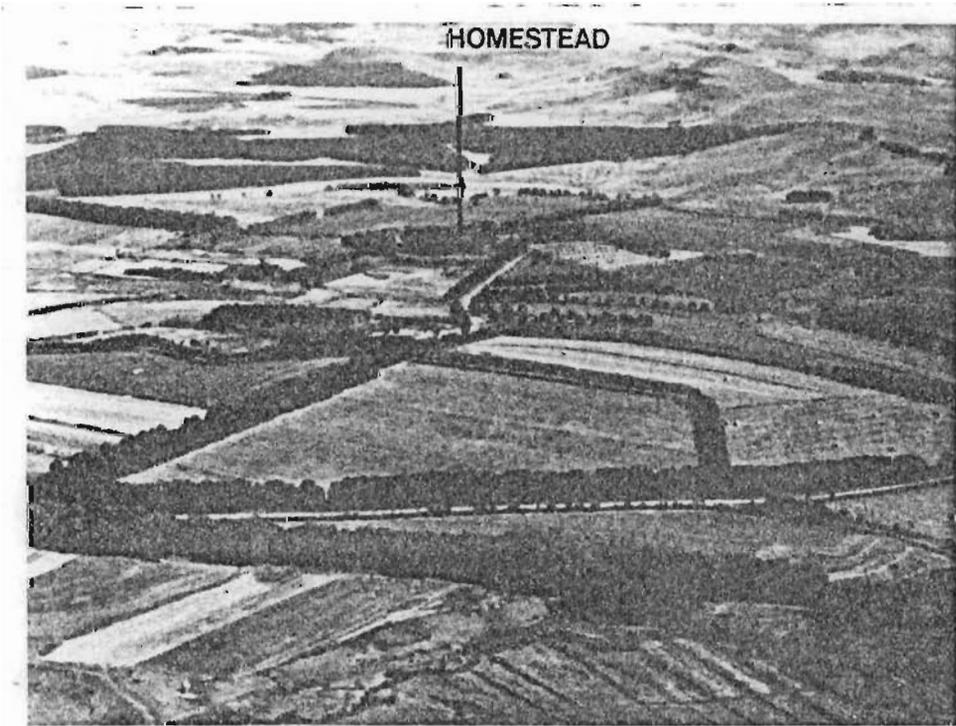
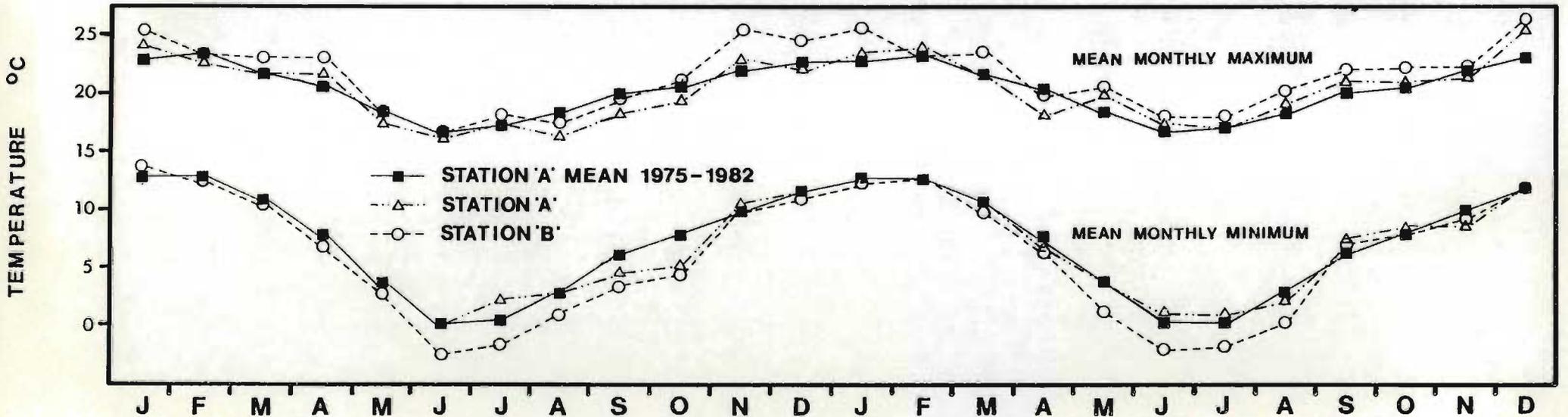
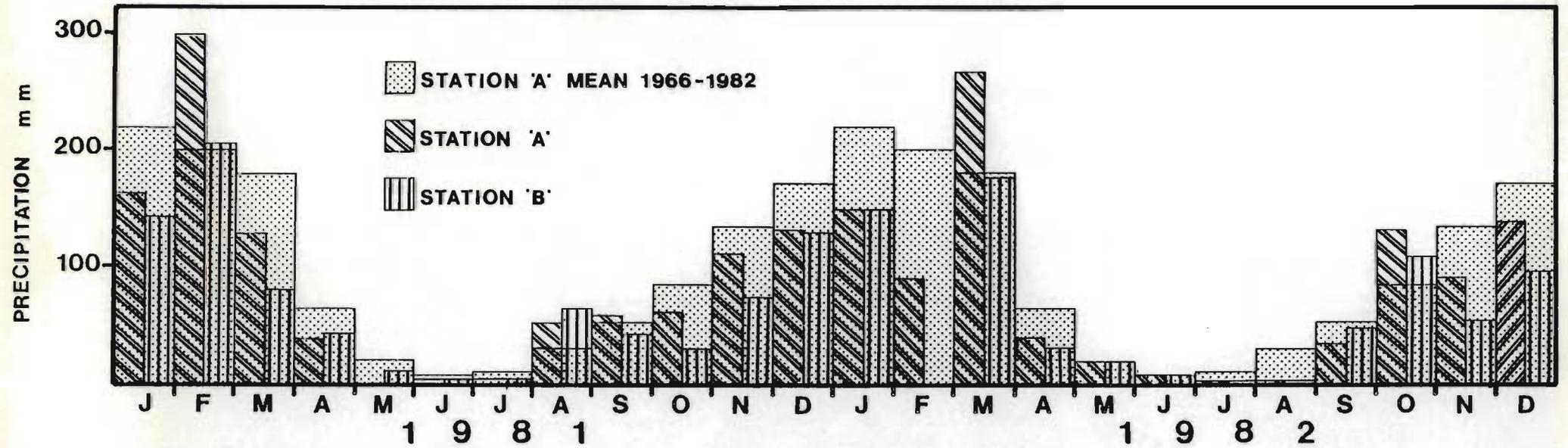


PLATE 3: Hazeldene farm; view from the north-east 1982

FIG.1.5 : MONTHLY RAINFALL AND MEAN TEMPERATURE RANGES AT COBHAM (STATION A) AND MERRIFIELDS (STATION B) COMPARED WITH MEAN DATA FROM COBHAM



The period of fieldwork coincided with the end of a predicted ten year wet cycle, and the beginning of a predicted ten year dry cycle (Dyer and Tyson, 1977). A comparison of weather data at the two stations during the study period, with mean data from Cobham reveals the following:

- 1 1981 and 1982 were dry years. Rainfall at Cobham was 13 % below normal. Merrifields, which is more centrally situated in the study area, and about 12 km from Cobham, received only about 80 % of the rainfall recorded at Cobham;
- 2 diurnal temperature ranges are far greater at Merrifields than at Cobham, both in summer and in winter. Merrifields experiences heavier frosts, with sub-zero mean minima during June and July;
- 3 the spring of 1981 was cool, with below average temperatures in August, September and October;
- 4 in 1981 (the only year for which evaporation data are available) evaporation exceeded precipitation for more than ten months of the year.

FIG. 1.6 : The balance between evaporation (—■—) and precipitation (—□—) at station B during 1981

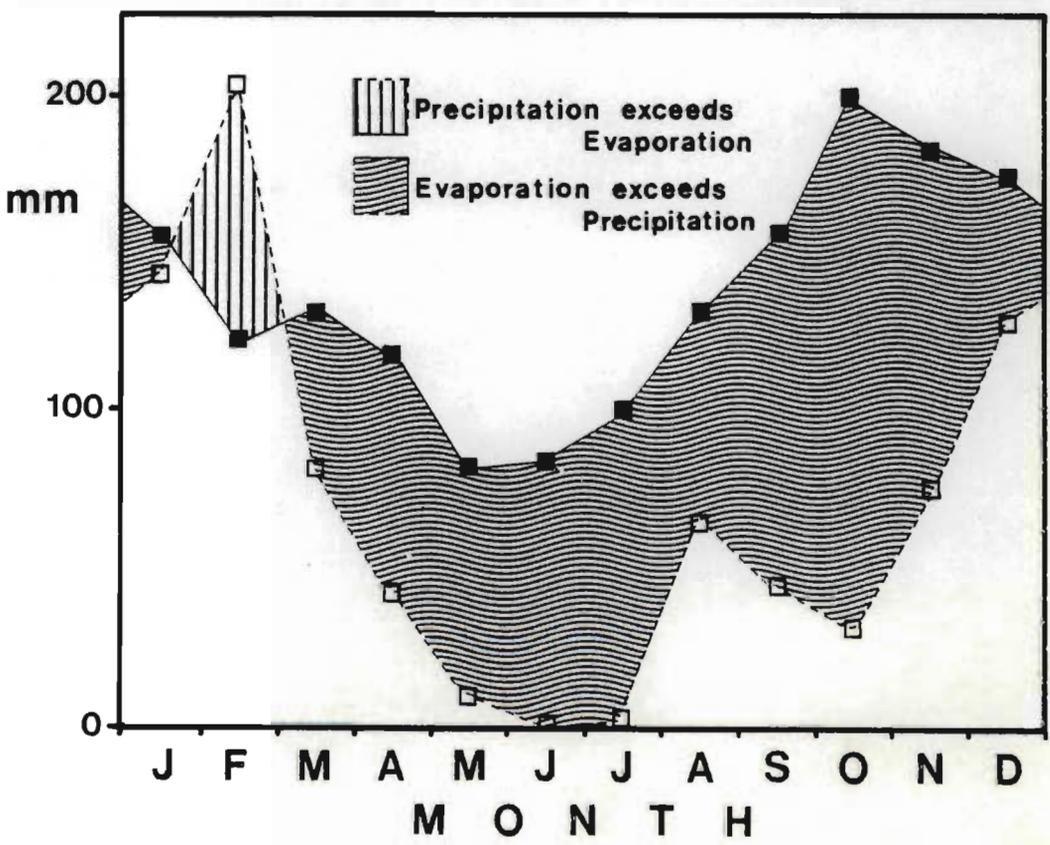


TABLE 1.1 : Summary climate statistics for the Extensive Study Area

	M E A N		1 9 8 1		1 9 8 2	
	STATION A (Cobham)	STATION A (Cobham)	STATION B (Merrifields)	STATION A (Cobham)	STATION B (Merrifields)	
Annual rainfall (mm)	1180	1079	829	970	784	
Mean diurnal temp. range JUNE (°C)	16,5	15,9	19,2	15,9	19,9	
Mean diurnal temp. range DECEMBER (°C)	11,1	11,0	13,6	14,0	14,8	

1.5.3.2 TOPOGRAPHY AND DRAINAGE

The Polela river descends the high Drakensberg rapidly, reaching Cobham Forestry Station, 1 200 metres below its source within 15 km. Here, it now enters the study area as a relatively mature river, and continues by meandering its way across a relatively wide, flat-bottomed valley, so that 40 km further on, but only 17 km (directly) from Cobham, it has dropped only a further 140 metres.

The Polela runs approximately from west to east, and in the south its watershed boundary with the Umzimkulu catchment is relatively indistinct. To the north, however, a high ridge running approximately northwest to southeast provides a more prominent boundary with the Umkomozana.

At the point of its entry into the study area at Cobham the Polela river has a mountain catchment of some 40 km²; by the time it flows out, the figure is more like 175 km². However, much of the water that would naturally fill the Polela in summer is now trapped in farm dams that have been constructed on many of the tributary streams (FIG. 1.4).

1.5.3.3 GEOMORPHOLOGY, GEOLOGY AND SOILS

The geomorphology and geology of the study area, situated as it is only about 15 km from the high basaltic wall of the Drakensberg escarpment (but some 1 200 metres below it) is the product of erosive forces during Intermision V (King, 1972). This is the period between the penultimate and final stages of the process of active

tilting that has led to the creation of the Natal Monocline (King, op.cit.). The Polela river displays basin planation, in a landscape underlain with shales and sandstones of the Beaufort series. These shales and sandstones are interrupted by dolerite intrusions that define the Polela's watershed with adjacent catchments, and control detail in the landscape.

Derived from these underlying rock types are three principal soil types (Van der Eyk et al., 1969). All are generally ferralitic, heavily leached and of low natural fertility.

1 Red, apedal soils, low in bases

These deep, permeable and well-aggregated soils are derived from dolerite and underlying shales. They have good physical characteristics, which make them suitable for agriculture despite their low nutrient content and strongly acid character (Van der Eyk et al., op.cit.).

2 Yellow, apedal soils, low in bases

These soils are derived from shales and sandstones of the Beaufort series and are more acid, with lower base status and greater amounts of active aluminium than other soils in the study area.

3 Acid gley soils

These are wet soils of bottomland sites that predominantly consist of a moderately or strongly acid, often humic A1 horizon overlying firm gley. These are the soils of the wetlands that provide the reedbuck's natural habitat. They originate when a river or stream flattens its profile and deposits its load of suspended material. The process is accelerated when hygrophilous vegetation is established, as this then filters out further suspended matter.

1.5.3.4 BURNING

In accordance with normal agricultural practice, most natural grasslands in the study area are burned in late winter or early spring to promote early grazing and prevent the build-up of excessive amounts of moribund material. Indeed the grasslands of the highlands are sub-climax to low woody communities, and are fire-maintained. They are commonly burnt each year, although some farmers prefer to burn biennially such that only half the grasslands on a property are burnt in any one year.

Owing to the very real threat of runaway fires, landowners are

legally required to burn firebreaks 15 metres wide on either side of their boundaries and alongside any public road, in late autumn. These firebreaks commonly flush green during late winter (depending on the weather) and provide the first natural grazing, available not only to domestic stock, but also to game on the farm. It should be noted that with the exception of firebreaks, soil conservation legislation prevents widespread burning of natural grasslands until after the first significant spring rains, and outlaws any burning after the 30th of October.

1.5.4 The biotic environment

1.5.4.1 VEGETATION

The study area lies within the Highland Sourveld bioclimatic group (Phillips, 1973), and supports vegetation communities characteristic of this group. Originally, the whole area probably supported forest and scrub forest (Acocks, 1975), but very little of this still remains (TABLE 1.2), and the dominant vegetation type is today

TABLE 1.2 : Vegetation communities in the Extensive Study Area

COMMUNITY TYPE	PERCENTAGE OF STUDY AREA	DOMINANT SPECIES	DESCRIPTION
Vlei	9,5	Reeds (<i>Phragmites</i> sp.) Sedges (<i>Cyperus</i> sp.)	Seasonally flooded and perennial wetlands including old ox-bow lakes of the Polela
Annual pasture	14,5	Ryegrass (<i>Lolium multiflorum</i>) Oats (<i>Avena</i> sp.)	Planted annual pasture, that may or may not be under irrigation. Frost tolerant species of northern hemisphere origin
Permanent pasture	5,9	Kikuyu (<i>Pennisetum clandestinum</i>) Cocksfoot (<i>Dactylis glomerata</i>) Fescue (<i>Festuca arundinacea</i>) Weeping lovegrass (<i>Eragrostis curvula</i>)	Permanent planted pasture, normally replanted each 5-10 years. Certain species (Cocksfoot, Fescue) frost tolerant
Crop lands	9,0	Maize (<i>Zea mays</i>) Japanese Radish (<i>Brassica</i> sp.)	Crops grown as winter stock feed
Plantation	7,0	Gum (<i>Eucalyptus</i> sp.) Pine (<i>Pinus</i> sp.) Poplar (<i>Populus</i> sp.)	Plantations of exotic trees, grown as windbreaks and commercially on sloping lands and marginal river lands
Natural scrub	1,4	umChichi (<i>Leucosidea sericea</i>)	Low woody scrub, 1-5 metres tall, found in gulleys and along river banks
Bramble	1,5	Bramble (<i>Rubus</i> sp.)	Bramble, commonly occurring in small patches (±0,01ha) on disturbed land
Rank herbs	6,4		Field boundaries and old cultivated lands
Flat veld	14,2	Redgrass (<i>Themeda triandra</i>) Trident grass (<i>Alochaete hispida</i>)	Flat, open fire-maintained natural grasslands
Sloping veld	30,6	Redgrass (<i>Themeda triandra</i>) Trident grass (<i>Alochaete hispida</i>) Highveld protea (<i>Protea multibracteata</i>)	Hillsides, ridges and gulleys providing broken country without arable potential. Principally fire-maintained natural grasslands, with a few scattered patches of Protea savanna

Themeda-Apochaete fire-maintained grassland. Natural woody plant communities are found in the study area principally as Leucosidea scrub along parts of the Polela river (representing 1,4 % of the total area - TABLE 1.2), and as a few isolated patches of Protea savanna on mountain slopes.

From TABLE 1.2, which summarises the vegetation communities of the study area, it can be seen that 44,3 % of the area is, or has recently been cultivated. The remainder still supports natural grassland communities, although trampling and selective grazing by cattle in many parts has favoured Eragrostis plana, a species characteristic of degraded veld.

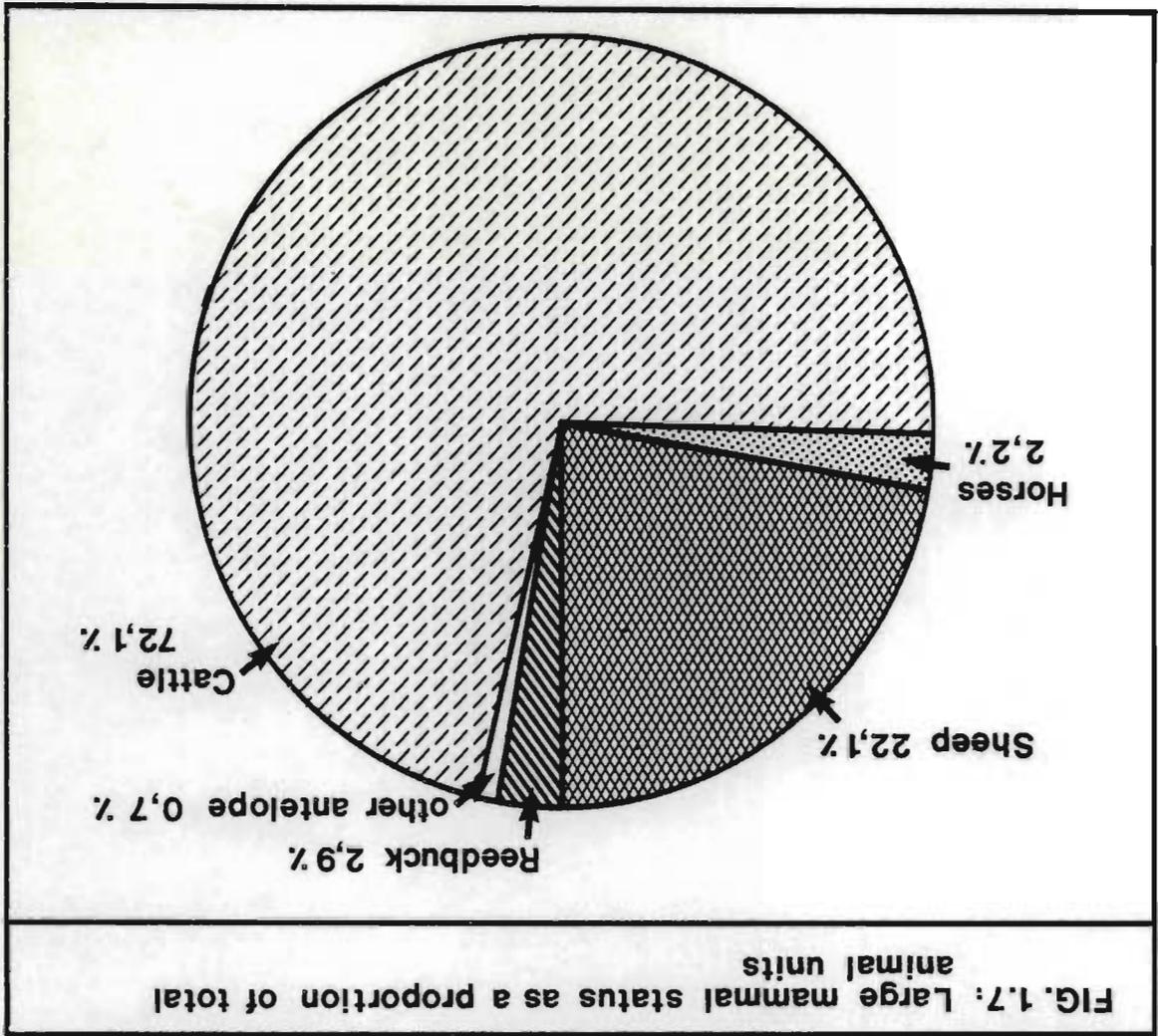
1.5.4.2 LARGE MAMMAL STATUS

As the study area is primarily a farming area, domestic stock are the principal large mammals (FIG.1.7), which together represent 96,4 % of total animal units (AU - Mentis and Duke, 1976). Their numbers, ascertained by personal interview with the landowners concerned, as at July 1982, were:

Cattle	5 000	animal units
Sheep	1 540	animal units
Horses	150	animal units

In addition, relatively small numbers of various antelope occur probably not exceeding the following personal estimates:

Eland	10	animal units	(occasional visitors)
Common reedbuck	200	animal units	(resident)
Grey rhebuck	10	animal units	(visitor/resident)
Oribi	1	animal unit	(visitor/resident)
Blesbok	1	animal unit	(introduced resident)
Grey duiker	30	animal units	(resident)



PART ONE: ECOLOGY

CHAPTER TWO

DISTRIBUTION AND STATUS

2.1 INTRODUCTION

2.1.1 Definitions, and purpose of determining distribution and status

The distribution of an animal is its pattern of occurrence over a given area, and its status defined as its potential for long-term survival. Status is governed not only by population density but by the many factors that control a population's rate of increase: these are discussed in CHAPTER NINE.

Monitoring distribution will always be an essential part of conservation management, because without it the effects of applied management practices are unknown. Ideally any wildlife management programme should begin with an evaluation of the distribution of the species, and this information should be continuously updated to assess the effects of management practices as they are applied.

2.1.2 Methods of determining distribution and status

On the provincial, national or continental scale it is usually not practical to assess animal distributions by any of the standard methods of census described in CHAPTER THREE. Instead the wildlife worker must depend on information gathered or supplied from other sources. Possible sources of information include:

- 1 publications referring to the occurrence of a particular species at a particular location;
- 2 records submitted by amateur observers;
- 3 records submitted by professional officers of wildlife organisations;
- 4 records procured from residents of a particular area or areas on request (i.e. questionnaire surveys).

Distribution information derived from sources 1, 2 and 3 above is likely to show at least some degree of bias dependent upon the number and distribution of observers. On the other hand, careful survey design in an investigation of type 4 will ensure less bias, although this may be

achieved at the expense of accuracy.

In questionnaire surveys the following sampling options are available:

- 1 random sampling, in which sampling is based on the 'laws of chance';
- 2 systematic sampling, in which sampling is done in a regular manner;
- 3 stratified sampling, in which sampling intensity, whether random or systematic, is zoned for different areas;
- 4 complete enumerative survey, in which the entire area is covered.

Methods of evaluating the status of animal populations are reviewed in CHAPTER NINE. One aspect in the evaluation of status, which will be considered in this chapter, is apparent population trend.

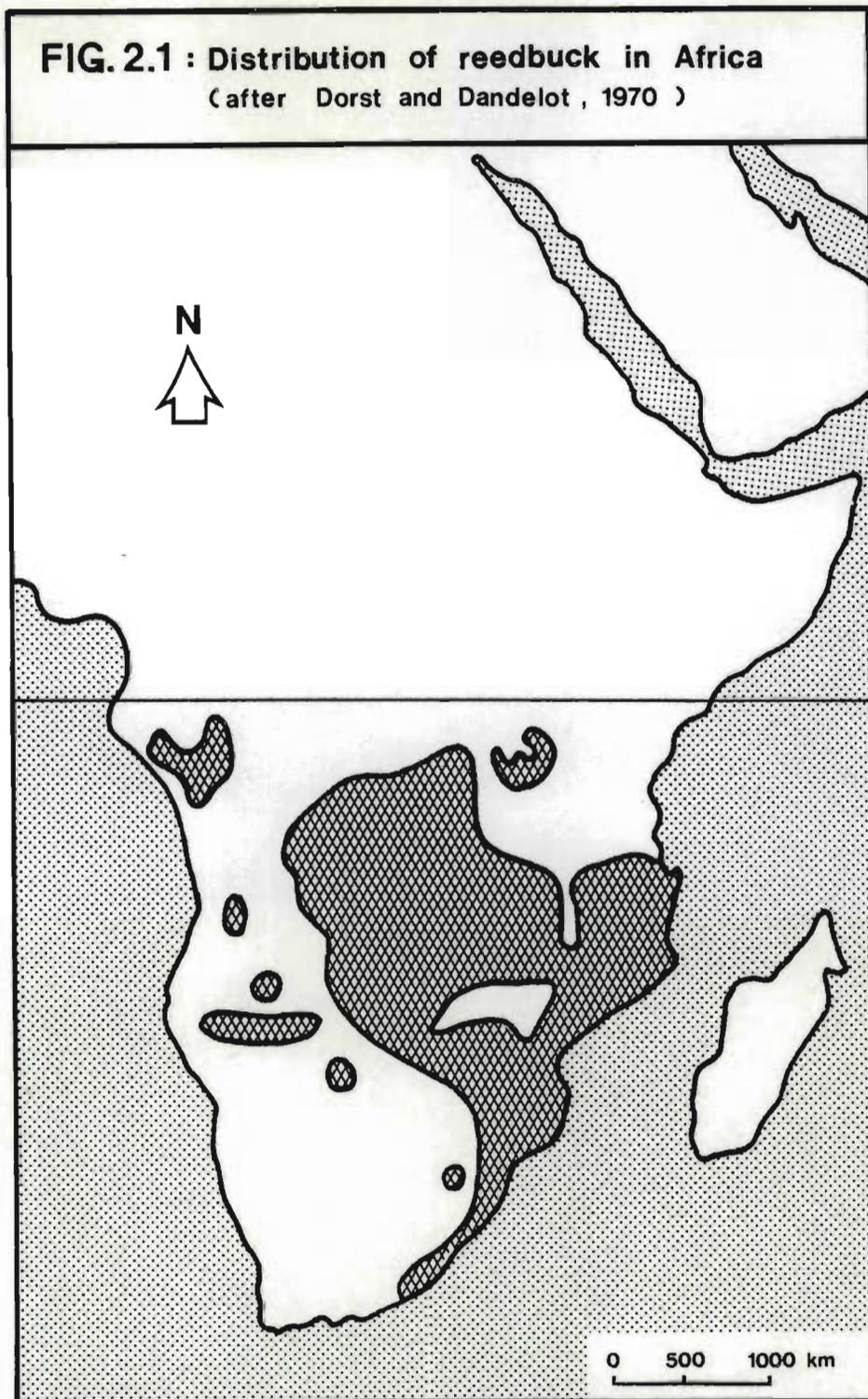
2.1.3 Previous work, and the state of existing knowledge of the distribution and status of reedbuck

Numerous authors report on the occurrence and distribution of reedbuck, and a synthesis of available information is given in the form of distribution maps in works of a general nature such as Roberts (1951), Sidney (1965), Du Plessis (1969), Dorst and Dandelot (1970) and Zaloumis and Cross (1974).

Recently published data on wildlife distributions considered on a regional basis in southern Africa include Joubert and Mostert (1975) for Namibia, Mentis (1974) for Natal, Rautenbach (1978) for Transvaal, and Lloyd and Millar (in press) for the Cape Province. All existing distribution information is descriptive, and no attempt has been made to describe what combination of factors makes the environment suitable for a particular species.

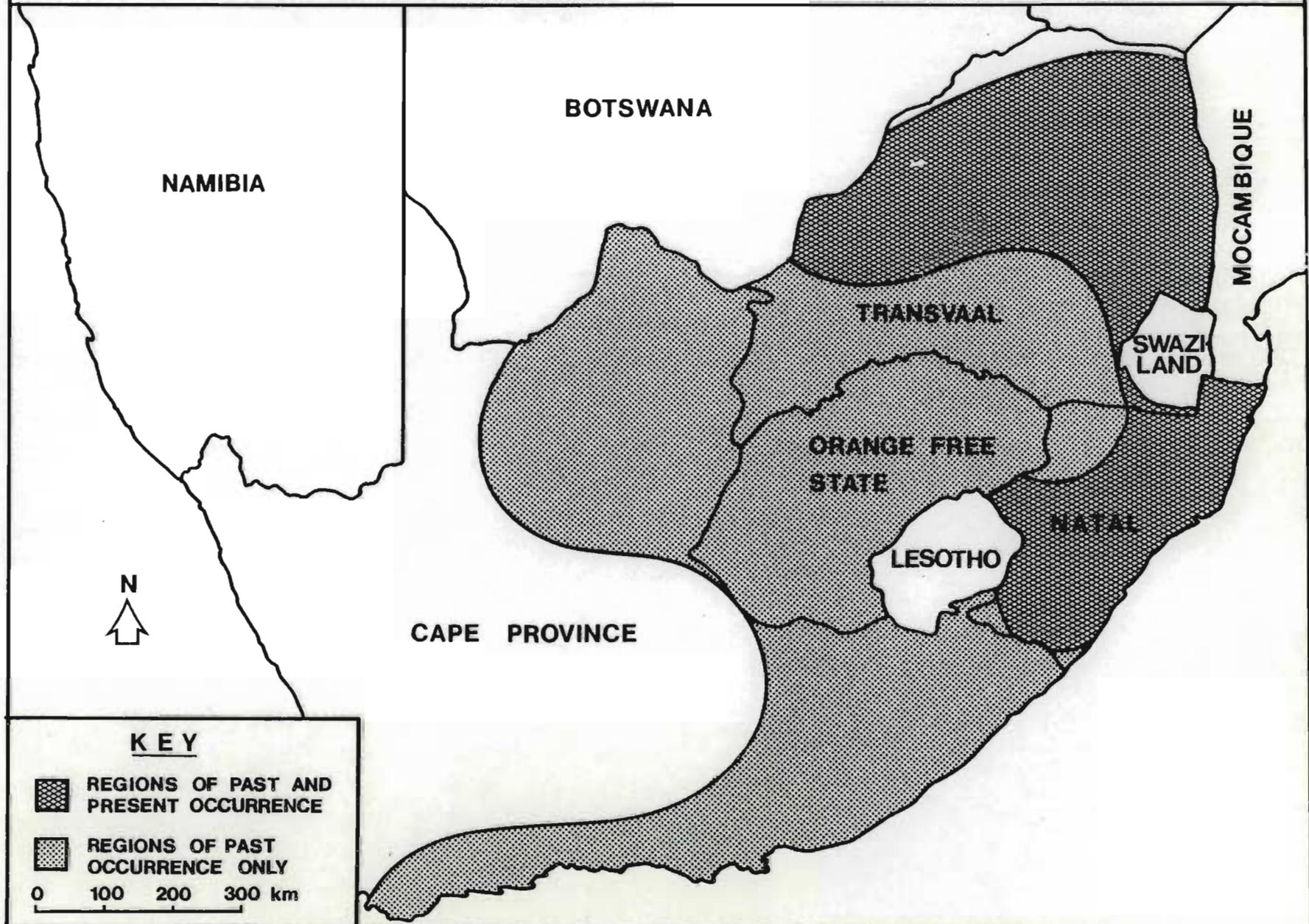
In Africa the southern reedbuck is widely distributed, occurring in Angola, Botswana, Congo, Gabon, Malawi, Mocambique, Namibia, Tanzania, Swaziland, Zambia, Zimbabwe and parts of South Africa (FIG. 2.1). To the north of South Africa its conservation status is described as 'apparently safe' in Angola, Botswana, Mocambique, Malawi and Zimbabwe (Bothma, 1975), but 'rare' in Swaziland and 'endangered' in Namibia (Joubert and Mostert, 1975).

Within South Africa, Von Richter (1974) considers the status of reedbuck as endangered, and Zaloumis and Cross (1974) point out that the species has disappeared from 80 % of its former range (FIG. 2.2). In the list of endangered large mammals compiled for the South African Red Data Book, the species is described as 'rare, common locally in parts of Zululand' (Skinner *et al.*, 1978). The reedbuck has recently disappeared from the Cape Province (Stuart, 1981) and survives in the Orange Free State only in the Golden Gate Highland National Park from introduced stock (van Zyl,



cited by Venter, 1979). Numbers appear to be increasing in the Kruger National Park (Brynard and Pienaar, 1960; Pienaar, 1963), and in the rest of the Transvaal the species is safeguarded in game reserves. In Natal the status of reedbuck is secure (Vincent, 1962; Dixon, 1964) with healthy populations in the coastal and low-lying regions of northern Natal, and the midland and upland regions south of 29°S (Mentis, 1974). In contrast to the situation in the Transvaal, where reedbuck numbers on farmland are declining and can be expected to continue doing so (Du Plessis, 1976), the species appears to be thriving on farmland in the midland and upland regions of Natal.

FIG 2.2: Past and present distribution in South Africa (after Du Plessis, 1969 ; Rautenbach, 1982 ; Howard and Marchant, in prep.)



2.1.4 Objectives of this study with respect to distribution and status

It is a common failing of distribution information that, because of the scale at which species distributions are mapped, and the fact that the basic data often lack detailed habitat descriptions, ecological interpretations are impossible. Such distribution information fulfils the primary requirement of providing a basis for monitoring the future decline or expansion of a species range, but it can neither explain the ecological reasons for the observed distribution, nor can it attempt to predict possible changes or identify unoccupied areas that are likely to provide suitable habitat for particular species. The objectives of this study are to fulfil the need for a definitive ecological interpretation of the distribution of common reedbuck on private land in Natal. More specifically the objectives are:

- 1 to document the present distribution of common reedbuck on private land in Natal at a finer, more meaningful scale than has hitherto been attempted;
- 2 to identify environmental factors that correlate with reedbuck density;
- 3 in view of the factors identified in 2 that might affect the status of reedbuck on farmland, to identify areas of privately-owned rural land in Natal that are potentially suitable for reedbuck;
- 4 to consider the relative advantages of natural animal dispersal and translocation in improving the conservation status of reedbuck on farmland in Natal.

Of these objectives, only the first is considered in this chapter. Objective 2 is considered in CHAPTER FIVE, 3 in CHAPTER NINE, and 4 in APPENDIX B, a short paper submitted to The Lammergeyer.

2.2 METHODS

2.2.1 Gamequest : a questionnaire survey

The most comprehensive and up-to-date information available on the distribution of reedbuck in Natal is provided by Mentis (1974), who used Natal Parks Board farm game records, and reports from officers of the Board as his data source. As Mentis (1974) himself points out, the absence of a record from a particular locality does not necessarily imply the absence of that species, since some areas of Natal are rarely visited by Natal Parks Board officers. A need was thus identified to survey systematically over the entire province.

There are approximately 8 700 farming units in Natal, and a complete enumerative survey of these would be beyond the scope of this study. A sample questionnaire was considered to be the most feasible method of obtaining the required data. In order to derive the maximum benefit from the questionnaire survey, it was decided that it should be designed in such a way as to include all naturally occurring species of antelope, and should request relevant information on available habitat types, farming practices and attitudes of landowners to game on their farms. This information, collected from a random sample of farmers, could then be used to evaluate bias in the 'Farm Detail Sheets' that are routinely collected by Natal Parks Board extension (zone) officers.

The following procedure was adopted in the development and implementation of the survey:

- 1 A draft questionnaire was drawn up and circulated to Natal Parks Board and University staff for comment. Copies were taken to all farmers in the extensive study area, who were asked to complete the form and return it with appropriate comments.
- 2 In view of comments received, a revised questionnaire was drawn up and printed in English and Afrikaans (APPENDIX A).
- 3 A sample of farmers was considered, taking one at random from within each of 345 eighth degree square compartments systematically covering privately-owned land in Natal. To qualify for inclusion in the sample farms had to be in excess of 200 ha (farms smaller than this were considered unlikely to be representative of the range of antelope and habitat types characteristic of that compartment), and more than half the farm had to be in the compartment. Addresses were obtained from the Department of Agriculture, from the list of farmers who had taken part in AGRIQUEST, the questionnaire survey of farming in Natal (Fotheringham, 1981).
- 4 Questionnaires were distributed in August 1981, with a stamped addressed envelope for the return of the completed form, and a covering letter. The survey was referred to as GAMEQUEST.
- 5 Reminder letters were sent out to those who had not replied after three weeks and again after six weeks; this period conforming to that prescribed by Babbie (1973). At this stage Natal Parks Board extension (zone) officers were also asked to telephone non-participants to enquire after the form, and farmers who did not wish to participate were invited to send the form back uncompleted.
- 6 Unfortunately zone officer involvement did not significantly improve

the level of return on the initial questionnaire distribution, and a second batch of questionnaires was distributed to new participants through zone officers.

- 7 From the completed forms a reedbuck distribution map was plotted, showing within each compartment presence or absence, the year when animals were last seen on the farm (if appropriate), and whether the population appears to be increasing, stable or decreasing.
- 8 Natal Parks Board farm detail sheets were used to plot a comparable distribution map for reedbuck. Such sheets have been routinely collected by inland zone officers over a period of about ten years, and contain similar information to that requested in the Gamequest survey.
- 9 The location of farms participating in Gamequest was plotted on a 1 : 500 000 scale map showing Phillips' (1973) bioclimatic subregions, and apparent population trend was considered for each bioclimatic group: the results of this analysis follow in CHAPTER FIVE.

2.2.2 Evaluation of translocation as a conservation management tool

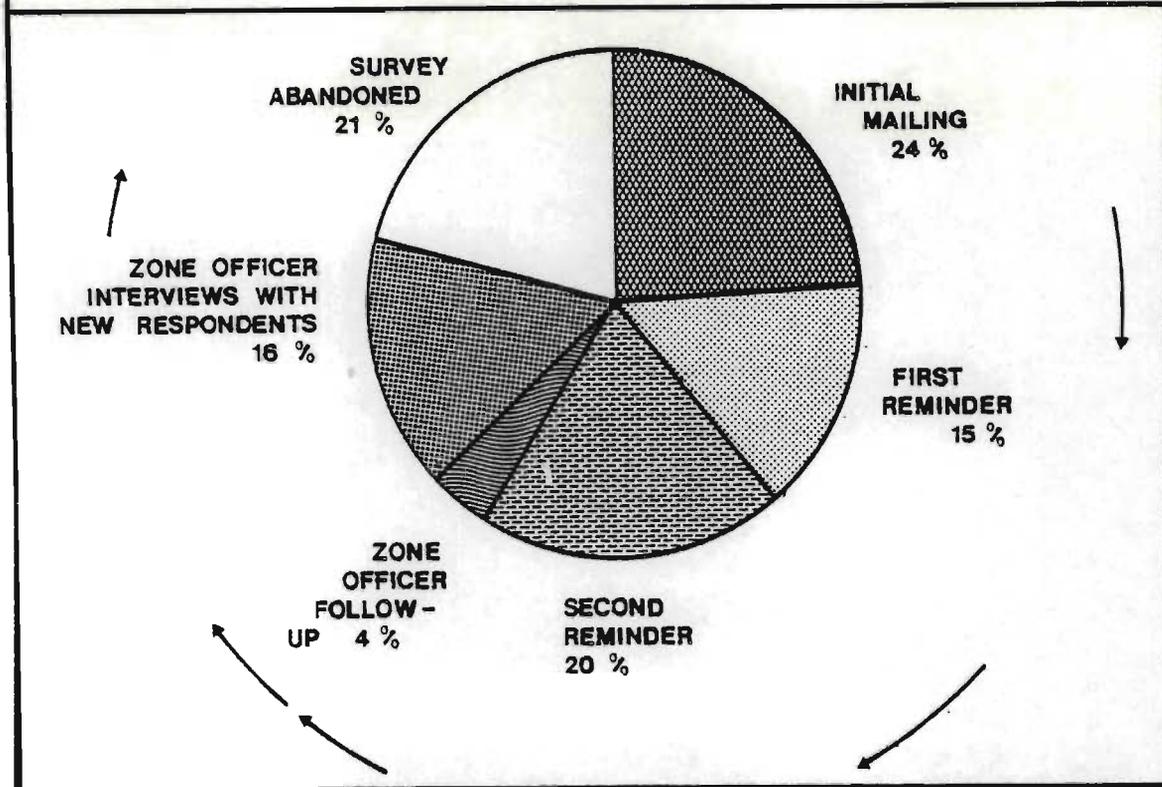
The value of translocation as a means of extending the present distribution of reedbuck was investigated by reviewing current progress with the movement of animals from the Eastern Shores of Lake St. Lucia. Fifteen hundred reedbuck were moved live from St. Lucia over the period 1978 to 1982, to destinations in all four provinces of South Africa. A questionnaire was sent to all recipient landowners to assess the success of the translocations, details of which are given in APPENDIX B.

Pertinent to the success of translocations over long distances is the genetic suitability of the introduced animals to their new environment. A simple comparison was made between the genetic make-up of reedbuck from St. Lucia with those from the extensive study area in the Natal Highlands, by examination of blood serum protein differences. This aspect has been written up as a separate paper, included as APPENDIX C.

2.3 RESULTS

The proportion of the 345 landowners responding to the Gamequest survey request at different stages in the survey is illustrated in FIG. 2.3. Seventy four percent of the initial batch of questionnaires were returned, including 11 % returned blank. Thus, useful completed forms were received from 63 % of the initial sample.

FIG. 23: The proportion of GAMEQUEST respondents participating at different stages in the survey



The second sample of questionnaires, distributed to Natal Parks Board zone officers for completion by personal interview with new respondents, achieved a 43 % response. This left 21 % of the potential sample unsurveyed.

Over the five year period from 1978 to 1982 Natal Parks Board zone officers completed farm detail sheets for a total of 913 properties throughout Natal. The distribution of sampling intensity is illustrated in FIG. 2.4, by considering the proportion of privately-owned land that was surveyed in each quarter degree square. In 42 % of the quarter degree squares less than 10 % of privately-owned land was surveyed. On an area basis, sampling was concentrated particularly in the Zululand lowveld.

FIG. 2.5 illustrates the present distribution of reedbuck on privately-owned land in Natal, as determined by means of the Gamequest survey, and NPB farm records. Reedbuck are widely distributed in Zululand as far south as 28°45'S and as far west as 31°15'E. They appear to be declining in the coastal areas, but are increasing inland. They are also widely distributed throughout the highlands and midlands between 29°00' and 30°30'S and east as far as 31°00'E. Populations in this area appear to be generally stable or increasing. In other parts of Natal there are few records of reedbuck occurrence, and those there are probably represent introduced animals (APPENDIX B). There are two records of extinctions in northern Natal in 1933 and 1940, and three in the coastal areas of Zululand during

FIG.2.4: The proportion of land surveyed for NPB farm detail sheets in each quarter degree square, over the five year period from 1978 to 1982

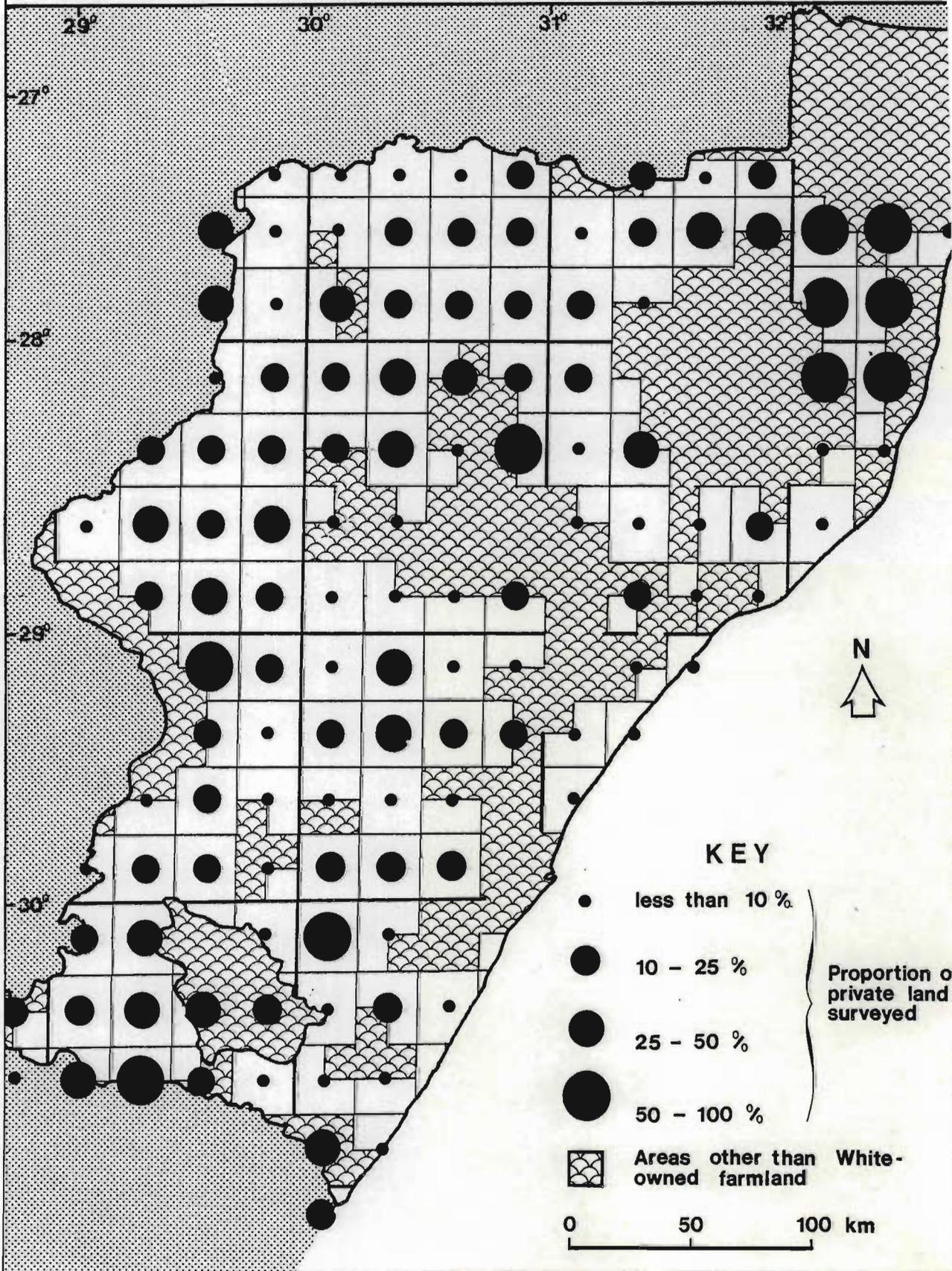
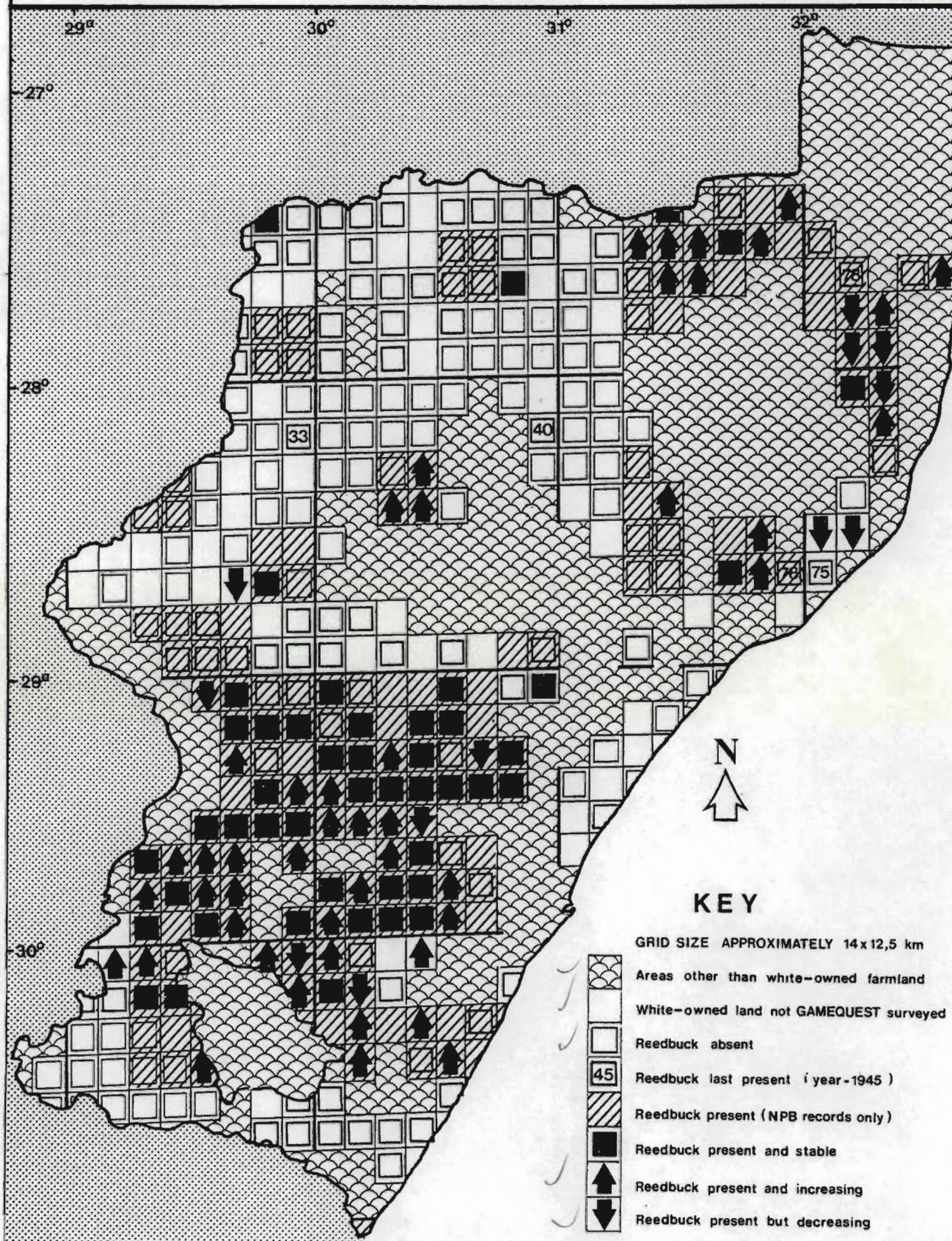


FIG.2.5 : Reedbuck distribution on farmland in Natal



the 1970's.

2.4 DISCUSSION

The purpose of this chapter is to document the present distribution of reedbuck on farmland in Natal, so that changes in distribution can be identified in future. It is therefore pertinent to consider how much confidence can be placed in the accuracy of the derived distribution map.

As far as the NPB farm records are concerned, FIG. 2.4 demonstrates a high degree of regional sampling bias, favouring the Zululand lowveld - a species rich area - at the expense of coverage in other areas such as the extreme north-eastern parts of the province, the coastal lowlands, and the midlands. Nevertheless, over the province as a whole, more than three times as many farms were surveyed by this method than by Gamequest, and on this basis we might expect a more thorough coverage. In practice, we find that reedbuck are recorded in seven quarter degree squares exclusive to Gamequest, and in eleven exclusive to NPB records, and we must conclude that the greater number of farms surveyed by NPB officers does not appear to have significantly improved on the more systematic coverage afforded by the Gamequest survey. Altogether a mean of 14 farms was sampled in each quarter degree square (70 000 hectares), and it is considered that this sampling intensity should be sufficient to identify reliably areas of reedbuck occurrence, except where the species is rare.

Babbie (1973) considers a 50 % return on questionnaire surveys to be 'good', and in this respect Gamequest was successful in eliciting such a full response. The first reminder letter stressed to potential respondents that the questionnaire was part of a sample survey, and that the addressee's farm had been especially selected for inclusion on the basis of its size and locality. The second 'threatened' the addressee that an enquiry from his local NPB zone officer would be forthcoming if the questionnaire was not returned. The effect of these two reminders on the overall response is clearly illustrated in FIG. 2.3, from which it is apparent that useful replies were increased from 24 % after the initial mailing to 59 % after the second reminder. Lloyd (pers. comm.) achieved a 41 % response to an extensive questionnaire survey of mammals in the Cape Province without any reminders, Boshoff (1980) achieved 48,4 % with one reminder in a bird-of-prey survey in the Cape, and Lloyd (pers. comm.) achieved an 80 % response from farmers associations for a survey of baboons in the Cape in which two reminders were used. By comparison with these surveys the response to Gamequest was, perhaps, a little poor, especially in the initial stage. However this is not surprising in view of the heavy 'response burden' (Corbin, 1977; Filion, 1981) of this rather complex questionnaire.

The importance of question wording to the success of questionnaire surveys is widely recognised (Filion, 1981), and in this respect Lloyd (pers. comm.) improved response to his mammal survey from 35 % to 48 % simply by providing alternative synonyms and descriptive notes, and by reminding readers that the alternative official language was overleaf. In Gamequest, ambiguities in question wording were ironed-out at the pilot study stage. There was some apparent confusion in the identification of certain antelope species (especially duikers: Howard and Marchant, in prep.) that might have been avoided had notes been provided, but only at the expense of increased 'response burden'.

The Gamequest respondents were not a truly random sample, but the recognised biases were considered unlikely to affect the overall survey results. The most significant bias occurred in the selection of respondents, whose addresses were acquired from the Department of Agriculture, from a list of known questionnaire participants. From the list, only landowners with comparatively large land holdings (>200 ha) were considered. Boshoff (1980), in a bird-of-prey survey, found that questionnaire response was highest amongst:

- 1 English-speaking respondents, compared with Afrikaans-speaking;
- 2 respondents aged 35 - 59 years, compared with older and younger classes;
- 3 owners of large land holdings.

The most important purpose of distribution information is to monitor change in species' ranges. There are two previous descriptions of reedbuck distribution in Natal, made in 1962 (Vincent) and 1974 (Mentis), but in neither case were there sufficient data to provide definitive descriptions, allowing subsequent rigorous comparison. Vincent (1962) describes the reedbuck as being 'ubiquitous throughout the province', whereas Mentis (1974) had no records of occurrence in northeastern Natal to the north of 28°30'S and east of 31°00'E. Today, the distribution appears little changed, except that reintroductions have been made in several parts of northern Natal. The apparent decline in reedbuck populations in the Zululand coastal regions is noteworthy, and probably related to loss of habitat through extended cultivation (CHAPTER FIVE).

The importance of long-term monitoring programmes for animal species and habitat types cannot be overemphasised, and a questionnaire survey similar to Gamequest could prove to be the most cost-effective method of data collection in such a programme. Priority should then be given to developing systems of computerised data-storage, so that the information is readily available to potential users (Boshoff et al., 1978).

CHAPTER THREE

POPULATION MONITORING AND DYNAMICS

3.1 INTRODUCTION

3.1.1 Definitions, and purpose of monitoring animal abundance and other population parameters

At any given time, a population is composed of a finite number of individuals, and an accurate knowledge of population size, or animal abundance, is often of key importance in management decisions. When data from comparable counts are available over a time interval population trend can be determined, and may highlight the need to conserve, manage, or control the population under investigation. However, it has been cautioned (Caughley, 1977) that simple estimates of abundance have no intrinsic value, and should not be considered ends in themselves. Populations are dynamic; and even within those that are numerically stable the factors governing recruitment and loss - reproduction, movement and mortality - may be continually changing. These processes then, govern the population's structure - its unique birth and death rate, age and sex structure, size, and productivity. Examination of population structure often leads to an understanding of the causes and processes underlying population change, or governing stability. From such an understanding it becomes possible to predict and manipulate populations.

3.1.2 Methods of population monitoring

Because animal populations are not stable in time and space, sound management depends on the development of methods to monitor them. Grimsdell (1977) identifies the three main components in animal population monitoring as numbers, distributions and condition plus dynamics.

Monitoring animal numbers is the subject of an extensive literature, and many different methods of counting animals or estimating animal numbers have been developed. Aerial census methods (Norton-Griffiths, 1978) are in common use where the terrain is suitable and the cost justified. Otherwise any of a number of ground census methods are adopted, which may attempt a total search of an area (Sinclair, 1973) or sample through different habitats usually along a transect (Anderson *et al.*, 1979). The various ground and air census methods available for ungulate population monitoring

have recently been reviewed by Collinson (1982). For species with a stable social structure it is often possible to estimate numbers fairly accurately from a detailed knowledge of the composition and movements of herds or groups (Melton, 1978), and where a large proportion of a population can be marked for individual recognition (Anderson, 1962) a Petersen estimate may also be used. Other methods are based on indirect evidence, such as pellets (Neff, 1968) and footprints (Tyson, 1950). Some methods necessarily sample only a part of the study area (e.g. transects), while others (e.g. aerial census) can be either total or sample counts. Choice of methods depends not only on the behaviour and type of animal under study, but also on the purpose of the census. If population trends only are investigated then a precise estimate, within narrow confidence limits, is of more value than a more accurate one, which, although less biased, has wide confidence limits (Grimsdell, 1977).

Distributions are also an important part of animal population monitoring, and this subject is given more detailed consideration in CHAPTER TWO and CHAPTER FIVE. In the context of this chapter the most important aspect of animal distributions is the way in which movement patterns affect recruitment and loss through immigration and emigration.

The 'condition' of the individuals that go to make up an animal population is intimately linked with that population's dynamics, because the general level of 'well-being' (or 'condition') of each individual affects its chances of living or dying (Caughley, 1971; Hanks, 1981), and hence the demography of the population. The concept of 'condition' is often ill-defined, and although it can be indexed for any individual by the level of fat reserves, aspects of body growth, and various other physiological and reproductive criteria, a problem arises because these indices are specific for sex and age, and it is therefore difficult to express the 'mean condition' of a population. Caughley (1971) proposes that the condition of a population should be expressed by a single statistic that weighs up and combines the vigour of each sex and age class in the population. He called this statistic r_s , the survival-fecundity rate of increase, that is calculated from age-specific survival and fecundity tables. Hanks (1981) argues the inadequacy of this statistic as a measure of demographic vigour per se and stresses the importance of other parameters; these are discussed at length in CHAPTER FOUR.

The methods used in an assessment of demographic vigour as defined by Caughley, must provide the following data:

- 1 mortality rates as a function of age and sex;
- 2 fecundity rates as a function of age.

Mortality rates are usually assessed indirectly by looking at the

frequencies of animals in different age classes that have either died of natural causes (time-specific life table data), or are 'standing' in the population (age-specific life table data), or by following the fate of a large number of individuals of known age. Fecundity rates can be calculated from the pregnancy rates of culled or captured adult females of known age. Clearly implicit in the use of these techniques is a reliable method of age determination.

3.1.3 Previous work on the population dynamics of members of the Reduncinae

Within the sub-family Reduncinae work on population monitoring is available for the waterbuck (Kobus ellipsiplymnus) (Spinage, 1967; Melton, 1978), kob (Adenota kob thomasi) (Modha and Eltringham, 1976), lechwe (Kobus leche) (Robinette and Child, 1964; Sayer and Van Lavieren, 1974; Grimsdell and Bell, 1972, 1975; Williamson, 1975), and common reedbuck (Ferrar and Kerr, 1971; Venter, 1979).

Populations of the common reedbuck, from widely separated areas of the species range, have been shown capable of rapid population increases (Ferrar and Kerr, 1971; Venter, 1979; Bell, pers. comm.) and in one case (Ferrar and Kerr, op.cit.) a crash followed. Deane (1966) has documented the impact of community succession on a declining reedbuck population in 'the corridor', Zululand.

In Zimbabwe and South Africa the adult sex ratios have been biased significantly in favour of females (Dasmann and Mossman, 1962; Venter, 1979). Venter (op.cit.) concluded that a disproportionately large number of young adult males of between three and four years of age were dying, probably due to intraspecific fighting, and it is at this age that Jungius (1971a) estimates young males first compete successfully for territories.

Venter (1979) estimated infant mortality at approximately 52 % and Mitchell et al. (1965) also record high juvenile mortality. In Zambia, wild dog (Lycaon pictus) and leopard (Panthera pardus) are the main predators (Mitchell et al., 1965), whilst in Umfolozi Game Reserve over 70 % of total predation can be attributed to leopard and cheetah (Acinonyx jubatus) (Venter, 1979).

3.1.4 Purpose of monitoring abundance and other population parameters in this study

The purpose of population studies in the context of this study is broadly:

- 1 to develop methods of animal census that are as precise and accurate as possible, which can be used by inexperienced personnel;

- 2 to relate observed grazing pressures, and patterns of habitat use to a measure of animal abundance;
- 3 to monitor trend in the population under intensive study;
- 4 to investigate population age and sex structure and demography, towards an understanding of the factors underlying population change;
- 5 to attempt to predict probable population changes in future under different management programmes.

3.2 METHODS

3.2.1 Census techniques

Choice of census methods was largely determined by the need for a technique that can be applied by laymen, on comparatively small land holdings. This requirement immediately precludes any form of aerial count and favours simple methods of ground coverage on foot or from a vehicle. The census methods chosen as potentially suitable for use by farmers and unqualified game rangers in assessing reedbuck numbers on farms, which were tested in this study, are as follows:

3.2.1.1 TOTAL COUNTS

The intensive study area was subdivided into four counting blocks (FIG. 3.1), each of which was covered on foot shortly after dawn and shortly before dusk once each month. Each block took approximately two and a half to three hours to cover, and since the object was to sight every animal within the block, special attention was paid to areas of cover in order to flush concealed animals. A fixed route was walked and all counting blocks included at least one vantage point from which the entire block was scanned using 8x30 binoculars and a 30x75 telescope. As most sightings were made from vantage points, the count was timed such that the observer was at a vantage point at sunrise/sunset.

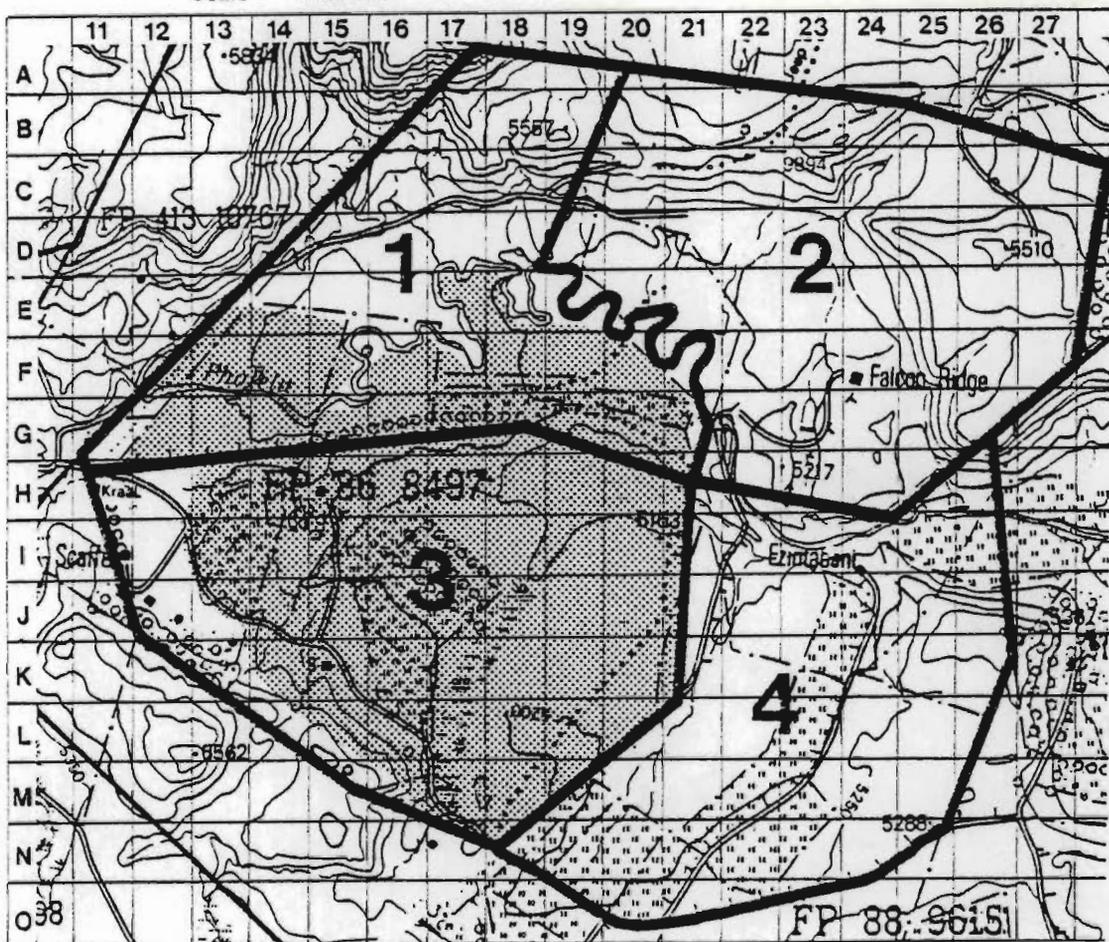
3.2.1.2 NIGHT PASTURE COUNTS

The central cultivated area of the intensive study area (FIG. 3.1) was searched three times each month shortly after dusk using a hand-held spotlamp operated from the back of a truck. Two people were required, the spotlamp operator/spotter and the driver/spotter/recorder. All habitats within the central area were given a total search, and the location and habitat type occupied by

each animal sighted was recorded, to assess whether simple pasture counts provide a usable index of animal abundance, suitable for management purposes.

FIG. 3.1 : The Intensive Study Area, showing the location of the four counting blocks, and the night census area (shaded)

Scale : 1 : 25 000



3.2.1.3 PETERSEN ESTIMATES

Seventy reedbuck were marked within the intensive study area for individual recognition (CHAPTER SIX), enabling the calculation of a Petersen estimate (Caughley, 1977), based on the ratio of marked to unmarked animals seen during subsequent counts. A monthly reassessment of the number of marked animals still 'in circulation' was made, and a mean estimate was calculated from Petersen estimates derived from dawn count, dusk count and three separate night pasture counts each month. The technique was believed to be particularly appropriate in this study because, when the animals congregate to feed on insular food resources in winter they are probably mixing freely. In addition, since up to about 35 % of the animals within the intensive study area were marked, the limitations of a small marked sample (Anderson, 1962; Strandgaard, 1967) were obviated.

3.2.1.4 CENSUS EVALUATION

In order to ascertain the degree of repeatability obtainable with these census techniques, the effect of the following variables was examined:

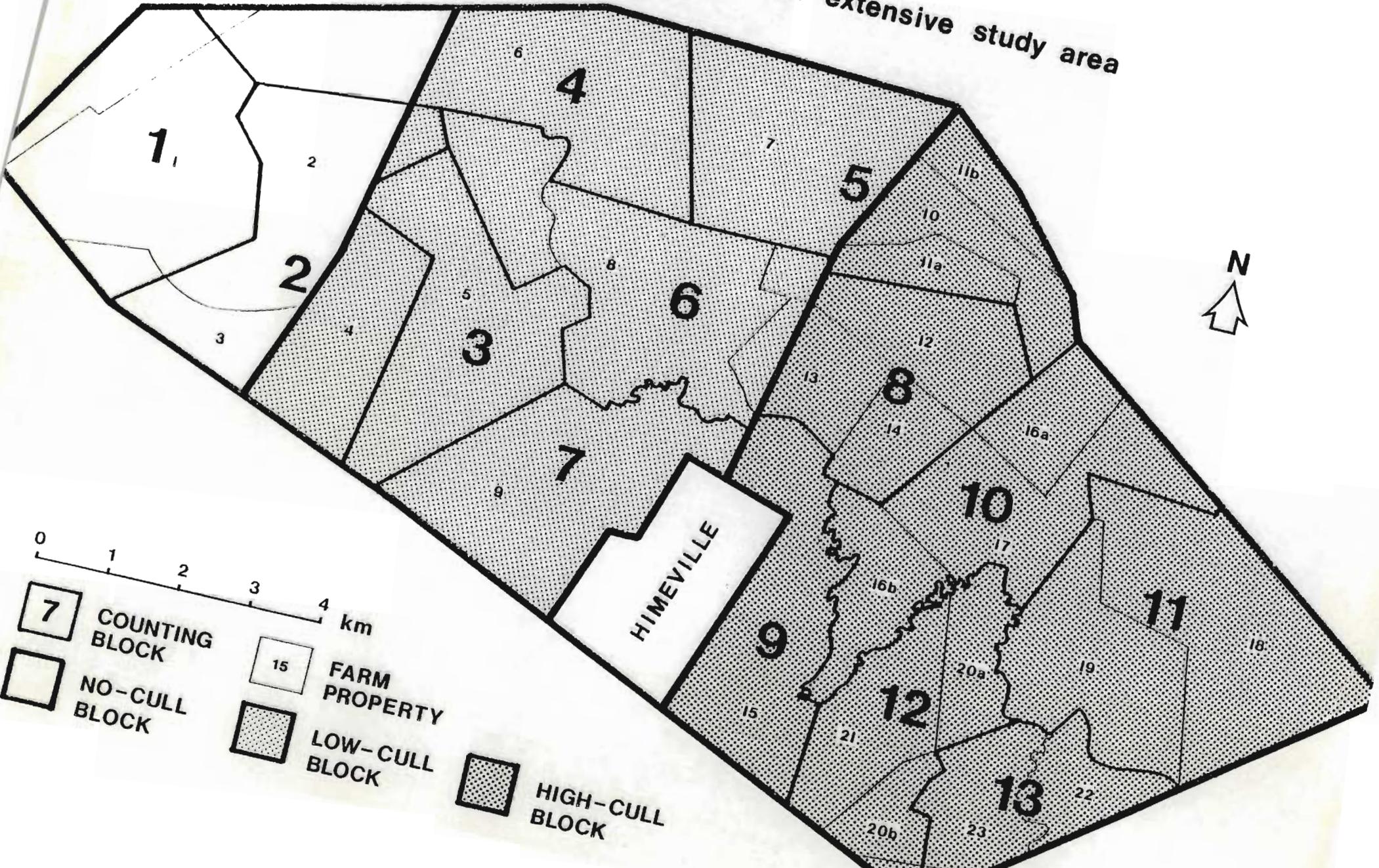
- 1 season: counts were made within the intensive study area each month of the year;
- 2 time: night pasture counts were conducted at different times of the evening; starting at nightfall, one and a half hours after nightfall, and three hours after nightfall;
- 3 phase of moon: the results of night pasture counts were examined in relation to the phase of the moon;
- 4 weather: weather conditions were recorded at the end of each count. Cloud cover was scored on an eight point scale, wind speed on the ten-point Beaufort scale, and shade temperature in degrees Celsius. For between-season comparisons temperature records were 'standardised' by subtracting the mean temperature for that month, so that the standardised temperature score became an expression of whether the particular day was above or below average for the time of the year.

In the analysis of the data, a 'count index' was derived by dividing the number of reedbuck observed and counted, by the number that would have been expected in that particular counting block. The expected value for dawn and dusk counts was calculated as the mean number counted in that particular block over the three month period including the previous and subsequent months. In the case of night pasture counts the expected value for any particular month was the mean of the three counts made during that month. Thus a 'count index' score of unity resulted when the number of reedbuck counted was as expected, greater than unity when more than expected were counted, and less when fewer were counted. The strength of correlations between the count index score and cloud cover, wind speed, and standardised temperature scores was examined, to see whether any clear relationships existed that may be helpful in deciding upon optimum weather conditions for censusing.

3.2.2 Population trend and manipulation

The 10 500 hectare extensive study area was subdivided into 13 counting blocks (FIG. 3.2), each of which could be adequately covered and searched with a spotlamp in about three hours. Some of these blocks comprised single properties, while others were made up of several smaller ones. Each of these counting blocks was searched in the manner described in SECTION 3.2.1.2 (Night Pasture Counts) once each month in June, July and August 1981, again in February 1982, and then subsequently in July 1982 and July

divisions in the extensive study area



7 COUNTING BLOCK

□ NO-CULL BLOCK

15 FARM PROPERTY

▨ LOW-CULL BLOCK

▩ HIGH-CULL BLOCK

1983. The 1981 series of counts was intended to give some indication of repeatability over a wide range of different farms during winter. The February 1982 count was made primarily to examine patterns of distribution and habitat use in summer, compared with winter (CHAPTER FIVE), and the July 1982 and 1983 counts were made to examine population trend.

From the project's inception one end of the extensive study area (the 'intensive study area') was designated a no-cull block, and no artificial removal of reedbeek (except a few capture mortalities) occurred on the three properties concerned. By contrast, approximately 10 % of the number of reedbeek counted at night were shot on most farms in the rest of the study area during the 1981-1982 growing season. Subsequently, the extensive study area was further sub-divided into a high-cull and a low-cull block (FIG. 3.2), and during the 1982-1983 growing season approximately 20 % of the animals counted were removed from the former, and 10 % from the latter.

3.2.3 Population parameters

3.2.3.1 BIRTH RATES

Birth rates were calculated by two independent methods. The first of these was the examination of reproductive condition in a sample of 91 female reedbeek shot, at random, on farmlands in Underberg district (CHAPTER FOUR). The age of each animal was estimated by examination of the teeth (APPENDIX D), such that a pregnancy rate could be calculated for animals in the sub-adult, prime and post-prime adult age classes.

The second method was the close monitoring of births to marked adult females observed over periods long enough to cover at least one inter-lambing interval. A mean inter-lambing interval was calculated.

3.2.3.2 DEATH RATES

(a) First year mortality

Mortality amongst the youngest age group was assessed by observation of marked adult females and their offspring. Youngsters were considered successfully weaned if they were seen accompanying their mothers up to a minimum estimated age of six months (APPENDIX D). The number successfully weaned was compared with the number of calculated births (SECTION 3.2.3.1), to give an estimate of survival.

Adult female : juvenile ratios observed in the field are commonly

used as a measure of infant survival in wildlife studies. In such cases the assumption is made that, firstly, adult females and juveniles are equally visible; secondly, that animals under one year of age can be readily distinguished from older groups, and, thirdly, that the cause of an adult female : juvenile ratio lower than calculated birth rates must be mortality. In this study, it was considered that none of these assumptions holds because:

- 1 the reedback is not a strictly seasonal breeder, and first year animals are not a distinct class easily distinguished from older groups (CHAPTER FOUR);
- 2 young reedback have a particularly long lying-out period when they are difficult to observe, although their mothers may be visible;
- 3 many young reedback move away from their birthplace before they reach twelve months of age (CHAPTER SIX).

For these reasons adult female : juvenile ratios were not considered to be a useful measure of first year mortality.

(b) Sub-adult and adult mortality

Mortality in the older age groups was examined by three independent methods:

Firstly, a shot sample, comprising 97 male and 77 female reedback over the age of one year was considered to be random with respect to age. The age of each animal was determined by means of its teeth (APPENDIX D), and age distributions calculated for each sex. Assuming a stationary age distribution, the number of survivors per age group (the f_x series; Caughley, 1977) was re-expressed as the probability (l_x) that any particular animal would reach a specified age. Before deriving the l_x series, it was necessary to 'smooth' the age frequencies (f_x) in cases where older age classes contained more individuals than younger ones. This was done by grouping the frequencies in threes, and attributing the mean of each group to the second age class. The mean mortality rate, \bar{q} , for each sex was then calculated as:

$$\bar{q} = 1/\Sigma l_x \quad (\text{Caughley, 1977})$$

Secondly, a collection of 43 male and 24 female skulls found in the field, and assumed to be the remains of animals that died of 'natural' causes, was made. Age distributions for each sex were derived, representing mortalities per age group. This information was again re-expressed as an l series, and treated as detailed above.

Finally, a sample of 44 male and 40 female reedbeek were marked for individual recognition (CHAPTER SIX), and monitored for periods of up to two years. Although the ages of these animals were not determined, an estimate of minimum survival was possible by considering the proportion of the marked animals that continued to be seen after specified periods of time. Thus, a 20 % loss of marked adult females over a one year period would, for example, suggest a five year life expectancy in this age and sex class.

3.2.3.3 MOVEMENT

The movement of animals out of the study population was examined by means of 84 marked animals (CHAPTER SIX). Details of these were circulated by mail to all landowners in Underberg district, and illustrated posters requesting details of any collared animals seen by members of the public were posted widely throughout the district.

A total removal exercise was envisaged to monitor possible immigration in a 'vacuum' situation, but this exercise was considered to be politically inexpedient by the Natal Parks Board, and consequently abandoned.

3.2.3.4 POPULATION STRUCTURE

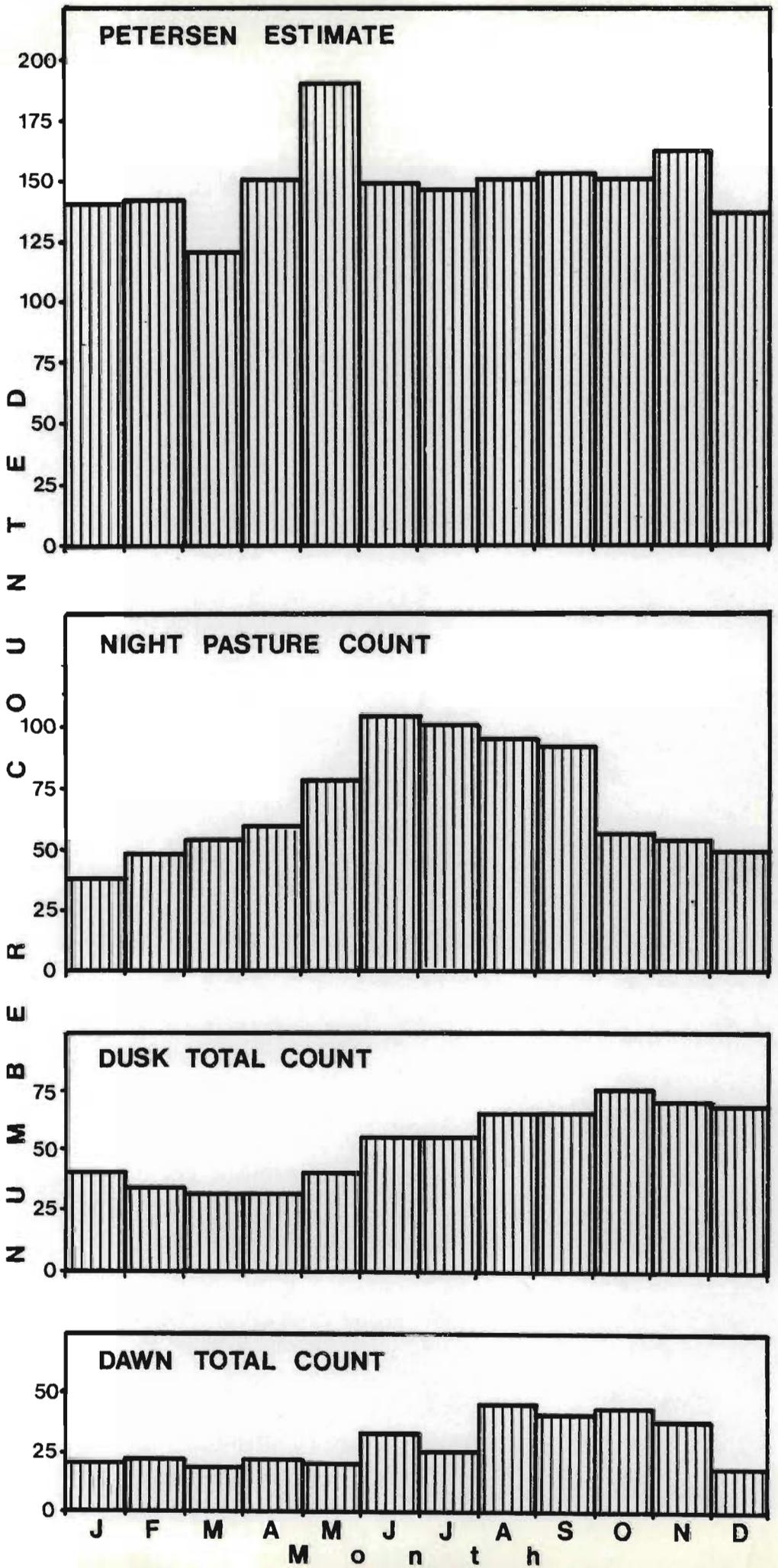
Field age and sex classifications were made of as many animals as possible during dawn and dusk total counts in the intensive study area (SECTION 3.2.1.1). Young females could only be reliably distinguished up to an age of approximately 12 months, but the ages of males could be determined until they reached about three years of age (APPENDIX D). A 30x75 'Optolyth' telescope was used for these classifications.

3.3 RESULTS

3.3.1 Census techniques

The results of all counts made in the intensive study area are presented in FIG. 3.3. Monthly mean Petersen estimates indicate that this area supports approximately 150 reedbeek, which are resident throughout the year. The proportion of these counted at night on the cultivated pastures rises from a mid-summer low of approximately 25 % to a mid-winter high of about 66 % in June, July and August. This is the highest proportion of the population counted by any method. Dawn and dusk total (foot) counts are lowest in autumn when available cover is greatest, and highest in early spring, shortly after most natural vegetation has been burnt. Dusk counts usually reveal approximately twice the numbers counted at dawn, and rise to a

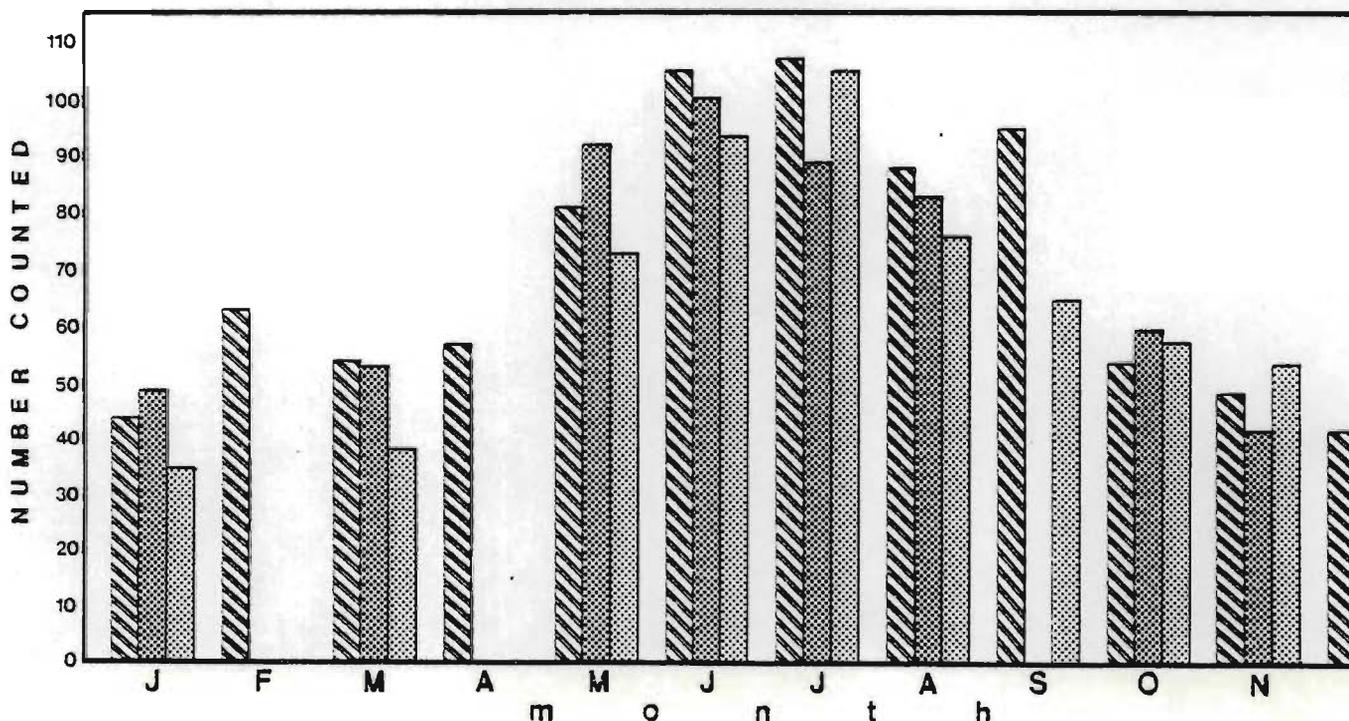
FIG. 3.3 : Mean monthly population estimates within the intensive study area for 1981 and 1982 combined



'high' of about 50 % of those present, when counted in early spring.

These results clearly illustrate the potential utility of mid-winter night pasture counts, and of early spring dusk total (foot) counts for ascertaining reedbuck numbers on farms. A summary of the number of reedbuck counted on each census in the intensive study area is given in TABLE 3.1. From the table, a high level of repeatability is indicated by the close agreement between counts made at night within any one month. The results of night pasture counts made at different times of the evening are presented in FIG. 3.4. Late counts were not made in February, April or December, but from the results obtained in other months, it is apparent that fewer animals tend to be seen during counts started three hours after nightfall than are seen earlier. Certainly, animals tend to be lying, rather than grazing, later in the evening, especially in winter when pastures are often frosted within a few hours of dusk (pers. obs.). As some animals also seek cover, they may be missed later in the evening. Perhaps surprisingly, the reduction in numbers counted when a census is started three hours after nightfall, as opposed to being started at nightfall, was never more than 25 %, and usually closer to 10 %.

FIG. 3.4: Results of Night Pasture Counts made in the Intensive Study Area, starting at nightfall one and a half , and three hours  after nightfall



The effect of the phase of the moon on the count index was examined (FIG.3.5), but no significant relationship could be demonstrated. The results of correlation analyses between the count index and cloud cover, wind speed and temperature are presented in TABLE 3.2. No significant correlations were established, nor was there any significant difference between mean count indices for censuses made under different wind direction conditions (TABLE 3.3).

TABLE 3.1 : Results of counts made in the intensive study area each month during 1981 and 1982

M O N T H	T Y P E O F C O U N T					
	DAWN COUNT	DUSK COUNT	First	Second	Third	MEAN
JANUARY 1981		45	26	33	31	30
FEBRUARY	20	36	38	42	34	38
MARCH	21	18	60	62	38	53
APRIL	27	28	62	61	61	61
MAY	25	23	57	75	83	72
JUNE	41	43	98	106	105	103
JULY	23	56	105	94	86	95
AUGUST	30	57	109	113		111
SEPTEMBER	46	72	96	97	92	95
OCTOBER	31	70	58	43	62	54
NOVEMBER	37	55	41	53	53	49
DECEMBER	15	74	35	50		42
JANUARY 1982	21	37	36	46	49	44
FEBRUARY	25	32	64	62		63
MARCH	15	44	51	56	54	54
APRIL	14	33	58	62	50	57
MAY	15	58	97	84	62	81
JUNE	25	68	106	100	108	105
JULY	26	55	103	96	121	107
AUGUST	60	73	82	76	94	84
SEPTEMBER	36	59	79			79
OCTOBER	55	80	69	52		61
NOVEMBER	37	83	65			65
DECEMBER	20	62	61			61

TABLE 3.2 : Correlation coefficients (r) between the count index score and cloud cover, wind speed and temperature for night pasture counts, dawn and dusk total counts

Count Index with:	Night count	Dawn count	Dusk count
Cloud cover	- 0,09	- 0,25	- 0,26
Wind speed	- 0,17	0,15	0,04
Temperature	- 0,07	0,11	0,03

TABLE 3.3 : Effect of wind direction on the count index, applied to night pasture counts, dawn and dusk total counts
Means are shown \pm standard deviation

Wind Direction	Count Index for:		
	Night count	Dusk count	Dawn count
N	1,05 (n=1)	1,75 (n=1)	0,89 \pm 0,78 (n=6)
NE	1,00 \pm 0,09 (n=7)	1,02 \pm 0,30 (n=10)	1,13 \pm 0,33 (n=10)
E	1,06 \pm 0,07 (n=8)	1,03 \pm 0,31 (n=11)	1,18 \pm 0,48 (n=7)
SE	1,03 \pm 0,11 (n=6)	0,34 \pm 0,38 (n=5)	1,25 (n=1)
S	1,05 \pm 0,05 (n=4)	(n=0)	0,96 \pm 0,68 (n=6)
SW	0,94 \pm 0,11 (n=9)	0,98 \pm 0,41 (n=4)	1,41 \pm 0,25 (n=5)
W	1,02 \pm 0,12 (n=5)	0,80 (n=1)	0,87 \pm 0,15 (n=3)
no wind	0,98 \pm 0,13 (n=16)	0,95 \pm 0,26 (n=12)	0,85 \pm 0,27 (n=6)

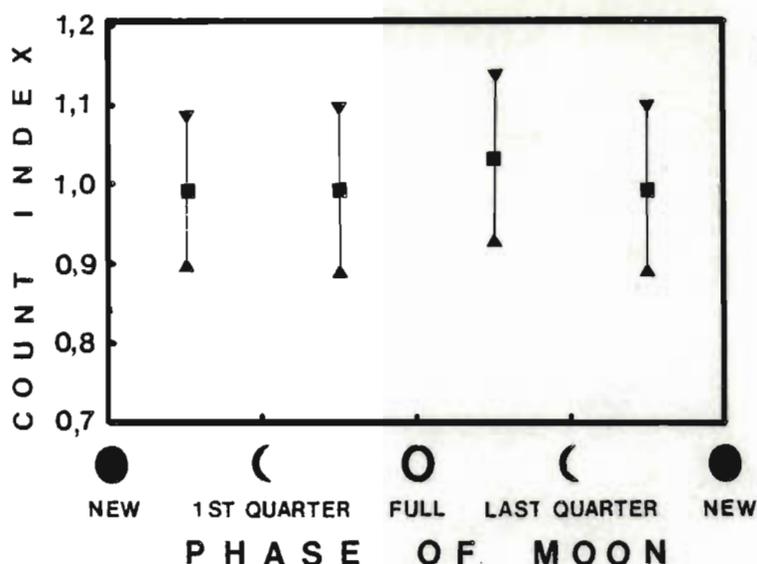


FIG.3.5: Effect of Phase of Moon on Count Index

Mean values are shown
± standard deviation

3.3.2 Population trend and manipulation

The results of counts made on all farms in the extensive study area, three times during winter 1981 and once in summer 1982 are presented in TABLE 3.4. The total number of animals counted was 631, 644 and 662 in June, July and August 1981 respectively, representing a mean monthly increase of 2,5 %. Only 60 % of winter numbers were counted in February 1982, presumably because of a shift in distribution away from the pastures during summer (CHAPTER FIVE).

Reedbuck numbers counted throughout the extensive study area in July 1981 are compared with 1982 and 1983 values in TABLE 3.5. Interestingly, there were no significant changes in numbers present in either the no-cull block, the low-cull block, or the high-cull block over this two-year period.

3.3.3 Population parameters

3.3.3.1 BIRTH RATES

Of the sample of 75 post-pubertal female reedbuck shot 59, or 78,7 % were found to be pregnant (CHAPTER FOUR). Since the gestation period for reedbuck is 233 days (Wilhelm, 1933), a lambing interval of 296 days is indicated (CHAPTER FOUR). A lambing interval of 296 days implies an annual birth rate of 1,22 lambs per female.

A summary of presumed progeny seen in the close company of marked adult females is given in TABLE 3.6 for the period of intensive fieldwork. Nineteen inter-lambing intervals were observed, with a mean duration of 268 days. This implies an annual birth rate of 1,36 lambs per female.

TABLE 3.4 : Results of night pasture counts on all properties in the extensive study area, made three times during winter 1981, and once in summer 1982

PROPERTY	COUNTING BLOCK	NUMBER OF REEDBUCK			
		JUNE 1981	JULY 1981	AUGUST 1981	FEBRUARY 1982
1	1	106	105	113	48
2	} 2	12	12	11	5
3		16	25	26	5
4		22	22	36	15
5	3	44	27	30	27
6	4	55	58	64	18
7	} 5	50	59	56	23
10		19	34	33	18
11		8	10	4	14
8	6	0	4	12	17
9	7	77	60	84	29
12	} 8	29	22	24	17
13		6	6	7	4
14		0	3	4	2
15	9	18	28	19	9
16	} 10	35	42	30	22
17		14	11	15	5
18	} 11	33	30	26	
19		28	34	34	
20	} 12	23	12	2	9
21		12	12	10	6
22	} 13	3	4	5	10
23		16	28	17	9
TOTAL		631	644	662	399
PERCENTAGE OF PREVIOUS COUNT		100	102	103	60

TABLE 3.5: POPULATION TREND ; Results of Night Pasture Counts on all properties , in 1981, 1982 and 1983

	PROPERTY see FIG.3.2	COUNTING BLOCK	NUMBER OF REEDBUCK							
			JULY 1981	CULL	JULY 1982	CULL	JULY 1983			
NO CULL	1	1	105	1	103	1	89			
	2 } 3 }	2a	12 } 25 }	37	20 } 21 }	41	0 } 22 }	47		
	TOTAL		142	4	144	1	136			
	PERCENT of previous count		100	3	101	1	94			
LOW CULL	4	2b	22	0	14	3	26			
	5	3	27	6	18	2	8			
	6	4	58	4	74	7	70			
	7	5a	59	5	72	7	77			
	8	6	4	2	5	2	4			
	9	7	60	3	62	1	61			
TOTAL		230	26	245	22	246				
	PERCENT of previous count		100	11	107	9	100			
HIGH CULL	10 } 11 }	5b	34 } 10 }	44	8	35 } 5 }	40	7	55 } 7 }	62
	12 } 13 }	8	22 } 6 }	31	2	38 } 11 }	53	9	33 } 9 }	42
	14 }		3 }			4 }		0 }		
	15	9		28	4		17	3		9
	16 } 17 }	10	42 } 11 }	53	8	8 } 24 }	32	4	27 } 19 }	46
	18 } 19 }	11	30 } 34 }	64	4	44 } 48 }	92	20	47 } 49 }	96
	20 } 21 }	12	12 } 12 }	24	4	19 } 11 }	30	7	7 } 15 }	22
	22 } 23 }	13	4 } 28 }	32	3	11 } 11 }	22	3	14 } 5 }	19
	TOTAL		230	32	286	53	296			
		PERCENT of previous count		100	12	104	19	103		

TABLE 3.6: Youngsters seen in close company of marked adult females, during the period of intensive fieldwork

FEMALE I.D. NUMBER	OBSERVATION PERIOD												INFANTS WEANED	INFANTS PRESUMED LOST	OBSERVATION PERIOD mths														
	1981				1982				1983																				
	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A			
11			J	J	S		S	S	S	†		I	J	...	S	S	S	...	S	†	J	J	...	S	S	†	3	0	22
13			J	J	S	S	†					I	J	S	S	S	†			...	S	...	†			3	0	22	
15			***																							0	3	21	
16				I	J	S	S	S	S	S	S	S	†		J	J	...	S	†		I	...				2	0	22	
19												I	J	...	J	S	...	S	S	†	J	...	S	...	S	†	2	0	23
20			J	S	...	S	S	†				J	S	S	...	S	†	J	J	S	S	...	S	†		3	0	22	
23			***																							0	3	22	
24			*															J	J	...	S	†				1	2	23	
27			J	S	S	S	S	...	S	†		I	J	J	...	S	S	S	†	...	S	S	†		3	0	23		
28			J	...	S	...	S	S	S	†		I	J	J	S	...	S	S	†	...	S	†				3	0	23	
34							J	J	S	S	S	†		*				J	...	S					1	1	24		
35			J	S	S	S	S	†	J	J	J	S	S	S	S	†		I	J	J	S	...	S	†		3	0	22	
50							J	J	S	S	S	S	S	S	S	S	†	J	...	S	S	S	S	†	2	0	19		
53															J	J	S	S	S	S	†	J	...	J	...	1	0	11	
59																		S	S	S	...	S	...	S	†	1	0	11	
64												S	S	S	S	S	†		I	J	...	S	S	†	I	2	0	14	
68															J	...	S	...	S	†					1	0	8		
82																		seen	infrequently		?	?			?	?	10		
83																		seen	infrequently		?	?			?	?	10		
												TOTAL		31	9	352													

I : INFANT J : JUVENILE S : SUBADULT

* INFANT PROBABLY BORN AND LOST

† INFANT WEANED

3.3.3.2 DEATH RATES

(a) First year mortality

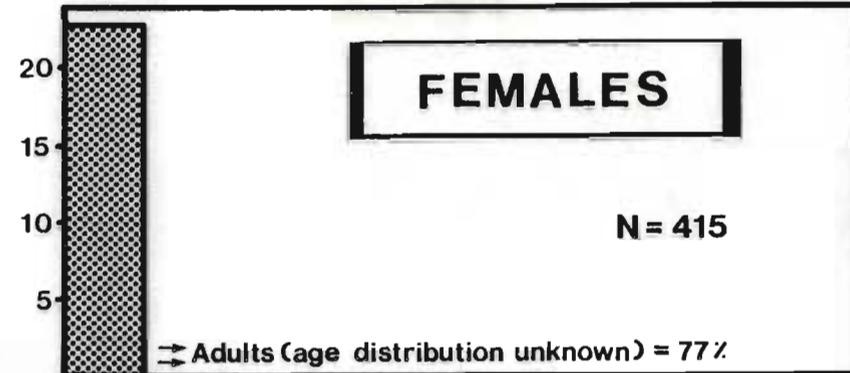
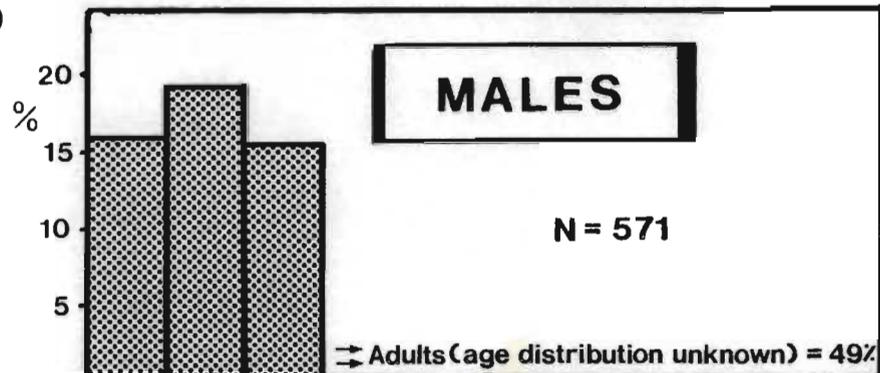
The total number of lambs considered successfully weaned by known adult females (TABLE 3.6) during the study period was 31, against nine which were presumably lost. The nine were never observed with their mothers, but their existence was implied by the indicated lambing interval, and the high level of reproductive activity noted amongst the shot sample. Six of the presumed deaths were attributed to two adult females (Nos. 15 and 23) which were very rarely seen in the close company of a youngster. Female No. 15 was on one occasion seen with a very young lamb, which showed some interest in her, but this interest was not reciprocated. It is possible that these two adult females had a behavioural block, preventing the successful rearing of youngsters. Thus, of the 40 implied births to known adult females 31, or 78 % were successfully raised and weaned.

(b) Subadult and adult mortality

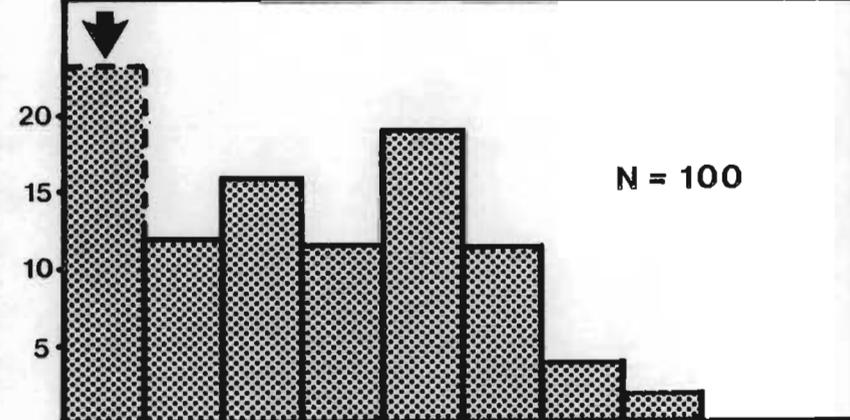
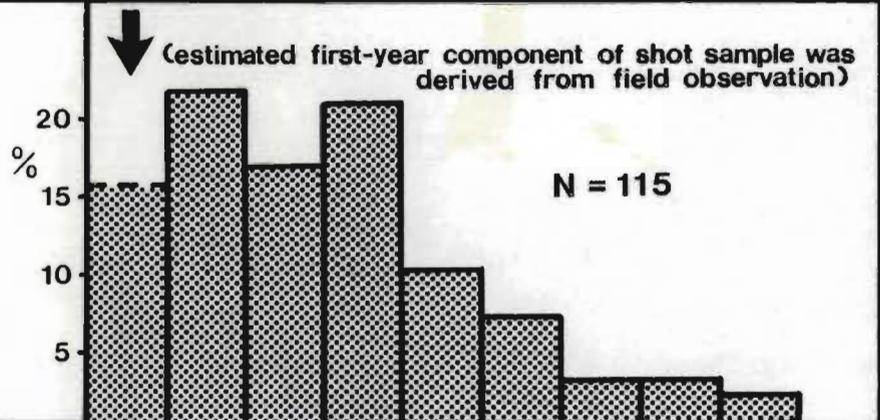
The age distributions of the shot sample, skulls collected in the field, and animals observed in the field are presented in FIG. 3.6,

FIG. 3.6 : AGE DISTRIBUTIONS

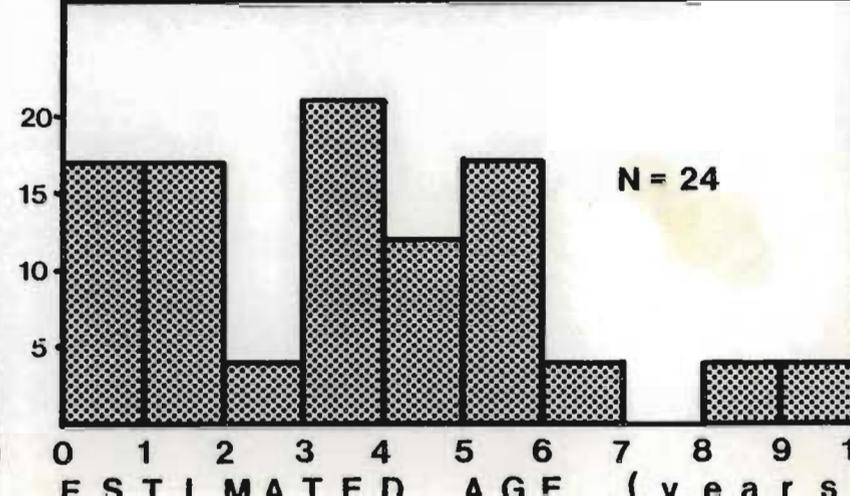
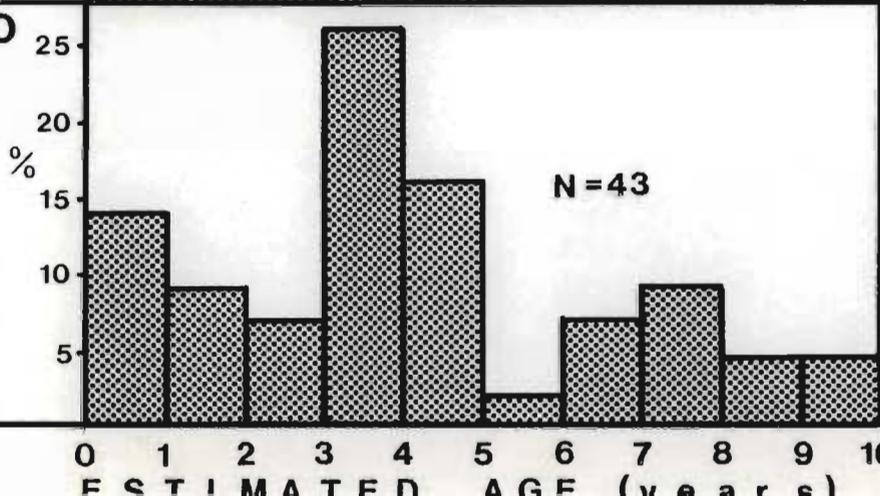
**OBSERVED
IN THE
FIELD :**



**SHOT
SAMPLE :**



**COLLECTED
SKULLS :**



and calculated survivorship, assuming a stationary age distribution, tabulated in TABLE 3.7.

TABLE 3.7: Survivorship, calculated for males and females from skulls collected in the field, and a randomly shot sample, assuming a stationary population

AGE (yrs)	M A L E S		F E M A L E S	
	lx (skull collection)	lx (shot sample)	lx (skull collection)	lx (shot sample)
0	1,00*	1,00*	1,00*	1,00*
1	0,78	0,78	0,78	0,78
2	0,70	0,72	0,62	0,78
3	0,63	0,58	0,58	0,78
4	0,40	0,37	0,38	0,78
5	0,25	0,25	0,27	0,78
6	0,23	0,09	0,12	0,26
7	0,17	0,09	0,08	0,13
8	0,08	0,06	0,08	0,0
9	0,04	0,0	0,04	0,0
TOTALS (Σlx)	<u>4,28</u>	<u>3,94</u>	<u>3,95</u>	<u>5,29</u>

* First year mortality was estimated at 22 % on the basis of observed survival of progeny born to marked adult females

The two male survivorship series show close similarity. From the collection of skulls, a mean mortality rate of 0,23 p.a. is calculated (i.e. a life expectancy at birth of 4,3 years), and from the shot sample a mean mortality rate of 0,25 p.a. (i.e. a calculated life expectancy at birth of 4,0 years). There is a peak in deaths at between three and four years of age. The female survivorship series show less close similarity, and a mean mortality rate of 0,25 p.a. (a 4,0 year life expectancy) calculated from the age of skulls collected

in the field compares with one of 0,19 p.a. (a 5,3 year life expectancy) calculated from the shot sample. The largest class of females represented in the shot sample was between four and five years of age.

Nineteen adult males (over three years of age, as classified from field observation; APPENDIX D) were marked for individual recognition, and over 25 reedbuck-years of observation, eight were lost. This gives an implied 'life expectancy' of $25/8 = 3,1$ years. Only one of the eight animals lost is known to have died, however, and one was sighted, alive, over 30km away. So the losses are at least partly due to dispersal as well as death, and the figure of 3,1 years is clearly an underestimate of life expectancy for these animals. It is however longer than the life expectancy estimates made for adult males (at three years of age) calculated from collected skulls (2,9 years) or the shot sample (2,5 years) (TABLES 3.7 and 3.8).

The nineteen marked adult females were observed over a total period of 29,3 reedbuck-years (TABLE 3.6), and not one animal was lost during this period. This gives an implied 'life expectancy' of at least $29,3/1 = 29,3$ years. This is, of course unrealistic, and doubtless results from a marked population biased in favour of young animals. It does, however, highlight the very high levels of survival enjoyed, and the high degree of fixed residency characteristic of this section of the population.

The causes of mortality amongst the sample of 43 male and 24 female natural mortalities are summarised in FIG. 3.7. In 60 % of cases the cause of death could not be ascertained. The single most important cause of death was snaring, and predator kills were mostly by domestic dogs. Reedbuck also died of other man-related causes, including deaths in fences, and road accidents. As far as the male reedbuck is concerned, injuries incurred in fighting also accounted for a large proportion of deaths (36 % of those where the cause was known).

3.3.3.3 MOVEMENT

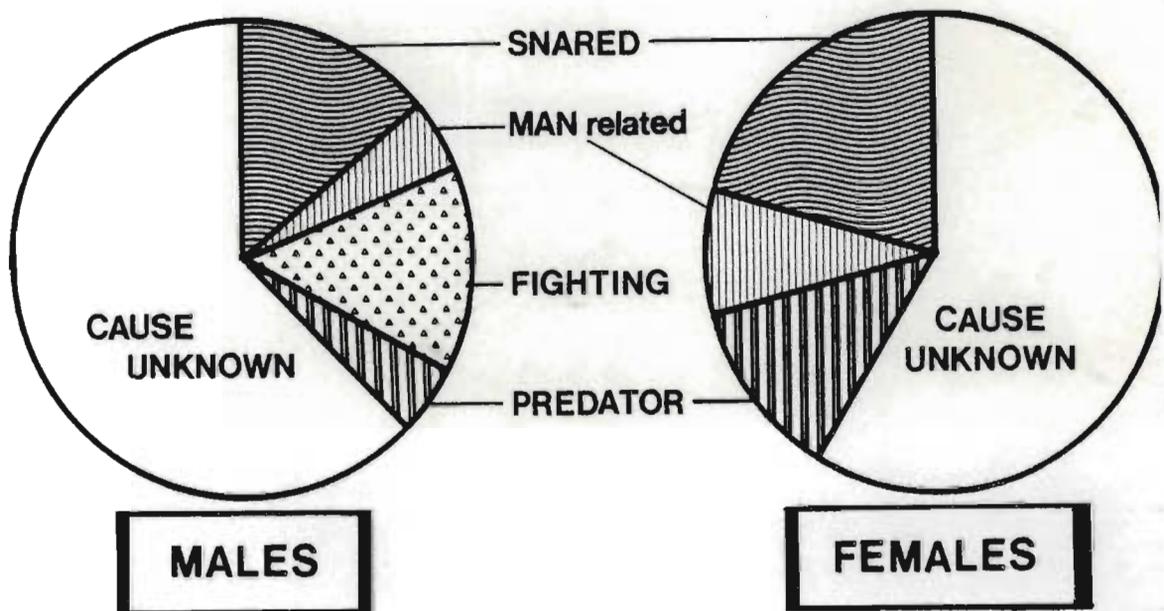
The movement and spatial organisation of animals will be discussed at greater length in CHAPTER SIX. In this section it is sufficient to record that 81 % of the 21 marked subadult females, 42 % of the 24 marked subadult males, and 50 % of the marked adult males were lost during the period of study. Of these 41 % of the subadult females, 10 % of the subadult males, and 12 % of the adult males were reported from farms outside the study area. Only 6 % of subadult females, and

TABLE 3.8 : Summary of population parameter estimates

PARAMETER		ESTIMATE	SOURCE
First year mortality		22% p.a.	Progeny of marked adult females
Life expectancy	males	4,0 years	Shot sample
		4,3 years	Skull collection
	females	5,3 years	Shot sample
		4,0 years	skull collection
	adult males (over 3 years)	3,1 years	Marked sample
		2,9 years	Skull collection
2,5 years		Shot sample	
adult females (over 2 years)	29,3 years	Marked sample	
	3,5 years	Skull collection	
	4,1 years	Shot sample	
Birth rates	infants per subadult female (aged 1-2 years)	1,2 p.a.	Shot sample (CHAPTER FOUR)
		1,2 p.a.	Shot sample (CHAPTER FOUR)
		1,36 p.a.	Marked sample
Emigration	subadult males (aged 1-3 years)	25% p.a.	Marked sample
	subadult females (aged $\frac{1}{2}$ -1 $\frac{1}{2}$ years)	70% p.a.	Marked sample
Population Structure	adult males (over 3 years)	28,5%	Field observation
	subadult males (aged 1-3 years)	19,6%	
	adult females	32,2%	
	youngsters (less than 1 yr)	19,7%	

12 % of adult males were, by comparison, found dead.

FIG. 3.7: The causes of mortality



3.3.3.4 POPULATION STRUCTURE

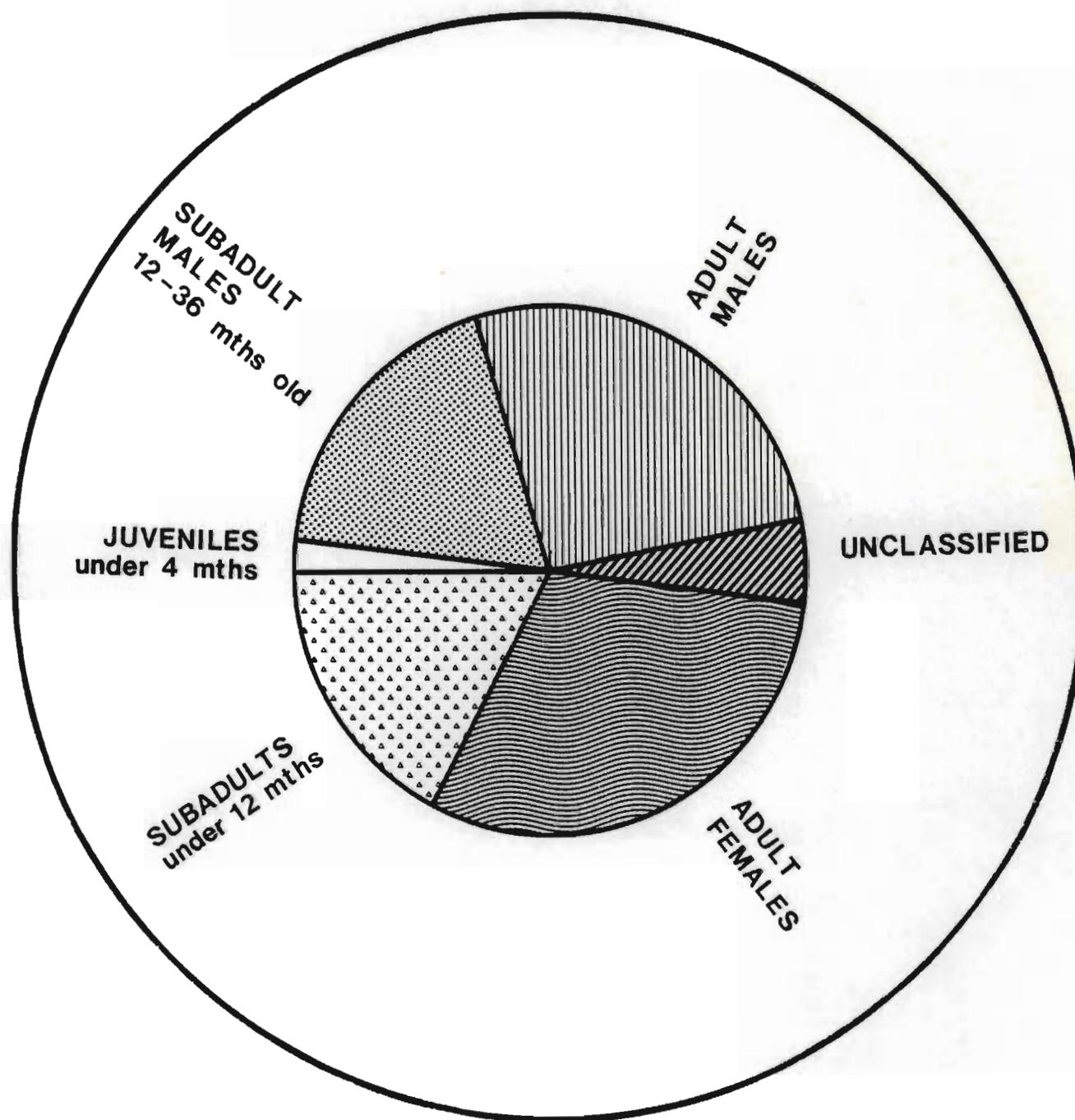
The structure of the population is illustrated in FIG. 3.8, and summary statistics included in TABLE 3.8. Adult females comprise 32 % of the population, and the adult male : adult female ratio is approximately 1 : 1,1, which does not differ significantly from unity (χ^2 ; $p > 0,1$).

3.4 DISCUSSION

3.4.1 Census technique

For the purposes of ungulate management the most important property of a census technique is its repeatability, or precision. A technique should consistently give the same result when applied repeatedly to the same population of animals, regardless of whether the population estimate derived represents 10 %, 50 % or 100 % of the real population size. Such a repeatable technique can then be used with confidence to ascertain changes in animal abundance over time, which may highlight the need for management action. The indicated action can then be applied to rectify any adverse change in population size, even without an accurate knowledge of the actual numbers of animals involved, and repeated census will reveal exactly what effect such management is having. Most wildlife management operations are undertaken in this way, without any real knowledge of the exact number of animals involved.

FIG. 3.8 : Population structure in the intensive study area



If actual numbers can be reliably ascertained, however, remedial population management is more likely to achieve the desired result first time around, without the need for repeated census and adjustment of management intensity. So accuracy in population estimation improves on what can be achieved by a less accurate, but repeatable census method only inasmuch as it makes the operation easier.

Three census techniques were critically evaluated for repeatability and accuracy in this study. Accuracy was determined against a series of Petersen estimates, the limitations of which are considered below. For the present, however, let us assume that the Petersen estimate gave a precise and accurate measure of population size in the intensive study area.

DAWN AND DUSK TOTAL COUNTS

Dawn and dusk total foot counts were only made once each month for the duration of the study. So to examine repeatability the best we can do is look at counts made in successive months, viewed in the context of overall seasonal changes. In the case of dawn counts (TABLE 3.1), repeatability is very poor, and even the highest counts, made in spring, account for only about 25 % of the population present in the area. Reedbuck are generally inactive early in the morning, and many of the animals counted were flushed from their lying-up places; and since reedbuck commonly sit tight until the observer is very close, the number counted is probably more closely related to search effort than to the number present. Dawn counts, then, are neither repeatable nor accurate, and can be of little value in reedbuck management. In the case of dusk counts, however, repeatability is improved, and the proportion of the population observed rises to a peak of about 50 % in early spring. Considering the period from September to December, we have eight population estimates derived from dusk counts, four each in 1981 and 1982: the estimate has a mean of 69 animals, a range from 55 to 83, and a 95 % confidence interval from 61 to 77 animals. With this level of variability, we would expect to be able to detect changes in population size greater than 23 %. This is not a high level of precision, but probably adequate for most farmers, who are generally only interested in whether their reedbuck have doubled or halved, and not in minor changes of a few percent. The census method has the advantage that it can be made on foot, with only a pair of binoculars as equipment, and could be undertaken by conservancy game guards without direct involvement on the part of the landowner.

NIGHT PASTURE COUNTS

The most useful technique, however, appears to be the night pasture count from a vehicle. In mid-winter about two-thirds of the population present

are counted, and a high level of precision can be anticipated. Considering the twelve night counts made in June and July (both years) a mean population estimate of 102 animals, with a range from 86 to 121 and a 95 % confidence interval from 97 to 107 animals was made. With this level of variability, and sampling intensity, a 10 % change in the size of the population could be detected. This is beyond the limits of precision required for the practical application of reedbuck management on farms.

Since the night pasture count appears to offer a high level of repeatability, we must consider how close the derived population estimate comes to the actual number of reedbuck present on a farm. Until this point, I have assumed that the Petersen estimate was directly comparable with the other estimates. This is, in fact, not the case, because whereas dawn and dusk counts, and the Petersen estimate are estimates of the reedbuck population over the entire intensive study area, the night pasture counts were made on only a portion of the area. There were other pastures that were not routinely searched on 'Falcon Ridge' farm immediately adjacent, also within the intensive study area (FIG. 3.1). Counts were made on this farm (property 2: TABLES 3.4 and 3.5), and revealed an additional 11 to 20 animals feeding there. These animals should be added to the night pasture count total to derive a value that is directly comparable with the Petersen estimate. Adding a mean of 16 animals to the original 102 animals gives 118 reedbuck counted, equivalent to 79 % of the Petersen estimate. It is apparent from these figures that this census method is not only repeatable, but also remarkably accurate. It is noteworthy, too, that of all the farms in the extensive study area, none has as much low woody cover as is found in the intensive study area, and it is this particularly favoured habitat type (CHAPTER FIVE) that probably shelters a large proportion of the 21 % of 'missing' animals. On other farms, it is suggested, the proportion of the animals present that are seen during a night pasture count is likely to be higher than 79 %.

PETERSEN ESTIMATES

These conclusions are based on the assumption that the Petersen estimate gives a precise and accurate estimate of population size. As this assumption rarely holds for studies of large mammals, it is worth considering some of the limitations of the method. One of the most common factors limiting its success is an inadequate sample of marked animals. This aspect has been the subject of a study on roe deer in a forested estate in Denmark (Anderson, 1962; Strandgaard, 1967), after which the conclusion was reached that, under the conditions described, two thirds of the population had to be marked to obtain a reliable measure of population size. In the present study, although 73 animals were marked in the intensive study area, the most that were there at any one time was 50, or approximately one third of the total population. This falls far short of

the requirements described by Strandgaard (*op.cit.*), but conditions are very different, particularly with regard to visibility. The very close agreement between Petersen estimates made in different months appears to suggest that marked sample size was adequate. Another important consideration is whether or not all marked and unmarked animals have an equal chance of being seen: bias will result if the marks are so conspicuous as to attract attention, or if the individual animal's activities are so localised that particular animals are 'expected' in particular locations and are consequently actively 'sought after'. In these cases the Petersen estimate would tend to underestimate the actual population size. This possibility cannot be ignored, although the night census information from which the Petersen estimates were largely derived was collected in such a way as to minimise these effects. Reedbuck were normally first seen from as far as 300m away as their eyes reflected back light from the spotlight - the visual key being the shining eyes, and not any collar the animal might be wearing - and, as these counts were made at 'congregation centres' - the pastures - the effect of localised home ranges was largely overcome. Another limitation in the use of Petersen estimates to determine population size is that marks, or marked animals may be lost from the population without account being taken of the losses. In this study the monitoring intensity was sufficiently high (over 3000 resightings in 18 months) that such losses were quickly apparent, and monthly reassessments of animal numbers 'in circulation' adjusted accordingly. In conclusion, a combination of factors, including the congregation of animals on pastures in winter, and the fact that a large proportion of the total population was marked, probably enabled accurate determination of population size by means of the Petersen estimate.

EFFECT OF ABIOTIC VARIABLES

In evaluating the influence of various abiotic variables on the number of reedbuck counted during any particular census, a count index score was derived for each count. The method of derivation was crude, based on a sample of only three consecutive counts, but the index should nevertheless have revealed any significant correlations, if any existed.

Season clearly has a strong influence on the results of a census, with highest numbers recorded on pastures at night in winter, where the animals congregate to feed. The availability of cover influences daytime counts, and when cover is short, soon after burning in spring, counts reach their highest levels.

In devising census techniques cognizance should be taken of time-related behaviours of the animals to be counted, so that observations can be timed to coincide with periods when most animals can be seen. Casual observations of reedbuck made early in this study indicated daytime

activity peaks just before nightfall, and to a lesser extent, within a couple of hours of dawn. Dawn and dusk counts were therefore undertaken and compared with night pasture counts made at different times of the evening. Clearly, from the results, the reedbuck's early evening activity peak can be used to good advantage to ascertain population size. Timing is particularly critical for dusk counts because they are made right at the start of the activity peak, and if they are completed too early, animals will be missed. It is worth noting that during winter and autumn there is a 50 % increase in numbers counted between the period when dusk counts are made and that when night pasture counts are made, only one hour later. In other words, over this short period, many animals are starting to become active and visible. The evening activity peak lasts for only a few hours, and by three hours after dusk many animals are lying down and others are no longer visible (FIG. 3.4).

A number of ungulate species (for example, kudu (Tragelaphus strepsiceros) and oryx (Oryx gazella) (Gaerdes, cited by Joubert and Eloff, 1971) and Thomson's gazelle (Gazella thomsoni) (Walther, 1973)) appear to be more active on moonlight than on dark nights, and this could influence night census results. The presence of moonlight might also affect an animal's reaction to the spotlight, and as the detection of animals depends to some extent upon their reaction, moonlight might again influence census results. However this did not prove to be the case in this study.

The influence of daily weather on ungulate activities has been the subject of several studies reviewed by Leuthold (1977). The most thorough of these was made by Lewis (1975), who concluded that activity patterns vary mainly in relation to the 'heat load' acting on the animals. The overall effect is usually a reduction in mobile activities (feeding, moving) under conditions of high heat load, and a corresponding increase in static activities (standing, lying). In my own experience, this would seem to be borne out by the observation that on clear hot days the start of the evening activity peak is later, and more synchronised. Ozoga and Gysel (1972) found that white-tailed deer (Odocoileus virginianus) made increased use of dense protective cover during periods of low temperature and high calculated air chill, and Zagata and Haugen (1974), working on the same species, established relationships between the number of individuals counted and air temperature, wind speed and wind direction.

Although the correlation analyses undertaken in the present study did not reveal similar relationships this may be because the results were too few to be considered by season. Observation of reedbuck under different weather conditions at different times during winter evenings suggest that they tend to lie down and/or seek cover earlier on cold or windy nights, and this might reasonably be interpreted as a temperature regulatory response. So, although there are no quantitative data to support this, my

recommendation would be to avoid night census work on especially cold or windy nights, when fewer animals may be seen as a result of their shelter-seeking activity.

3.4.2 Population dynamics

For stability to be achieved in animal populations the number of individuals recruited must be equivalent to the number lost. Recruitment is through births and immigration, whilst losses arise by death and emigration. The population ecologist is therefore concerned with the four components of the equation:

$$\text{BIRTHS} + \text{IMMIGRANTS} = \text{DEATHS} + \text{EMIGRANTS}$$

An important feature of the reedbuck population studied here is that stability appears to be maintained, even under quite different harvesting regimes. The purpose of this discussion is to examine the mechanisms involved in the maintenance of stability, by considering the four components concerned.

BIRTHS

Approximately 32 % of the population are reproductively active adult females, each of which is capable of producing between 1,2 and 1,4 lambs per annum, or one each eight and a half to ten months (TABLE 3.8). A realistic estimate of recruitment through reproduction under present conditions would, then, be $32 \times 1,3 = 41,6$ % each year. For the foreseeable future reedbuck are likely to be able to continue enjoying the benefits of cultivated pastures and a high plane of nutrition throughout the year, so that lambing intervals are unlikely to change significantly in the absence of intervention. Recruitment through births into the population could, however be subject to change if management were directed at altering the proportion of the population represented by adult females.

DEATHS

Life expectancy was studied in three quite distinct ways, each of which possessed particular advantages and disadvantages.

The most direct method used was to follow a sample of marked individuals over as long a period as possible, noting relevant details about observed deaths. The aim was to calculate average life expectancy figures, based on the proportion of the marked animals that died in any one year. The value of this method could have been further enhanced had the age of the marked

animals been known, but unfortunately the need to handle animals quickly during capture (CHAPTER SIX) precluded examination of teeth for age determination. Inadequate sample size, and a period of only two years observation of an animal with a potential longevity of about ten years limited the value of the method. When animals were lost, it was seldom possible to ascertain whether the animal had died or emigrated. However, because the method was so direct, great confidence could be attached to the results. Thus, regardless of the age of the nineteen marked adult females studied over 29 reedbuck-years, the fact that none disappeared over the entire period of study did indicate a much higher level of survival than was suggested by life table analysis.

Life table analysis is a useful technique of calculating survival and life expectancies in stable populations with a stationary age distribution. The tables can even be adjusted to take into account an observed rate of population increase, provided such an increase has been constant for some time (Caughley, 1977). In this study the population does appear to be stable, but that does not necessarily imply a stationary age distribution because we cannot be certain that the population has been stable for a generation or so. In this study survivorship data were calculated from the age distributions of animals that died of 'natural' causes, and from the age distributions of animals living in the population. By comparing the two survivorship tables we can get some idea of the level of agreement between the two, which will give us some measure of their validity.

One noteworthy feature of the tables (TABLE 3.7) is that, in the case of both sexes, the oldest animals were recorded as natural mortalities, and animals of similar age were not sampled from the living population, despite the larger sample size in this group. This feature tells us that some animals are living longer than would seem to be indicated by sampling the living population.

For males the agreement between the two survivorship tables is otherwise good (TABLE 3.7), and as they represent independent estimates of survival, they probably are as true a reflection of reality as we might expect. They give us an expected longevity of 4,3 years (skull collection) or 4,0 years (shot sample), and both methods indicate high mortality between the ages of three and five years. Over this period of life at least 60 % of animals die. Fighting is a major cause of mortality (FIG. 3.7), and is probably especially prevalent at this age when young adults attempt to achieve social dominance.

Until recently ethologists believed that intraspecific combat was rarely fatal (Lorenz, 1966; Tinbergen, 1969; Eibl-Eibesfeldt, 1970). Today there is growing evidence (Geist, 1971, 1974; Wilkinson and Shank, 1976; Crowe and Liversage, 1977; Venter, 1979) to suggest that this previously

held notion is obsolete, and that socially induced mortality, as defined by Wynne-Edwards (1962), is very often the result of direct and mortal combat. Whether the deaths arise 'deliberately' (Geist, 1974) or 'accidentally' (Maynard Smith and Price, 1973) seems immaterial: the fact that they occur is undeniable and the consequences unavoidable. As far as the reedbuck is concerned combat mortality amongst males is clearly widespread and commonplace (Ferrar and Kerr, 1971; Venter, 1979), and the consequence of it is a considerably shortened natural life-span.

For females the agreement between the two survivorship tables is not good. The collection of skulls indicates that, of the animals entering their second year of life only 35 % reach five years of age. By contrast, survival according to the shot sample is 100 % over the same period of life. If the population were expanding, this discrepancy could be readily explained, as a life table derived from a shot sample would tend to underestimate mortality in the younger age classes, and that derived from a collected sample would overestimate mortality in these age classes, under these conditions. However, the population does not appear to be expanding and, moreover, the observations on marked adult females endorse the view that the population is heavily biased in favour of young animals experiencing exceptional survival rates. From the age distribution of the living population (i.e. shot sample), we find that 78 % of adult females are aged between two and five years, over which period survival is calculated as 100 %. This is in accord with observations on marked adult females. If, then, we accept that the shot sample of 77 adult females is representative of the true situation in the living population, we must consider why so few animals over six years of age were sampled. Since we know from the collection of skulls that animals do live on into these older age classes, the obvious explanation, that females have lived out their natural life-span by the time they reach five to seven years of age, is clearly erroneous.

A possible alternative explanation is that some natural disaster five to seven years ago devastated the population. Such a disaster could take the form of an epidemic disease, or adverse weather conditions. Nineteen seventy six was a particularly wet year in the study area, and this could have been the direct or indirect cause of such a disaster. A reedbuck population crash has been documented in Kyle National Park in what was then Rhodesia (Ferrar and Kerr, 1971), and I have personally received vague reports from farmers of periods when more reedbuck carcasses than usual were found. However, in this regard it should be noted that die-offs are normally associated, at least indirectly, with an inadequate supply of food (Keep, pers. comm.), and that food is unlikely to be limiting in the study area (CHAPTER FOUR). Moreover, if such a disaster did affect the study population at about this time, the return to stability was achieved remarkably quickly. Furthermore, the age distribution of the living

population is not typical of an exponentially increasing population in which each younger age class contains more animals than the previous one.

With regard to the female survivorship table derived from collected skulls, an important consideration is whether the collection in fact represents age at death information. The table is derived from a collection of only 20 skulls, of which six were collected from snares, fences or road accidents. Whilst these are very real mortality agents, they are in fact sampling randomly with respect to age from a living population. Consequently the skull collection is probably more representative of the living, than of the dying population, and a more appropriate treatment of the data might be to treat them as such. The collection is, in any case, much too small to really tell us much about survivorship, and the much larger shot sample probably provides more reliable information, particularly when combined with observations on the marked animals.

To conclude, the three methods used to assess female mortality gave confusing results. The best estimate for longevity, derived from a randomly shot sample, is 5,3 years, but this may be an underestimate if, as is speculated, the older age classes were under-represented, possibly because of some natural disaster five to seven years before sampling.

EMIGRATION

Of the marked subadult males aged between one and three years, 42 % were lost, which is equivalent to a rate of loss of 50 % had all animals been observed over the entire subadult lifespan (CHAPTER SIX). Life table analysis reveals that loss through mortality accounts for between 19 % and 25 % of these animals. The remainder - about 28 % - probably move out of the area in which they were born. Only one such emigrant was positively identified as such (CHAPTER SIX), but the evidence is considered sufficiently strong to support the conclusion that most do emigrate (CHAPTER SIX). As subadult males are added to the population at an annual rate equivalent to half the birth rate minus the first year mortality rate, or 16 %, loss of subadult males through emigration is approximately $28 \times 0,16 = 4,5$ % per annum.

Ninety one percent of subadult females were also lost from the population, of which 84 % were probable emigrants (CHAPTER SIX). As they are added to the population at approximately the same rate as males, the total loss through emigration of this class is approximately $84 \times 0,16 = 13,4$ %. Thus the total annual loss through emigration of both sexes is approximately 18 %.

IMMIGRATION

Of the four components in the equation characterising a stable population (Births + Immigrants = Deaths + Emigrants), the level of immigration was the only one that was not examined experimentally in this study. However, because we know something of births, deaths and emigration, it should be theoretically possible to deduce levels of immigration.

Using the calculated annual recruitment rate through births of 41,6 %, an average expected longevity of 4,65 years (based on a figure of 4,0 years for males, and of 5,3 years for females - from the shot sample) and an emigration rate of 18 %, the equation for the stable, unmanaged population in the intensive study area, looks like this:

$$42 \text{ BIRTHS} + x \text{ IMMIGRANTS} = 22 \text{ DEATHS} + 18 \text{ EMIGRANTS}$$

The equation does not balance, and even without any immigration, the recruitment side of the equation is 2 % higher than the losses. This is a quite acceptable 'error' component, in view of the methods used. In any case the census method used would not detect such a small increase in population size. The figures are sufficiently close to reach the conclusion that immigration is insignificant. They also tell us that the study population has a potential rate of increase of about 20 % p.a., which, interestingly, is similar to the observed 19 % increase of the St Lucia reedbuck population (Venter, 1979).

This situation applies where mortality is achieved through natural causes, as in the experimental 'no cull' block. Where culling was undertaken, however, because of the increase in losses through deaths, two possible population responses would be required to maintain stability. Firstly, the number of animals leaving as emigrants might decrease ; and in this regard 18 % of the population are 'available'. Or, secondly, emigration might remain at 18 %, but immigration into the area might increase by an amount equivalent to the level of culling implemented. Under the culling regimes implemented in this study, there is no way of telling to what degree each of these two possibilities applies. If dispersal is an innate movement, genetically 'programmed' into a reedbuck, then stability would be maintained by means of increased immigration. If, on the other hand, dispersal is a behavioural response to unfavourable environmental conditions, such as shortage of space, then additional mortality through culling may ameliorate conditions so that emigration is no longer necessary. These aspects of dispersal are considered at some length in CHAPTER SIX. For the present it is sufficient to appreciate the significance of animal movement in population regulation, as has been demonstrated in this study.

POPULATION SEX RATIO

Having established birth, death, immigration and emigration rates, it is a relatively simple process to derive an 'expected' population sex ratio, and compare this with the one observed. This then provides a useful check on calculated population parameters.

Since the sexes are born in equal numbers (CHAPTER FOUR), the ratio of males to females standing in the population must be the result of the sexes' different lifespans and migration rates. Males have a calculated life expectancy of 4,0 years, compared with the female's 5,3 years (data from the shot sample), so that in a population experiencing no immigration or emigration, the sex ratio would be $4,0 : 5,3 = 1 : 1,3$ in favour of females. However, of the 16 % 'increment' of males born each year, only 4,5 % are lost through emigration, compared with 13,4 % of the females. This implies that $(16-4,5)/(16-13,4) = 4,4$ times as many males as females remain behind and are recruited into their parent population. The 'life expectancy' of males within the population thus becomes 4,4 times as great as was previously calculated, and so the 'expected' sex ratio is $4,4 \times 1 : 1 \times 1,3$ or $3,4 : 1$ in favour of males.

In the real population I observed 58 males : 42 females (TABLE 3.8; assuming unsexed youngsters of < 1 yr old to represent equal numbers of each sex), which is a ratio of 1,4 : 1 in favour of males. Since the observed sex ratios are considered realistic, it is clear that, in the derivation of the 'expected' ratio, either female losses have been overestimated, male losses underestimated, or a combination of the two. There are many possibilities which could account for the disparity, but the 'weakest link' appears to be in the derivation of longevity from the shot sample. In particular, the high survival rates observed amongst the nineteen marked adult females cast very serious doubts on the validity of the 5,3 year life expectancy calculated from the shot sample.

3.4.3 Theories of population regulation and their relevance to this study

The results presented in this chapter raise a number of interesting questions about the mechanisms of regulation that enable a population of animals to maintain a stable population size. In this discussion I intend to examine some theories of population regulation, some of the evidence in support of each, and to then relate these to my own observations of reedbuck. I will be returning to this theme in subsequent chapters of this thesis, as I examine more thoroughly the reasons for population stability, and the mechanisms by which it is brought about.

There are essentially three types of theory relating to the ways in which animal populations are regulated. Although a great deal of compromise is apparent in recent work, the principal proponents of these theories

believed that they had universal application. The theories will be considered independently under the headings abiotic mechanisms, biotic mechanisms and self-regulation, before turning attention to compromise theories.

ABIOTIC MECHANISMS

A number of workers, of whom Andrewartha and Birch (1954) are perhaps the chief proponents, believe that animal populations are controlled by environmental factors, of which weather is by far the most important. Andrewartha and Birch are entomologists, and in the invertebrate world the disturbing influences of weather on population size are undeniably conspicuous. There is also a sizeable body of evidence that inclement weather conditions can severely reduce populations of large mammals: Clutton-Brock and Albon (1982) have shown that winter temperatures and late winter rainfall together account for 82 % of observed variation in mortality of adult red deer (Cervus elaphus) on the Isle of Rhum; weather severity has been linked to natal mortality in white-tailed deer (Verme, 1977), and to calf loss of red deer in Norway (Wegge, 1975); in the lowveld of Natal natural mortalities of large herbivores occur differentially at times of the year when air temperatures are low or rainfall high (Brooks, 1973), and under natural conditions in the Natal Drakensberg, most antelope deaths occur in late winter and are associated with cold, wet periods (Rowe-Rowe, pers. comm.).

BIOTIC MECHANISMS

Biotic mechanisms of population regulation are of two distinct types. Regulation through competition for food is possibly the most widely recognised of all regulatory processes, whilst predation, disease and parasitism may also be important regulatory agents. Disease and parasitism are essentially the same as predation, except that the causative organism is smaller than its host (Tamarin, 1978).

Lack (1954) was one of the early proponents of the theory that competition for food could regulate populations, at least in birds, and numerous authors have subsequently contributed more evidence in support of this theory. Sinclair (1975) has demonstrated that the green component of the primary production during the dry season is the limiting resource for grazing herbivores in East Africa and Rowe-Rowe (1983a) has shown that most antelope deaths in the Natal Drakensberg occur when the quantity and quality of available forage is at its lowest. Population limitation via an animal's food supply need not involve obvious mortality, as Hanks and McIntosh (1973) have shown: they found that as elephant population density increased and food resources became scarce, both the age of puberty and the calving interval were increased.

For population regulation to be achieved as a result of disease, predation and parasitism, the controlling organism must have an increased effect on the host population as that population's density increases, so that a balance is achieved between 'predator' and 'prey' (Nicholson, 1933; Gause, 1934; Holling, 1959). Some of the most convincing evidence of this type of regulation is provided by Slobodkin et al. (1967), and by the work of Mech (1963) and Jordan et al. (1971) who demonstrated stability in the wolf-moose relationship on Isle Royale.

SELF-REGULATION

Self-regulation is the process whereby a population of animals is able to limit its own size at or below the level of resource shortage, by means of 'internal' mechanisms that serve to increase mortality or reduce fertility. This can be brought about within a population phenotypically as each individual responds to stressful conditions associated with increased population density in the same way (Christian and Davis, 1964), or genotypically if the population stress results in a changing gene pool over several generations favouring certain types of behaviour that in the long term curtail population growth (Chitty, 1971).

Self-regulation of this kind is the basis of Wynne-Edwards' (1962, 1965) controversial theory of 'group selection' whereby the individuals within a population limit their reproductive output in order to avoid starvation by all. Wynne-Edwards' theory is essentially one of regulation by intraspecific competition, where the competition is brought about artificially through an animal's social relationship with conspecifics, so that the real carrying capacity of the environment is never reached. Wynne-Edwards thus sees territorial and hierarchical social behaviours as the mechanisms enabling group selection: both systems admit a limited quota of individuals to share the food resources, and exclude the extras, which may actually die of starvation in periods of food shortage.

There is a considerable body of evidence in support of the self-regulation hypothesis of population regulation. Much work in this connection has been done on small mammals, which may show inhibition of reproductive function or increased adrenocortical secretion resulting in mortality through the lowering of resistance to disease, parasitism, or adverse environmental conditions as a direct result of increased population density (Christian and Davis, 1964). The self-regulation mechanism has been shown so effective as actually to cause the near demise of a population of mice raised in an artificial 'Utopian mouse universe' (Calhoun, 1973).

Amongst large mammals, Siniff et al. (1977) inferred that the McMurdo Sound Weddell seal (Leptonychotes weddelli) population was self-regulated by a physiological or social connection between the number of adult females at

the pupping colonies and the subsequent year's pup population. Grey seals (Halicoerus grypus) are regulated by pup survival which decreases disproportionately at high population densities due to desertion and injury (Harwood, 1981), and in grizzly bears (Ursus arctos horribilis) recruitment of juveniles is inversely related to the size of the adult population by means of social factors (McCullough, 1981).

COMPROMISE THEORIES

It is now widely recognised that the approach of the original proponents of the three opposing theories of population regulation was in many ways too simplistic to explain fully the complexities of the natural world. As Botkin et al. (1981) point out, one of the problems in much of the existing population theory for large mammals is its failure to view the animals within an ecosystem context. Bell (1982), too, has stressed the need for a holistic view of community structure and ecosystem function. In East Africa the size of a population of large mammals is not simply governed by rainfall (as one might infer from Coe et al., 1976), but also by that animal's role in nutrient cycling and the maintenance of a complex ecosystem that can in turn support the animal. There is evidence that herbivores in African ecosystems are limited, at least under some conditions, by the nutritional quality and not the quantity of vegetation (Sinclair, 1975). The nutritional quality of vegetation depends, over long periods of time, on the retention of essential elements by the ecosystems, and this involves mechanisms that are biotic at moderate to high rainfall, and abiotic at low rainfall (Botkin et al., 1981).

A second problem which arises with the traditional theories of population regulation is, as Sinclair (1977) points out, one of semantics. Thus, whilst Andrewartha (1961) argues that weather can act in a density-dependent way by increased mortality on populations that are too large for the available cover to protect from climatic extremes, the proponents of the 'regulation by biotic mechanisms' theory would say that this was competition for space as a resource, and that weather was the limiting factor, and not the regulating one.

3.4.4 Conclusion

These are the mechanisms by which animal populations may be regulated. In conclusion I would like to refer back to the results of this chapter and examine the evidence for any such regulatory mechanisms that might be demonstrable for reedbed.

The fact that a stable population size was maintained in the study area under conditions where as many as 20 % of the population, or as few as 1 %, were artificially removed, suggests that regulation is indeed taking place,

and that such regulation is density dependent. It remains to be asked why such regulation is necessary, and how it is brought about.

For some initial ideas we might look to previous published work on reedbuck. Ferrar and Kerr's (1971) reported population crash appears to be a classic example of density dependent regulation through intraspecific competition where food is the limiting resource, and inclement weather the controlling factor. Not enough evidence is cited in their paper to exclude the possibility of some kind of self-regulation, but in this regard it is noteworthy that the study was made within a relatively small fenced area, and the natural process of animal dispersal was not possible.

Dispersal of reedbuck from the Eastern Shores of Lake St. Lucia in the Natal lowveld is also very severely restricted because this area is a peninsula providing only limited access to the mainland; here the reedbuck population is apparently too young to demonstrate clearly population regulation, and was increasing at 19 % p.a. between 1974 and 1977 (Venter, 1979). Under present interventionist management, it is unlikely that the natural regulation of reedbuck numbers will occur on the Eastern Shores.

There is some evidence from a number of sources (Jungius, 1971a; Ferrar and Kerr, 1971; Venter, 1979) that reedbuck males suffer mortality in combat, and that this is a significant mortality agent particularly amongst young adults. This must be regarded as evidence of self-regulation, as must the high incidence of emigration observed in this study. Deane's (1966) paper describing the effects of community succession on a declining population of reedbuck has demonstrated the environmental sensitivity of the species, and since deaths are not reported, we might infer some kind of self-regulation.

The hows and whys of population regulation as observed in this study will be the subject of subsequent chapters of this thesis. In CHAPTER FOUR I examine the possibility that food is limiting, in CHAPTER FIVE I look at other habitat resources, CHAPTER SIX examines spatial relationships of the species in some detail, with especial reference to animal movements as these might affect the regulation of population size, and in CHAPTER SEVEN social organisation and behaviour are considered in the context of Wynne-Edwards' (1962) concepts of self-regulation.

3.5 CHAPTER SUMMARY

Three animal census techniques were applied to reedbuck in the intensive study area. The effects of season, time of day, prevailing weather conditions and phase of moon on the numbers counted were evaluated, and the accuracy of the three methods gauged against Petersen population estimates. The most useful census technique proved to be a systematic search of

planted winter pastures made soon after dark in June or July. Prevailing weather conditions and the phase of the moon had no significant effect on numbers counted, which amounted to about 80 % of the animals present.

The extensive study area was subdivided into a no-cull, a low-cull and a high-cull block. Animal numbers were assessed throughout the area in July 1981 before implementing appropriate culling regimes in which removal quotas varied between zero and twenty percent. Animal numbers were reassessed in July 1982 and July 1983, revealing great stability in population size, regardless of harvesting level.

Parameters pertinent to an understanding of population dynamics were assessed. The birth rate, calculated from a randomly shot sample of females, and from observation of a sample of free-living marked animals, was approximately 1,3 lambs per adult female per annum. Death rates were assessed through observation of free-living marked animals, from life table data derived from a randomly shot sample, and from a collection of skulls of animals found dead of natural causes. Males were subject to 'social' mortality, resulting in a mean longevity of about 4,0 years by comparison with the females' 5,3 year life span. Dispersal was found to be important in population regulation, with approximately 84 % of a sample of marked subadult females, and 28 % of marked subadult males disappearing, presumably through dispersal. The higher number of females leaving the population meant that population structure in the intensive study area was biased in favour of males, despite their shorter life span.

CHAPTER FOUR

POPULATION CONDITION

4.1 INTRODUCTION

4.1.1 Definition

The term condition is commonly used in wildlife studies, but often poorly defined. It may be used to describe reproductive state, the levels of various types of body reserves, or the demographic vigour of a population. The last of these has already been considered for this study population (CHAPTER THREE), and the term is used here to describe an animal's physiological responses to its plane of nutrition as these affect rates of survival and reproduction.

4.1.2 Factors affecting condition and the use of condition indices

These physiological responses can be broadly classified into three groups: the first are those concerning the levels of stored body reserves ('physiological' condition); the second those affecting reproductive rates ('reproductive' condition); and the last, those affecting mortality through disease ('pathological' condition). These physiological responses, which are quantified by means of specific condition indices, are closely linked with an animal's chances of living, dying and reproducing.

These facets of condition are intimately inter-related. We know that simple measures of body reserves are not a true reflection of an animal's nutritional status, because an animal's energy requirements change from time to time dependent on its growth stage, reproductive state and many other factors (Caughley, 1970; Bear, 1971; Hanks *et al.*, 1976). Physiological condition simply reflects the balance between the demands for energy and nutrients and their supply. If, as managers of wildlife, we want to know whether the supply is adequate we have to look not only at this 'left-over balance', but also at the animal's changing demands with time, and at whether these demands are being adequately met.

4.1.3 Possible methods of assessing condition

4.1.3.1 PHYSIOLOGICAL CONDITION

The various criteria used in the assessment of physiological condition have been extensively reviewed by Hanks (1981), and fall into three broad categories:

(a) Deposited Fat Reserves

Ideally, wildlife workers would like to quantify all body fat (Ledger and Smith, 1964), but this is unrealistic as a workable field technique, and the kidney fat index (KEI) method proposed by Riney (1955) has gained wide acceptance (Bear, 1971; Sinclair and Duncan, 1972; Hanks et al., 1976). A number of studies have quantified the fat content of the bone marrow (Bone Marrow Fat - BMF) expressed as a percentage of the marrow's fresh mass (Neiland, 1970; Sinclair and Duncan, 1972). Further, for more sensitive comparative studies, perinephric fat and the fat contents of different limb bones can be assessed, since fat mobilisation follows a definite sequence (Riney, 1955; Ransom, 1965; Sinclair and Duncan, 1972; Brooks et al., 1977).

(b) Stored Protein Reserves

Two indices of condition indirectly quantify levels of stored protein. The first is simply the measurement of body mass. Klein's (1968) study of reindeer on St. Matthew Island, in which average body masses were found to decrease by about 40 % over a six year period as food and space became limiting, provides a good example of the use of body mass as an index of condition. DeCalasta et al. (1975) further demonstrated the linear relationship that exists between mass loss and length of starvation in mule deer (Odocoileus hemionus hemionus). Measurements of body mass should be corrected for skeletal size (Taber and Dasmann, 1958; Grimsdell and Bell, 1975), and in view of Payne and Hutchinson's (1963) observation that live mass of zebu steers may increase by as much as 7 % after a single drinking, carcass dressed mass is preferable to live mass (see also Park and Day, 1942). Even when these precautions are taken it is impossible to identify the particular body components that account for a decline in mass, since water, minerals and lipids are lost, as well as proteins (Young and Scrimshaw, 1971). The second condition index that attempts to quantify levels of stored protein is that of liver mass. McDonald et al. (1969) state that dispensable protein reserves in the liver are the first to be mobilised in times of nutritional stress, and Williamson (1979) concluded that liver mass showed promise as an index of protein status in lechwe.

(c) Physiological and biochemical methods

Various standard medical techniques have been used to derive condition indices in wildlife studies. The use of blood constituents, particularly serum cholesterol, serum protein, blood urea nitrogen, packed cell volume and plasma glucose has met with mixed success (Hanks, 1981). So, too, has the measurement of hydroxyproline - derived from the breakdown of collagen in growing animals - in the urine (McCullagh, 1969; Malpas, 1977; Woodall, 1977). One further technique that has been widely used is the assessment of adrenal cortical hypertrophy, that results from environmentally or socially induced stress. Most studies of this have been made on small mammals (e.g. Chitty, 1952; Christian and Davis, 1966; Andrews, 1968), and work on large mammals (e.g. Welch, 1962; Smith, 1970) has so far been largely inconclusive.

4.1.3.2 REPRODUCTIVE CONDITION

As far as a general assessment of population condition is concerned, pertinent aspects of the reproductive state of individuals are assessed by a demographic approach. However, because reproductive cycles affect the levels of an animal's body reserves, indices of physiological condition should not be used without reference to reproductive condition.

Attwell (1977) identifies the following aspects of reproduction in the female which are subject to variation. Most are applicable to the male also, although the male is relatively dispensable in most polygamous mammals, and may show less marked variations. Methods used in the examination of reproductive condition attempt to quantify the extent of variation in:

- 1 the onset of the breeding season;
- 2 the duration of the breeding season or rut;
- 3 the age of attainment of puberty;
- 4 the extent of out-of-season breeding;
- 5 the pregnancy or conception rate;
- 6 the extent of intra-uterine mortality and the ratio of successful to unsuccessful pregnancies;
- 7 the duration of lactation;
- 8 the age of reproductive senescence.

4.1.3.2.1 Field methods

Field observations of free-ranging animals can often furnish information on 1, 2 and 4 above, and for intensively studied populations information may also be available on 3, 5 and 8. If animals can be handled (Grimsdell and Bell, 1975) a captured sample

will provide more detailed information, particularly with respect to pregnancy and lactation, than can be provided by simple observation.

4.1.3.2.2 Post mortem examination

Reproductive physiology is a complex subject and post mortem material has been studied in a wide variety of ways. Only those methods likely to be applicable to general studies of an ecological nature are listed below:

(a) Methods relevant to the study of reproduction in the female include:

- 1 assessment of lactational state (fresh mass of mammary gland, histological examination of tissue);
- 2 assessment of pregnancy (position and sex of fetus, mass of fetus - from which conception and birth dates are calculated (Huggett and Widdas, 1951), and the extent of reproductive seasonality derived);
- 3 ovarian examination (counts and measurement of follicles, corpora lutea and corpora albicantia, following Cheatum (1949), Golley (1957) and others);
- 4 steroid analyses from blood samples (Attwell, 1977).

(b) Methods relevant to the study of reproduction in the male include:

- 1 assessment of changes in testis mass (Robinette and Child, 1964);
- 2 assessment of change in seminiferous tubule diameter (Watson, 1969);
- 3 assessment of changes in epididymal sperm number (Skinner and Huntley, 1971);
- 4 assessment of changes in the mass of accessory glands (Chapman, 1972);
- 5 measurement of sperm motility (Skinner, 1971), and spermatogenic activity (Johnson and Buss, 1967);
- 6 hormone (Fairall, 1972) and biochemical assays (Skinner and Huntley, 1971).

4.1.4 Previous work on condition in reedbuck

Ferrar and Kerr (1971) documented a reedbuck population crash in Kyle National Park, Zimbabwe, that followed reports that reedbuck were generally in very poor condition. For several years prior to the crash, environmental resistance had successfully controlled and virtually halted

population growth by almost eliminating recruitment to the adult sector. Ferrar and Kerr 'guessed' that this was achieved by factors such as high post-natal mortality, increased predation, poor lactation, abortion, reduced fertility and conception rates, but presented no quantitative data on these aspects, or on levels of body reserves.

Venter (1979) measured kidney fat indices, bone marrow fat, aspects of blood chemistry and adrenal mass and linear dimensions in a sample of 107 culled animals of which 92,5 % were classed as being in good physical condition (Riney, 1960). Venter could show no seasonal changes in KFI or BMF indices, and concluded that the animals were under no nutritional stress at the end of winter. He made no attempt to relate body reserves to reproductive condition, and though there were significantly more juveniles present in the population in August, he found no significant birth peak in any one month.

4.1.5 Purpose of monitoring condition in this study

It seems likely that in the farm environment reedbuck would be able to compensate for the decline in the quality of 'natural' winter forage by feeding on high quality crops, and thus maintain an artificially high plane of nutrition. This should be reflected in good condition, increasing the individual animal's chances of survival and affecting the demographic vigour of the population.

The demographic state of the population under intensive study has already been described (CHAPTER THREE), and the purpose of this chapter is to help examine whether the observed population stability can be explained in terms of physiological processes related to nutritional plane. Measurements of physiological condition are, of course, of greatest value when comparisons can be drawn between populations, and since few data are yet available for most African ungulates, much contemporary work in this field has to be presented as baseline data in the expectation that it will be of some value to wildlife managers tackling similar problems in the future.

In terms of the present study the purpose of monitoring condition is:

- 1 to document baseline data for a population of common reedbuck under intensive autecological study;
- 2 to attempt to ascertain whether this population is food-limited (Melton, 1978; Scotcher, 1982) by monitoring seasonal changes in the levels of various body reserves, reproductive seasonality, and rates of growth, and drawing comparisons with other populations.

4.2 METHODS

4.2.1 Field methods

The physical condition of animals recorded during regular censusing was assessed by Riney's (1960) method of field classification, by which animals are classed as being in good, moderate or poor condition on the basis of obvious external characters.

4.2.2 Assessment of physiological condition

The physiological condition of the population under intensive study was examined by use of a number of the standard autopsy techniques outlined above (SECTION 4.1.3.1). Post mortem sampling was undertaken throughout the year, and every effort made to ensure an even distribution of sampling effort between each two-month period. With few exceptions, animals were randomly shot between 18h00 and 24h00 and routine autopsies carried out only after the last animal had been collected on any one night. In total 106 male and 91 female reedbuck were collected. Linear body measurements, blood smears and PCV values were the only measurements to be taken in the field at the time of death. On return to the field laboratory carcass mass measurements were taken using a 100 kg Salter spring balance to the nearest 0,5 kg, and the masses of different organs were taken using two triple beam balances, such that measurements were accurate to within 1 % of the organ's mass.

The various measurements taken are listed below.

(a) Body growth

- 1 dead mass, being the dead mass of an animal without correction for blood loss (Williamson, 1979);
- 2 dressed mass, being the dead mass minus the entire contents of the body cavity, and the head;
- 3 total length, being taken 'over the curve' along the mid-dorsal line from the top of the upper lip to the tip of the tail (Ansell, 1965);
- 4 body girth, being taken around the body immediately behind the front legs;
- 5 neck girth, being the circumference of the neck at the mid-point between the head and shoulders;
- 6 shoulder height, being the linear distance from the base of the hoof to the top of the scapula, when light upward pressure is applied to the foot, and the knee held straight;
- 7 horn length, being taken around the curve, along the front

edge of the horn, and excluding the boss of hardened skin at the base (Best, 1981).

Measurement data were analysed by computer, using the program developed by Hanks (1972) for the Von Bertalanffy (1938) growth equation.

(b) Body reserves

The following measures of an animal's body reserves were made:

- 1 liver mass (Williamson, 1979), recorded fresh with the gall bladder cut away;
- 2 dressed mass (Taber and Dasmann, 1958);
- 3 kidney fat index: Riney's (1955) method was adopted unchanged;
- 4 bone marrow fat percentage: the right femur only was used, since mobilisation of marrow fat begins in the bones of the upper leg (Brooks et al., 1977), and these bones are consequently likely to be the most sensitive indicators of a drop in condition, where a population is known to be in generally good condition. The percentage fat content was predicted from the percentage dry mass, using the regression equation for reedbeek of Brooks et al. (1977).

(c) Stress Indicators

- 1 Adrenal mass (Christian, 1955)

4.2.3 Assessment of reproductive condition

In terms of the stated objectives (SECTION 4.1.5), examination of reproductive condition is intended to quantify:

- 1 the extent of any seasonality in the reproductive cycle;
- 2 the rate at which live births are made;
- 3 the age at puberty;
- 4 the age at sexual senescence (if apparent).

It was considered that only these four aspects were likely to be of any practical value in either helping to explain the demographic state of the study population, or as baseline data for comparison with other populations. Since reproductive activity (particularly later pregnancy and lactation) is a drain on an animal's body reserves, examination of the relationship between reproductive state and the levels of these reserves was made, to help provide an understanding of the underlying cause of any

seasonal changes in body reserves.

Reproductive condition of the sample of 106 male and 91 female reedbuck was assessed in the following ways:

4.2.3.1 MALES

As soon after death as possible, the testes were removed from the scrotum, and the mass of testes and epididymides recorded separately. A small portion of the testes, and the whole of the caput epididymis were fixed in 10 % buffered neutral formalin for later histological processing. After routine embedding, testis and epididymis samples were sectioned at 7 μ m and stained with haematoxylin and eosin. These were then examined microscopically as follows:

- 1 Epididymides were examined from each animal, and all animals in which sperm were present were regarded as being sexually active.
- 2 For animals in which no sperm were apparent in the epididymides, testis sections were examined for the presence of spermatogenesis. Testes were regarded as prepubertal if no spermatids were found in the lumen of the seminiferous tubule, and only a single layer of cells was apparent at the basement membrane of the tubule.
- 3 Seminiferous tubule diameters (taken for each animal as the mean of 30 diameters in circular cross-sections) were measured in a select sub-sample, to examine the possibility of a male sexual cycle, and of sexual senescence. Since a peak in conceptions was inferred from pregnancy data (SECTION 4.3.3.2) during March, April and May, seminiferous tubule diameters were measured in all adults aged three to six years shot during this period of the year, and compared with those shot in September, October and November, during the 'conception lull'. These measurements were then compared with those from all animals over six years of age, to examine the possibility of sexual senescence.

4.2.3.2 FEMALES

Before opening the body cavity the mammary gland was dissected away, weighed and its activity noted. The reproductive tract was then removed, noting the site of implantation in pregnant animals. Fetuses were weighed and, where possible, sexed to provide information on natal sex ratios and birth and conception dates (Huggett and Widdas, 1951). Both ovaries were removed, weighed, and stored in 10 % buffered neutral formalin for later macroscopic

examination. To quantify the variables listed above (SECTION 4.2.3) the following procedures were adopted:

- 1 Reproductive seasonality was investigated by examining the seasonal distribution of birth dates derived from fetal masses (Huggett and Widdas, 1951). The number of births recorded in any one month was expressed as a proportion of the 'births potential' for that month, given that sampling of adult females was not evenly distributed throughout the year. The maximum possible number of births that could be recorded in any month (the 'births potential'), obviously depends on the number of adult females sampled in the period of (possible) gestation preceding that month. In this study, the 'births potential' for any month was calculated as being equivalent to the total number of sexually mature females shot in a period of 233 days (the gestation period) prior to the last day of the month, plus the sums of the proportions of the month in question during which a female, shot in a period of 233 days prior to the first day of the month, could potentially have given birth, plus the sums of the proportions of the month in question during which a female, shot during that month, could potentially have given birth. Thus an adult female shot on 15 March (which could have a fetus due at any time between that date and 3 November, 233 days later), would contribute a 0,5 'births potential' score to the March total, a 1,0 score to each month from April to October, and a score of 0,1 to the November total.
- 2 Birth rates were calculated from the pregnancy rates of randomly culled females and considered with respect to age (Caughley, 1977).
- 3 Age at puberty was calculated in two ways. Firstly, pregnant females with immature mammary glands were considered to be in their first pregnancy, and the mass of the fetus was used (Huggett and Widdas, *op.cit.*) to calculate the conception date. The tooth eruption table of Venter (1979) (APPENDIX D) was then used to calculate age at first conception. Secondly, the ovaries of all non-pregnant females were examined (Cheatum, 1949; Golley, 1957) macroscopically for presence of corpora lutea, corpora albicantia and large Graffian follicles. Thirty one pairs of ovaries were examined in this way. Ovaries in which one or more corpus luteum or corpus albicans was recorded were regarded as being post-pubertal. The diameter of the larger follicles was measured with Vernier slide calipers, and the largest of these was considered to be on the point of rupture at 7,1 mm. Thus an arbitrary value of 5,0 mm for the

diameter of the largest follicle was taken as indicative of an animal very close to puberty (Sayer and Rakha, 1974).

- 4 The age at sexual senescence was not calculated as only two mature post-pubertal females were reproductively inactive, and in neither case was reproductive senescence considered to be the cause.

4.2.4 Assessment of pathological condition

The following methods were used:

- 1 Animals were examined for external parasites, and tick loads assessed quantitatively by counting ticks on the ears. Tick loads were classified on a four-point scale ranging from very light (less than 5 ticks > 2 mm in diameter) to heavy (more than 50 ticks > 2 mm in diameter) infestations.
- 2 Packed Cell Volume (PCV) (Wilson and Hirst, 1977) was assessed on a fresh blood sample taken from the jugular vein, using a battery operated mini-centrifuge in the field.

Of particular interest in the farming community is the possibility that reedbeek transmit parasites and disease organisms affecting domestic stock. A need was identified to carry out a more detailed project on these aspects of pathological condition than could be adequately covered within this study. Such a project was initiated in April 1983 by Dr M. Keep of the Natal Parks Board, and post mortem sampling began in May 1983 on farms within the extensive study area. The results of this investigation, a collaborative project between Dr Keep and Dr Boomker of the Faculty of Veterinary Science at the University of Pretoria, will be written up after completion of the field-work in mid-winter 1984.

4.3 RESULTS AND DISCUSSION

4.3.1 Field methods

Very few (<0,2 %) of the animals observed in the field were in sub-optimal physical condition (Riney, 1960), and of a total of approximately 10 000 animal observations, only seven were of animals considered to be in poor condition. These statistics alone provide a general estimate of the condition of the study population, that might be valuable as one measure of the response of a study population to a given ecosystem (Riney, 1956).

4.3.2 Physiological condition

4.3.2.1 CHANGES IN RELATION TO AGE

The relationship between age and various measures of body size is summarised in TABLE 4.1, using the Von Bertalanffy growth equation (Von Bertalanffy, 1938; Hanks, 1972). Changes in dead mass with age are illustrated for males and females in FIG. 4.1, and changes in body length, neck girth, shoulder height and horn length are illustrated in FIG. 4.2 for males only.

TABLE 4.1 : Von Bertalanffy equations for growth in males and females

PARAMETER	SEX	VON BERTALANFFY EQUATION	AGE IN YEARS AT ASYMPTOTE - 2,5 %
Mass	M	$m_t = 69,11 (1 - e^{-0,76(t + 1,31)})^3$ kg	5,5
	F	$m_t = 46,74 (1 - e^{-2,13(t + 0,29)})^3$ kg	2,5
Total length	M	$l_t = 171,87 (1 - e^{-0,72(t + 1,83)})$ cm	3,5
	F	$l_t = 154,65 (1 - e^{-2,35(t + 0,30)})$ cm	1,75
Neck girth	M	$l_t = 54,07 (1 - e^{-0,42(t + 1,06)})$ cm	6,5
	F	$l_t = 27,89 (1 - e^{-0,95(t + 1,12)})$ cm	3,5
Body girth	M	$l_t = 89,92 (1 - e^{-0,66(t + 1,70)})$ cm	4,5
	F	$l_t = 76,09 (1 - e^{-2,74(t + 0,26)})$ cm	1,25
Shoulder height	M	$l_t = 91,17 (1 - e^{-0,40(t + 4,51)})$ cm	4,5
	F	$l_t = 81,60 (1 - e^{-1,62(t + 0,92)})$ cm	1,75
Horn length	M	$l_t = 316,68 (1 - e^{-0,91(t - 0,37)})$ mm	4,5

FIG. 4.1 : Theoretical Von Bertalanffy growth curves for dead mass (mean values are shown \pm two standard errors)

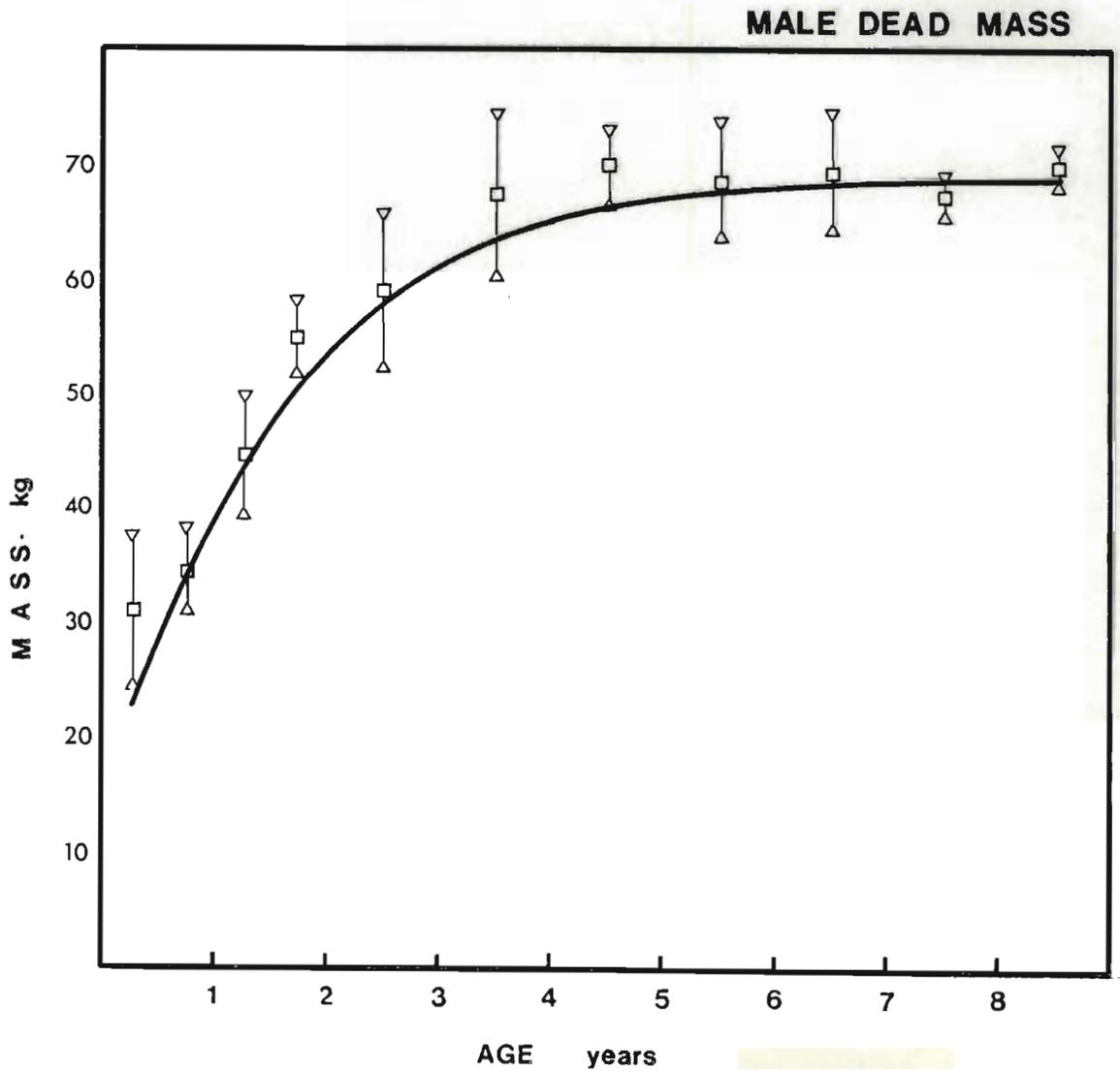
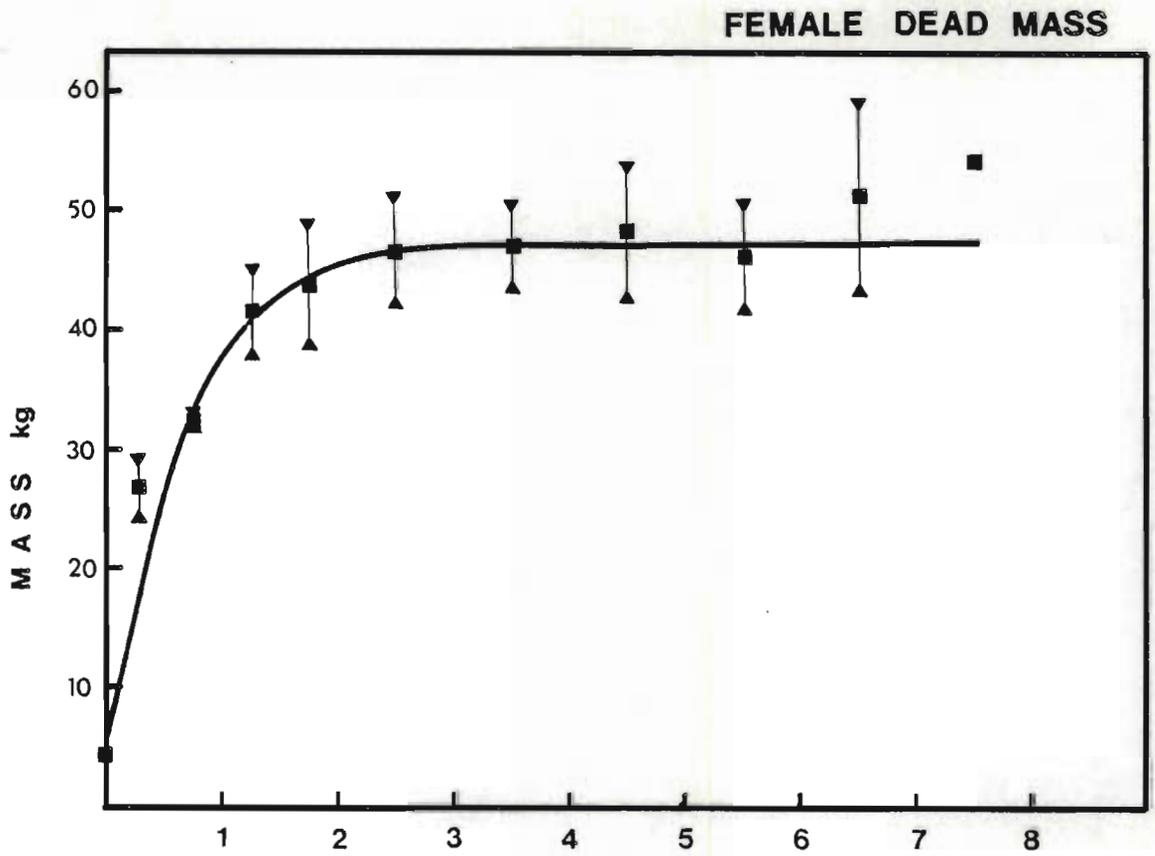
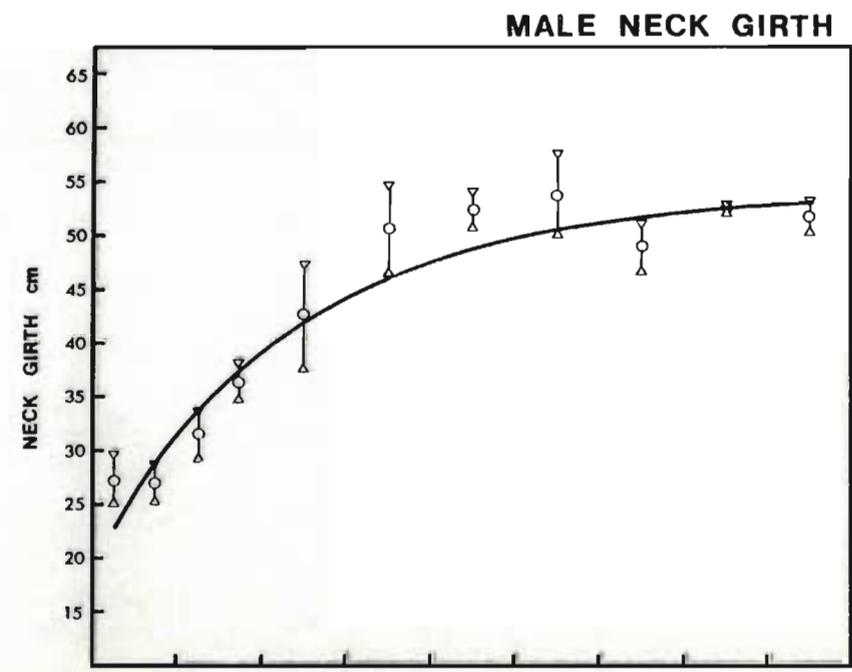
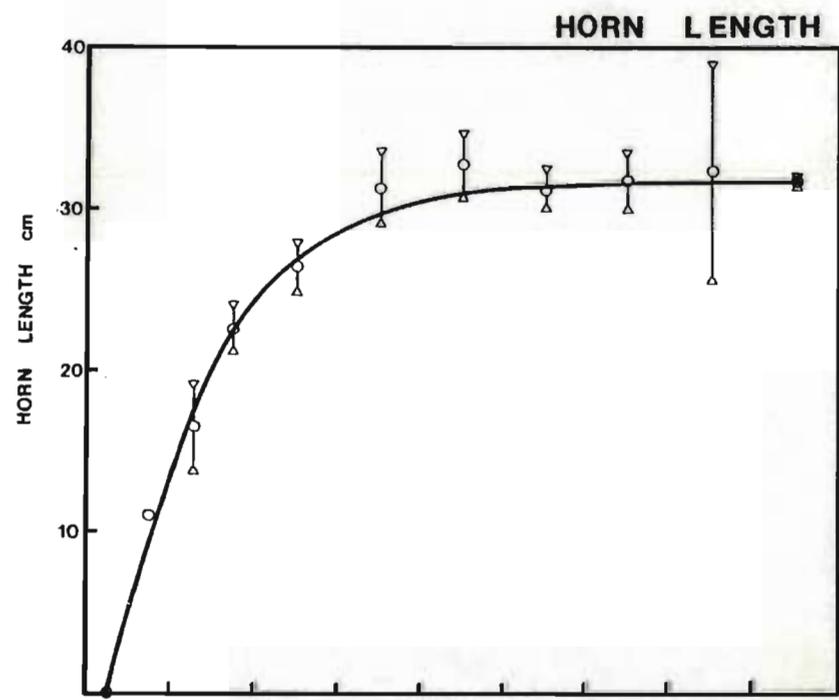
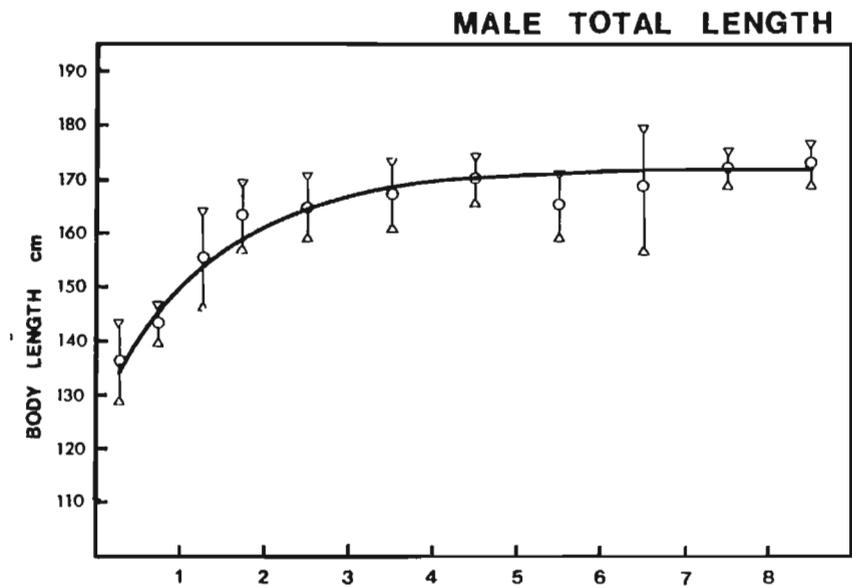
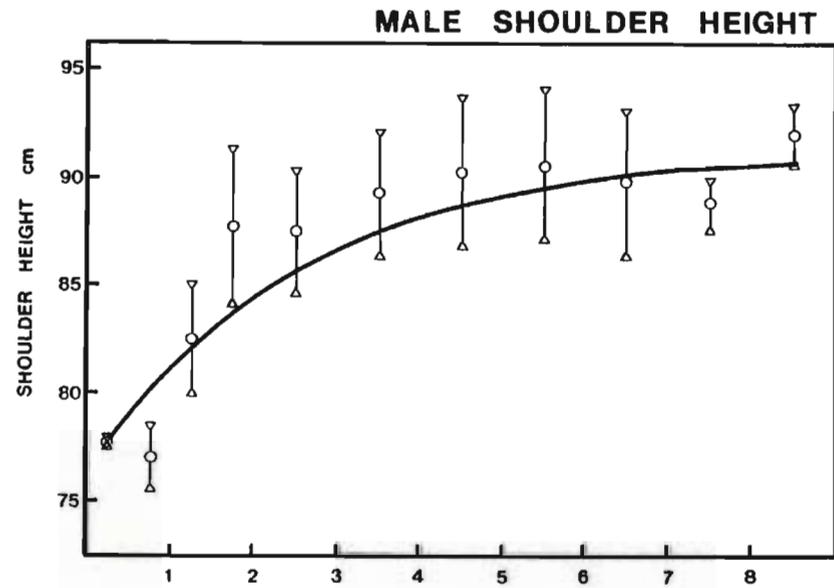


FIG. 4.2 : Theoretical Von Bertalanffy Growth Curves (Mean values are shown \pm two standard errors)



The relationships established here must be regarded as baseline data, as no previous work on rates of growth are available for this species. Some mean adult values have, however, been established (Venter, 1979) for a number of parameters. Two particular aspects are of interest and value in between-population comparisons. The first of these is the asymptotic value for particular parameters, as this will be influenced by plane of nutrition (as well as the animal's genetic make-up). The second is the rate at which that asymptote is reached, which is most easily expressed as the age at which the fitted curve achieves 97,5 % of the asymptotic value (Attwell, 1980; Jeffery and Hanks, 1981). The worth of asymptotic values as indices of condition reflecting nutritional status has been clearly demonstrated by studies such as those of Taber and Dasmann (1958), Klein (1968), others reviewed by Klein (1970), and Wegge (1975). Body mass in particular, has become a universally used criterion reflecting nutrient status of ungulate populations, and there are many examples where large body size is correlated with good forage quality (Klein, 1970). A comparison of simple mean values for the dead mass, total length, neck girth, body girth and shoulder height of adult reedbuck at Lake St. Lucia (Venter, 1979) with those in this study population (TABLE 4.2) reveals that there are no significant differences between them with respect to dead mass or body girth. Observed differences in the total length of males from these populations, and in female neck girth are more difficult to explain than those involving measurements of shoulder height; in the latter case the amount of pressure applied on the hoof at measuring introduces unknown observer bias. Despite these anomalies, the condition of adult reedbuck in these two populations cannot be considered to be significantly different on the basis of measurements of mean values for the growth parameters taken.

There are no comparative data describing rates of growth in other reedbuck populations, and so the ages at which the asymptotic values are reached (TABLE 4.1) must be considered as descriptive baseline data. It can be seen that, as in other sexually dimorphic African ruminants, males attain a greater mature size than females not simply by growing faster, but, more importantly, by continuing to grow after female growth has stopped (Georgiadis, in press) (TABLE 4.1; FIG. 4.1).

Body growth undoubtedly makes heavy demands on an animal's supply of nutrients (Young and Scrimshaw, 1971; Hanks *et al.*, 1976) such that little or nothing is available for storage. Numerous recent studies (for example, Attwell, 1977; Williamson, 1979) have demonstrated this by simply comparing the levels of various types of recognised body reserves in growing and mature animals; the results of these

TABLE 4.2 : Comparison of mass and linear measurements of adult reedbuck from the highlands (this study) and Eastern Shores of Lake St Lucia (Venter, 1979). Means are shown \pm 1 standard error

PARAMETER	SEX	HIGHLANDS POPULATION (this study)	EASTERN SHORES POPULATION (Venter, 1979)	SIGNIFICANCE OF DIFFERENCE (t-test)
Dead mass (kg)	M	67,7 \pm 0,78 (n=60)	67,8 \pm 1,9 (n=12)	p > 0,1
	F	47,2 \pm 0,63 (n=70)	49,4 \pm 0,7 (n=46)	p > 0,1
Total length (cm)	M	168,7 \pm 0,87 (n=60)	163,5 \pm 1,8 (n=12)	p < 0,02
	F	155,0 \pm 0,65 (n=70)	157,1 \pm 1,0 (n=46)	p > 0,1
Neck girth (cm)	M	50,2 \pm 0,60 (n=59)	53,7 \pm 1,6 (n=12)	p > 0,1
	F	27,7 \pm 0,30 (n=64)	34,1 \pm 1,3 (n=46)	p < 0,001
Body girth (cm)	M	88,7 \pm 0,47 (n=60)	88,0 \pm 1,1 (n=12)	p > 0,1
	F	77,3 \pm 0,46 (n=67)	77,5 \pm 0,6 (n=46)	p > 0,1
Shoulder height (cm)	M	89,3 \pm 0,40 (n=60)	92,9 \pm 0,7 (n=12)	p < 0,001
	F	81,2 \pm 0,40 (n=70)	85,2 \pm 0,6 (n=46)	p < 0,001

studies are regarded as conclusive, and changes in physiological condition in relation to season and reproductive condition are consequently only considered for physically mature animals in this study.

There is a moderately good positive correlation between age and adrenal mass in both male and female reedbuck (TABLE 4.3). Even when these data are corrected for body size, the same significant trends occur (FIG. 4.3). In females the index increases throughout life (with considerable within age class variation), by an amount described by the regression equation $y = 0,14x + 0,77$ ($r=0,64$), where y is the adrenal mass index in gm^{-1} and x the age in years. In males the increase only occurs up to three to four years of age ($y = 0,12x + 0,68$; $r=0,49$ between birth and three and a half years of age), levelling off thereafter ($y = 0,004x + 1,02$; $r=0,03$ for all age groups above three and a half years). This results in significant differences between the sexes in animals over four years of age.

FIG. 4.3 : Changes in Adrenal Mass Index with age
(mean values are shown \pm two standard errors)

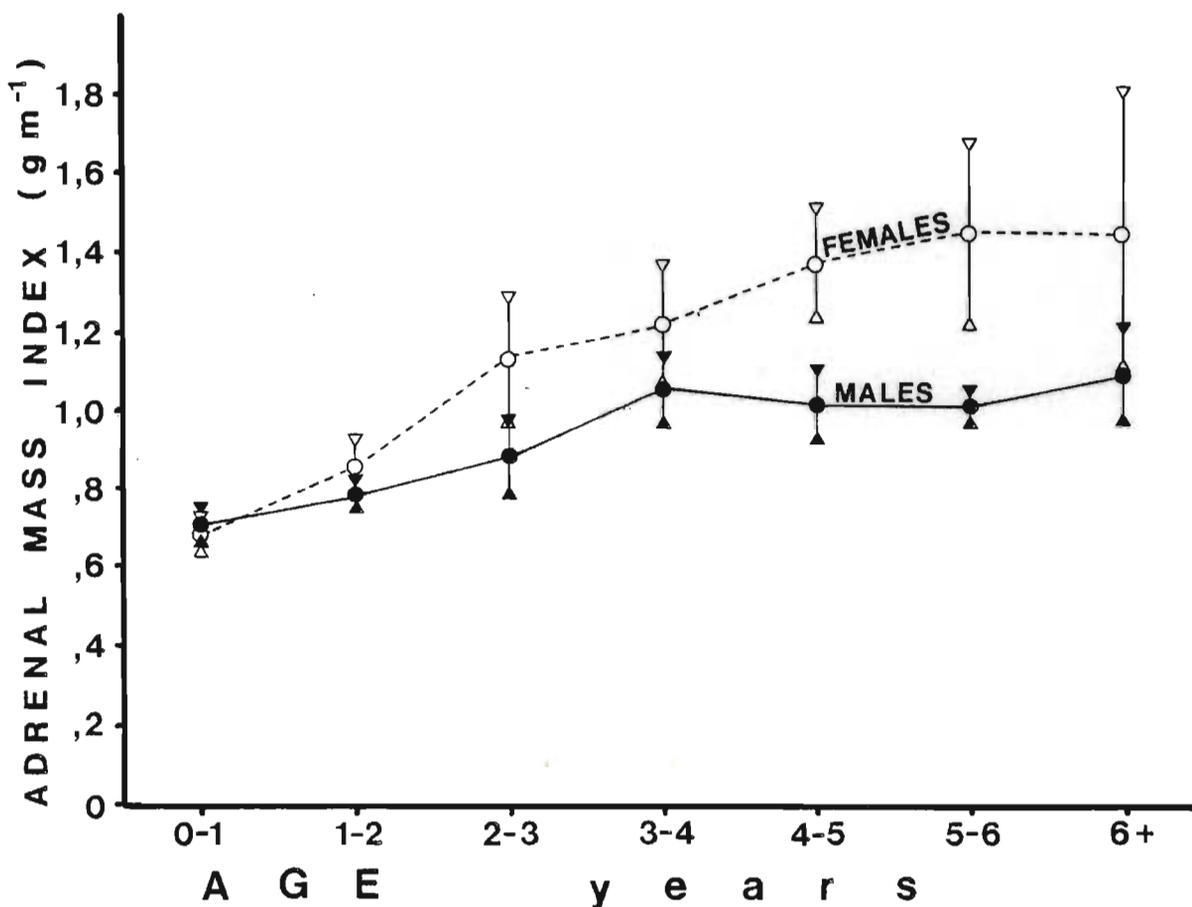


TABLE 4.3 : Changes in mean adrenal mass with age (means are shown \pm 1 standard error)

AGE	FEMALES	MALES
0 - 1	0,93 \pm 0,038 (n = 12)	0,99 \pm 0,04 (n = 8)
1 - 2	1,30 \pm 0,06 (n = 10)	1,25 \pm 0,04 (n = 20)
2 - 3	1,74 \pm 0,13 (n = 15)	1,45 \pm 0,09 (n = 18)
3 - 4	1,89 \pm 0,12 (n = 11)	1,76 \pm 0,08 (n = 24)
4 - 5	2,10 \pm 0,11 (n = 15)	1,72 \pm 0,08 (n = 10)
5 - 6	2,26 \pm 0,19 (n = 11)	1,66 \pm 0,04 (n = 7)
> 6	2,32 \pm 0,30 (n = 4)	1,86 \pm 0,11 (n = 8)

Differences in adrenal masses between the sexes have been reported in several species, with larger glands consistently recorded in the female (Goertz, 1965; Kumfrey and Buss, 1969; Rana *et al.*, 1975). Christian and Davis (1966) found that adrenal mass increased sharply at sexual maturity in female voles (*Microtus pennsylvanicus*), and attributed this to increased secretion of oestrogen. They found no change in adrenal mass with reproductive state once maturity had been reached, and in this regard their observations are at variance with those of Bell and Weber (1959) and Kumfrey and Buss (1969), but in agreement with observations made on reedbuck in this study (SECTION 4.3.2.3). Moreover, where Christian and Davis (1966) found a marked increase in adrenal mass with increased population density of voles, Rana *et al.* (1975) established exactly the opposite in Cutch Rock-rats (*Rattus cutchicus*). Clearly, from these results and others (Hughes and Mall, 1958; Smith, 1970; Attwell, 1982) it is clear

that insufficient is currently known with regard to adrenocortical hypertrophy for adrenal measurements to be of any practical value in wildlife management. If we could attribute an increase in adrenal mass to social stress, as appears to be indicated for small mammals (Andrews, 1968, 1970; Christian, 1975; To and Tamarin, 1977), then the observed changes in adrenal mass with age in male reedbeek might be regarded as further evidence in support of a theory recognising the importance of socially induced mortality amongst three to four-years olds, as a mechanism of population regulation (CHAPTER THREE).

4.3.2.2 CHANGES IN RELATION TO SEASON

The extent of seasonal changes in the levels of various body reserves are illustrated for males in FIG. 4.4 and FIG. 4.5, and for females in FIG. 4.6 and FIG. 4.7, where the summer 'season' is the period from November to February inclusive, and the winter 'season' from May to August. There are no significant seasonal differences in kidney or femur marrow fat, nor in dressed mass or liver mass indices of adult males. There are, however, some significant seasonal differences in the body reserves of adult females.

Among females, femur marrow fat is significantly lower ($p < 0,05$) in December/January than during any period between April and November. Kidney Fat Index is significantly lower ($p < 0,05$) in October/November than in June/July. This period of lowered body fat reserves coincides with an observed birth peak (SECTION 4.3.3.2 below) and probably reflects endogenous events associated with the reproductive cycle. It is widely accepted (Robbins and Moen, 1975) that late pregnancy and lactation create heavy demands for nutrients, and we should expect this to be reflected in lowered physiological condition at this time. Scotcher (1982) has shown that in female eland fat is laid down during early pregnancy in preparation for this drain on resources. As in the present study, Scotcher found that fat levels were highest in mid-winter, when the quality of available forage was at its lowest, and that this preceded a birth peak in spring. This provides a good example of where simple measurements of an animal's body reserves can be misleading if interpreted as being indicators of nutritional status. In this regard Verme and Ozoga (1980) also concluded that in white-tailed deer lipogenesis comprises an obligatory physiological event in autumn, regardless of nutritional plane.

The results presented here also seem to indicate that mobilisation of fat reserves is underway in mid-summer, coinciding with the birth peak (SECTION 4.3.3.2). Several studies (for example, Sinclair and Duncan, 1972; Brooks et al., 1977) have described a sequence of

FIG. 4.4 : Bi-monthly changes in body fat reserves of adult males
(mean values are shown \pm two standard errors)

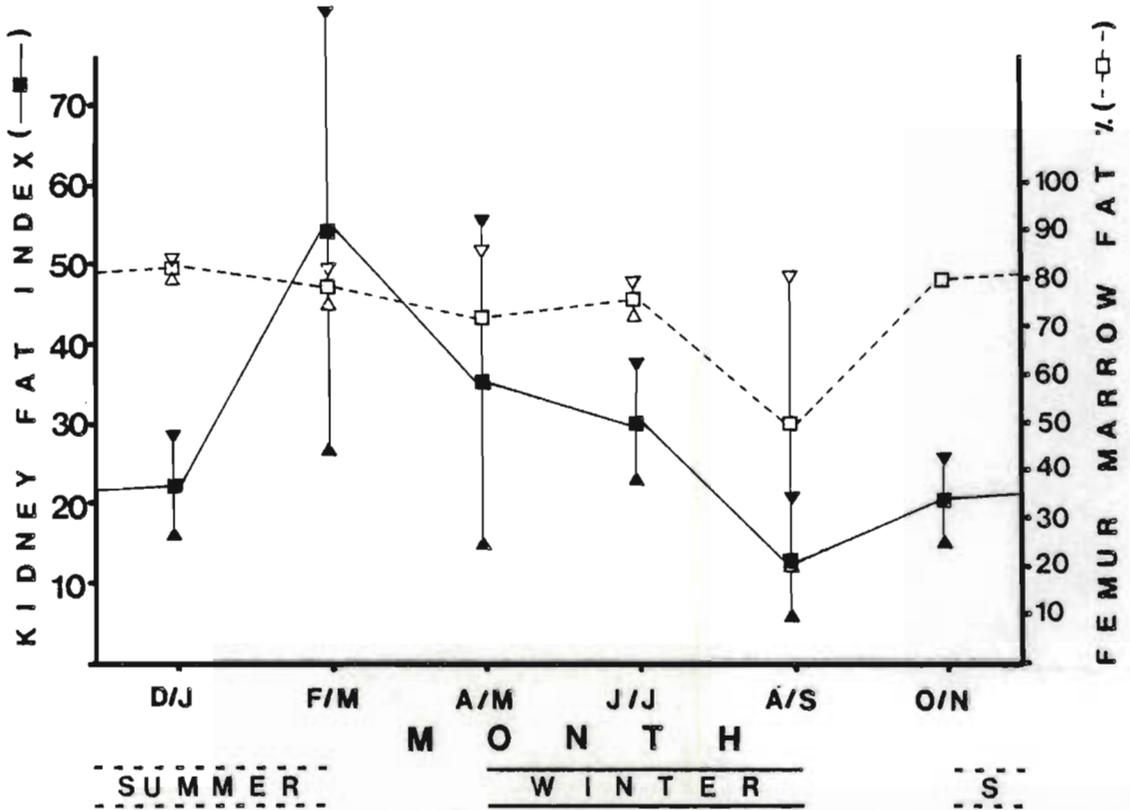


FIG. 4.5 : Bi-monthly changes in protein reserves of adult males
(mean values are shown \pm two standard errors)

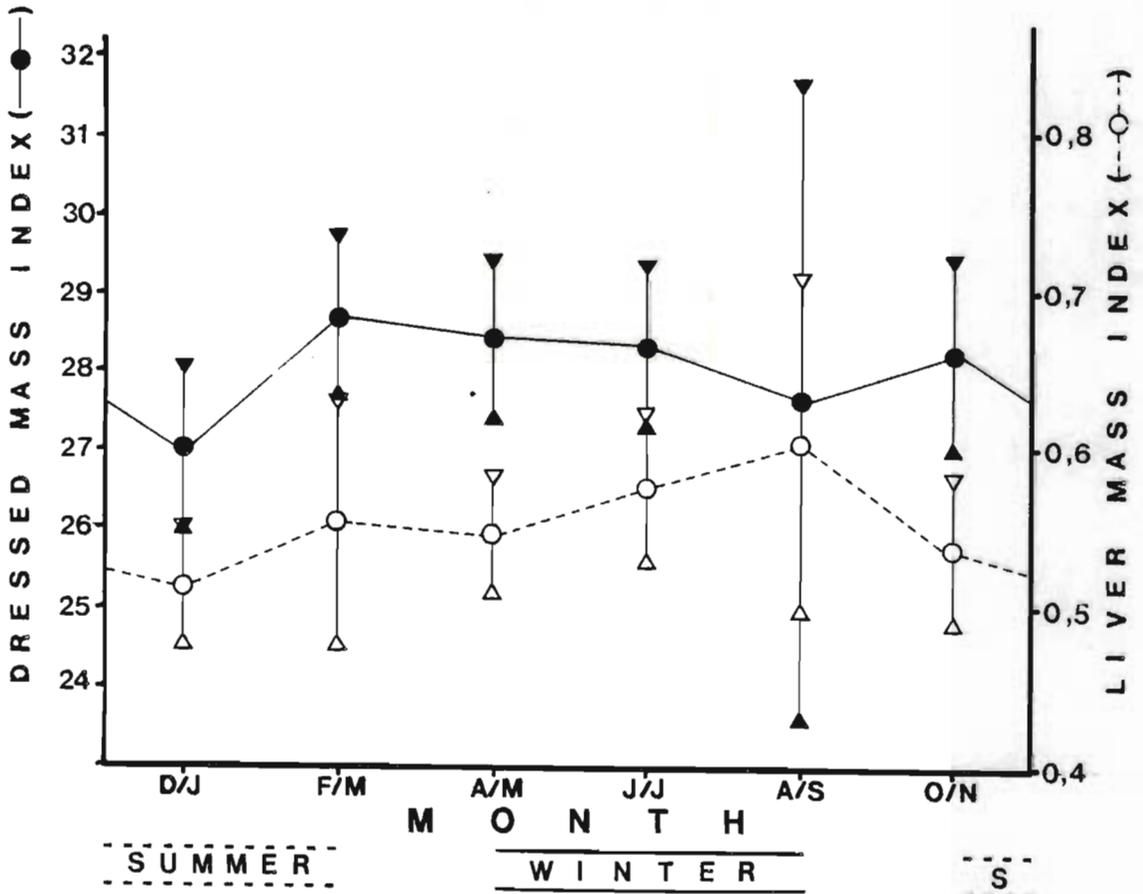


FIG. 4.6 : Bi-monthly changes in body fat reserves of adult females
(mean values are shown \pm two standard errors)

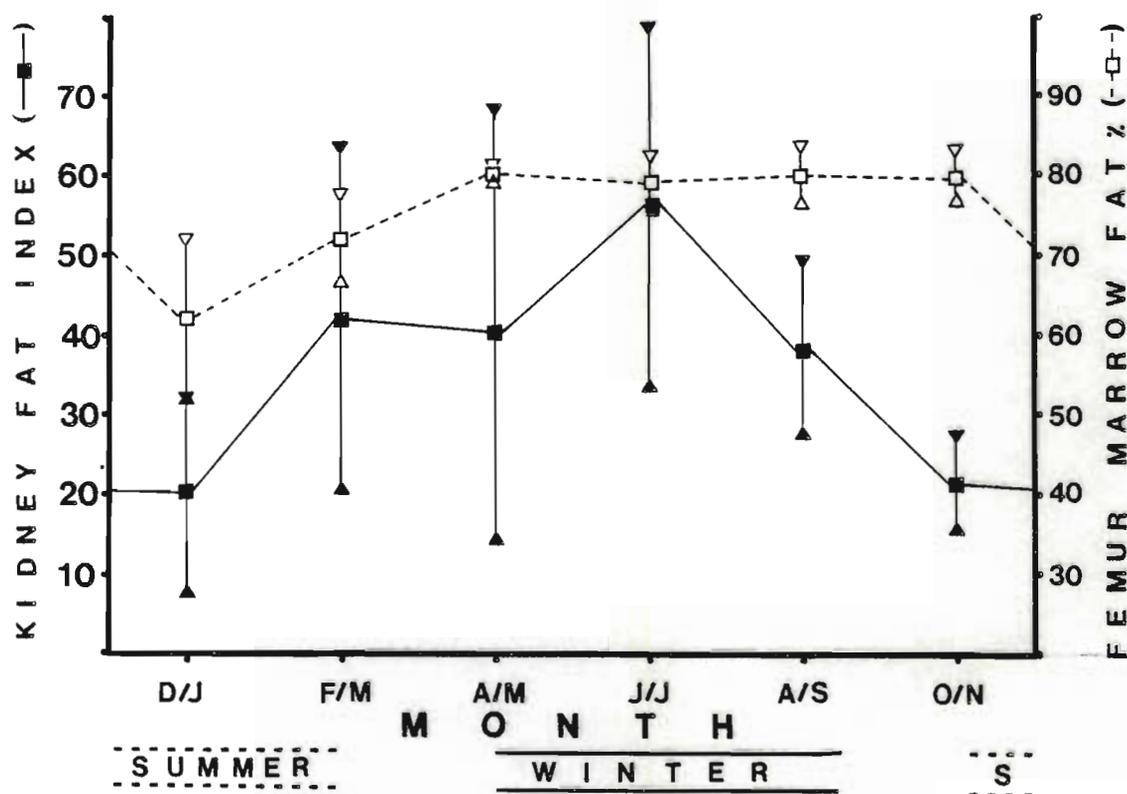
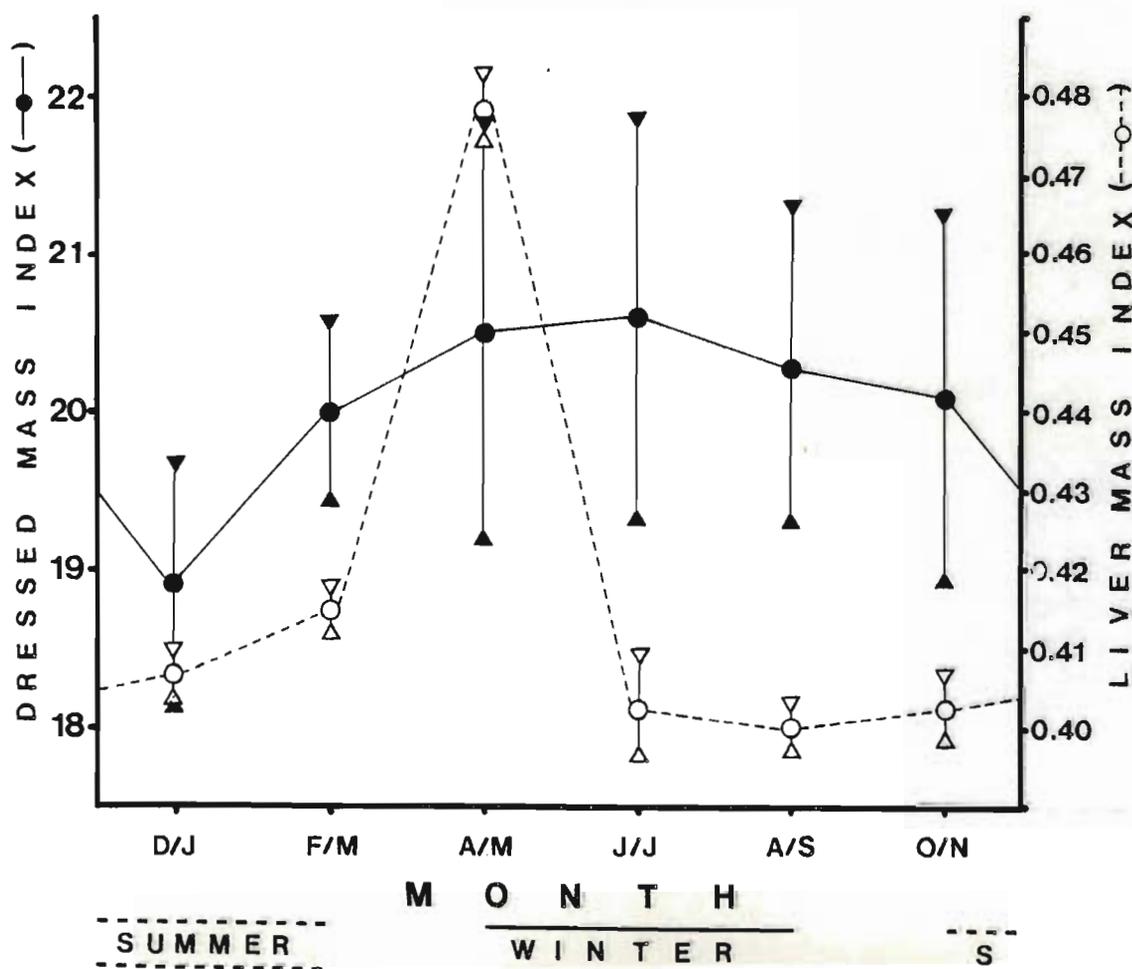


FIG. 4.7 : Bi-monthly changes in protein reserves of adult females
(mean values are shown \pm two standard errors)



mobilisation of fat from different parts of the body, that begins subcutaneously, later affecting perinephric fat, and moving finally to the bone marrows. In view of this, the results presented here would seem to indicate that mobilisation of kidney fat is well underway in October/November, while fat reserves in the marrows of the femur remain intact until December/January, when those too are mobilised.

Hanks (1981), citing Dauphine's (1975) observations of pronounced seasonal changes in kidney mass of caribou (Rangifer tarandus), cautions against the indiscriminate use of kidney mass in the standardisation of measurements of perinephric fat. Thus, in this study, a comparison was made between adult female kidney mass in June/July and October/November, which revealed no significant ($p > 0,1$) difference between samples, thus confirming the observed trends.

The protein reserves of adult females, indexed by dressed mass index, show a slight but insignificant ($p > 0,1$) increase in mid-winter, in line with the observations made on fat reserves. Indexed by liver mass index, mean values in April/May are very significantly ($p < 0,001$) higher than at any other time of the year, but there are no significant differences ($p > 0,1$) between any other mean values. Since the April/May value is based on a mean of 11 samples, no single one of which was extraordinary, and which originated on a number of different farms throughout the study area we must accept that the phenomenon is real. It may be significant that fat reserves are accumulating at this time of the year (FIG. 4.6), and since the liver is involved in lipogenesis, the increase in its mass may reflect an accumulation in the liver of the various metabolites involved.

Seasonal changes in mean adrenal mass index are illustrated in FIG. 4.8 for adult males and females. There are no significant seasonal differences.

4.3.2.3 CHANGES IN RELATION TO REPRODUCTIVE STATE

The influence of reproductive state on selected indices of physiological condition was examined in adult females only, since significant seasonal differences were apparent in this class only (SECTION 4.3.2.2). The two adult females that were neither pregnant nor lactating were excluded from the analysis, and the remainder categorised as lactating only; pregnant only, fetus less than half term; pregnant only, fetus greater than half term; pregnant and lactating. Mean values for dressed mass index, liver mass index, kidney fat index, and mean adrenal mass index in each of these categories are presented in TABLE 4.4. The relationship between

FIG. 4.8 : Bi-monthly changes in Adrenal Mass Index for adult males (●) and females (○) (means \pm 2 std. errors are shown)

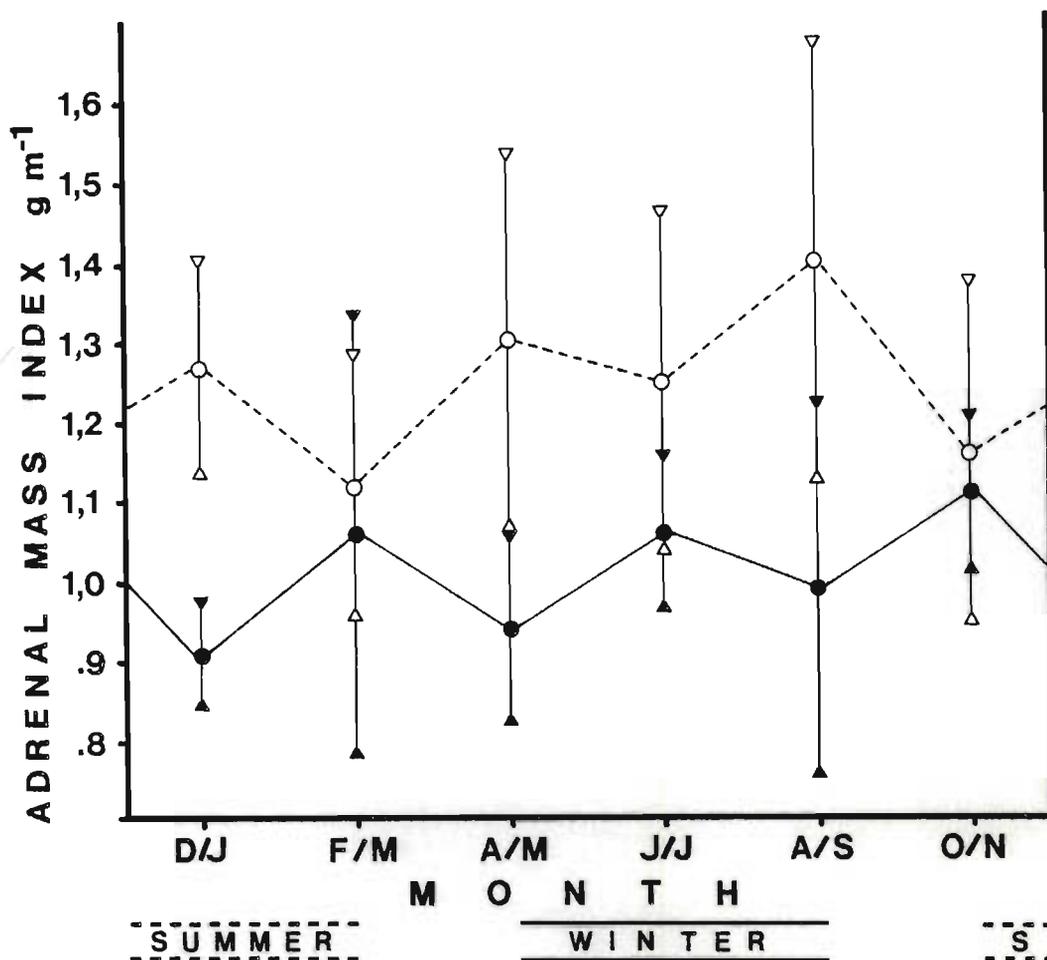


TABLE 4.4 : The relationship between reproductive status and dressed mass, liver mass, kidney fat and mean adrenal mass indices. Mean values are shown \pm 1 standard error.

REPRODUCTIVE STATE	n	DRESSED MASS INDEX (kg m ⁻¹)	LIVER MASS INDEX (kg m ⁻¹)	KIDNEY FAT INDEX (%)	MEAN ADRENAL MASS INDEX (g m ⁻¹)
Lactating only	13	19,85 \pm 0,50	0,412 \pm 0,017	18,15 \pm 4,16	11,94 \pm 0,54
Pregnant and lactating	30	19,26 \pm 0,28	0,408 \pm 0,013	28,52 \pm 4,38	12,60 \pm 0,67
Pregnant only < half term	11	20,21 \pm 0,41	0,396 \pm 0,029	62,45 \pm 12,35	11,82 \pm 1,15
Pregnant only > half term	11	21,45 \pm 0,65	0,444 \pm 0,024	42,54 \pm 10,16	12,96 \pm 1,06
Significance of difference between highest and lowest values (t-test)		p < 0,001	p > 0,1	p < 0,002	p > 0,1

using the 'grab technique' of Hanks *et al.* (1976), bone marrow fat was assessed from the metacarpus, and adrenal data were not considered by age and sex class.

In view of the obvious need for comparative data to facilitate in the interpretation of the possible effects planted pastures may have, physiologically, on farm-dwelling reedbuck, a small sample of adult males was shot in the nearby Loteni and Giant's Castle reserves at the end of winter 1982. The results and their implications are discussed in APPENDIX F.

4.3.3 Reproductive condition

4.3.3.1 CHANGES IN RELATION TO AGE

The reproductive condition of 196 randomly culled reedbuck was examined, and the results are presented in TABLE 4.5 for particular age and sex classes.

The presence of abundant sperm in histological sections of the epididymides of all males over an estimated age of nine months, indicated that these animals were postpubertal. Puberty is reached in the male at between six and nine months of age; one of four animals examined in this age class was considered to be at the point of puberty, as there was only a trace of sperm in the epididymides, and examination of a testis section revealed the presence of spermatids in only a few of the seminiferous tubules.

Macroscopic ovarian examinations showed that 50 % of females achieved a Graffian follicle of at least 5,0 mm in diameter between the ages of nine and twelve months, and since more than 50 % had conceived by the time they had reached fifteen months of age, an estimated age of puberty in the female is given as twelve months. This is corroborated by the calculation of an average age at first conception from seven reproductively active yearling females of 11,8 months, with a range from 7 to 15,5 months. The considerable range is probably more an expression of the variability associated with the use of tooth eruption as a criterion for age determination (APPENDIX D), than a real expression of variability in age at puberty.

Age at puberty is widely recognised (Joubert, 1963; Sadleir, 1969; Verme, 1969) as being a good indicator of a population's condition, and this makes between population comparisons particularly valuable. In the ungulate male puberty is reached long before social maturity is achieved (Altmann, 1960; Emlan, 1973; Williams, 1975; Leuthold, 1977), whereas the female becomes reproductively active as soon as

TABLE 4.5 : The number of individuals in a given reproductive state, considered by age class

AGE CLASS (mths)	M A L E S			F E M A L E S									
	PREPUBERTAL	PUBERTAL	POSTPUBERTAL	PREPUBERTAL	PUBERTAL *	}} not pregnant not lactating		}} pregnant not lactating		}} not pregnant lactating		}} pregnant lactating	
0 - 6	2	0	0	1	1	0	0	0	0	0	0	0	0
6 - 9	0	1	3	4	1	1	0	0	0	0	0	0	0
9 - 12	0	0	5	2	2	0	0	0	0	0	0	0	0
12 - 15	0	0	3	0	3	0	3	1	0	0	0	0	0
15 - 18	0	0	12	0	0	0	1	0	0	0	0	0	0
18 - 24	0	0	8	0	0	0	1	1	1	1	1	1	1
24 +	0	0	72	0	0	2	22	13	30	13	30	13	30
TOTAL	2	1	103	7	7	3	27	15	31	15	31	15	31

* Females were regarded as pubertal when the largest follicle reached 5,0 mm

she is physiologically capable. Consequently, age at puberty in the female is of more practical significance to the wildlife manager, in that it will have a direct effect on the demographic vigour of the population.

There are some comparable data available for age at puberty in females from the Eastern Shores of Lake St. Lucia (Venter, 1979). Venter (*op.cit.*) found that one of three females with a mean estimated age of fifteen months had conceived, and that the other two in this age class had ovulated. At twelve months the only animal examined had not ovulated. With respect to age at puberty there does not

appear to be any difference between these two populations, although this judgment is made on very small sample sizes.

The other age-related aspect of reproductive state that is of interest in wildlife management, is the age at which reproductive senescence occurs. Farmers, particularly, commonly argue in favour of shooting older rams because of their supposed reproductive inadequacy. Reproductively inactive individuals, whether young or old, are a liability to any population of animals, reducing that population's potential for increase; and they are a segment of the population that managers would like to minimise in order to achieve the maximum possible harvest.

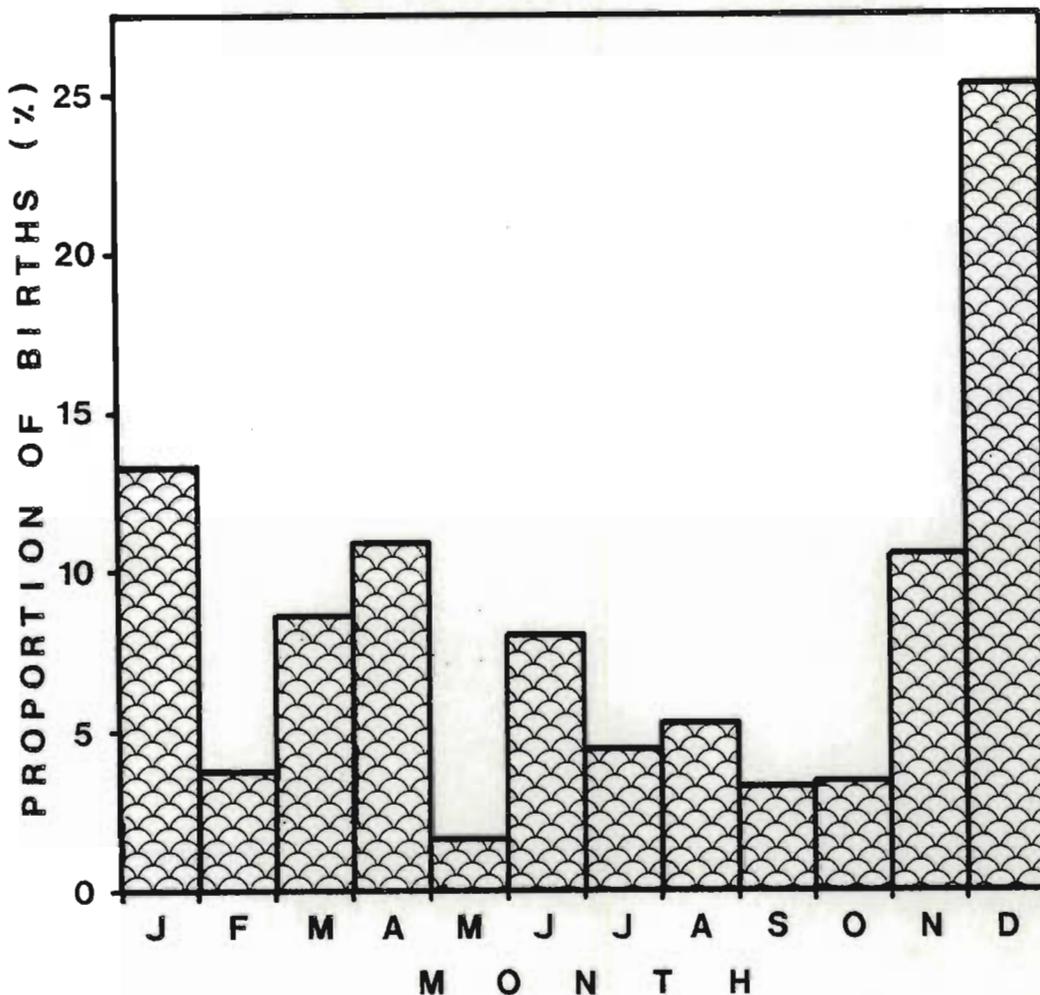
In this study, of 75 post-pubertal females examined, only three were neither pregnant nor lactating (TABLE 4.5); one of these was a nine month-old ewe that had clearly recently ovulated; one, of about six and a half years was considered abnormal in that it was a giant (63,2 kg compared with a class mean of 47,2 kg for adult females), with apparently immature mammae, but normal ovaries with a corpus luteum and a large follicle; and the other, a female of an estimated four and a half years, appeared to be reproductively normal, with a large corpus luteum signifying that it may possibly have been in the early stages of pregnancy following the loss of its previous infant. Thus, none of the 'reproductively inactive' females examined in this study could be considered senescent. The oldest female examined was between seven and eight years of age, and she was pregnant.

As previously stated, sperm were found in the epididymides of all post-pubertal males. The comparison of seminiferous tubule diameters in animals over six years old with those of between three and six years revealed no significant ($p > 0,1$) differences between the two groups: in fact, the mean tubule diameter of the older group ($235 \pm 8 \mu\text{m}$ (S.E.)) was slightly greater than that of the younger group ($229 \pm 7 \mu\text{m}$ (S.E.)). The oldest male examined was between eight and nine years old; and had a mean seminiferous tubule diameter of $244 \mu\text{m}$. Again, there appears to be no evidence of reproductive senescence.

4.3.3.2 CHANGES IN RELATION TO SEASON

The proportion of (potential) births made each month is shown in FIG. 4.10. Forty nine percent of births occur in the three summer months November, December, January, and only 25,8 % in the previous six months, May to October. On the basis of the 57 pregnancies used for this analysis the birth distribution appears also to be rather skewed, with a long 'tail' of births through autumn and into winter.

FIG.4.10 : The proportion of births made each month, calculated from fetal masses



To help explain this we must consider what factors are likely to control breeding seasonality. Proximate factors govern conceptions, which peak sharply during March/April/May, but continue declining gradually throughout the winter. Amoroso and Marshall (1960) suggest that light, temperature and nutrition are the three important stimuli involved and Lofts (1970) points out that species tend to evolve responses to those environmental changes which constitute the most stable source of predictive information. As far as ungulates outside the equatorial zone are concerned, change in daylength is the most stable source of information, and the importance of photoperiod as a cue for breeding has been demonstrated for many species (Sadleir, 1969; Spinae, 1973b). If conceptions in reedbuck are synchronised by a photoperiodic response, then they are clearly initiated by decreasing daylength, which would make the reedbuck a 'short-day' species such as sheep, goats and deer (Spinae, 1973b). There is no way of telling, from the very limited observations of this study whether reedbuck do respond to decreasing daylength in this way, but a photoperiodic response is a plausible explanation for the observed

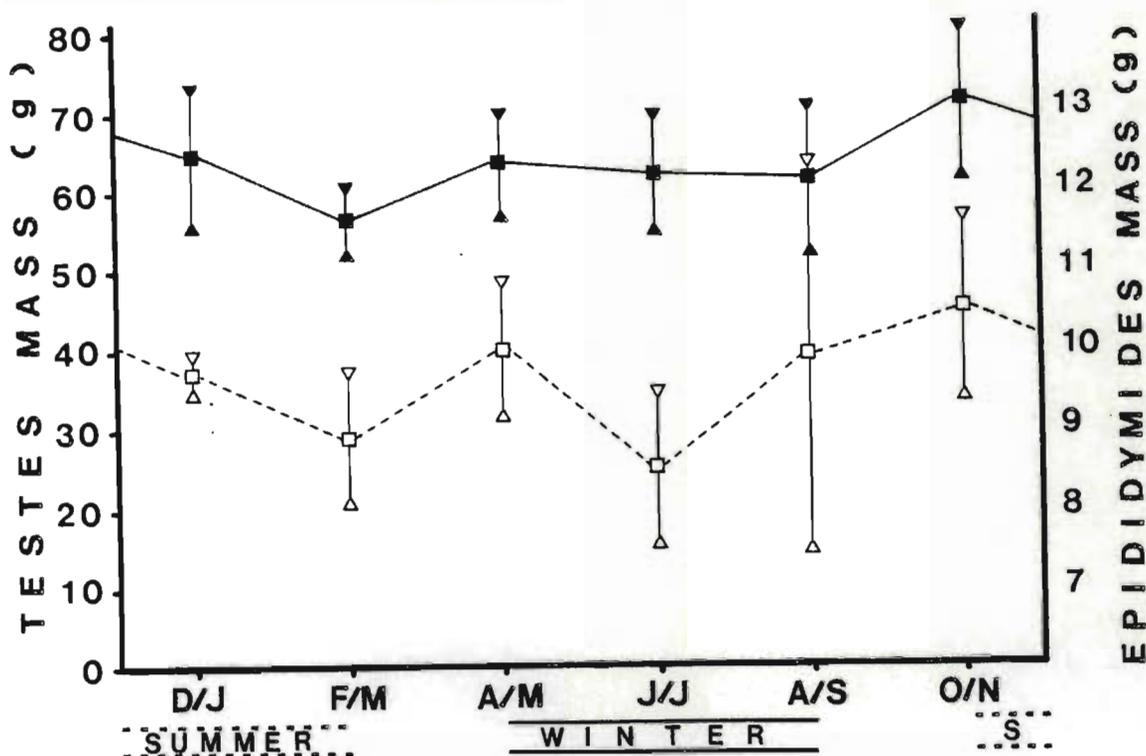
sharp increase in conceptions. It is equally plausible that, where the conception peak would naturally be clearly defined as the limitations of a declining winter food supply curtailed reproductive activity, under the present favourable nutritional regime on farmland the breeding 'season' continues much longer. Taken to its ultimate extreme, this 'extension' of the breeding season could merge one breeding season into the next.

The fact that there is still a marked seasonality in births suggests that one or both of two possibilities applies. Firstly, breeding seasonality may be genetically 'programmed' into the reedbuck's physiology. Lofts (1970) and others believe that such a well developed endogenous rhythm is common to many mammals, and that this rhythm is so strong that even if the photoperiodic breeding cue were removed, seasonal breeding would still occur as this endogenous rhythm came into play. The second possibility is that food supply is not the ultimate factor governing the seasonality of births, and that some other factor still favours a seasonal birth peak in mid-summer. There is circumstantial evidence to support this view, in that the behaviour (CHAPTER SEVEN) and habitat requirements (CHAPTER FIVE) of reedbuck highlight the importance of cover to this species, and cover is most abundant in summer. It would seem logical to produce young when environmental conditions are optimal for the survival of mother and infant (Amoroso and Marshall, 1960; Sadleir, 1969; Lofts, 1970).

Despite the observed seasonal birth peak, there are no significant seasonal changes in the mass of testes and epididymides of adult males (FIG. 4.11). The difference between highest and lowest values was 26 % for the testes, and 23 % for epididymides, expressed as a proportion of the lower value.

Since the gestation period is 233 days (Wilhelm, 1933) a conception peak during March/April/May is indicated. The comparison of seminiferous tubule diameter of adult males shot during this period with those shot six months later revealed that mean values were significantly smaller ($p < 0.02$) in the March/April/May group ($212 \pm 7 \mu\text{m}$ c.f. $244 \pm 9 \mu\text{m}$). This is contrary to what one would expect, as seminiferous tubule diameters are generally regarded (Skinner, 1971; Chapman, 1972) as being a good indication of male sexual activity in ungulates, and one would have expected larger tubules in more active testes. Viewed against maximum between season differences in other species (for example in blesbok, 35 %; impala, 33 %; kudu, 56 %; springbok (*Antidorcas marsupialis*), 22 % (Skinner, 1971)) the observed difference of 15 % is, however, small. It is concluded that male reedbuck in this population exhibit no seasonality in their physiological ability to reproduce.

FIG.4.11 : Bi-monthly changes in testes and epididymides mass of adult males (mean values are shown \pm two standard errors)



The seasonality of births in reedbuck has been considered for populations in the Kruger National Park (Jungius, 1970), and on the Eastern Shores of Lake St. Lucia in Zululand (Venter, 1979). Jungius's (*op.cit.*) study lacked quantitative data, but he concluded from his own observations and a thorough review of available literature that the reedbuck is not a strictly seasonal breeder, although there is a peak in births between December and May. Venter (*op.cit.*) concluded that reedbuck show no significant breeding peak on the Eastern Shores. The data presented here serve to confirm Jungius's general conclusions.

4.3.3.3 CHANGES IN RELATION TO PHYSIOLOGICAL CONDITION

It has been shown (SECTION 4.3.2.3) that reproductive activity, particularly the latter stages of pregnancy and lactation, tends to drain away an animal's body reserves and lower its 'physiological condition'. It is also true that elevated body reserves in an animal of given age can serve to enhance its reproductive ability. This has been demonstrated for domestic cattle (Lamond, 1970) which must, firstly, achieve a critical mass before they can attain puberty, and in which, secondly, there is also a critical mass above which adult cows are more fertile. More recently this association has been investigated in red deer (Lowe, 1971; Wegge, 1975) and lechwe (Williamson, 1979) where similar relationships were found.

The possibility of a critical mass below which the fertility of adult

females is inhibited cannot be investigated in this study because of the lack of 'infertile' animals in the adult segment of the population. The dressed mass of females was, however, considered by age class and reproductive state, and the results are presented in TABLE 4.6. In what might be termed the 'pre-prime' age class (12 to 18 months) postpubertal animals (which had all conceived) were significantly larger ($p < 0,05$) than those that had not conceived but which were considered to be on the point of puberty. On the basis of these results, a dressed mass of 25 kg appears to be the minimum mass for a reedbuck to conceive. Assuming a dressing out percentage of 66 % (based on real figures for adult females), the critical live mass for conception to occur would be approximately 38 kg, or 80 % of mean adult mass. In lechwe, Williamson (1979) found that the critical mass for first conception fell between 70 and 84 % of adult mass, and that non-reproductive adults had a mean mass of 78 % that of reproductively active adults. It could be that further studies will show that the critical mass for conception is a fairly fixed proportion of adult mass in many species, in which case simple measurement of body mass might serve as a useful measure of age at first conception, and might even be used to predict the demographic state of a population.

TABLE 4.6 : Dressed mass (kg) of females, by age class and reproductive state. Mean values are shown, number of animals, and in brackets the range of masses.

Age Class (months)	Prepubertal	Pubertal	Postpubertal
0 - 6	16,0 n = 1	15,0 n = 1	-
6 - 12	20,9 (19,5 - 23,2) n = 6	20,2 (18,7 - 21,5) n = 3	20,0 n = 1
12 - 18	-	25,0 (22,0 - 28,0) n = 3	30,2 (27,5 - 33,0) n = 4
> 18	-	-	31,0 (24,5 - 41,0) n = 69

4.3.4 Pathological condition

Tick counts were discontinued after the first 97 post mortems, made over fourteen months of fieldwork, because of the very low numbers of external

parasites found. Twenty seven percent of culled animals had no ticks at all, 41 % had very light infestations (< five ticks on the ears), 19 % had light infestations (five to twenty ticks), and the remaining 13 % had moderate infestations of up to fifty ticks on the two ears. In all cases the ticks were found deep inside the ears.

The results of blood packed cell volume (PCV) analyses are shown in FIG. 4.12 for males and females. There appears to be a similar seasonal trend in both sexes, where PCV reaches a peak in August/September, but only in the male is it significantly ($p < 0,05$) higher at this time than at any time over the period December to July. The interpretation of these results is difficult because the physiological basis underlying observed seasonal trends in PCV is not understood (Hanks, 1981). Nevertheless, of 19 techniques of condition evaluation tested on blood samples from populations of Alaskan moose (*Alces alces gigas*) PCV values were considered to be the most useful (Franzmann and LeResche, 1978), and a value of 50 % or greater was considered indicative of an animal in average or better condition.

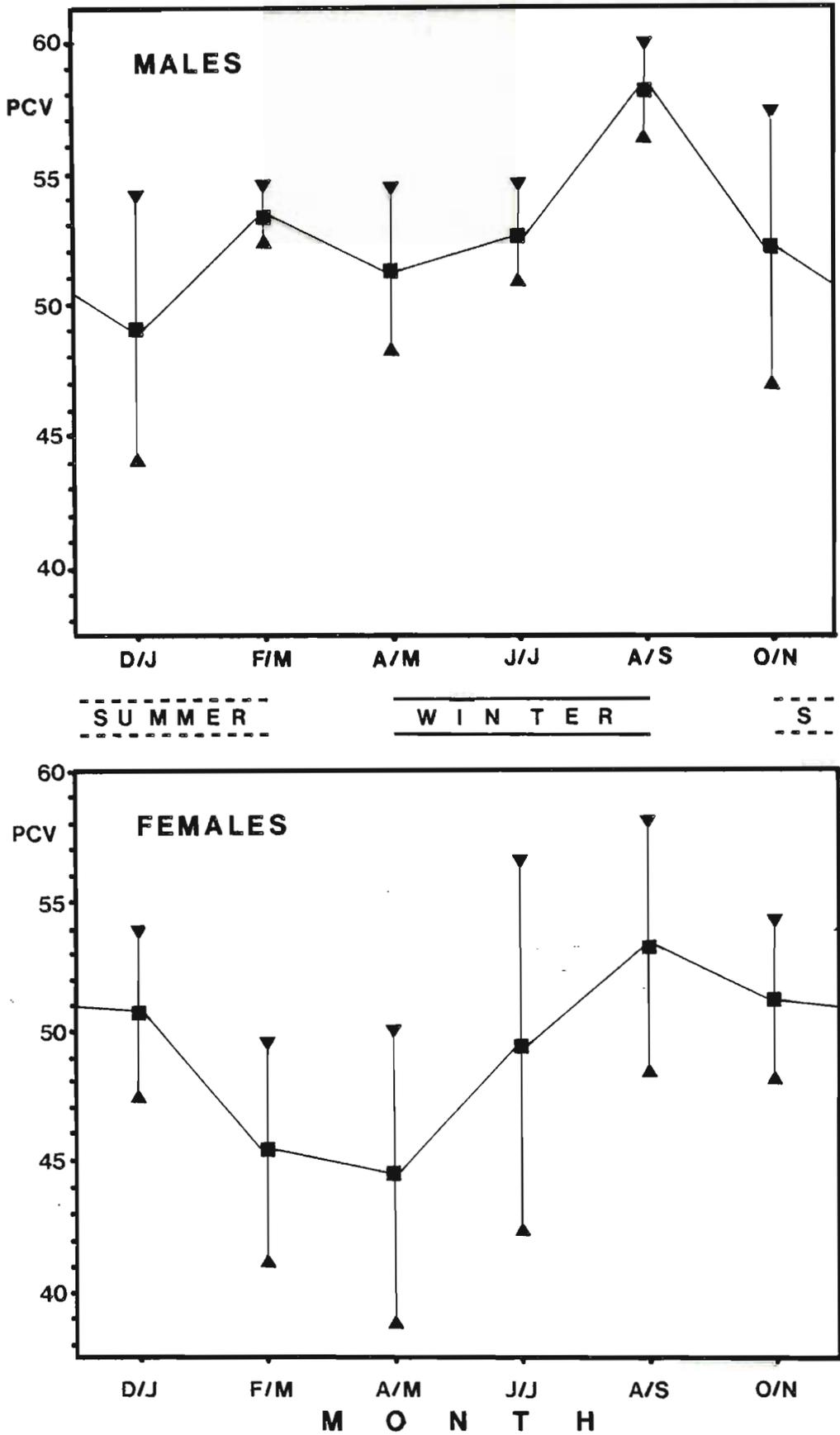
Some comparative PCV measurements were taken in this study from blood collected on the Eastern Shores of Lake St. Lucia in June 1981. In both adult males and females the values were lower than those of the highlands population (males: $43,0 \pm 1,8$ c.f. $52,5 \pm 1,1$; females: $45,0 \pm 1,1$ c.f. $49,5 \pm 3,7$ ($\bar{x} \pm S.E.$)), and this is very probably an altitudinal effect: Hall (1937) and Marshall and Matthias (1971) have shown that oxygen carrying capacity is greatly increased at high altitudes because of more rapid proliferation of red blood cells. As much of the value of condition assessment comes from comparisons between populations, this altitudinal effect is a severe limitation to the use of PCV as an index of condition.

4.4 CONCLUSION

Many of the results presented in this chapter have, of necessity, been descriptive. It is hoped that they have been presented in such a way as to be of value to future workers in the field, as without comparative data measurements of condition lose much of their value. In this study lack of comparative data from other populations have severely limited the scope of interpretation.

However, a few clear trends are apparent, and the interpretation of these is unambiguous. Firstly, whilst many African ungulates show marked seasonal fluctuations in the levels of their body reserves, this population of reedbuck does not. The only significant drop in physiological condition occurs in adult females in mid-summer, coinciding with a seasonal birth peak. The general conclusion from this is that, unlike most other African ungulate populations (Sinclair, 1974; Mentis, 1978; Scotcher, 1982), these reedbuck are not food limited. This is, of course, hardly surprising

FIG. 4.12 : Bi-monthly changes in blood Packed Cell Volume (PCV) of adult males and adult females
 mean values are shown \pm two standard errors



as they do have access to particularly nutritious food at all times of the year (CHAPTER FIVE).

Despite this high plane of nutrition, the study population of reedbuck exhibited a seasonal birth peak in mid-summer, which may be an indication that cover, and not food, is the ultimate factor governing the seasonality of births.

Secondly, this population of reedbuck is very productive: lambs are born at the rate of 1,3 per reproductively active female per year (CHAPTER THREE); there is no evidence of sexual senescence in either males or females; and puberty is reached by the age of nine months in males, and by twelve months in females. In view of evidence cited by Western (1979) suggesting that parameters such as growth and maximum rates of reproduction can be scaled to the size of mammals, these reproductive rates would appear to be at, or close to the reedbuck's genetic potential.

4.5 CHAPTER SUMMARY

The purpose of this chapter was to examine whether the observed stability in population size could be attributed to limitations imposed by the inadequacy of the food supply.

Research techniques were based on post-mortem sampling from 197 reedbuck shot at random; body growth, the levels of various types of body reserves, and the reproductive and pathological condition of these animals was examined.

Male reedbuck exhibited no significant seasonal changes either in the levels of their body reserves, or in their physiological ability to reproduce. Females showed a decline in body reserves in mid-summer, which was attributed to the physiological strain of late pregnancy and lactation at this time.

A seasonal birth peak was inferred from pregnancy data in mid-summer, and the possible reasons for the existence of such seasonality discussed. It was concluded that cover, and not food, is the probable likely ultimate factor governing this.

Puberty is reached by the age of nine months in the male, and by twelve months in the female. This, together with other reproductive data was considered indicative of a population at, or close to its genetic potential as regards productivity.

The conclusion was reached that this population of reedbuck is not food limited.

CHAPTER FIVE

HABITAT PREFERENCE AND DIET

5.1 INTRODUCTION

5.1.1 Definitions, and purpose of habitat preference and diet determination

All the resources that an animal requires to survive and reproduce - food, water and protection from climatic extremes and predation - must be provided by the area, or habitat, in which it lives.

The fact that an animal lives in a particular area usually implies at least some degree of selection, dependent on its ability to move elsewhere; and even within the area where it carries out its routine activities, it uses particular sites for particular activities in preference to others. An animal exhibits habitat preference by selecting sites for particular activities from the range of sites available to it. The purpose of determining habitat preference is to enable description of the physical and biological properties of an animal's preferred habitat. Such knowledge is the key to successful conservation, because preservation of an animal's habitat is a precondition for the conservation of that species. The same knowledge might also facilitate the control of problem species, enabling manipulation of key habitat factors that are essential to the animal's survival.

Year-round availability of food is a particularly critical aspect of a species' habitat requirements and an analysis of diet should lead to an understanding of the ways and the extent to which an animal accommodates seasonal variations in the quality and the quantity of its food supply. Once such an understanding has been gained, it may be possible to manage a population of animals simply by appropriate management of that animal's food resources.

5.1.2 Possible methods of determining habitat preference and diet

5.1.2.1 HABITAT PREFERENCE

Leopold (1933) was one of the first to recognise that 'distribution is often an excellent and accurate index usable in the diagnosis of

food and cover questions'. It is a principle that is now so well established that scarcely a study is made of habitat preference without cognizance of it. With very few exceptions habitat preference studies attempt to relate the distribution of animals at a particular time to selected environmental parameters measured or assessed throughout that animal's potential range. There is a multitude of techniques available to the wildlife worker for assessing animal distributions and measuring potentially important habitat parameters, and those selected will depend on the level at which the investigation is undertaken:

- 1 at the regional level animal distributions may be recorded as simple presence or absence, or as relative densities in different areas, and considered in relation to gross regional bioclimatic differences. The possible methods used in this type of investigation have been reviewed in CHAPTER TWO.
- 2 at the local level the locations of a large number of individuals within a finite population may be recorded. The possible methods of counting individuals within a population have been reviewed in CHAPTER THREE, and include not only direct observations of the animals themselves, but also indirect methods based on the distribution of animal signs (e.g. lying-up places, wallows, footprints, faeces (Anderson et al., 1972)).
- 3 at the individual level animals, suitably marked for visual recognition (Hanks, 1969; Taylor, 1969; Twigg, 1975) or remote sensing (Cumming, 1971) can be monitored over long periods, as they move between, and use, different habitats.

Having established exactly where the animals are, the wildlife worker goes about describing the occupied and unoccupied sites available to them (Johnson, 1980). The way in which he describes the sites, and subsequently analyses the data, depends on the particular objectives of the investigation. In many instances (for example, Lamprey, 1963; Pienaar, 1974; Mason, 1977; Tomlinson, 1981; Irby, 1982) it is sufficient to classify each occupied site into one of a number of broad habitat categories, and compare the observed frequency of occurrence of the animals in each habitat with that expected had those same animals distributed themselves randomly in the study area. Indeed the method can be further refined to consider not only the habitat type that an animal is using, but also its association with other types that occur close by (Cole, 1949; Sinclair, 1977). This type of investigation can provide a useful insight into gross habitat preferences of particular species, and the ways in which animals use different habitat types at different times for different activities:

the principles of grazing succession (Bell, 1969) and ecological separation in space and time (Lamprey, 1963).

However this method is limited in that the habitat categories are often far too broad to isolate adequately the attributes of the habitat that make it more or less preferred. To achieve this isolation a number of more complicated multivariate techniques have been developed (for example, Anderson *et al.*, 1972; Ferrar and Walker, 1974; Hudson *et al.*, 1976; Stocker and Gilbert, 1977; Dyer, 1978; Strahler, 1978; Euler and Thurston, 1980; Clark and Gilbert, 1982; Rowe-Rowe, 1982; Duncan, 1983). These have been particularly useful in studies of species interactions and community structure (Ferrar and Walker, *op.cit.*; Melton, 1978), revealing aspects of habitat use that differ between species occupying the same broad habitat type: the principle of niche differentiation. Multivariate statistical techniques can be immensely useful to the wildlife manager, but there are many cases in which their use is inappropriate. Two of the most common pitfalls seem to be that, firstly, the inadequacies and limitations of the original field data are ignored or brushed over, and secondly, the computer generated discriminant statistics are so complex as to lose much of their practical value.

5.1.2.2 DIET

Food supply is such a critical aspect of an animal's habitat, that the analysis of diet has become a central theme in many ecological studies. In the case of grazing animals the approach and methods adopted may be plant-based or animal-based, depending on the specific objectives of the study.

Animal-based methods can be considered in four separate categories:

- 1 direct observation of tethered or free-ranging animals (examples of this approach include the studies of Field, 1970; Jungius, 1971b; Duncan, 1975; Venter, 1979; Bryant *et al.*, 1980). This method normally only yields food plant species lists (Jungius, *op.cit.*; Venter, *op.cit.*), but may give some quantitative indication of diet by measuring feeding times (Dixon, 1934), counting the number of bites (Duncan, *op.cit.*), and plucking equivalent quantities by hand.
- 2 using oesophageal and ruminal fistulated animals to collect samples of the forage grazed for analysis of the botanical and/or chemical composition (Short, 1962; Duncan, 1975);

- 3 faecal analysis (Dusi, 1949; Storr, 1961; Bredon et al., 1963; Stewart, 1967; Stewart and Stewart, 1970; Scotcher, 1979). This is a popular and widely used technique, because of the ease with which material can be collected. However, despite many attempts at a quantitative interpretation of the results of this type of analysis, it is now clear (Smith and Shandruk, 1979; Scotcher, 1979) that the technique has severe limitations in the assessment of food preference.

- 4 rumen analysis (Baumgartner and Martin, 1939; Norris, 1943; Field, 1972; Westoby et al., 1976; Rees, 1978; Staines et al., 1982). This is perhaps the most widely used technique in the study of ungulate diets, and although many of the limitations applicable to faecal analysis also apply here, this is generally accepted as being more quantitatively representative (Sparks and Malechek, 1968; Westoby et al., 1976; Smith and Shandruk, 1979). Its use extends far beyond microscopic food plant species identifications (Field, 1972; Irby, 1977), to include analysis of the chemical composition and nutritive value of the food ingested (Staines et al., 1982). Stanley Price (1977) has further described a method whereby the daily intake of food could be calculated from the specific gravities (and thus, retention time in the rumen) of components of the rumen content.

There are three broad categories of plant-based methods in the analysis of herbivore diets:

- 1 sampling plants that are known to be important components of the diet, to determine their chemical composition and nutritive value (Radwan and Crouch, 1974; Field, 1976; Von Richter and Osterberg, 1977; Sinclair, 1977; Oldemeyer et al., 1977; Everitt and Gonzalez, 1981);

- 2 estimating the production and utilisation of individual plants;

- 3 clipping plots in the herb layer before and after grazing to determine use by the difference (Brown, 1954; 't Mannetje, 1978).

5.1.3 Previous work on habitat preference and diet of reedbuck

Work on the habitat preference and diet of reedbuck is confined to that of Jungius (1971a, 1971b) and Venter (1979), with additional observations by Field (1970), Royal (1979), Vesey-Fitzgerald (1960) and van der Schijff (1957). Only Venter (1979) has attempted any quantitative assessment of

habitat preference, and analysis of diet is limited to food plant species lists derived from observation of free-ranging animals in Kruger National Park (Jungius, 1971b) and at Lake St. Lucia (Venter, 1979; Royal, 1979), and from rumen and faecal analysis for plant species composition of a total of 26 animals. The most pertinent observations are summarised below:

(a) Habitat selection

Reedbuck show a preference for the earlier pioneer seres in the plant succession (Jungius, 1971a; Venter, 1979), particularly where there are some woody elements present (Venter, 1979). Suitable reedbuck habitat will provide water and cover throughout the year (Jungius, 1971a). Venter (1979) and Jungius (1971a) record a switch of preference between the summer, when low-lying hygrophilous grasslands are the preferred habitats, and the winter months when there is a movement up to the higher lying short and medium shrubland.

(b) Diet

Reedbuck are classed with those medium sized antelope that are either grazers or browsers, and are very selective (Jarman, 1974). The closely related bohor reedbuck of East Africa is classed as being a fresh grass grazer dependent upon water (Hofmann and Stewart, 1972). Seasonal preference for different grass species has been shown (Field, 1970), as has plant part selection (Venter, 1979) and occasional browsing (Field, 1970; Jungius, 1971b; Royal, 1979). It is of interest that the food of reedbuck allegedly consists mainly of 'unpalatable' grasses which are avoided by other antelope species (Jungius, 1971b).

5.1.4 Purpose of habitat preference and diet determination in this study

The primary objective of this study, as set out in CHAPTER ONE, is to make recommendations for the management of reedbuck populations to improve their conservation status on farmland in the province, and assess the extent of any conflict between the interests of the farming community and these antelope. Habitat preference and diet determination are clearly key issues.

Specifically, the purpose of habitat preference and diet determination in this study is:

- 1 to describe the physical and biological nature of optimal reedbuck habitat on farmland;

- 2 to assess the extent to which the farmland habitat provided within the extensive study area fulfils the requirements of reedbuck, and examine the possibility of resource shortage as this might affect the regulation of population size;
- 3 to assess the extent to which habitat manipulation might be used in the management of reedbuck populations on farmland;
- 4 to determine which crops are most vulnerable to damage by reedbuck, and the extent of seasonal variation in reedbuck's dependence on these crops;
- 5 to determine the adequacy of the diet of reedbuck on farmland, and the extent of seasonal changes in the use of principal foods;
- 6 to relate observed seasonal changes in diet with seasonal changes in the quality of principal foods.

5.2 METHODS

5.2.1 Determination of habitat preference

Five techniques were used to determine habitat preference, at three distinct information levels:

5.2.1.1 AT THE PROVINCIAL LEVEL

Gamequest, the postal questionnaire survey of farm game conducted systematically over Natal (CHAPTER TWO) provided information on the distribution of reedbuck at a provincial level. The exact location of each farm participating in the survey was plotted on a 1:500 000 scale map of the province, showing Phillips' (1973) bioclimatic subregions, and the subregions occurring on each farm were listed on the completed questionnaire form for that farm. The 'status' (present and stable, increasing or decreasing, or absent) of reedbuck in each bioclimatic group was then assessed by expressing the number of farms reporting reedbuck in each of the status categories as a proportion of the total number of farms of which a portion or the entire fell within that bioclimatic group. In many cases, two or even three bioclimatic groups were represented on a single farm, in which case the status of reedbuck was scored for each group separately.

5.2.1.2 AT THE POPULATION LEVEL

Three methods of habitat preference determination were used at the population level:

(a) Habitat Preference Index

The dawn and dusk total counts described in CHAPTER THREE provided monthly coverage of the intensive study area, during which the exact locations and habitat types occupied by reedbuck were recorded. The habitat categories used are listed in TABLE 5.1. Data from each two-month period were pooled and 1981 and 1982 results totalled. For each habitat sub-type a seasonal habitat preference index was calculated as the proportion of animals recorded in that sub-type divided by the proportion of the entire intensive study area represented by that habitat. The data were later pooled and plotted as habitat preference indices for the five major habitat types represented.

TABLE 5.1 : Habitat categories used in habitat preference determination

HABITAT TYPE	PROPORTION OF INTENSIVE STUDY AREA (%)	HABITAT SUB-TYPE	DESCRIPTION	
VLEIS	6,3	2,9	Perennial vlei	Perennially wet vlei - tall reeds, sedges, etc.
		3,4	Seasonal vlei	Seasonally dry vlei - shorter marginal wetlands
AGRICULTURAL LANDS	34,4	21,7	Annual pasture	Annually planted winter pasture (ryegrass, etc.)
		4,5	Permanent pasture	Pastures infrequently replanted (clover, cocksfoot, etc.)
		4,5	Crop lands	Cultivated lands under maize, rootcrops, or garden produce
		3,7	Mature plantation	Planted exotic trees, without understorey vegetation
COVER	15,5	1,4	Woody scrub	Low woody vegetation, providing at least 50 % aerial cover
		4,1	Invading scrub	Low woody vegetation, providing 10 % to 50 % aerial cover
		2,0	Bramble	Patches of bramble
		8,0	Rank herbs	Old cultivated lands, and other areas of rank herbaceous cover
FLAT VELD	18,7	Flat veld	Flatish veld, potentially suitable as arable land	
BROKEN VELD	25,1	0,5	Upland basin	Ledges and basins on hillslopes
		0,6	Ridge	Stony ridges along hilltops
		0,0	N.Slope (boulders)	North-facing slopes strewn with boulders bigger than a reedbuck
		2,9	" (stony)	North-facing slopes covered with smaller stones
		2,5	" (grassy)	North-facing grass-covered slopes
		0,1	" (gulleys)	North-facing slopes interrupted by drainage lines
		1,5	S.Slope (boulders)	South-facing slopes strewn with boulders bigger than a reedbuck
		4,9	" (stony)	South-facing slopes covered with smaller stones
		10,7	" (grassy)	South-facing grass-covered slopes
1,4	" (gulleys)	South-facing slopes interrupted by drainage lines		

Coefficients of Association (Cole, 1949; Sinclair, 1977) between reedbuck and the various habitat sub-types were also calculated, using a 250 m square grid to determine 'associated' habitats. The results of this analysis are not presented because of the low levels of significance achieved. It was concluded that animal densities in the intensive study area were too high, and animals were too well dispersed for the effective use of this method.

(b) Changes in Animal Distribution

During night counts on all farms in the extensive study area (CHAPTER THREE) the locations of all animal sightings were recorded. These were plotted on maps of the area to show gross seasonal changes in distribution between August 1981 and February 1982 in relation to available habitats.

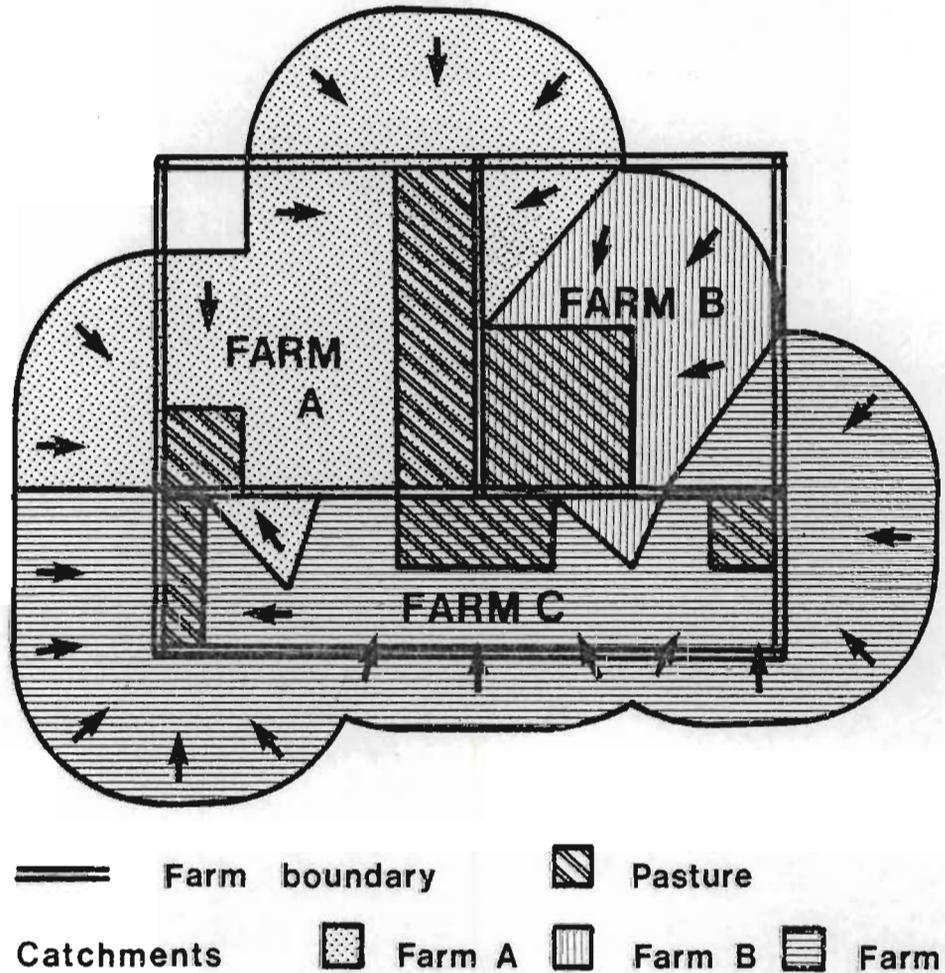
(c) Multivariate Analysis of Reedbuck-Habitat Relations

On the basis of counts made on the twenty three farms in the extensive study area, a stepwise multiple regression technique was used in the analysis of reedbuck-habitat relations. The procedure adopted was as follows:

- 1 Night pasture counts were made on all farms in July 1982 as detailed in CHAPTER THREE.
- 2 The area of each of the habitat sub-types listed in TABLE 5.1 was calculated from recent 1:10 000 scale aerial photographs of each farm. This was achieved by superimposing a grid representing squares 250 m x 250 m, or 6,25 ha over the photographs, and estimating the approximate percentage cover (to ± 5 %) of each habitat type within each grid cell.
- 3 Studies of known animals indicate that in winter reedbuck feeding each night on planted pastures generally spend the daytime within a radius of about 1,5 km of that food source, and generally feed at the closest food source to their preferred daytime habitat. These observations led to the derivation of the 'catchment' concept, whereby each pasture has an associated 'catchment' from which reedbuck are 'drawn'. The size of a catchment associated with any particular property depends on the location of winter food sources (i.e. pastures) both on the property and on neighbouring farms, and so farms of the same size with the same area of pasture may have very different catchments. This is illustrated in FIG. 5.1. Three farms, A, B, and C have exactly the same area, and the same area of pasture is planted on each. If we assume there are no pastures on the surrounding farms, then the catchments are as illustrated. The area of farm B's catchment is actually smaller than the area of the property, because some of the reedbuck that live on the farm by day go to feed on farms 'A' and 'C', and so fall within their catchments. On farm C however, the pasture is well dispersed in three blocks, attracting buck from way outside the property on three sides, and the farm's catchment is well over twice the size of the property. The catchments of all

farms in the extensive study area were mapped in this way, and the areas of each of the habitat sub-types in the catchment were calculated.

FIG. 5.1 ILLUSTRATING THE PASTURE CATCHMENT CONCEPT
see text for explanation



- 4 Two other variables that were considered to be potentially important in explaining reedbeek densities were the amount of boundary between cover and pasture, and the diversity, or patchiness of the habitat. The former was measured for each property from aerial photographs, and a habitat diversity score was derived for each property and each catchment by summing the total number of habitat sub-type/grid cell scores and dividing this total by the number of grid cells to give a mean number of habitat sub-types per 6,25 ha grid cell.
- 5 The datasets for each of the twenty three farm properties/catchments were punched onto computer cards, and the University of Natal's Univac 1100 computer was used to execute various routines from the SPSS statistical package.

- 6 The first analysis requested was a series of scattergrams and their associated statistics describing the relationship between reedbuck numbers and the areas of each of the habitat sub-types, the major habitat types, pasture-cover boundary, habitat diversity and domestic stock numbers for property and catchment considered separately.
- 7 The next step was to examine the strength of relationships between the habitat variables themselves. A strong correlation between any pair of habitat variables would clearly influence apparent reedbuck-habitat relationships, producing spurious results. Each habitat variable was measured against each of the others by means of Spearman Rank Correlations.
- 8 Having examined these results, it was decided to look at the correlations between reedbuck numbers and certain of the habitat variables that had appeared to be strongly correlated, whilst controlling for the effects of certain other variables. This is the method of partial correlation: it enabled re-examination of the reedbuck-habitat relationships established earlier, now controlling for other habitat variables that had clearly influenced the initial results. First order partial correlations were used to control for single variables, and second order correlations to control for pairs of habitat variables.
- 9 The penultimate phase of the analysis was to conduct a number of stepwise multiple regressions of selected habitat variables that had been shown to have a strong influence on reedbuck numbers, and establish the relative importance of these as predictors of reedbuck numbers. The objective here was twofold: firstly, to determine as precisely as possible what habitat factors are of importance to reedbuck, and secondly, if possible, to generate a simple equation whereby anybody could predict the number of reedbuck likely to occur on a farm, simply by looking at the habitat on that property/catchment.
- 10 Finally, having generated a number of equations to predict reedbuck populations on individual farms, these equations were used to calculate 'expected' populations on the study farms, thus providing a measure of their utility. Strictly, the equations should be tested against a completely new set of data, but in view of the large amount of work involved, this was not possible.

5.2.1.3 AT THE INDIVIDUAL LEVEL

A total of 84 reedbuck was marked with collars and/or eartags for individual recognition (CHAPTER SIX) of which 45 animals were used in an analysis of home range habitat composition. To qualify for home range habitat analysis an animal had to be seen over a minimum period of ten months (over which period a satisfactory annual range could be ascertained), and had to be sighted on a minimum of 16 different days (see CHAPTER SIX for further explanation of the derivation of the minimum number of sightings required for home range calculation). Home ranges were plotted on a 1:10 000 scale habitat map of the intensive study area (APPENDIX E; produced from aerial photographs, updated by personal survey) using the minimum area method (Mohr, 1947). Within each home range the areas of each habitat type were calculated, and results presented for different age and sex classes of animal.

5.2.2 Analysis of diet

5.2.2.1 QUANTITY AND QUALITY OF INGESTED FOOD

The rumen contents of 199 freshly shot reedbuck were weighed on a 10 kg Salter spring balance as part of the routine autopsy procedure. The contents were well mixed, and two samples taken for subsequent analysis. One was oven dried to enable the conversion of fresh rumen content mass to a dry matter equivalent, while the other was stored in formal acetic alcohol (FAA). From these preserved samples those of five adult males and five adult females were selected in each two-month period for analysis of protein content.

Laboratory analysis of protein content of these samples was undertaken by staff of the Department of Agriculture at their feed analysis laboratory, Cedara Agricultural College, Natal.

The relationship between rumen content mass and dead mass was examined separately for males and females by linear regression analysis, and the established relationships compared with values derived for concentrate feeders and for bulk and roughage feeders (Anderson, 1978) in a simple evaluation of the degree of dietary selectivity shown by this species.

5.2.2.2 QUALITY OF AVAILABLE FOOD

Green leaf samples of annual ryegrass (Lolium multiflorum) and redgrass (Themeda triandra), believed to be principal foods of reedbuck on farmland, were taken approximately monthly for routine

analysis of dry matter, fat, crude fibre, crude protein, Calcium (Ca) and Phosphorus (P) percentages. Samples of Themeda were taken from burnt and unburnt sites, for comparison.

5.2.2.3 CROP PREFERENCE ANALYSIS

Within the night census area of the intensive study area, weekly assessments of land management activities (ploughing, planting, fertilizing, irrigating, mowing, grazing) and vegetation condition (green leaf and ground cover percentages, height of living and moribund components) were made for all cultivated land units. The number of reedbuck recorded on each land unit during each night pasture count (CHAPTER THREE) was then expressed as a proportion of the total seen that night and divided by the mean proportion seen on that particular land unit over the entire year, to give an idea of the animals' relative preference for the unit at that particular time. As fertilization and irrigation normally succeed planting, grazing or mowing, the relationships between these activities and reedbuck preference were not considered independently of planting, grazing and mowing. Correlations were drawn between reedbuck preference and time since planting, grazing or mowing, and between preference and height of the living component of the vegetation.

5.3 RESULTS AND DISCUSSION

5.3.1 Habitat preference

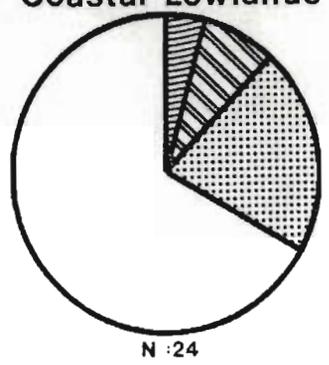
5.3.1.1 AT THE PROVINCIAL LEVEL

The status of reedbuck is considered by bioclimatic group in FIG.5.2, and TABLE 5.2 summarises the main features of each bioclimatic group (after Phillips, 1973). The number of farms sampled in bioclimatic groups five, seven and eleven was too few to give meaningful results but examination of apparent trends on farms in all other groups reveals the following:

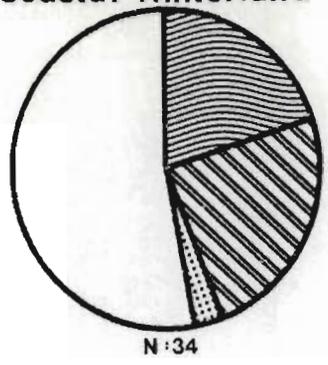
- 1 In most bioclimatic groups reedbuck are reportedly increasing on more farms than they are declining. The exception is in the coastal lowlands (group one) where reedbuck are declining on 64 % of farms where they occur: this is a high rainfall area well suited to agriculture, and we might reasonably suppose that habitat destruction for agricultural development is the main cause of this decline.
- 2 Reedbuck are most widespread, and appear to be generally increasing on farms in the mistbelt (group three) and in the

FIG. 5.2: Status of reedbuck by bioclimatic group

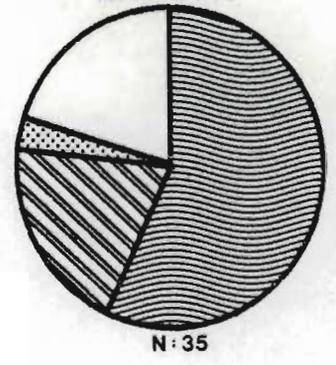
GROUP 1
Coastal Lowlands



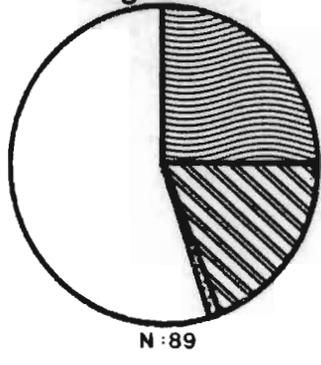
GROUP 2
Coastal Hinterland



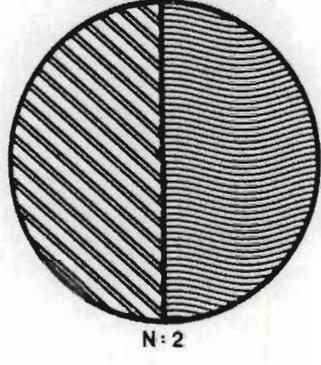
GROUP 3
Mistbelt



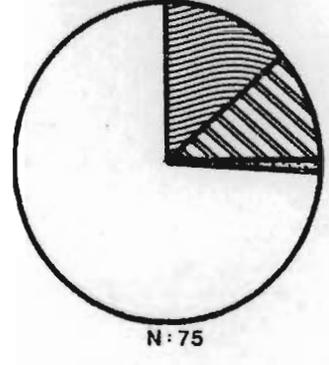
GROUP 4
Highland



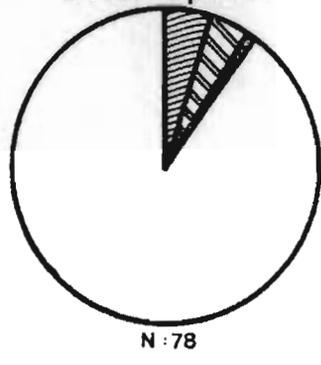
GROUP 5
Montane



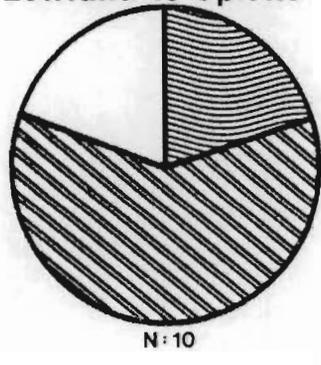
GROUP 6
Moist Upland



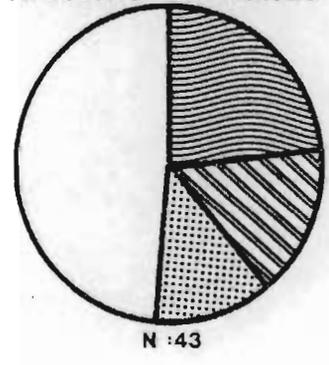
GROUP 8
Drier Upland



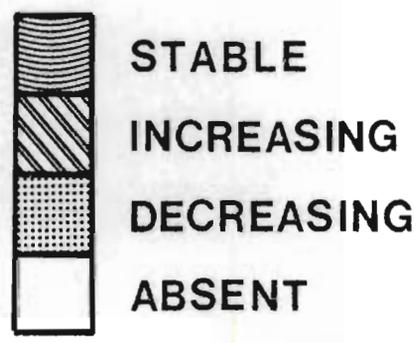
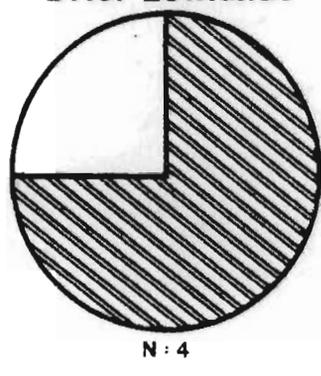
GROUP 9
Lowland to Upland



GROUP 10
Riverine Lowlands



GROUP 11
Drier Lowlands



N REFERS TO THE NUMBER OF FARMS SAMPLED

TABLE 5.2 : The bioclimatic groups of Natal (after Phillips, 1973)

No.	BIOCLIMATIC GROUP (potential)	ELEVATION (metres)	RAINFALL mean ann. (mm)	TEMPERATURE mean ann. (C)	HUMIDITY RANGE
1	COASTAL LOWLANDS	0 - 457	850/1400	20/22,5	H - SSH
2	COASTAL HINTERLAND	457 - 915	850/1300	17,5/20	H - SSH
3	MISTBELT	915 - 1372	800/1600	16/18	H - SH
4	HIGHLAND TO SUBMONTANE	1372 - 1981	800/1500	13/15	H - SH
5	MONTANE	1981 - 3353	1500+	13	H - H/SH
6	UPLAND (MOIST)	915 - 1372	800/1000	16/18	SH/MSA
7	RIVERINE (Tugela)	305 - 610	700/800	17/18	SH/MSA
8	UPLAND (DRIER)	915 - 1372	600/800	16/18	MSA - MSA/SA
9	LOWLAND TO UPLAND (Zululand)	152 - 1067	700/850	21/22	SH/MSA - MSA/SA
10	RIVERINE/ INTERIOR LOWLAND	152 - 915	600/700	18/23+	MSA/SA - SA
11	DRY LOWLAND	152 - 457	320/600	21/23	A

transitional Zululand lowland to upland (group nine) regions, where they occur on more than 75 % of farms sampled. The latter is a relatively low rainfall area, where 60 % of farms have increasing reedbuck populations. It is probably significant that both these regions are physiographically disrupted, since broken country appears to favour (SECTION 5.3.2.1) the species.

- 3 Reedbuck are least widespread on farms in the drier upland (group eight) regions of the province. In view of habitat requirements established in this study (SECTION 5.3.1.2) it is not surprising that these extensive open plains fail to provide suitable habitat for reedbuck.

5.3.1.2 AT THE POPULATION LEVEL

(a) Habitat Preference Index

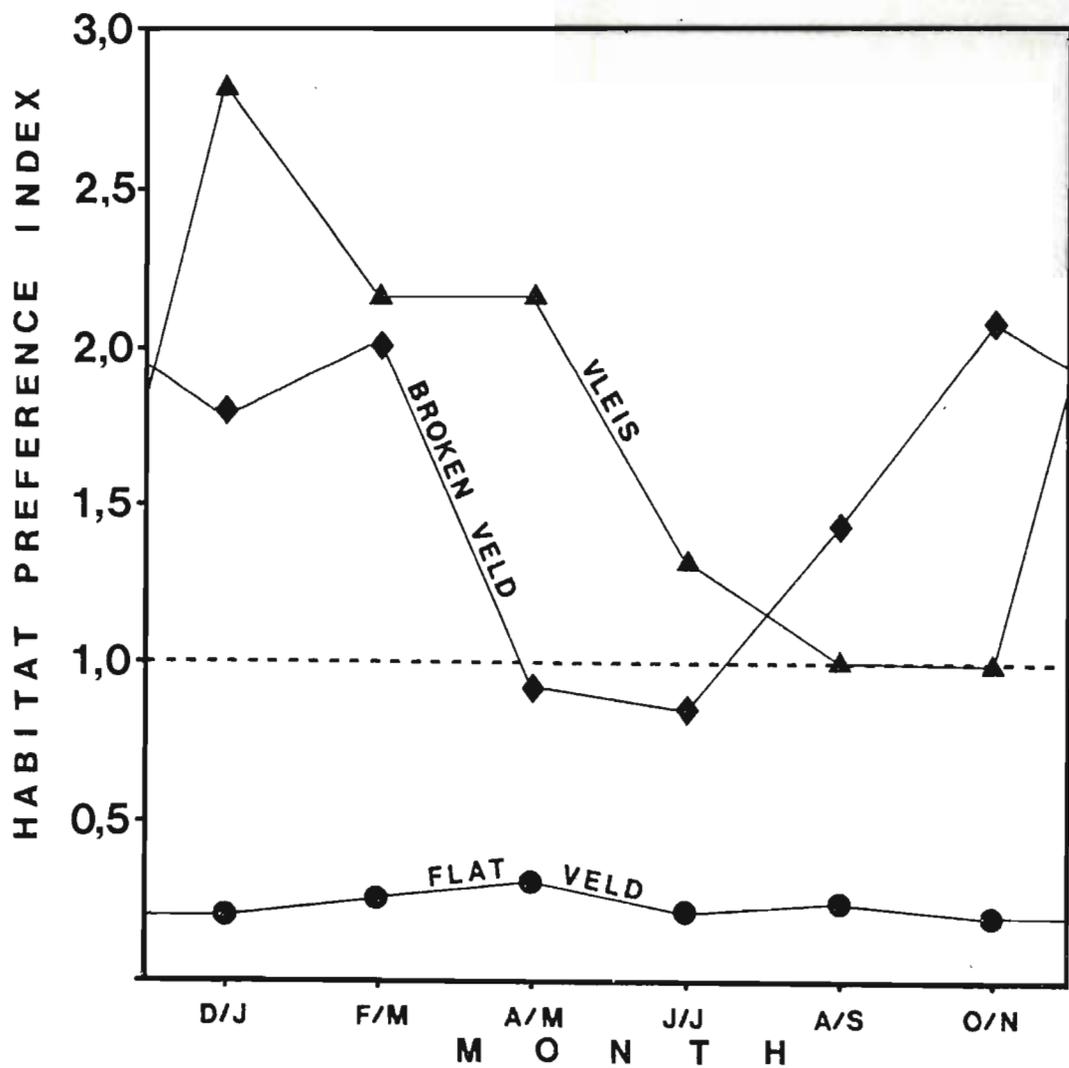
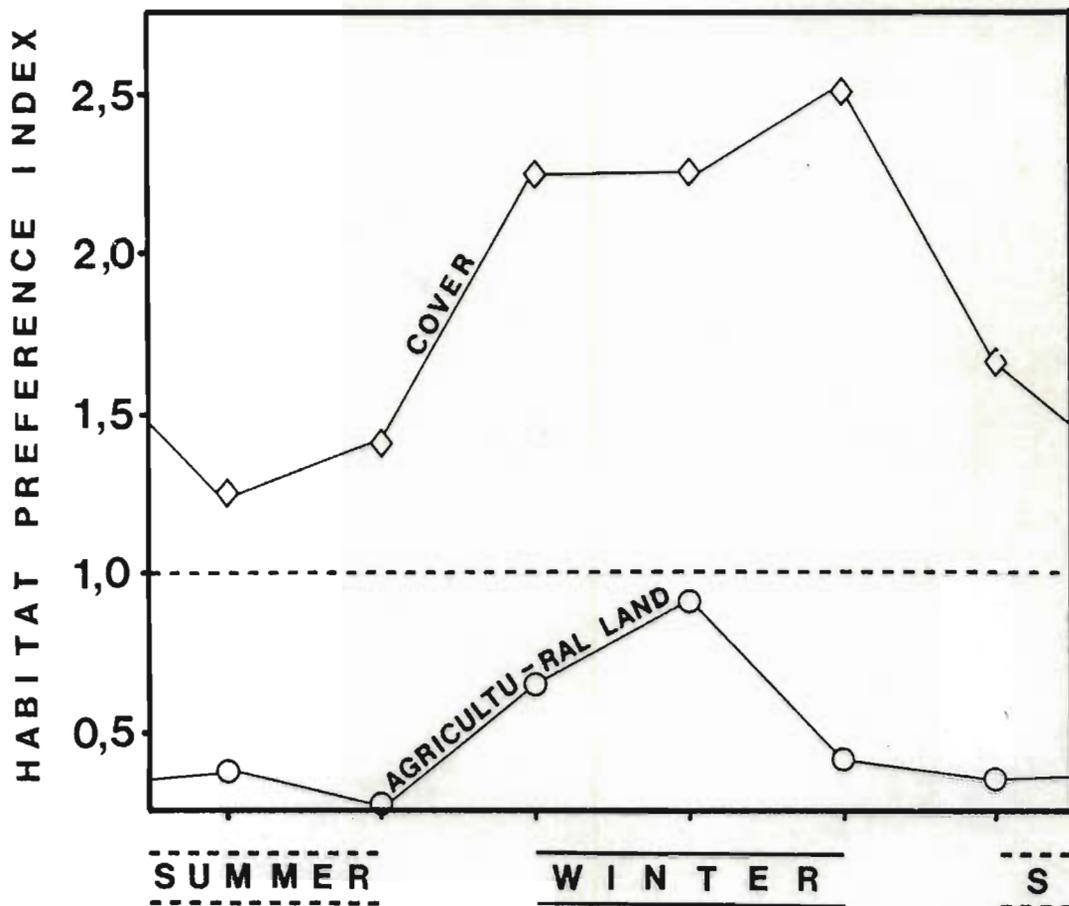
Seasonal changes in habitat preference for the five major habitat types are shown in FIG. 5.3. A habitat preference index value of one signifies random distribution with respect to the habitat, greater than one signifies preference, and less than one, avoidance of a habitat. From the results it is possible to distinguish three distinct trends in habitat use:

- 1 Cover and agricultural land are 'winter' habitats that are more highly preferred at this time than in summer. The animals are feeding on the pastures, and using nearby cover for shelter.
- 2 Vleis and broken veld are 'summer' habitats, that become highly favoured only at this time of the year. These habitats can provide food and adequate shelter simultaneously in summer, but in winter forage quality is low (SECTION 5.3.2.1).
- 3 Flat open veld is avoided at all times of the year, and this is interpreted as being the result of the inadequate provision of suitable cover.

(b) Changes in Animal Distribution

The distribution of reedbuck sighted shortly after dusk throughout the extensive study area is mapped, and presented in FIG. 5.4. FIG. 5.4a shows the distribution of the major habitats where 'other cultivated lands' includes crop lands, rested lands and plantations, and where 'veld' includes all natural vegetation other than vleis. For a more detailed breakdown of these habitats the reader is referred to TABLE 1.2 of CHAPTER ONE. FIG.5.4b (an overlay to FIG.

FIG. 5.3 : Seasonal changes in preference for major habitat types



5.4a) shows the distribution of reedbuck in August 1981, and FIG. 5.4c (also an overlay) the corresponding distribution in February 1982. The proportion of animals in each of the major habitat types is shown in TABLE 5.3, for August 1981 and February 1982.

TABLE 5.3 : Proportion of animal sightings made in each of the major habitat types of the extensive study area

HABITAT	PROPORTION OF SIGHTINGS (%)	
	August 1981 (n = 673)	February 1982 (n = 398)
Annual pasture	53	23
Other cultivated lands	20	12
Vlei	13	44
Veld	14	21

These survey results clearly indicate the following trends:

- 1 Animals are concentrated on annual pastures during the winter, and the greatest concentrations of animals are found around the edge of the valley floor on pastures closest to the steeper hillsides. This winter concentration of reedbuck is more marked than TABLE 5.3 would seem to indicate because many animals that were recorded from habitats other than annual pasture were, in fact, close to pastures, and had clearly been attracted by them.
- 2 Particularly in the centre and east of the study area, where there is extensive cultivation, reedbuck densities are lower than elsewhere.
- 3 In summer (FIG. 5.4c) not only is the number of reedbuck sighted far smaller, but they are also more widely scattered. Vleis are clearly important summer habitats, and one could speculate that areas of veld that were inaccessible were inhabited by many of the 'missing' animals that congregate on the pastures in winter.

FIGURE 5.4b : REEDBUCK DISTRIBUTION IN THE EXTENSIVE STUDY AREA : AUGUST 1981



FIGURE 5.4c : REEDBUCK DISTRIBUTION IN THE EXTENSIVE STUDY AREA : FEBRUARY 1982

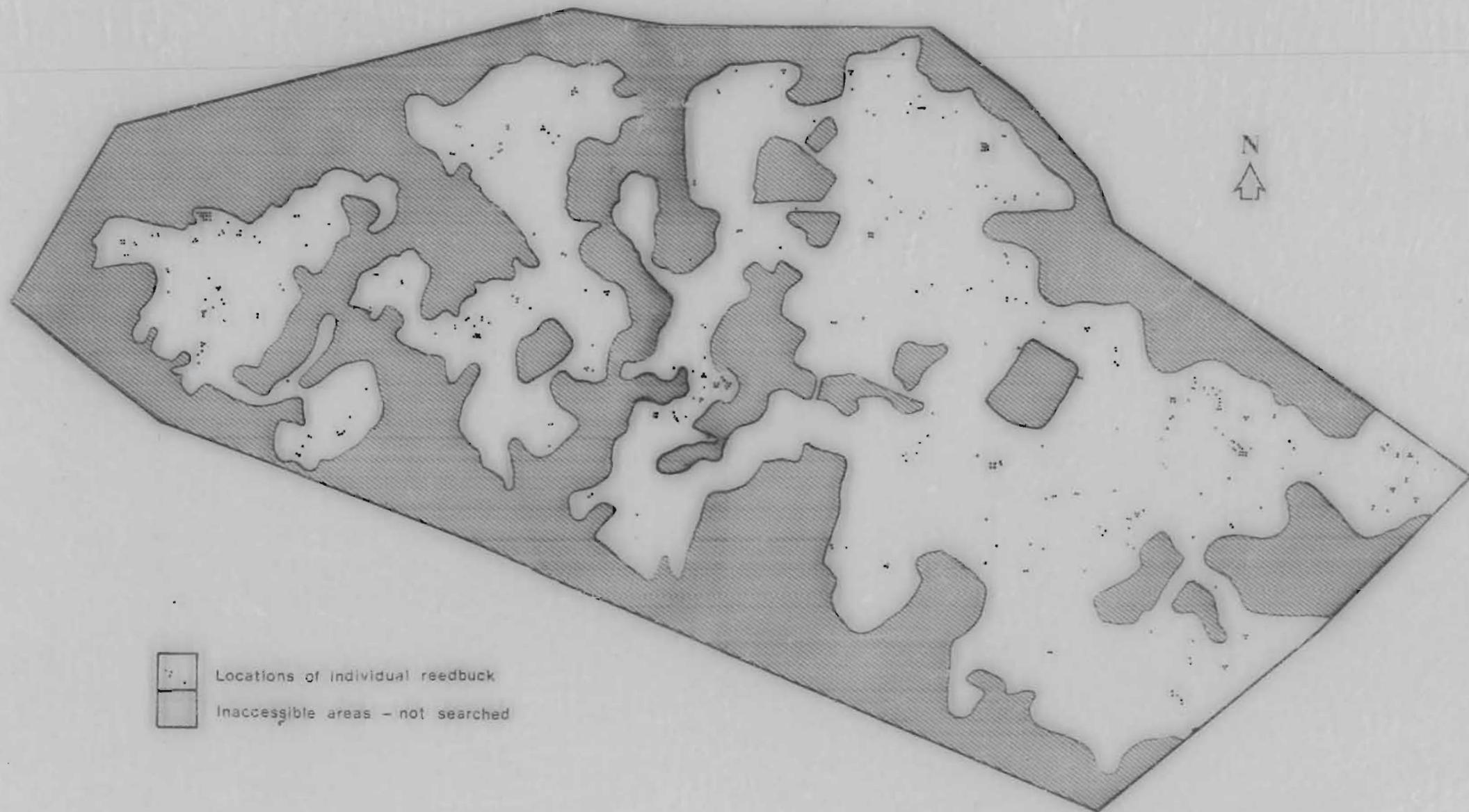
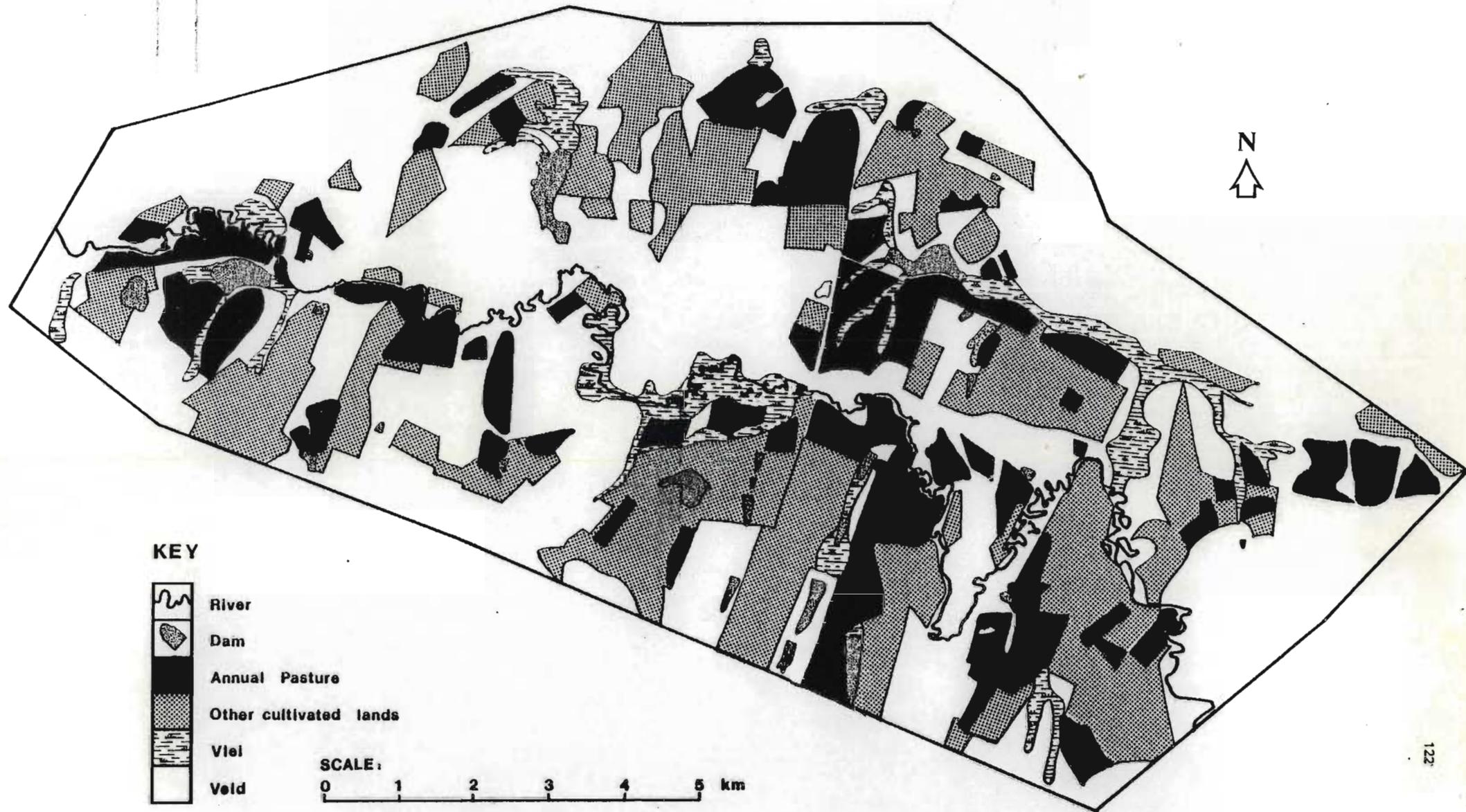


FIGURE 5.4 a : DISTRIBUTION OF HABITAT TYPES IN THE EXTENSIVE STUDY AREA



(c) Multivariate Analysis of Reedbuck-Habitat Relations

The initial series of scattergrams examining the relationship between reedbuck numbers and each of the habitat variables, showed consistently higher correlations between reedbuck and the areas of the various habitats considered for the catchment compared with corresponding areas on the property. These results confirmed the value of the catchment concept. The ten strongest correlations were, in rank order:

Rank	Habitat Variable	Correlation (r)
1	Catchment habitat diversity score	0,87
2	Catchment total area of low woody cover	0,86
3	Catchment area of bramble	0,85
4	Catchment total area of natural vegetation	0,84
5	Catchment total area	0,84
6	Catchment area of rank herbs/old lands	0,82
7	Catchment area of gulleys in N-facing hillsides	0,80
8	Catchment area of N-facing hillsides	0,79
9	Catchment total area of broken veld	0,77
10	Catchment area of woody scrub	0,75

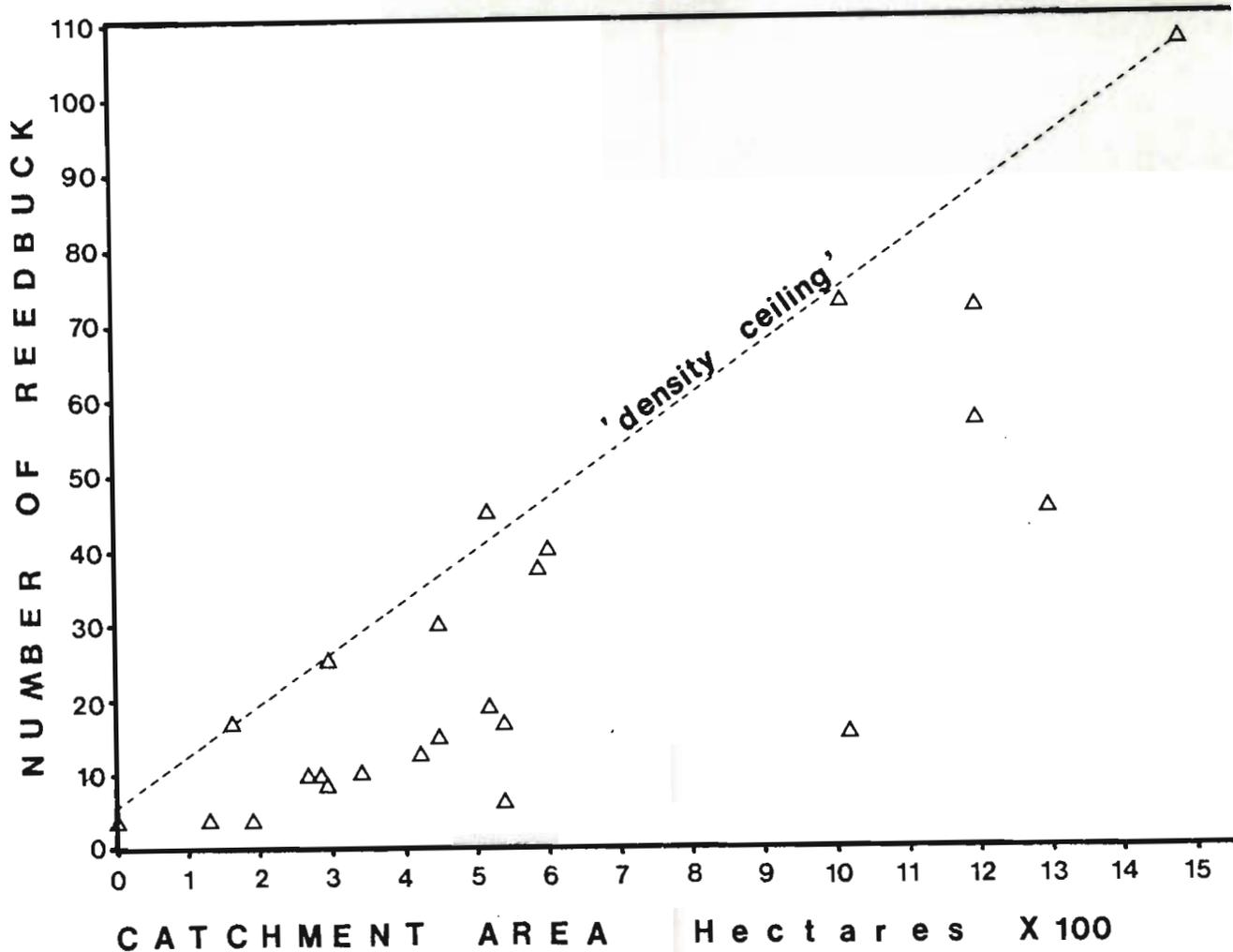
The closest correlation between reedbuck numbers and any of the habitat variables considered for the property was with the area of low woody cover on the property ($r=0,69$).

The results presented above clearly indicate the importance of cover to reedbuck: variables ranked 2nd, 3rd, 6th and 10th being simple measures of cover components, while all other variables occupying high rank positions contain at least some cover element. It is interesting to note, too, that the areas of pasture ($r=0,36$) and vlei ($r=0,63$), being possible winter food sources, do not rank highly in correlations with reedbuck numbers. These results then, suggest that food is super-abundant, and that cover is the most important factor governing reedbuck densities.

The relationship between reedbuck numbers and the total area of the catchment is a particularly interesting one, and one which may add some weight to the tentative conclusion drawn above. From FIG.5.5 it can be seen that the six uppermost points have an almost straight linear relationship, and that all other points fall below this (dotted) line. In other words, there appears to be a 'ceiling' above which reedbuck densities cannot go, which has been reached on just six farms, with all other farms supporting lower animal densities. On these lower density farms something is, presumably, limiting the

achievement of the 'ceiling' density, and this limiting factor could, judging from the above correlation list, be the availability of cover. If that limiting factor were removed, all farms would, we might suppose, achieve the density 'ceiling'.

FIG. 5.5 : The relationship between catchment area and reedback number



We must conclude from this examination of simple correlations that the catchment concept is a particularly useful one, but that a simple measure of total catchment area is inadequate as an expression of anticipated reedback numbers because the important factor is normally what habitats that catchment contains.

The strength of Spearman rank correlations between all the major habitat categories is shown in TABLE 5.4. They show that the diversity score, vlei areas, and the total areas of property and catchment are strongly correlated with a number of the other habitat variables, and these variables are shown to be, in themselves, of limited value in habitat preference determination. Controlling for the effects of these variables in second order partial rank

correlations (TABLE 5.5), the unambiguous results again demonstrate the importance of low woody cover (bramble and riverine scrub communities) as determinants of reedbuck numbers.

Several combinations of habitat variables were used in stepwise multiple regression analyses, and the best predictive equation, accounting for 87,4 % of variation in reedbuck numbers was:

$$y = 0,74 + 0,079 a + 0,69 b - 0,054 c$$

(±0,018)
(±0,18)
(±0,039)
(S.E.)

where

- y = number of reedbuck on a property
- a = the habitat diversity score of the catchment
- b = the area of low woody cover in the catchment
- c = the area of annual pasture on the property

Considered alone the habitat diversity score accounts for 75,3 % of variation in reedbuck numbers, and this is improved by a further 10,9 % by consideration of the area of low woody cover in the catchment. The use of a third correlate (annual pasture) adds only a further 1,2 %. It is interesting that the equation predicts an increase in reedbuck numbers for improvements in habitat diversity score as such improvements are a normal feature of farm development in the region of the study area. Two of the most obvious ways that this is occurring are, firstly, the breaking-up of extensive areas of flat veld into relatively small fields interrupted with windbreaks and rank field boundaries, and, secondly, the failure to remove invasive woody elements from non-agricultural sites where they begin to establish themselves. It should be stressed, however, that for each additional reedbuck on the farm, the average number of habitat types in each 6,25 ha grid cell has to be increased $1/0,079 = 12,7$ times, and the effect that habitat diversity has, per se, on reedbuck numbers is therefore, relatively small.

Of far greater importance is the effect of low woody cover on reedbuck densities: diversity and low woody cover are closely correlated variables (TABLE 5.4) and the woody cover component of the diversity score is obviously very important. From the equation it can be seen that for each additional three hectares of low woody cover in the catchment, there are an extra two reedbuck on the farm.

From a practical point of view, then, if habitat management were to become a significant tool in controlling reedbuck numbers, it could be achieved far more easily by manipulation of low woody cover elements than by attempting to alter the diversity, or patchiness of the habitat. Finally, in relation to the above equation, the area of

TABLE 5.4: The strength of Spearman rank correlations between all major variables in the multiple regression analysis of reedback-habitat relations. All correlation values of less than 0,5  were considered indicative of only weak associations between variables, correlations of 0,5 to 0,8  of moderate associations, and correlations of greater than 0,8  of strong associations

		PROPERTY										CATCHMENT												
HABITAT CATEGORY		REEDBUCK	VLEI	ANNUAL PASTURE	ALL CULTIVATED LAND	LOW WOODY COVER	BROKEN VELD	FLAT VELD	NATURAL VEGETATION - TOTAL AREA	TOTAL AREA	HABITAT DIVERSITY SCORE	SHEEP (ANIMAL UNITS)	BULK GRAZERS (ANIMAL UNITS)	VLEI	ALL CULTIVATED LAND	LOW WOODY COVER	BROKEN VELD	FLAT VELD	NATURAL VEGETATION - TOTAL AREA	TOTAL AREA	HABITAT DIVERSITY SCORE			
PROPERTY	VLEI																							
	ANNUAL PASTURE																							
	ALL CULTIVATED LANDS																							
	LOW WOODY COVER																							
	BROKEN VELD																							
	FLAT VELD																							
	NATURAL VEGETATION - TOTAL AREA																							
	TOTAL AREA																							
	HABITAT DIVERSITY SCORE																							
	SHEEP (ANIMAL UNITS)																							
BULK GRAZERS (ANIMAL UNITS)																								
CATCHMENT	VLEI																							
	ALL CULTIVATED LANDS																							
	LOW WOODY COVER																							
	BROKEN VELD																							
	FLAT VELD																							
	NATURAL VEGETATION - TOTAL AREA																							
	TOTAL AREA																							
	HABITAT DIVERSITY SCORE																							

TABLE 5.5 : Results of selected partial rank correlation (2nd order) analyses

	FIRST ANALYSIS	SECOND ANALYSIS	THIRD ANALYSIS
Control variables:	Catchment vleis Catchment diversity	Catchment vleis Catchment area	Catchment area Catchment diversity
Variables correlating best with reedback numbers (in rank order):	1 Catchment low woody cover	Catchment low woody cover	Catchment low woody cover
	2 Property low woody cover	Property low woody cover	Property low woody cover
	3 Catchment natural vegetation	Catchment diversity	Property cultivated land (correlation negative)

annual pasture is relatively unimportant as a determinant of reedbuck numbers, and is, in fact inversely correlated. Above a certain threshold the area of pasture seemingly contributes to reedbuck numbers only inasmuch as it replaces other habitat types which might be better able to support them.

The above equation is undoubtedly of considerable value in determining the habitat requirements of reedbuck on farmland, but as a predictive equation its utility is severely limited because two of the independent variables (viz. habitat diversity score and area of low woody cover) are difficult to estimate quickly without reference to aerial photographs. Accordingly, a series of stepwise multiple regressions were performed using selected habitat variables that were considered potentially useful in this regard, and the best predictive equation generated, accounting for 80,4 % of variation in reedbuck numbers, was:

$$y = 2,0 + 0,24 d - 0,18 e$$

(±0,05)
(±0,06)
(S.E.)

where y = number of reedbuck on a property
 d = the total area of all natural vegetation in the
 catchment
 e = the area of broken veld in the catchment

Using this equation it is fairly straightforward to estimate the number of reedbuck any particular farm is likely to support. The purpose of such prediction would be in the quick assessment of quotas in a harvesting programme.

TABLE 5.6 shows predicted values for reedbuck numbers on each of the 23 study farms, using each of the generated equations, and compares these predicted values with observed values and estimates made by the landowners concerned before any counts were made. The mean percentage deviation from observed values is given in the bottom row of the table, from which it appears that the predictive equations are far more reliable (worst mean deviation = 30 %) as methods of estimating reedbuck numbers on any particular farm than is the use of an estimate given by a farmer (mean deviation = 68 %). However, it should be stressed that farmers were asked what was the maximum number of reedbuck occurring on the farm at any time of the year, and that in several cases estimates were made of numbers in summer, as the animals move to adjacent farms in winter. The observed values are winter counts and as has been shown (SECTION 5.3.1.2) animal distribution patterns undergo considerable seasonal changes. If we look at the total number of reedbuck estimated by the farmers who

TABLE 5.6 : The number of reedbuck counted on each farm in the extensive study area, compared to the number predicted by each of the derived regression equations, and the landowner's estimate. See text for explanation.

FARM NUMBER	P R E D I C T E D N U M B E R		OBSERVED NUMBER	FARMERS ESTIMATE
	EQUATION ONE*	EQUATION TWO**		
1	113	81	107	-
2	24	20	28	-
3	25	24	21	-
4	28	23	14	-
5	32	35	18	-
6	57	68	74	14
7	54	53	72	-
8	1	2	5	40
9	65	76	62	-
10	35	31	35	40
11	8	4	5	25
12	24	33	38	25
13	4	8	11	6
14	5	3	4	-
15	24	35	17	-
16	18	15	8	28
17	21	20	24	35
18	50	66	44	40
19	37	35	48	35
20	7	7	19	6
21	20	16	11	20
22	19	21	11	30
23	16	8	11	5
TOTAL	687	684	683 (344) [@]	(349)
MEAN PERCENTAGE DEVIATION FROM OBSERVED VALUE	26	30	0	68
* EQUATION ONE:	$y = 0,74 + 0,079a + 0,69b - 0,054c$			
**EQUATION TWO:	$y = 2 + 0,24d - 0,18e$			
	see text for explanation of symbols used			
@	shown in brackets is the total number observed on those farms where a corresponding farmer's estimate was obtained.			

gave estimates, totalled for the study area as a whole (349 animals) they are remarkably close to actual figures (344 animals) totalled for those farms.

With regard to the second predictive equation, it is interesting that this equation also seems to attempt an estimate of reedbuck numbers from a measure of cover availability. Here cover is measured as the total area of natural vegetation less most of the broken veld: leaving vleis, bramble, low woody scrub, and flat veld. Flat veld has been shown to be poorly correlated with reedbuck numbers (TABLE 5.4) and it is probable that had this component been included in the regression, it would have been a further negative component.

5.3.1.3 AT THE INDIVIDUAL LEVEL

The results of home range habitat analysis for 45 known animals are presented in TABLE 5.7 and FIG. 5.6, in which the mean areas of the major habitat types occurring within the home ranges of animals of different age and sex classes are compared. In all cases there is a highly significant difference (χ^2 ; $p < 0,001$) between habitat occupancy and availability, where availability is measured as the areas of the different habitat types within the 1 050 ha intensive study area.

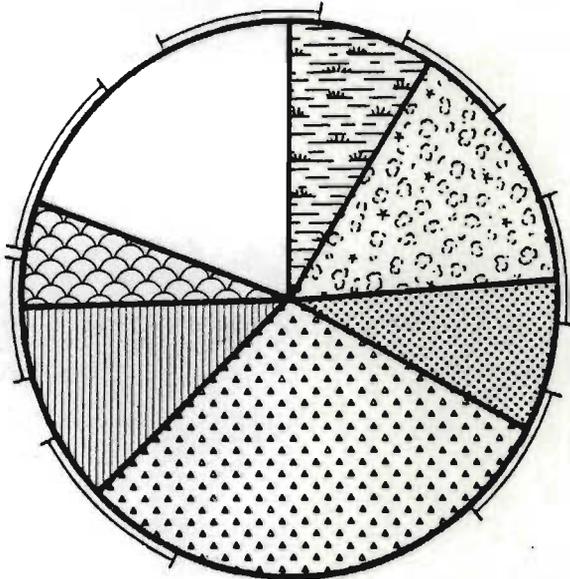
TABLE 5.7: Areas of the major habitats occurring within known home ranges, considered by age and sex class.
Mean values are shown ± 1 standard error

		M A L E S		F E M A L E S		Area
		Adult	Subadult	Adult	Subadult	availabl
		(n=9)	(n=15)	(n=16)	(n=5)	(ha)
H A B I T A T	VLEI	6,5 \pm 1,3	11,9 \pm 2,0	9,0 \pm 2,1	5,8 \pm 1,6	66
	LOW WOODY COVER	10,7 \pm 3,6	19,1 \pm 2,6	15,2 \pm 2,8	13,6 \pm 3,3	79
	RANK HERBS	6,6 \pm 1,8	8,5 \pm 1,2	6,2 \pm 1,3	4,3 \pm 1,8	84
	ANNUAL PASTURE	22,1 \pm 4,2	23,2 \pm 3,3	19,8 \pm 3,8	7,7 \pm 1,7	228
	AGRICULTURAL LANDS	8,8 \pm 3,0	14,1 \pm 1,6	8,7 \pm 2,3	6,2 \pm 3,0	134
	FLAT VELD	4,5 \pm 2,0	15,8 \pm 3,1	7,6 \pm 2,9	2,8 \pm 1,2	196
	BROKEN VELD	14,3 \pm 5,7	117,4 \pm 14,1	56,5 \pm 15,5	35,4 \pm 9,6	263
HOME RANGE SIZE		73,5 \pm 13,9	210,0 \pm 18,5	123,0 \pm 21,6	75,8 \pm 16,6	

FIG. 5.6: Habitat composition of known home ranges

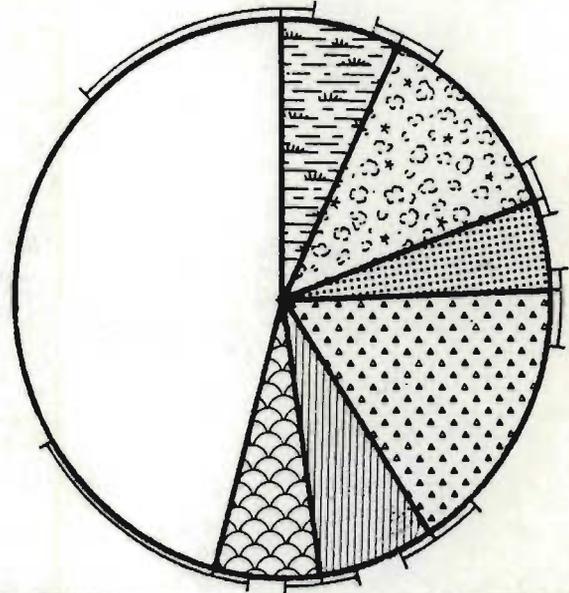
ADULT MALES

MEAN HOME RANGE SIZE 73,5 ha.



ADULT FEMALES

MEAN HOME RANGE SIZE 123,0 ha.



AVAILABILITY

Vleis



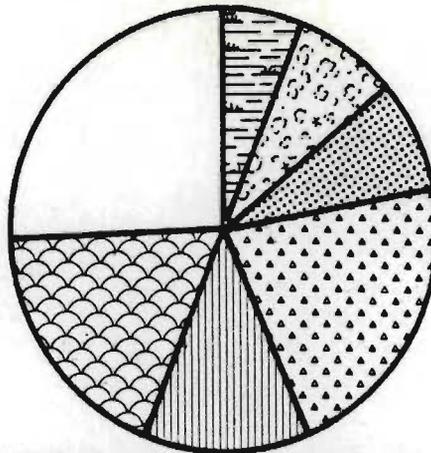
Flat open Veld



Broken Veld



Agricultural Lands



Low Woody Cover



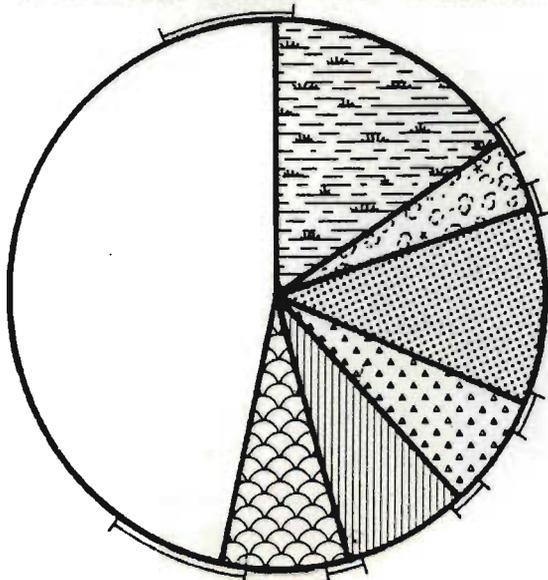
Rank Herbs



Annual Pasture

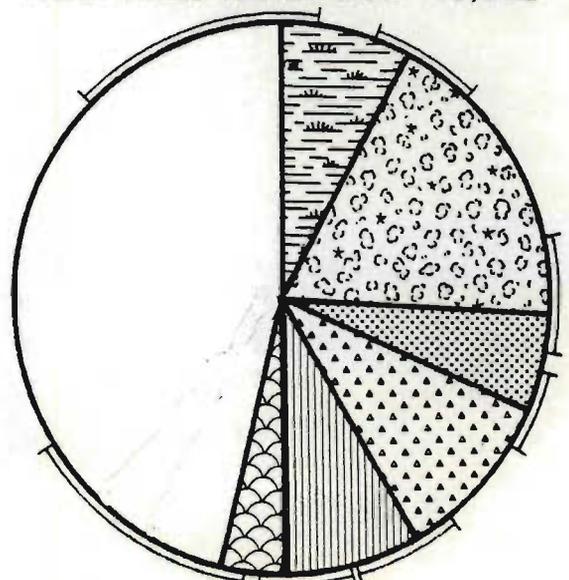
SUBADULT MALES

MEAN HOME RANGE SIZE 210,0 ha.



SUBADULT FEMALES

MEAN HOME RANGE SIZE 75,8 ha.



ARCS SHOW ONE STANDARD ERROR EACH SIDE, FOR EACH HABITAT

In all age and sex classes, individual home ranges tend to occupy vleis, low woody cover, and rank herbaceous cover areas to a greater extent than would be expected had the animals distributed themselves randomly with respect to habitat types. They also tend to avoid areas of flat open veld, although adult females and subadults of both sexes occupy broken hilly veld in preference to other habitat types. More than half the home range areas of adult females and subadults consists of veld, whereas in the adult male this habitat type constitutes only a quarter of the area occupied.

Although the calculated home range size of adult females is 67 % greater than that of males, the difference is not significant ($p > 0,1$). The only significant differences in home range sizes between age and sex classes occur between subadult males and all other classes, whose home ranges are significantly ($p < 0,01$) smaller. Home range size and spatial organisation is considered further in CHAPTER SIX.

As regards habitat preference the results presented in this section confirm the conclusions reached previously. Low cover, preferably with some woody elements present is of paramount importance to reedbuck. So too are extensive areas of broken veld: these provide adequate cover by way of boulder outcrops, gulleys and ledges that support rank vegetation, and generally broken physiography which allows escape from danger by running out of sight over a ridge, around a hillside, or over its top (pers. obs.).

It might have been reasonable to suppose that adult females would be more closely associated with 'prime' areas of cover than other age and sex classes, on account of the nursery function these areas undoubtedly perform. However, the home range data presented here do not reveal any such relationship. This is not to imply that none exists since there may be some temporal/seasonal spacing involved, whereby the nursing female is initially closely associated with the area of cover where its infant is concealed, later becoming more wide-ranging as the juvenile matures. Unfortunately, the type of analysis adopted here does not distinguish this kind of complexity. It is possible, too, that adult females become more wide-ranging as a result of ram-seeking activity associated with oestrous behaviour. Such activity has been reported in domestic sheep ewes (Lindsay and Fletcher, 1972).

Although adult females occupy extensive areas of broken veld during the course of a year, adult males do not; the home ranges of this group comprise a far greater proportion of cover and annual pasture. This is probably significant, as these habitat types seem to

represent the most important regions of a reedbuck's home range, and by maintaining dominance over his rivals in these key areas, a reedbuck ram is able to maximise his chances of meeting an oestrous ewe, and propagating his genes. The annual pasture in the adult ram's home range is considered to be significant, not simply as a feeding area, but also as a 'meeting and mating' ground. This probably explains why its area is proportionately greater than in the home ranges of the other age and sex classes where its primary function is as a feeding area.

5.3.2 Diet

5.3.2.1 QUANTITY AND QUALITY OF INGESTED FOOD

The relationship between wet rumen content mass and dead mass for females is described by the equation $y = 0,071x + 1,1$ ($r=0,48$, $p<0,01$, $n=48$), and for males by the equation $y = 0,075x + 1,4$ ($r=0,69$, $p<0,01$, $n=45$) where y = mass of the rumen content in kilograms and x = dead mass in kilograms.

Subsamples of the rumen content of 26 reedbuck, shot in April, were oven dried and a mean dry matter percentage of 17,1 ($\pm 0,49$ (S.E.)) % derived. The overall mean wet rumen content mass was 4,61 ($\pm 0,18$ (S.E.)) kg for adult females and 6,42 ($\pm 0,24$ (S.E.)) kg for adult males, the respective dry matter equivalents being 0,79 kg and 1,10 kg.

These values are not measures of daily forage intake, because nothing is known of retention times in the rumen. Retention times, which are highly variable, are governed by the digestibility of the food (McDonald *et al.*, 1973) and its succulence, or water content (Norris, 1943). The more digestible, succulent foods are retained for shorter periods. And, since the ruminant stomach works at nearly constant volume (Stanley Price, 1977), larger quantities of good quality foods can be consumed, because they are retained in the rumen for shorter periods than drier, less digestible ones (Stanley Price, *op.cit.*). In his study on hartebeest (*Alcelaphus buselaphus cokei*) Stanley Price (*op.cit.*) found that retention times varied from a mean value of 22,1 hours in January, to a mean of 90,2 hours in September.

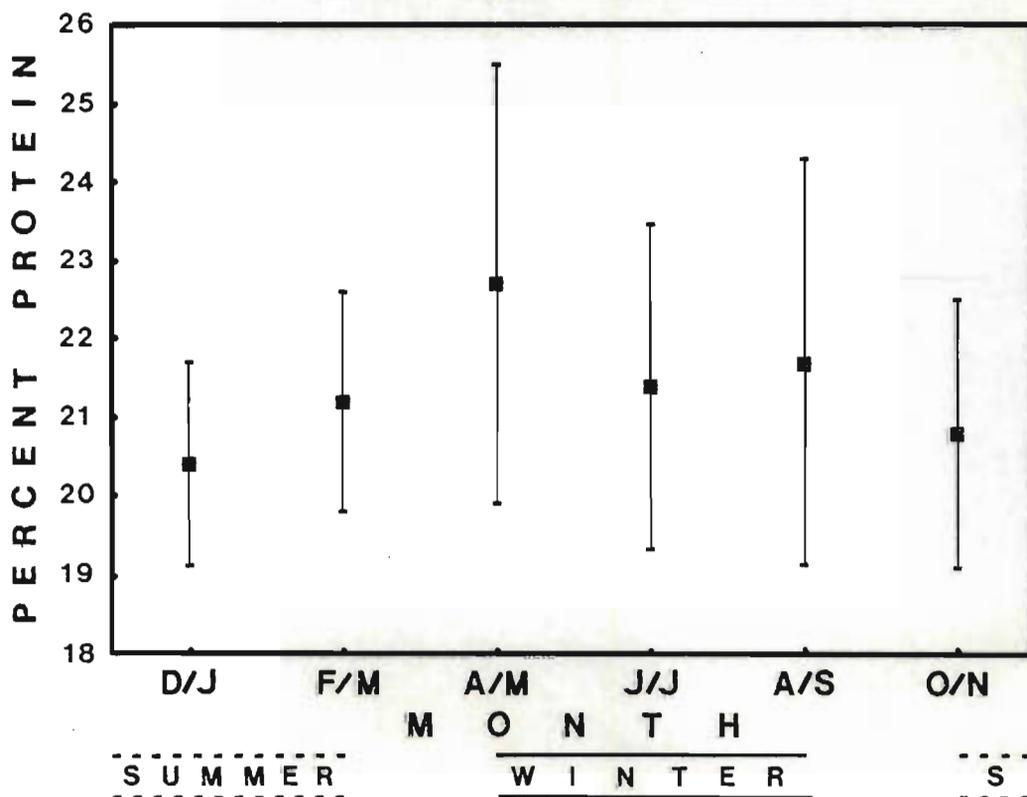
In view of the work of Stanley Price and others, it might be fair to assume that even the highest quality diet is unlikely to pass through the rumen in a period much less than 24 hours, in which case a measure of rumen content mass might be regarded as being approximately equivalent to the maximum daily intake that an animal is physiologically capable of consuming. The results of this study

(see below) show that rumen content quality is extremely high in reedbuck, which would ensure minimal retention times, and might enable the animals to consume close to this theoretical maximum intake.

An alternative approach to determine the likely daily forage intake of reedbuck is to examine published figures for domestic sheep, which is probably the closest ecological equivalent for which such figures are available. Reid (1968) gives a dry matter intake of 1,1 kg/day for a 70 kg adult sheep feeding on a 'fair quality' roughage diet containing 1,8 kcal. of metabolisable energy per gram. This figure agrees closely with the rumen content mass of adult male reedbuck of 1,10 kg for an average 68 kg animal in this study.

There was no significant difference in the protein content of male and female rumina in any month ($p > 0,1$), and the sexes were considered together in the preparation of FIG.5.7; here seasonal changes in the protein content of the rumina are illustrated. Mean protein content remained above 20 % throughout the year, without significant seasonal change.

FIG. 5.7 : Bi-monthly Changes in Rumen Content Quality of Adults
mean values are shown \pm two standard errors



5.3.2.2 QUALITY OF AVAILABLE FOOD

Seasonal changes in the dry matter, crude protein, crude fibre, fat, Calcium (Ca) and Phosphorus (P) percentages of ryegrass from autumn and spring plantings, and Themeda from burnt and unburnt sites are illustrated in FIG. 5.8. The dry matter component of all samples increased progressively through winter. The protein content of spring-planted ryegrass declined during late summer and autumn as the plants seeded and senesced before being ploughed out in mid-winter. Autumn-planted ryegrass, however, showed high protein content levels throughout the winter, fluctuating between 15 % and 30 % in response to successive grazing, fertilizing, and irrigation. The protein content of Themeda from both burnt and unburnt sites fell below 4 % in mid-June, and remained below this level until regrowth began in early September. Burning of the veld stimulated a substantial increase in protein content and in mineral levels in Themeda during early summer, but the improvement over unburnt sites was fairly short-lived and by late January Themeda from the two sites was of similar nutrient value. The burning of veld in spring is a widespread practice (SECTION 1.5.3.4) and the benefits obtained are only too evident from FIG. 5.8: in October, the protein content of Themeda rises above 20 %, and in this regard compares very favourably with planted pasture grasses, such as ryegrass.

5.3.2.3 CROP PREFERENCE

Changes in the pasture preference index of reedbuck for two ryegrass pastures are shown in FIG. 5.9 in relation to concurrent farm management practices. The results presented are considered typical of all land units, and serve to quantify the observed trend that reedbuck's preference for particular land units increases progressively after planting, but declines as soon as cattle begin to graze there. In all cases the fields were strip-grazed, and measurements of pasture preference during the course of a grazing period seem to confirm the observation that reedbuck use it to an extent dependent upon the amount of pasture still undisturbed. After grazing, the pasture becomes progressively more attractive although periods of irrigation also seem to reduce the level of use to some extent. To determine whether the observed changes in preference were related to factors associated with disturbance, or to the height of the living component of the grass, the relationship between grass height and pasture preference was examined (FIG. 5.10). The results indicate that grass height per se is not an important factor determining preference at any particular time, and one is drawn to the conclusion that disturbance by livestock is the chief cause of declines in preference. Similar observations have been made for

FIG. 5.8: Monthly Changes in Quality of Principal Foods

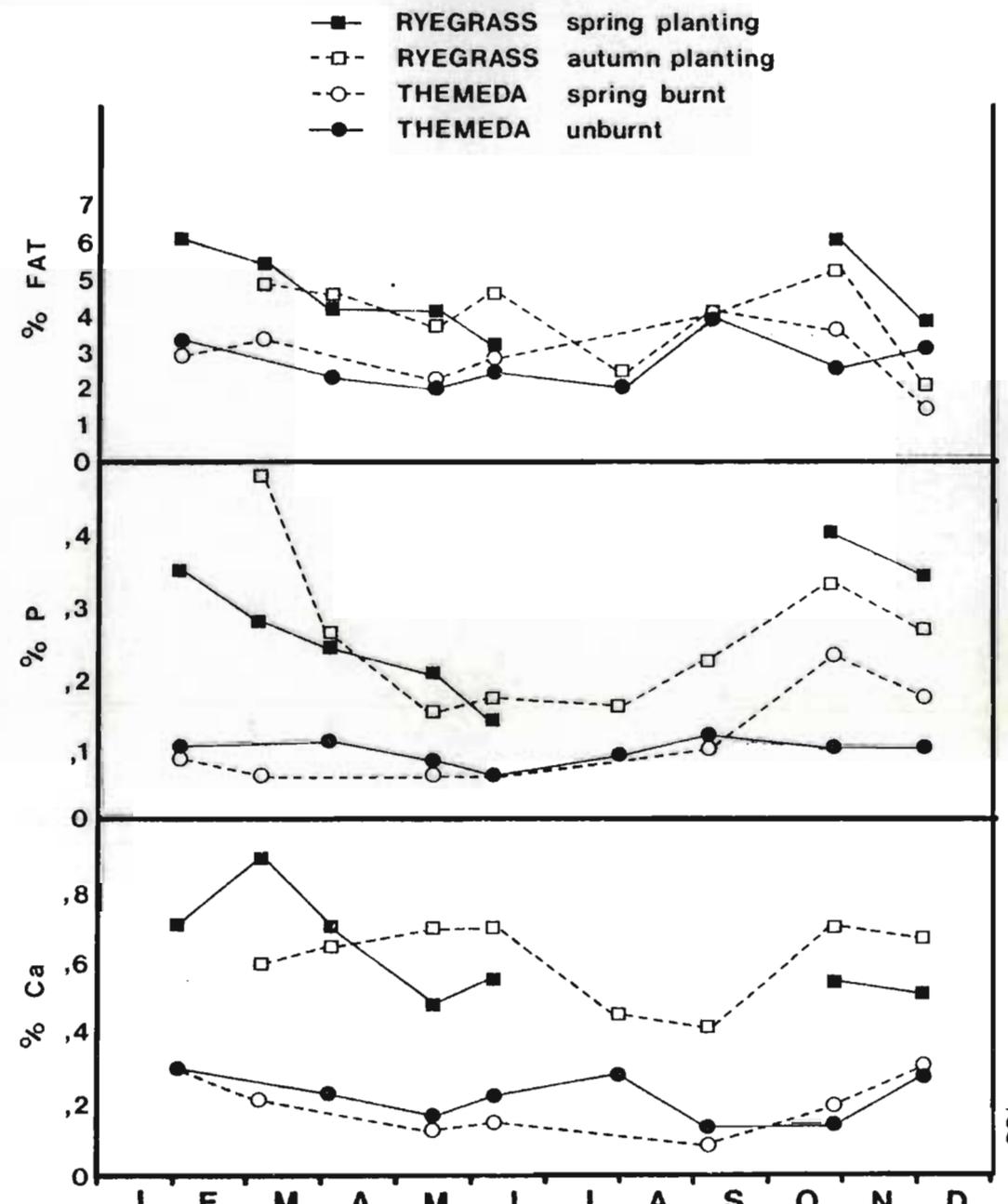
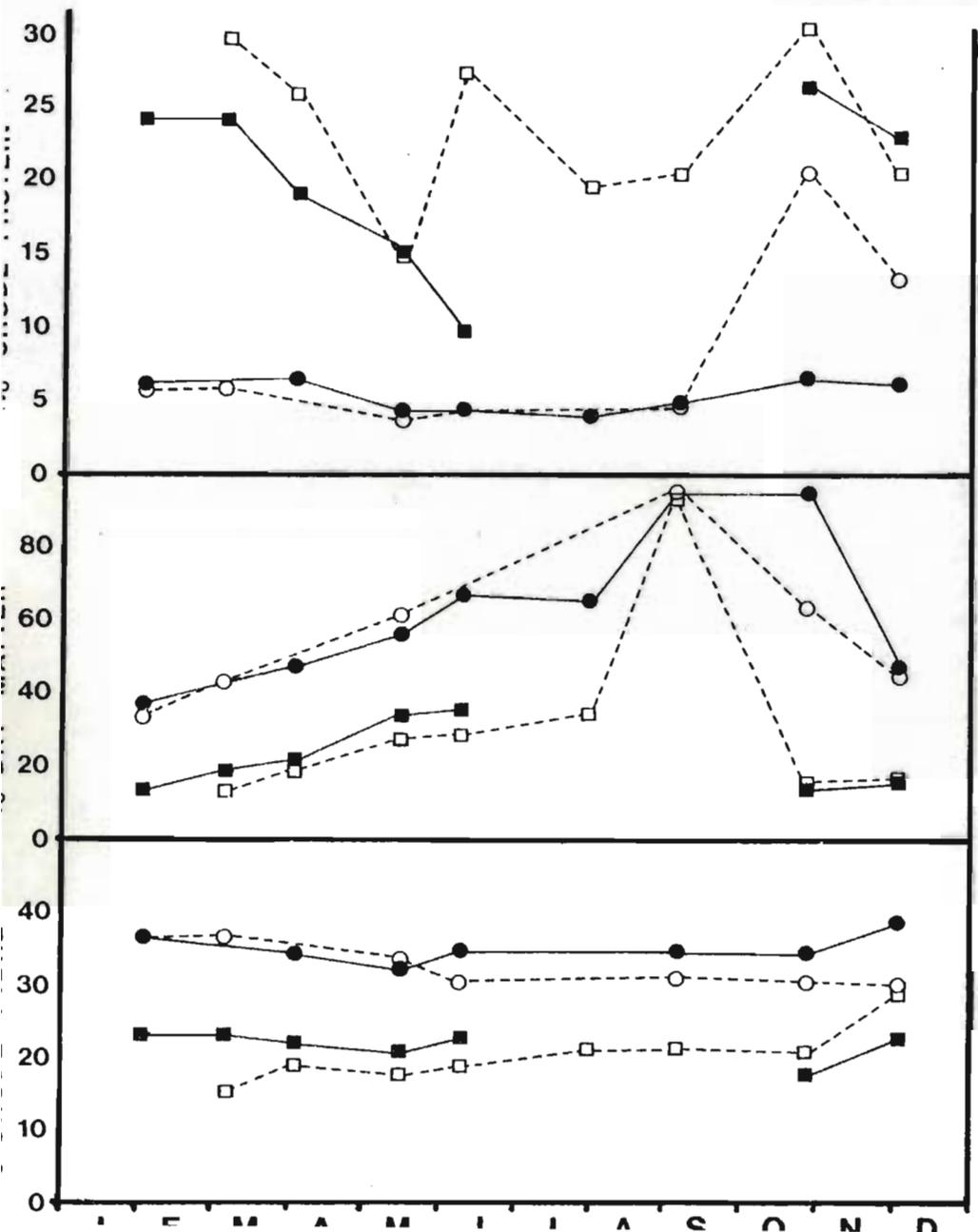
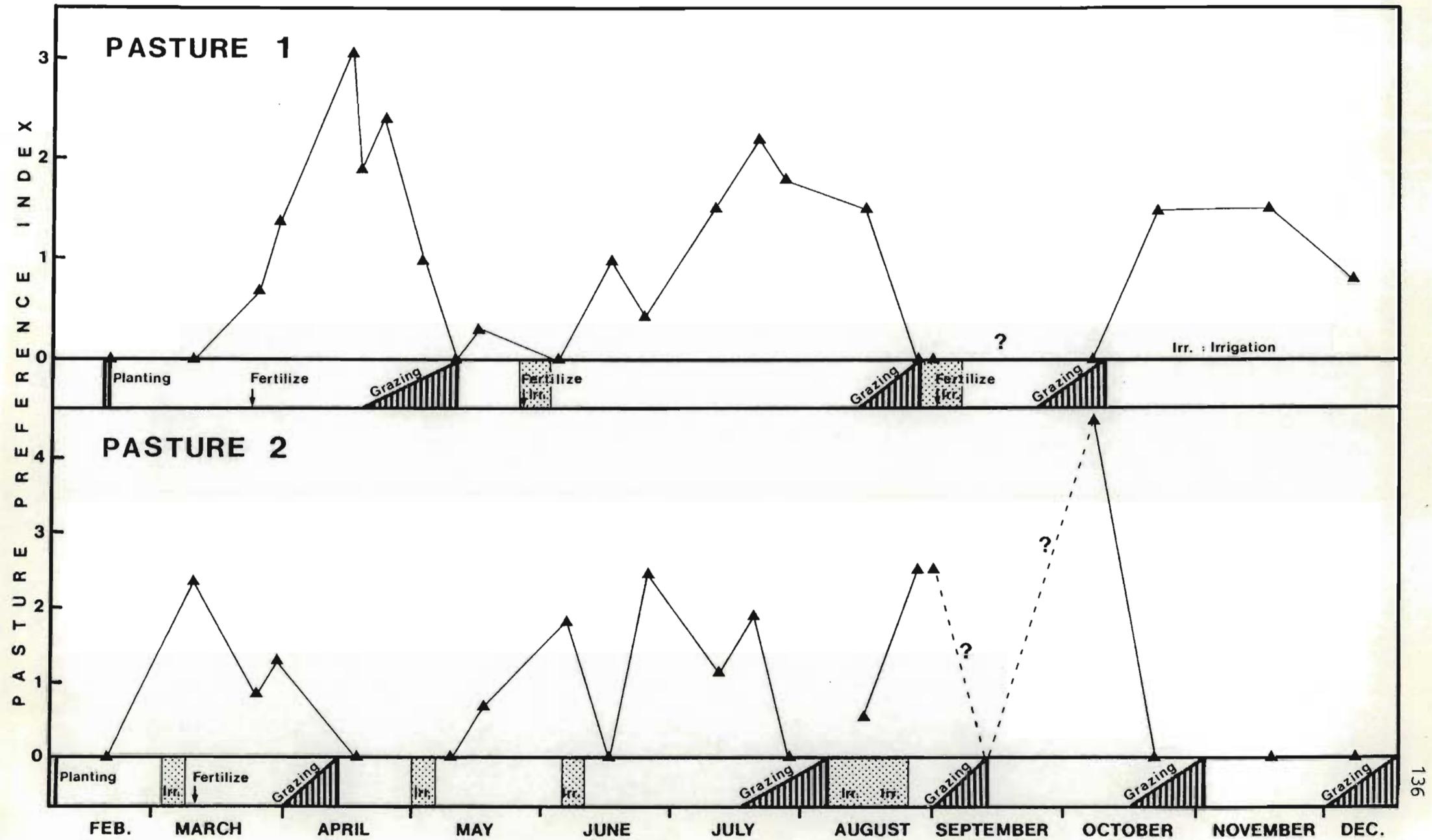
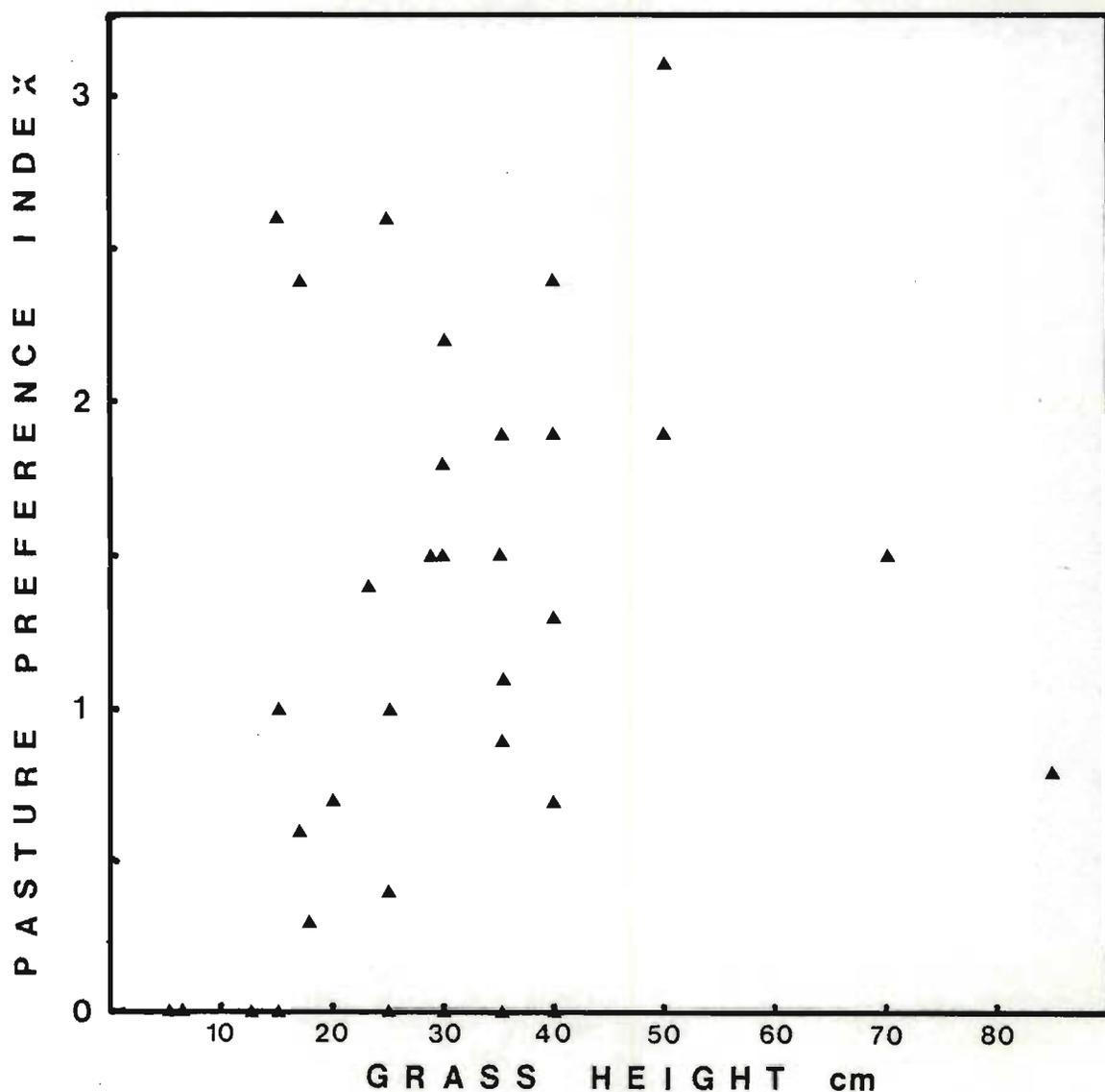


FIG. 5.9: Changes in pasture preference in relation to management activities on two pastures



brown hares (Lepus europaeus) in southern England (Barnes et al., 1983). These observations could have implications for management, in that lands that are particularly susceptible to damage by reedbeek can be stocked for longer periods at lower domestic stock densities, thus maintaining a continual disturbance. However, whilst such an approach may be theoretically applicable, there are many practical reasons for managing domestic animals in reasonably large herds that can be fed, watered, counted, inspected and managed with a minimum of effort.

FIG.5.10 : The relationship between grass height and pasture preference



How, then, do studies of crop preference assist in the control of crop damage on farmland? The answer to this question is that such studies enable the identification of least preferred crops, and, since we have a good idea of the general principles governing the susceptibility of particular areas to damage, based on their proximity to the reedbucks' preferred habitats (SECTIONS 5.3.1.2 and

5.3.1.3), we can now manage the most susceptible lands in such a way as to make them least desirable to reedbuck. This will have the effect of driving the animals elsewhere, which may either mean to the neighbour's crops, or on to less favourable (natural) grazing areas. In practice this means that the susceptible lands on the edge of the cultivated part of a farm should be planted to root crops (which are not eaten by reedbuck), or managed as dryland pasture under continuous grazing by young stock or sheep during winter.

5.4 GENERAL DISCUSSION

Having established preferences for particular habitat types, it is my intention in this section to consider some of the functional aspects of habitat use. In particular, I would like to consider the importance of cover and food resources, and develop an understanding of the ways in which these resources do, or might in the future, contribute to the success of reedbuck on farmland.

It has been recognised for some time (Walther, 1958) that a fairly clearcut dichotomy exists in the behaviour of female ungulates and their young. In the first group, the 'followers' (Walther, 1965), the precocious young associate with the mother's group from soon after birth where they are actively protected from predators (as, for example, in zebra (Equus burchelli), buffalo (Syncerus caffer) and elephant; Leuthold, 1977) or concealed within the group (as in wildebeest (Connochaetes taurinus); Estes, 1974). In the second group, the 'hidiers' (Lent, 1974), the young characteristically spend long periods lying alone in seclusion, and their chief means of defence against predators is to avoid detection. This is aided by isolation of the young from conspecifics, its prone response and general inactivity, and the ingestion of the infant's urine and faeces during irregular visits by the mother. 'Hiding' is the most common strategy for the protection of young bovids from predation (Leuthold, 1977), and is the strategy adopted by reedbuck, and all other members of the Reduncinae (De Vos and Dowsett, 1966; Spinage, 1969; Williamson, 1979). The adequacy of the habitat in providing suitable concealment sites is obviously of paramount importance. The concealment behaviour of young reedbuck has been described by Jungius (1970) in which 'it is assumed with great certainty' that the 'concealment period of the lamb is well demonstrated during the first one and a half to two months, but possibly even longer (three months)'. In my own experience, a number of observations of known adult females with young suggest that a three-month 'lying-out' (Gosling, 1969) period is normal. This is considerably longer than in many other 'hider' species (e.g. Gosling, 1969; Spinage, 1969; Jarman and Jarman, 1974; Clutton-Brock and Guinness, 1975), and this fact again points to the importance of adequate cover in the reedbuck's habitat.

Concealment of the young is, arguably, the most important function of rank herbaceous cover in the life-history of the reedbuck. It is, however, by no means its only function, for cover is also required by older animals for a number of reasons. One of these is, again, concealment from predators. The reedbuck is not a particularly agile animal, and its strategy for survival lies in avoiding detection by predators, rather than in running away from them (Jungius, 1971a; Leuthold, 1977; pers.obs.). Reedbucks spend most of each day lying concealed in rank herbaceous cover. When approached while active they commonly lie down on the spot, preferably in some long grass, and may press themselves as close to the ground as possible to avoid detection. Only if the predator approaches close by does the reedbuck bolt from directly in front of it, thus delaying the predator's reaction, by startling it. If it has to run, it escapes not by speed, but by running out of sight, changing direction, and later, hiding. These are the behavioural responses which determine the types of habitat that are suitable for reedbuck. An appreciation of them helps provide an understanding of the functional aspects of the habitat preferences described in this chapter. Of particular interest is the degree of preference shown for broken veld, compared with that for flat veld. Broken veld can provide adequate cover in the form of boulder outcrops and rocky ridges against which reedbuck can 'disappear': if detected, they do not have to run far before they are out of sight around a hillside, over a ridge or into a gully from where they can change direction, thereby foiling the predator. On flat veld this reaction is not possible, and a reasonably fast predator can easily run a reedbuck down (pers. obs.).

As well as its important function in concealment of adults and young, cover also provides an important 'escape facility'. It has been noted that a reedbuck's preference for particular feeding areas is directly related to the proximity and quality of adjoining cover. This is a demonstration of Leopold's (1933) observation that 'game is a phenomenon of edge'. Several more recent studies have also demonstrated this type of response in considering the importance of ecotones to wildlife (e.g. Clark and Gilbert, 1982). Indeed, so important is the escape facility that good quality feeding areas may remain totally unused if cover is not sufficiently close by (Robinette and Child, 1964; Sayer and Van Lavieren, 1975; Williamson, 1979).

One further very important function of cover, particularly in the extreme climate of the Natal highlands, is its provision of shelter against adverse weather conditions. During late winter particularly, when the peaks of the Drakensberg are commonly topped with snow, and strong 'berg' winds bring freezing air off the mountains, body heat loss is potentially severe. It is probably no coincidence, then, that the reedbuck's preference for low woody cover is greatest at this time of the year, for this is the habitat type where body heat loss can best be controlled. Grace and Easterbee

(1979) have demonstrated that heat loss from red deer in a Scottish glen would be nearly twice as much in an exposed position compared with that in a small area of woodland, where windspeed was reduced by up to 95 %, and Ralph (1981) has demonstrated that in domestic sheep loss of newborn lambs rises from 8,8 % where shelter is available to 35,5 % where it is not available and winds greater than 15 km per hour combine with rain and/or a temperature of less than 5°C during the six hours after birth.

Since cover provides a high threshold of security against many environmental factors (Errington, 1945), it might allow a population of animals to approach the limits set by food supply. This has been clearly demonstrated for mule deer (Picton and Mackie, 1980) in which the 'turnover' of animals was inversely correlated with cover availability in different habitats. Where cover was scarce 'turnover' was high because of the proportionately high rate of loss by emigration, predation and other cover-related factors, coupled with high rates of recruitment. Where cover was super-abundant, however, 'turnover' was low as a result of the proportionately low rates of population loss, and because food had become limiting, thus suppressing reproductive rates. Picton and Mackie's study is important because it demonstrates how a single species can be limited by cover in one part of its range, and by food in another. As far as the population of reedbuck studied here is concerned, food is clearly not a limiting factor (CHAPTER FOUR), recruitment rates are high (CHAPTER THREE), and so are population losses through emigration (CHAPTERS THREE and SIX). These are the characteristics of a cover-limited population. By contrast, Ferrar and Kerr's (1971) reported population crash of reedbuck in Kyle National Park, Zimbabwe, is a demonstration that under certain circumstances reedbuck are apparently food-limited.

Although little attempt was made in this study to ascertain the degree of dietary selectivity shown by reedbuck, there are three lines of evidence to suggest that the species is very selective. Firstly, Jarman (1974), in relating the social organisation of antelope to their ecology, distinguished five main groups based on their feeding styles, and found that within each group social organisation was similar. Jarman (*op.cit.*) placed the reedbuck in his class 'B', which comprised medium sized antelopes that are either grazers or browsers and are very selective. The food items are of high nutritive value, and show some seasonal variations. The home range does not change throughout the year, and may contain more than one vegetation type. The group size is commonly in the range of three to six, but can vary from one up to twelve, with females usually in the company of other females. Single males are probably always territorial. With the possible exception of the last point (CHAPTER SEVEN) the observations made in this study are in agreement with Jarman's classification. The second line of evidence for a degree of dietary selectivity comes from Hofmann and Stewart's (1972) classification based on

a comparison of the stomach structure of 26 of the 31 East African ruminants. In view of observed structural differentiation, especially with regard to rumen papillae shape and distribution, reticulum mucosal relief, and omasal leaflet mucosal relief, the reedbuck was classified as a 'fresh grass grazer dependent upon water'. Finally with regard to dietary selectivity, the coefficients in regression equations relating rumen content mass with body mass derived in this study, are much closer to values characteristic of concentrate selectors ($y = 0,075x - 0,204$) than of bulk and roughage feeders ($y = 0,199x - 0,649$) (Anderson, 1978).

Several recent studies have concluded that it is the quality and not the quantity of food that generally limits ungulate populations (Sinclair, 1975; Mentis, 1978; Scotcher, 1982). Selective grazers, such as reedbuck, are dependent upon a high quality diet, and the carrying capacity of any particular range for that species reflects the abundance of plant food material of sufficiently high quality. This is illustrated by the relative proportions of different antelopes in the Giant's Castle Game Reserve (Rowe-Rowe, 1983), where it is found that the overall standing crop of eland (a class 'E' bulk grazer: Jarman, 1974) is 54 animal units (AU) compared with only 4 AU grey rhebuck, 3 AU mountain reedbuck (class 'B' selective grazers: Jarman, op.cit.) and only 1 AU oribi (class 'B', but probably the most selective of the four species, and recently reclassified as class 'A' (Rowe-Rowe, 1982)). It seems reasonable to assume that reedbuck in the highlands of Natal would naturally be food-limited in a similar way. However, with the provision of a super-abundance of high quality food in the form of annual planted pastures, this limitation is removed. Indeed, a reedbuck feeding on a pasture does not have to exercise any high degree of selectivity because the vast majority of food there is of high quality. And so, whereas a large area of veld might be required to provide enough food of sufficiently high quality, a relatively small area of pasture is required. It would appear, then, that food is unlikely to limit reedbuck populations on farms with annual pastures, and it is likely that the carrying capacity of these farmlands has been raised considerably for reedbuck, as well as domestic stock (Sharkey, 1970).

Taitt and Krebs (1981) and Taitt (1981) examined the effect of extra food on small rodent populations, and some interesting analogies can be drawn between their results and the results of this study. They found that extra food affected the rodent populations in the following ways:

- 1 increased population density;
- 2 increased immigration;
- 3 increased reproduction, and lengthened breeding season;
- 4 decreased individual home range size;
- 5 reversed the normal winter body mass loss.

In order to ascertain what affect the provision of winter pastures has on reedbuck living on farmland it is necessary to compare the population with

another living under similar conditions, but without the extra food. Some comparative data were obtained from a small shot sample of adult male reedbuck from Drakensberg reserve areas (APPENDIX F) which suggest that the provision of pastures results in improved physiological and reproductive condition on farmland (analogous to 3 and 5 above). There is some circumstantial evidence that the improved food supply has resulted in an increased population density (1 above: CHAPTER THREE), but if immigration has increased at some time, net migration at present seems to be away from the areas with the extra food (2 above: CHAPTER SIX). Without comparative data on home range size it is impossible to ascertain what effect extra food might have on this aspect of the reedbuck's biology.

5.5 CHAPTER SUMMARY

The purpose of this chapter is to examine the resources available, and the ways in which reedbuck make use of these resources within the study area, so as to describe the attributes of an optimal reedbuck habitat. Such knowledge might then be of use in the control of overabundant populations, and in the maintenance and expansion of the species' range.

On a province-wide level, population trend was examined by means of the GAMEQUEST postal questionnaire survey, and examined in relation to gross bioclimatic differences. Reedbuck appear to be doing particularly well in areas of the province where the terrain is broken, but are declining in the coastal lowlands of Zululand, probably through loss of habitat to cultivation.

Habitat preference was examined in the intensive study area, where reedbuck tended to inhabit vleis and hilly veld in summer, switching to agricultural land and adjacent cover in winter. Areas of open flat veld were avoided at all times.

A multiple regression analysis was carried out to examine the relationships between available habitat types and reedbuck population size on the 23 farms in the extensive study area. The results of this analysis conclusively demonstrated the importance of low woody cover to reedbuck.

The habitat types represented within the home ranges of 45 known animals were examined. In all age and sex classes, habitat types offering rank cover were preferentially occupied, whilst open veld was avoided.

The diet of reedbuck was examined by chemical analysis of rumen contents. On farmland, reedbuck are able to enjoy an exceptionally high quality diet in which the protein content never falls below 20%, and shows no significant seasonal fluctuation. The quality of the diet is maintained in winter by feeding on planted pastures. Disturbance of these pastures by

domestic stock reduces their acceptability to reedbuck.

The functional aspects of habitat use are discussed with particular reference to the importance of cover and food resources, and their possible role in the regulation of population size.

CHAPTER SIX

SPATIAL ORGANISATION

6.1 INTRODUCTION

6.1.1 Purpose of examining spatial organisation in this study

An understanding of the spatial organisation of reedbuck is important for two main reasons. Firstly, because wildlife in South Africa has the legal status of res nullius (it belongs to nobody, but may be owned by anybody who takes possession of it in compliance with the Nature Conservation Ordinance), it is important for nature conservation authorities to know how far an animal is likely to range, and how many people (landowners) are likely to have a legitimate claim on that animal's life. Wide-ranging species would obviously be more vulnerable to overexploitation than more sedentary ones and might thus warrant a higher degree of legal protection. In this way an understanding of spatial organisation is important to the development of a management policy that safeguards the status of reedbuck, and the interests of the farmers who provide their living requirements.

Secondly, it was shown earlier in this thesis (CHAPTER THREE) that reedbuck are able to regulate their population size through animal movement. From the results already presented it is not clear whether such movement is an 'innate' response, the cause of which lies with the genetics of the dispersing individual, or an 'environmental' response to unfavourable conditions. To gain a more complete understanding of the role of animal movement in population regulation, we need to look more closely at the age and sex of the animals that move, at the distances and directions involved, and at the time of the year when these movements are made.

6.1.2 Definitions and concepts

All animal behaviour is related to the environment in one way or another, and that which is space-related determines an animal's spatial organisation. Intimately linked with this is the concept of 'home range' defined as 'the area over which an animal normally travels in pursuit of its routine activities' (Jewell, 1966).

This relatively simple concept is complicated by the fact that many species undertake seasonal movements between temporary home ranges, and make little

use of intervening areas. Jewell (1966) suggested the term 'lifetime range' to describe this entire system being 'the total area with which an animal has become familiar, including seasonal home ranges, excursions for mating, and routes of movement'.

Since the home range of an animal is also, by definition, its habitat, the purpose of studying spatial organisation and determining habitat preferences is to a large extent one and the same. This purpose has already been specified (CHAPTER FIVE): viz. to gain a knowledge of important habitat attributes that might be of value to conservation management or control. The emphasis in this chapter is on spatial aspects of habitat organisation.

Four types of animal movements are distinguished by Caughley (1977):

- 1 dispersal, which is the movement an animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate;
- 2 local movement within a home range;
- 3 nomadism, which is similar to a random walk, where movement is not restricted to a circumscribed area, and tends to take the animal further and further from its place of origin;
- 4 migration, which is a seasonal movement between areas, that is regular and predictable.

6.1.3 Factors affecting spatial organisation

An animal's spatial organisation is dependent on a variety of factors, some of which are attributes of the animal itself, and some of which are characteristics of the local environment.

Animal attributes that affect spatial organisation include size, species, age and sex. Within certain limits small animals have smaller home ranges than large animals of similar physical constitution (Leuthold, 1977). Hence the small dikdik antelope (Madoqua kirki) (Hendrichs and Hendrichs, 1971, cited in Leuthold, 1977) has a home range size about one thousandth that of the roan antelope (Hippotragus equinus) (Joubert, 1974). Even within species the smaller female often has a smaller home range than the male, as in bushbuck (Waser, 1975) and bohor reedbuck (Hendrichs, 1975). Differences in home range size between species are not simply related to size. Solitary animals usually have smaller home ranges than gregarious ones of similar size, which is what one would expect if the home range is considered as a reservoir of resources. Certain species (e.g. Thomson's

gazelle (Leuthold, 1977) show considerable mobility, while others (e.g. impala (Jarman, 1970)) demonstrate a high degree of attachment to their familiar surroundings. Age and sex differences within a species also affect spatial organisation such that only certain individuals of specific social status may hold territories, and habitat preference may even be sex related, as in giraffe (Giraffa camelopardalis) (Foster and Dagg, 1972).

A home range must contain all the resources needed by an animal, and if an animal can satisfy all its requirements for the year round in a small area, it is likely to have a small home range. If there are seasonal changes in, for example, food or water supplies, or suitable cover, the animal might be forced to move elsewhere temporarily, or use a larger area. This may involve relatively small-scale movements (e.g. Jarman, 1972; Simpson, 1972) or large scale annual migrations, such as occur in the Serengeti (Maddock, 1979).

6.1.4 Possible methods of studying spatial organisation

Studies of spatial organisation depend on the ability to recognise individuals. This can sometimes be achieved by use of natural characteristics, such as shape of horns, or patterns of skin markings, but it is often necessary to resort to artificial marking by means of collars, ear tags, paint, branding, etc.: such methods have been reviewed by Twigg (1975) and Hanks (1969). They usually involve the physical capture of the animal to be marked either by means of drug immobilisation, or mechanical capture using traps, nets, lassos and other devices (Young, 1973). Subsequent tracking of known individuals is usually achieved by visual observation, and sometimes by remote photographic sensing, radiotelemetric and radioisotopic (Harvey and Barbour, 1965) methods. Recently, radiotelemetric methods have become widely used (Cumming, 1971; Douglas-Hamilton, 1971; Leuthold and Sale, 1973), and have proved especially useful in the study of highly mobile and forest-dwelling species.

Following subsequent relocations, there are a number of methods whereby home range size is calculated, of which the minimum area method (Mohr, 1947) is the most widely used.

6.1.5 Previous work on the spatial organisation of reedbuck

The spatial organisation of reedbuck has received scant attention. From observations in Kruger National Park, Jungius (1971a) proposed a territorial system, in which the territory, being a certain part within the home range, is defended by the male and sometimes even by the female, against intruders of the same species. Based on observations of three such territories in winter, and two in summer, he records a mean winter territory size of 44,3 ha and a mean summer size of 54,0 ha, but he gives

no indication of the sizes of home ranges. He noted that in winter reedbuck migrate to areas where water is available from locations without sufficient water, and these were short-term daily excursions if the distance involved was not more than two kilometres.

Venter (1979) calculated the home range size of five known individuals occupying the same area on the Eastern Shores of Lake St. Lucia, and noted a large degree of overlap between male and female home ranges. Mean home range sizes were given as 5,04 ha for adult males and 6,33 ha for adult females, but no indication was given of the period over which observations of these animals were made.

6.2 METHODS

6.2.1 Capture

6.2.1.1 NETTING

During the winter months reedbuck were captured in nets whilst feeding at night on planted pastures. The technique took advantage of the animals' natural movement to these favoured feeding areas, and did not attempt to drive them out of their normal home range. The procedure adopted was as follows:

- 1 A suitable pasture was selected for the capture operation on the grounds of the numbers of animals seen feeding there, its isolation from other alternative food sources, its size, and the ease with which it could be 'enclosed' (see below).
- 2 The pasture, and an area of land surrounding it, were completely enclosed by the construction of a 2,5 m high 'wall' of opaque white plastic sheeting and 0,1 m square mesh game capture netting. The plastic sheeting was used because there was insufficient net to completely enclose the pastures where capture was undertaken, and was used only along edges of the enclosure where the natural movement of reedbuck was considered least likely.
- 3 This trap was constructed during the day, and on completion selected sections of the net were lifted and hooked up onto the supporting poles to enable the free passage of reedbuck into and out of the pasture.
- 4 The trap was left in position for a period of several days.
- 5 A dark windless night was chosen for the capture operation, which began approximately one hour after dark with the manual lowering of

the suspended sections of net. Thus the pasture was completely enclosed, with a number of reedbuck trapped inside.

6 Vehicles were taken onto the pasture, and the disturbed animals ran towards the net to get out. If they did not contact the net of their own accord, they were driven into it, and held manually until marking was complete.

7 The animals were released from outside the enclosure.

6.2.1.2 DRUG IMMOBILISATION

Some preliminary investigations were made into the feasibility of darting reedbuck at night. The method is included in this section not because it contributed significantly to the number of reedbuck marked in this study, but because it appeared to show great promise as a marking technique for reedbuck under farmland conditions. At night reedbuck can often be approached with a spotlight to within about 25 metres, and because of the open country in which they live, darted animals can be satisfactorily observed for the period of induction. Carbon dioxide and powder charged Cap-chur guns were used. Two animals were successfully immobilised, and there were two mortalities. The first mortality, an adult female, received an inadequate drug dosage and after prolonged following was lost into a farm dam and subsequently found drowned. The second mortality arose from the use of the powder charged gun at very close range, which lodged the dart into the spinal cord of the target animal. A 65 kg male reedbuck was successfully immobilised with a dose of 2 mg etorphine hydrochloride (M99) in combination with 25 mg xylazine with an induction time of approximately four minutes, and a 43 kg female receiving a dose of 30 mg Fentanyl in combination with 25 mg xylazine showed an induction time of approximately five to six minutes.

6.2.2 Marking

Three methods of animal marking were used in this study:

1 'Sterkolite' plastic collars were used initially to mark adults and older subadults where growth in neck girth was almost complete. These were constructed of a double layer of heavy duty coloured 'sterkolite' sheeting, reinforced with 2 mm gauge celluloid strips incorporated between the layers across the width of the collar to prevent folding. Large symbols were cut out of the top 'sterkolite' layer to expose the different colour plastic of the lower layer (Brooks, 1981). Collars were affixed to the animals by means of pop rivets or nuts and bolts.

2 Large coloured plastic eartags ('Lone Star' and 'Allflex') were fitted to any infants, juveniles and subadults in which potential growth in neck girth precluded the use of collars. The use of eartags was later extended to include adults as well, as a precautionary measure in case collars were lost. Tags of different colours were fixed to each ear.

3 The useful life of 'sterkolite' collars when fitted to adult males was considerably shorter than that required, and during 1982 some modified machine belting collars, similar to those described by Brooks (1981) were fitted. Clearly identifiable symbols were cut out of the machine belting, which was then riveted to a similar sized piece of 'sterkolite', the colour of which showed through the cut-out symbol.

6.2.3 Resighting

Resightings were made during regular censusing of the intensive study area (CHAPTER THREE), and during a large number of additional searches. Areas of adjoining Department of Forestry land and neighbouring farms were searched regularly on horseback and on foot to detect furthest dispersal points. Resighting of collared animals became a major component of the field work between July 1981 and July 1983, for both my assistant and I. Resightings were aided by use of 8x30 binoculars and by 30x75 'Optolyth' and 20-60x zoom spotting telescopes. With this equipment individuals could be clearly identified at over one kilometre. Group size and composition were recorded for all resightings, together with the exact location on a 0,25 ha grid map of the area (the grid was superimposed on the habitat map reproduced as APPENDIX E).

6.2.4 Data analysis

All resighting data were plotted on (1 : 10 000 scale) maps (reduced, and included in this thesis as APPENDIX E) of the intensive study area, one of which was kept for records of each known animal. Home ranges were calculated on a seasonal and lifetime basis, where the summer season comprised the four months November to February, the winter season May to August, and 'lifetime' any period of at least ten months.

The minimum number of resightings required for the calculation of a home range was determined by examining the relationship between the number of resightings of an animal and the proportion of the final home range represented at each successive resighting. Here, only animals seen at least 20 times during either season were used. An arbitrary value of 90 % of 'real' home range size was considered acceptable.

The outermost points of a home range were joined, and the convex polygons derived in this way used in the calculation of home range size. All

resightings were used because some 'outlying' areas were searched only occasionally and the exclusion of a percentage of the outermost sightings from home range calculations would exclude these 'legitimate' home range areas as well as excluding 'occasional sorties' (c.f. Murray, 1982).

It was reported earlier (CHAPTER THREE) that a large proportion of marked subadults - both male and female - were lost from the population. In its simplest form this was quantified with a figure for the number of animals that were lost as a proportion of the number marked. This is of limited value, however, because not all animals were observed for the whole of their subadult life. Consequently this figure underestimated losses as some of those observed might have moved either before or after the observation period. The figures were thus adjusted by considering the proportion of the marked animals lost in each of a number of shorter (six month) age intervals.

In analysing the characteristics of population losses the following were considered:

- 1 the month when animals were last seen;
- 2 the estimated age of the animals when last seen (APPENDIX D);
- 3 the proportion of marked animals observed over any particular age interval that were lost;
- 4 the distances and directions travelled by any known animals recovered outside the study area.

6.3 RESULTS

6.3.1 Capture

Five netting operations were conducted on pastures within the intensive study area in the winter months of 1981, and four during the winter of 1982. Together with two hand-caught infants and two darted animals, the number of animals captured in these operations is shown in TABLE 6.1. The age and sex structure of the marked sample is not significantly different from the observed population structure (χ^2 , combining adult and subadult females, which were not distinguished in field observations (CHAPTER THREE); $p > 0.05$).

In addition to these captured animals the population of known animals in the intensive study area included one adult male with a peculiar horn configuration. On a nearby farm outside the intensive study area (farm No. 9; CHAPTER THREE) an additional eleven animals were marked, but resightings of these were not used in home range analysis. The total 'known animal' sample thus comprised 84 individuals, of which 73 were within the intensive study area. As well as the 69 individuals

TABLE 6.1: The number of animals of each age/sex class captured in the intensive study area

		1981	1982	SAMPLE STRUCTURE (PERCENT)	POPULATION STRUCTURE (PERCENT)
Juveniles <1 year	M	5	3	25	20
	F	5	5		
Subadults	M	8	2	14	20
	F	6	4	14	--
Adults	M	8	8	23	28
	F	13	4	24	32
TOTAL		<u>45</u>	<u>26</u>	<u>100</u>	<u>100</u>

successfully netted and marked on pastures at night, there were three mortalities (5,5 %) using this technique. As far as use of this technique is concerned, it is noteworthy that where the same pasture was used more than once, the second and subsequent trappings yielded fewer animals.

6.3.2 Marking

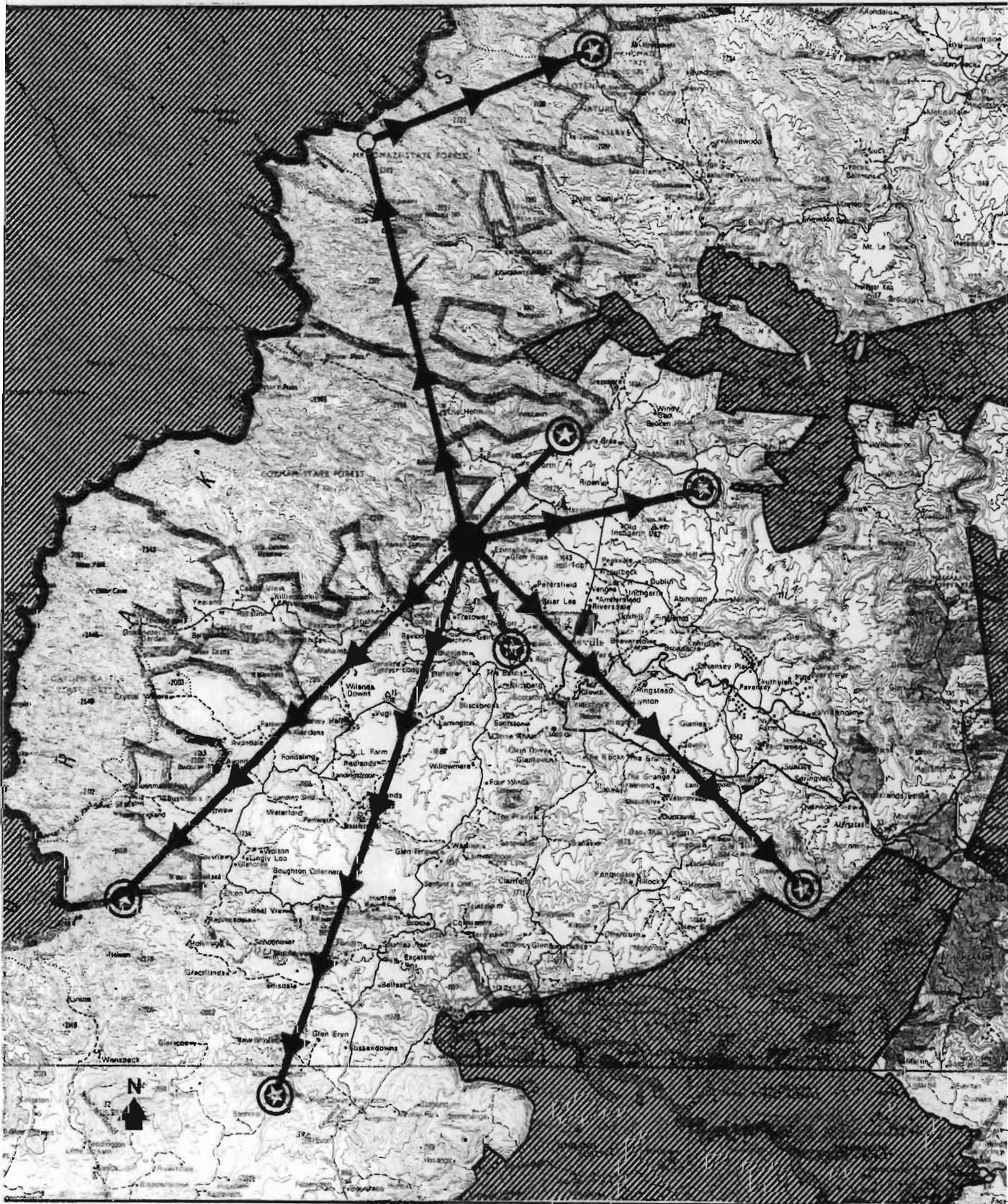
In 1981 'sterkolite' plastic collars were fitted to all suitable captured animals, but these became badly torn on all males over an estimated age of two years (APPENDIX D). The useful life of 'sterkolite' collars on adult males was very variable, with two animals losing their collars after 4,5 months, a further four losing collars within a year, and only one of eight adult males marked in this way retaining its collar for the two-year duration of field work. There was no loss or noticeable damage to 'sterkolite' collars when fitted to females, all of which outlived the project.

All machine belting collars outlived their required one-year period of use, and there was no loss of eartags in a total of approximately 75 eartag-years of use.

6.3.3 Resighting

Approximately 3 500 resightings of known animals were made, of which 3 400 were within the intensive study area. Reports of marked reedbuck were received from nine landowners/managers from outside the extensive study area, involving six different animals. One marked animal was resighted independently by myself on a farm outside the study area. The locations of these resightings and the distances involved are illustrated in FIG. 6.1: five out of six of these animals were subadults. In addition, one

FIG. 6.1: Resighting locations in relation to the capture centre and KwaZulu



● Capture centre Ⓢ Resighting locations [diagonal hatching] White-owned land [cross-hatching] KwaZulu, with Lesotho and Transkei

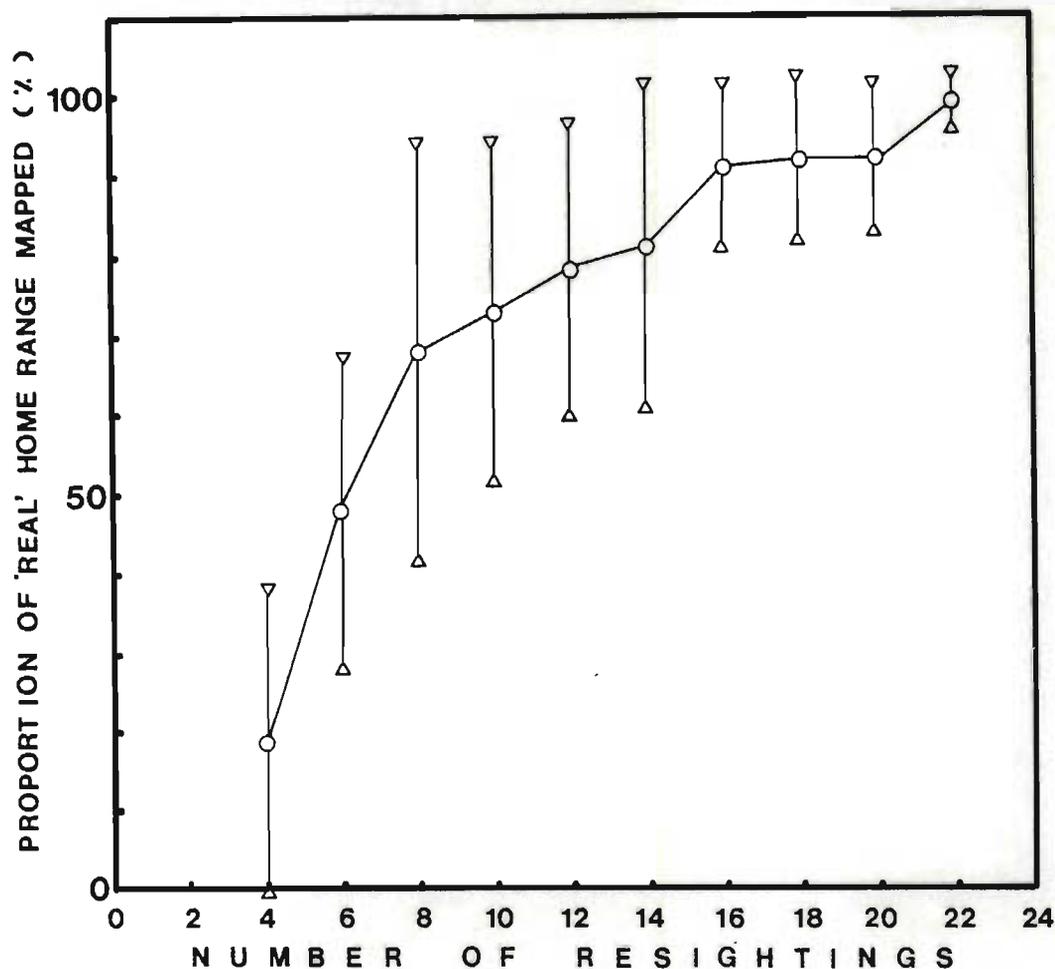
SCALE : 0 5 10 15 20 25 30 km

dispersing animal (subadult female) was resighted on a farm within the extensive study area some 4 km from its place of capture, where it was seen several times, apparently settled.

6.3.4 Home range analysis

Reedbuck movements are generally restricted to a well defined home range (FIG. 6.2), 90% of the area of which can be ascertained from consideration of 16 independent resightings (FIG. 6.2). All home range analyses presented in this chapter are based on a minimum of 16 resightings.

FIG. 6.2 : The relationship between the number of resightings and the proportion of the area of the 'real' home-range mapped. (means are shown \pm 95% confidence limits)



The home range sizes of different age and sex classes are compared in TABLE 6.2, together with some data on summer and winter home range sizes of adults. Subadult male home ranges are significantly larger than those of any other age and sex class (t-test; $p < 0.05$), but there are no other age and sex differences. Summer (November to February) and winter (May to August) home ranges do not differ significantly in size in either sex (t-test; $p > 0.1$), but both summer and winter ranges of adult females are

TABLE 6.2 : Home range size

HOME RANGE TYPE		n	SIZE (ha) (mean±S.E.)
Summer range	Adult MALE	4	32,2 ± 10,3
	Adult FEMALE	11	38,0 ± 6,7
Winter range	Adult MALE	3	22,0 ± 9,4
	Adult FEMALE	8	41,2 ± 9,9
Lifetime range	Adult MALE	9	73,5 ± 13,9
	Adult FEMALE	16	123,0 ± 21,6
	Subadult MALE	15	210,0 ± 18,5
	Subadult FEMALE	5	75,8 ± 16,6

significantly smaller than the lifetime range size (t-test; $p < 0,05$). The differences between lifetime, summer and winter home ranges of adult males are barely significant ($0,1 > p > 0,05$).

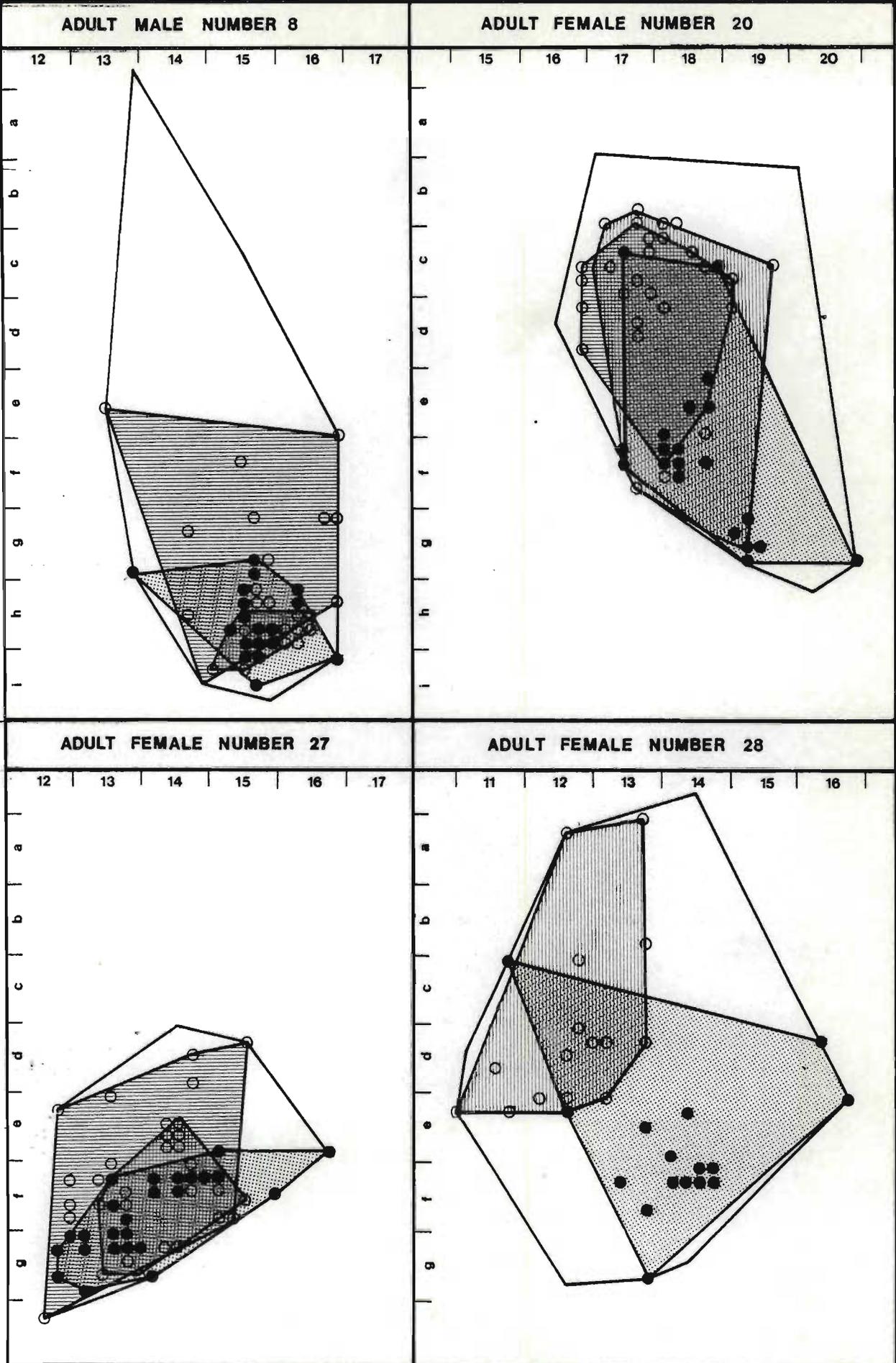
The summer and winter ranges of six adults (one male, five females) were compared, four of which are illustrated in FIG. 6.3. The mean percentage overlap between the seasons' ranges, expressed as a proportion of the smaller range, was 57 ± 22 (S.D.) %. Seasonal changes in habitat use vary between two extremes. At the one end, there is a quite distinct difference between areas occupied during summer compared with winter (FIG. 6.3; adult female 28), and at the other, the area used in winter is also used in summer, though the range may be extended slightly at this time (FIG. 6.3; adult female 27; adult male 8).

The home ranges of 13 adults (three males, ten females) were compared between the first and second years of observation. The mean percentage overlap between the two annual ranges, expressed as a proportion of the smaller range was 94 ± 7 (S.D.) %, illustrating that there is no shift of range once a home range area has been established. The normal situation is illustrated for adult female 20 in FIG. 6.4, and compared with adult female 23 which showed an exceptional 'contraction' of its 1981/82 range during the following year. It is possible that this animal was subadult during the first year of observation, as it was never seen accompanied by a youngster.

Age-related changes in home range size of subadult males are illustrated in FIG. 6.5. No clear trend is apparent, except that, as previously noted, home ranges of subadult males are larger than those of adults.

The locations and extent of all adult female lifetime ranges in the intensive study area is illustrated in FIG. 6.6, and of adult males in FIG.

FIG. 6.3: Seasonal changes in adult home ranges



Grid references relate to habitat map - APPENDIX E

Range, Nov. '82 - Feb. '83 (resighting location)

Range, May - Aug. '82 (resighting location)

Range, Nov. '81 - Feb. '82 (resighting location)

0 0,2 0,4 0,6 0,8 1 km

SCALE

Life-time range

FIG. 6.4: Annual changes in adult female home ranges

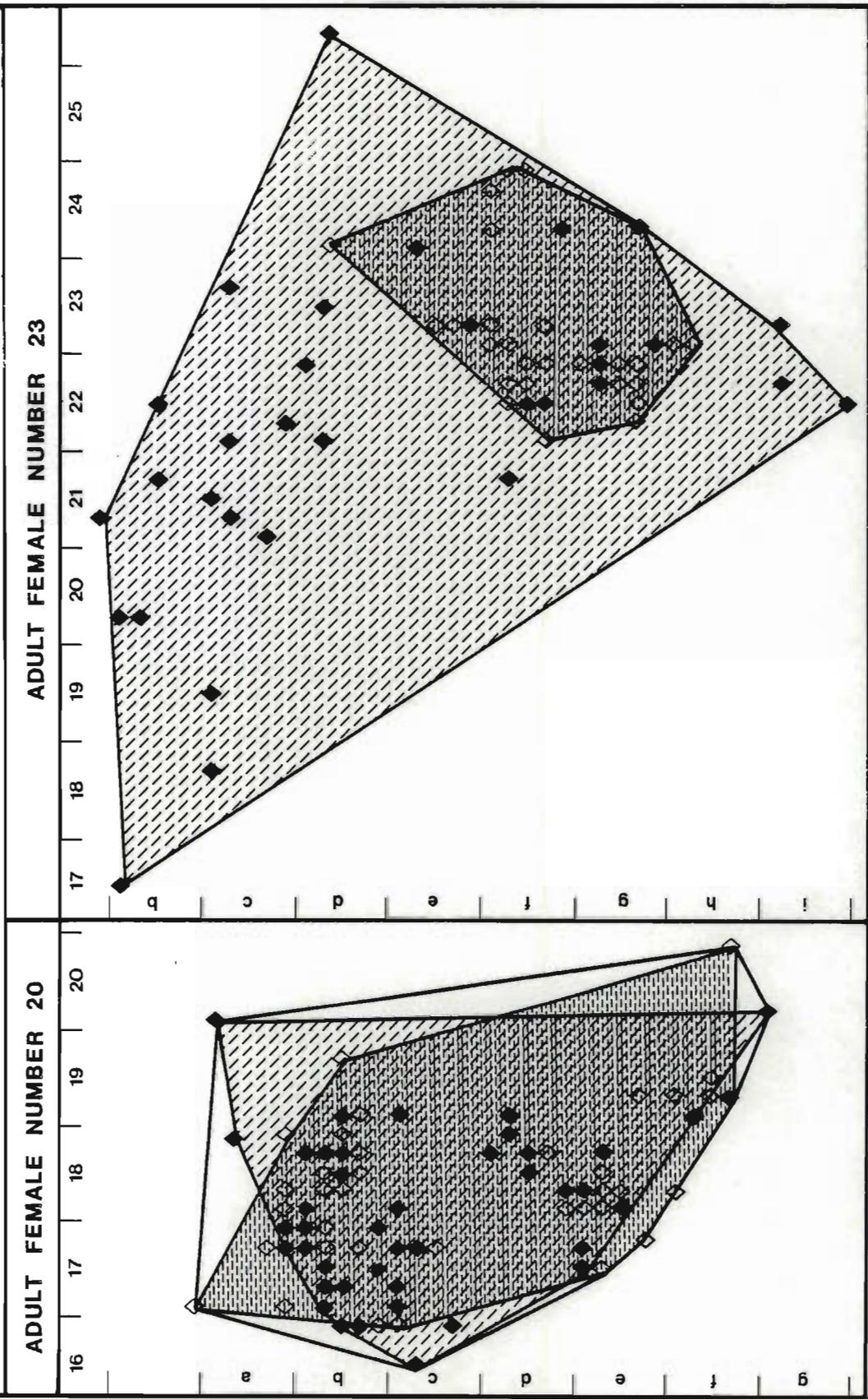
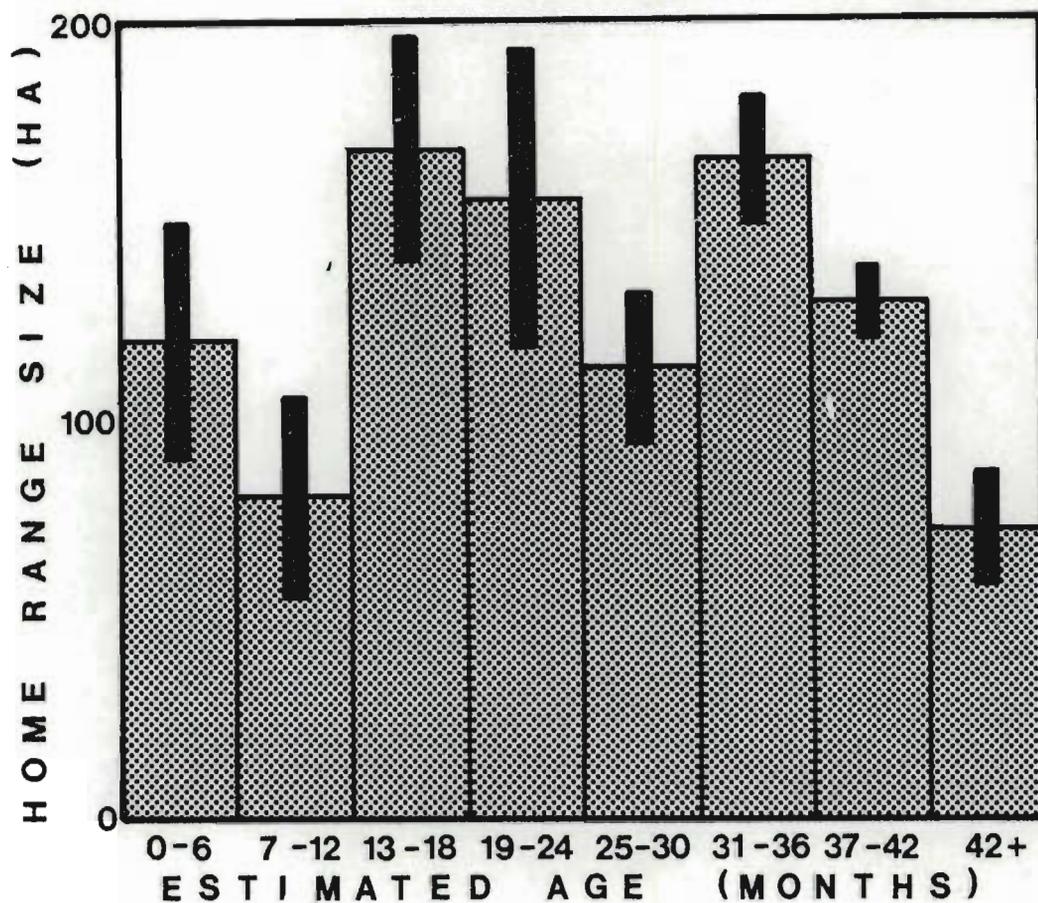


FIG. 6.5 : Home range size of sub-adult males relative to their age

(mean values are shown ; vertical bar represents ± 1 std.err.)



6.7. There is a very large degree of overlap in the home ranges of adult females, which is less apparent in males. However, only nine adult male ranges were plotted, compared with 19 adult female ranges.

6.3.5 Dispersal

The cumulative proportion of marked subadults lost at each age interval is illustrated in FIG. 6.8. Ninety one percent of females were lost from the population by the time they reached two years of age, including 47 % as confirmed dispersers, and 3 % confirmed deaths. Amongst males only 50 % were lost by the time they reached three years of age, including 5 % confirmed dispersals, and no deaths.

Of the subadult losses 96 % occurred in the spring/summer/autumn months from October to May (FIG. 6.9), and there were no losses in the harshest winter months of June, July and August. Losses were greatest in November, during which month 32 % of the total subadult losses occurred. There were no losses of adult females from the marked sample during the period of

FIG. 6.6 : Life-time home ranges of adult females

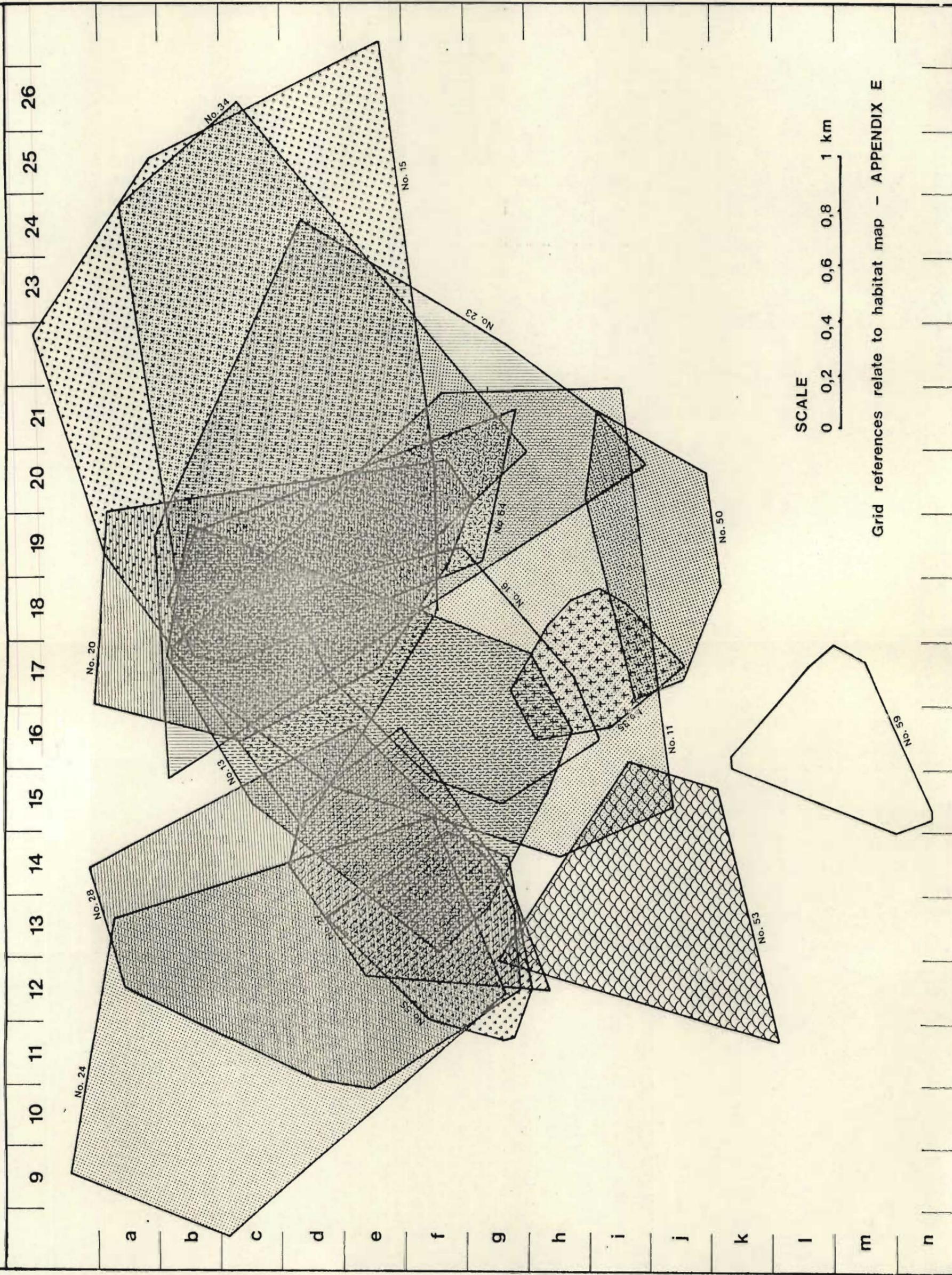


FIG. 6.7 : Life-time home ranges of adult males

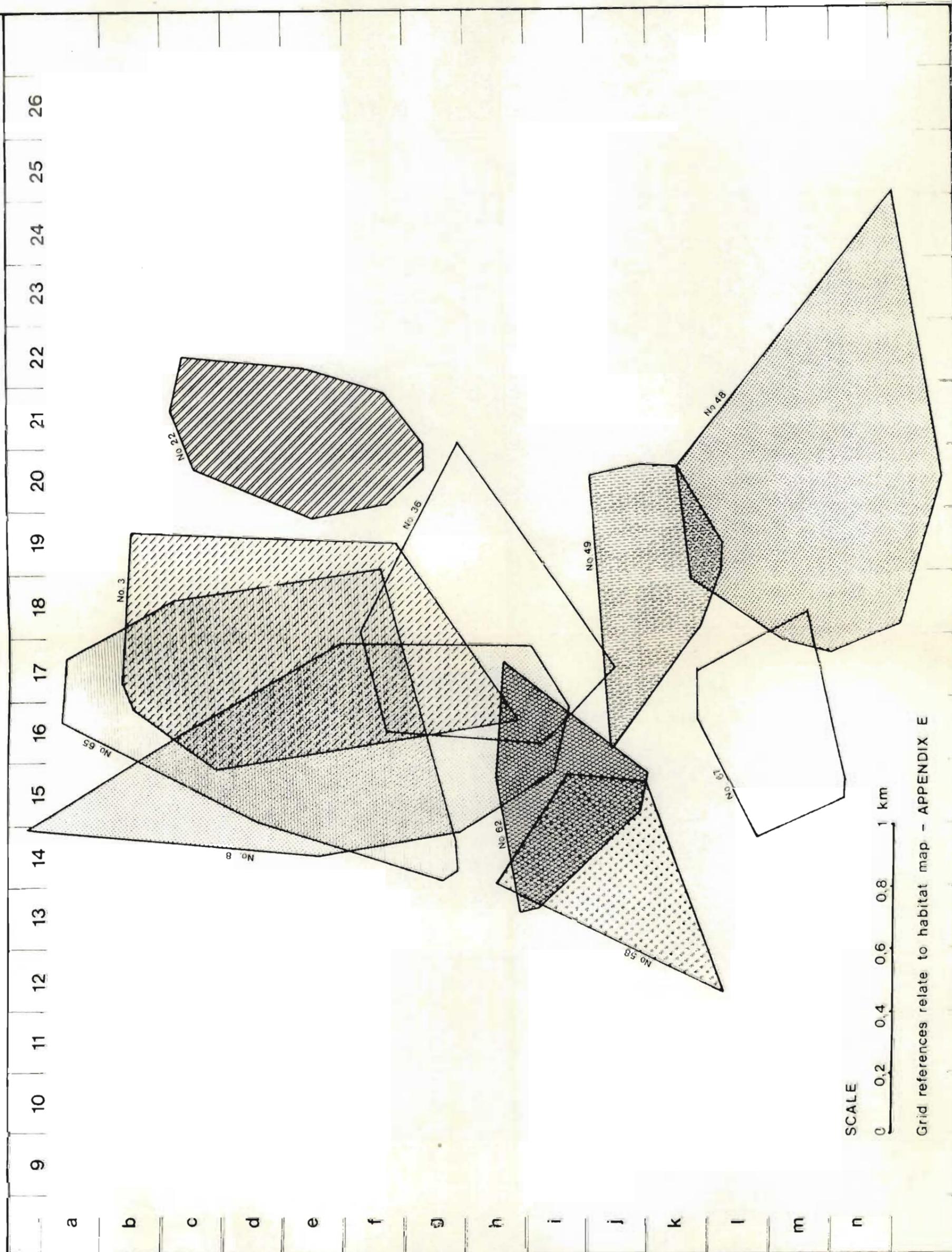
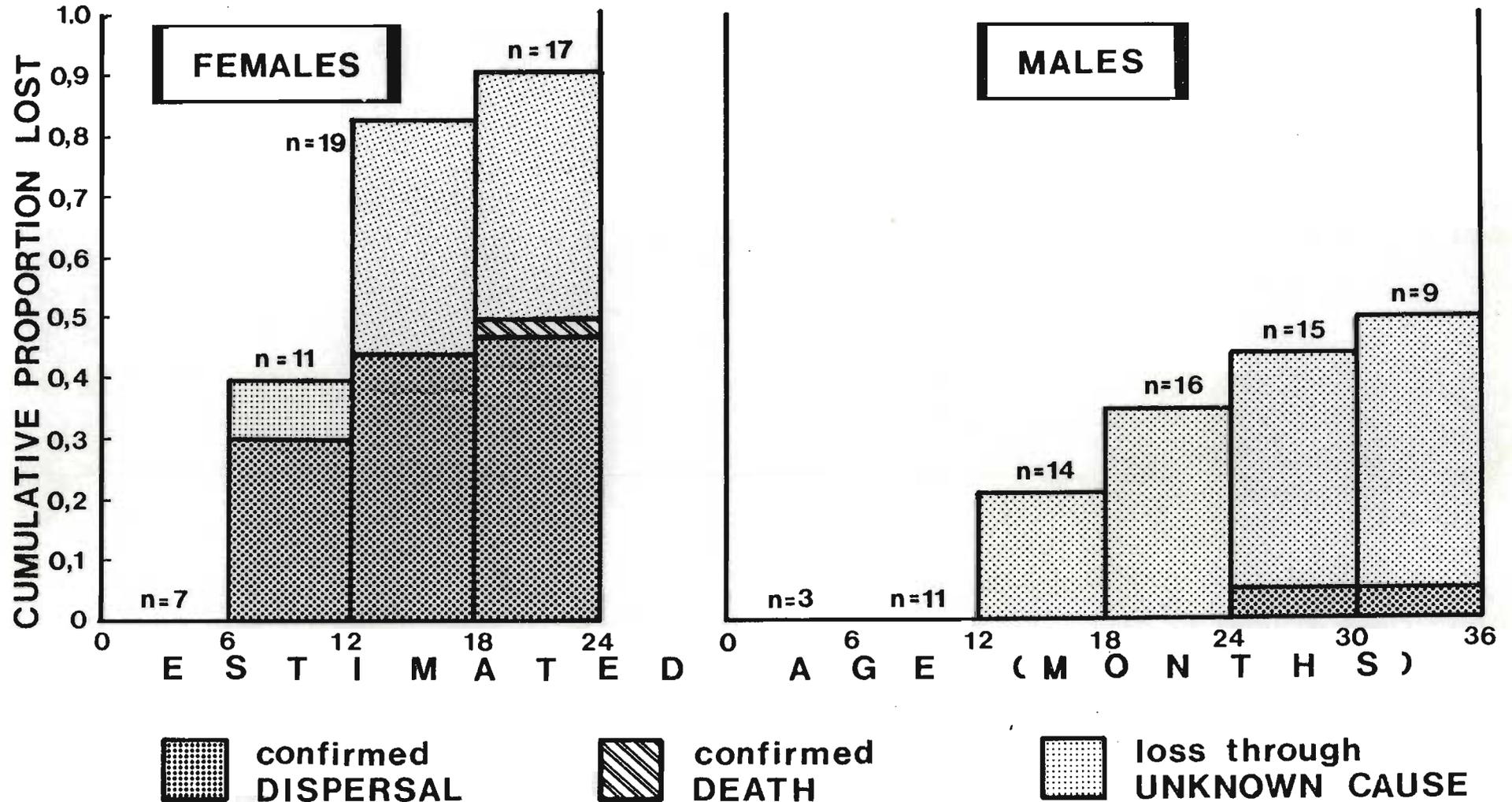


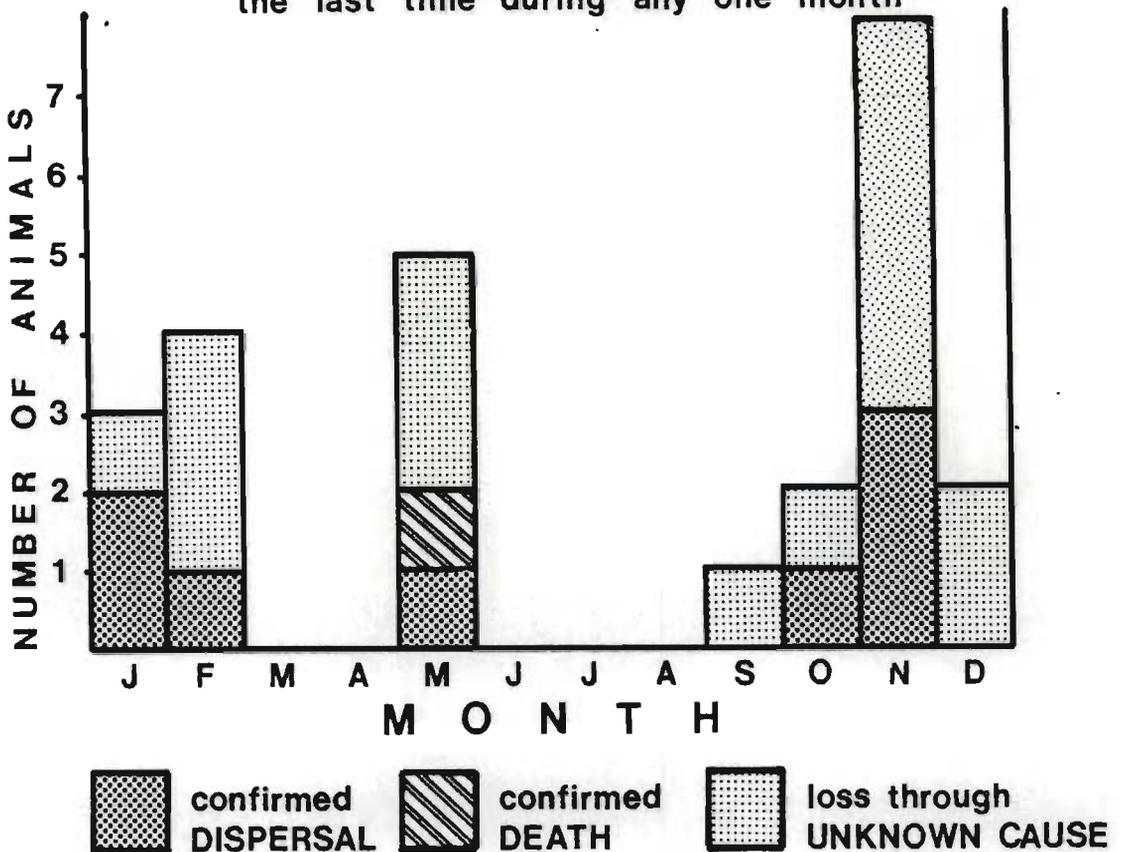
FIG. 6.8: Cumulative loss of marked subadults, considered by age class



n refers to the number of animals that could potentially have been observed, had none of the marked population been lost

field work (CHAPTER THREE), and of the seven adult males that were lost all were last seen during the period January to May; one was found dead in March, one dispersed out of the study area in May, and the other losses occurred in January (one), February (one) and March (three).

FIG. 6.9: Number of marked subadults seen for the last time during any one month



6.4 DISCUSSION

6.4.1 Home range

The estimation of home range as the area enclosing the limits of an animal's movements is the simplest of many available methods of home range estimation. These have been reviewed by Sanderson (1966), Flowerdew (1976), and others, and range from a multitude of relatively simple mapping techniques to more sophisticated statistical procedures which associate a particular area with a probability of the animal's occurrence there. As Sanderson (1966) points out, no one technique gives the best answer for all species and all situations. The minimum area method used in this study was first used by Dalke (1942), and subsequently recommended by Mohr (1947). It is still widely used in studies of African ungulates (e.g. references in Leuthold, 1977; Venter, 1979; Murray, 1982), although its use for small mammal studies has now been largely superseded by other methods that more

realistically represent the concept of home range as defined by Jewell (1966). The reasons for adopting the method in this study are threefold; firstly, to enable direct comparison of home range size with other African ungulates; secondly, because it was felt that the objectives of the study did not indicate a need for a more sophisticated analysis of home range than could be provided by use of the minimum area method; and finally, because recognised biases in the collection of resighting data largely invalidate the use of more sophisticated data analysis techniques.

The biases to which I refer arise because the relocation of animals is based on visual sightings. Thus the majority of them were made when the animal concerned was either active, or in an exposed position. Relocations of animals lying up in dense cover are few. The importance of cover was demonstrated in CHAPTER FIVE, but it takes no more than casual observation to realise its significance in the life of the reedbuck. Further, because relocations could most easily be made at times of the day when the animals were active, these times (particularly the two hours either side of nightfall) were selectively chosen for observation. Clearly the production of, for example, elaborate three-dimensional home range maps, where the level of utilisation of an area is plotted on the third axis (e.g. Inglis *et al.*, 1979; Don and Rennolls, 1983), would be beyond the scope of the data collected.

From the management point of view, one of the prime concerns is the degree of movement reedbuck make between farm properties, and in this respect the home range statistics presented give a clear indication of the limited extent of inter-season and inter-year movements. At the time of veld-burning in spring observations were made of several animals apparently outside their normal range, but in all cases they returned within a week at the most. Ungulates commonly show a degree of attachment to their range (Jarman, 1970; Sweeney *et al.*, 1971), which prompted Leuthold (1977) to redefine home range as 'the area that an animal is familiar with and does not leave voluntarily'.

Harestad and Bunnell (1979) have demonstrated that differences in mass alone account for a large portion of the differences between male and female, or subadult and adult home range size in mammals, the smaller animals occupying smaller home ranges. The observation that subadult male reedbuck occupy significantly larger home ranges than other age and sex classes, and that adult males, as the largest animals, occupy the smallest home ranges is at variance with their observations. An alternative hypothesis to account for these differences might be that subadult males are socially excluded from the best areas and have to increase the size of the range they occupy to compensate for its inferior quality. Leuthold and Sale (1973) concluded that elephant home range size was related to habitat quality in this way, and numerous other examples of this type of

relationship are to be found in the literature (Leuthold, 1977). Murray (1982) observed in impala that the home range size of both young and old males was greater than that of middle aged ones, and suggested that this was probably associated with different ontogenetic phases in reproductive strategy. A similar situation could pertain to reedbuck, where the possible advantages of wide-ranging behaviour include: assessment of the relative density of dominant males and adult females in different localities; information gained about personal rank by low intensity interaction with a wide range of peers; and an increased chance for opportunistic mating (Murray, 1982).

Although immaterial to management, it is interesting to note the observed extremes of seasonal ranging behaviour. Those animals that occupy the same range in summer and winter presumably find all their living requirements within that range, whereas those which largely move between a summer and a winter range presumably find some resource shortage in each of the seasonal ranges. A shortage of food would seem to limit winter occupancy of summer ranges, but the reason for the use of a different range in summer is not immediately apparent. A similar situation has been described for white-tailed deer by Inglis et al. (1979) who found that some animals showed a temporary dichotomy of range use related to differences in brush availability, and that others, in more homogeneous habitats, failed to show such a dichotomy.

Some previous work on home range size in reedbuck was reviewed in the introductory section of this chapter. The home ranges of the animals under study here are apparently considerably larger than those of reedbuck at St. Lucia (Venter, 1979). However, as seasonal and lifetime range sizes may differ considerably, and no indication is given by Venter (op.cit.) of the period over which his observations were made, firm conclusions cannot be drawn. Hendrichs (1975) has reviewed the social and spatial organisation of the Reduncinae, with special reference to the bohor reedbuck. There is obviously considerable variability between different members of the sub-family in home range size, the largest recorded home ranges being those of waterbuck at 650 to 700 ha (Spinage, 1969a), and the smallest, excluding Venter's (1979) observations, being those of bohor reedbuck at 15 to 60 ha (Hendrichs, 1975) although again these figures are suspect because of the short period (two months) of observation.

One of the most important aspects of studying spatial organisation in this study is that it might offer some clues as to the way in which resources are divided up between members of the population, which might help in our understanding of population regulation. We might get some idea of the probable social organisation of the species simply by examining the animal's general pattern of dispersion: for example, mutually exclusive home ranges, the centres of activity of which are dispersed regularly

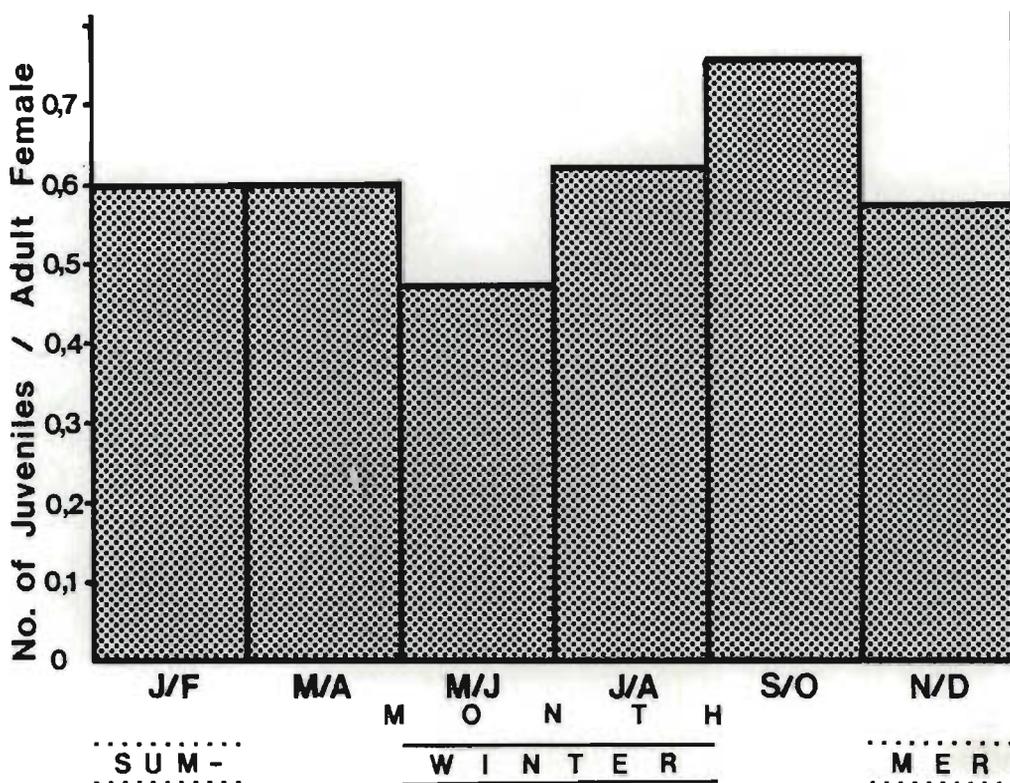
throughout the area would be highly suggestive of a territorial system. Social organisation is the subject of CHAPTER SEVEN, and its role in population regulation will be discussed at some length. It is important to note, at this stage, however, that male home ranges appear (FIG. 6.7) to be more mutually exclusive than those of females (FIG. 6.6), and the possibility of a territorial system cannot be dismissed. Certainly there is some overlap in male home ranges, but that does not exclude the possibility of an area within each home range that is used exclusively by the occupant, whilst peripheral areas are shared. In view of the very high degree of home range overlap apparent for females (FIG. 6.6), however, a territorial system in this group appears less likely.

6.4.2 Dispersal

The dispersal of young reedbuck clearly plays a key role in the regulation of population size (CHAPTER THREE), and is an important aspect of reedbuck ecology. It is my belief that the majority of those subadult animals that were lost 'through unknown causes', in fact dispersed. Indeed it is a reflection of the high degree of cooperation and participation afforded to the project by local landowners that such a good number of dispersals were confirmed, especially as reedbuck on farmland are largely nocturnal or crepuscular. Some of the dispersing reedbuck undoubtedly found their way into KwaZulu, which adjoins Underberg district on three sides (FIG. 6.1), where they would probably be hunted and eaten without a record being made of any markings they carried.

It is not unexpected to find that the loss of subadults occurs during the spring/summer/autumn months (FIG. 6.9), when adequate food is generally available throughout the district. Because animals are so dependent upon planted pastures for winter forage, they do not 'risk' dispersal in the harshest months of June, July and August, and this is reflected in a steady increase in the juvenile : adult female ratio observed in the population over these winter months (FIG. 6.10). It is interesting to note, too, that this ratio declines from a steady summer level of 0,60 : 1 to a level of 0,47 : 1 at the start of winter in May/June, as if some juveniles are being 'pushed out' prematurely by their peers in anticipation of subsequent crowding during winter. This is reflected in the disproportionately large number of subadult losses in May (FIG. 6.9). One could speculate as to the likely fate of these animals; unless they are able to find a new home with an adequate (artificial) winter food supply, they may well die in their first winter. At the end of winter juvenile : adult female ratios 'peak' at 0,75 : 1, which is 'corrected back' to the stable summer level by a surge of dispersal in November when natural grasslands are optimal for grazing (CHAPTER FIVE).

FIG.6.10: Bi-monthly changes in the ratio of animals under twelve months of age to adult females



One big question remains unanswered: is the observed dispersal an 'innate' or 'environmental' response? If it is an innate response, genetically 'programmed' into a reedbuck, by which a fairly fixed proportion of young animals move away from their birth place, then population regulation is presumably achieved by allowing only a certain number of immigrants to settle. If, on the other hand, dispersal is an environmental response to unfavourable conditions, such as crowding, the population will be regulated by adjusting the number of animals that disperse away from the population.

Caughley (1977) specifies seven types of information that are required for a detailed study of dispersal. I will restate these, and review the extent to which available information on reedbuck can contribute to our understanding of the mechanisms involved.

- 1 The sex and age of dispersing individuals, and the sex and age of individuals that do not disperse.

Clearly, reedbuck dispersal involves predominantly young animals, and females disperse more than males. Sexually mature females certainly do not disperse. These observations are contrary to the normal mammalian pattern where juvenile male dispersal tends to predominate (Greenwood, 1980; Dobson, 1982). Greenwood (*op.cit.*) argues that in birds and mammals sex differences in dispersal are a consequence of

the type of mating system. In those species where the defence of a resource by one sex to attract members of the opposite sex is practised, philopatry of the resource defender, and dispersal of the 'attracted' sex will tend to predominate; this is certainly borne out by observations of birds and some mammals, but there is as yet little evidence of this type of relationship for ungulates. Greenwood's (1980) hypothesis would predict that, since female reedbucks are the predominant dispersers, males should be resource defenders (i.e. 'territory holders'), and, as has been shown, their spatial organisation certainly does not preclude this possibility. The reason for predominantly male dispersal in mammals is that most species that have been studied are polygamous and organised on a system of mate defence which favours dispersal of the sex which is primarily concerned with gaining access to and defending its 'opposites'. Thus in red deer (Lowe, 1966), soay sheep (Ovis aries; Grubb and Jewell, 1966), white-tailed deer (Kammermeyer and Marchinton, 1976) and impala (Murray, 1982), all of which are considered to be mate rather than resource defenders, predominantly male dispersal has been demonstrated. Greenwood (1980), recognising the importance of dispersal in population control, concluded that, although population density can affect the degree of sex bias in dispersal, underlying sex differences tend to remain. To illustrate this, he cites the great tit (Parus major) as an example, where, although increased population density is accompanied by increased male dispersal, the underlying sex bias persists.

Dobson (1979) reported on an interesting experimental study of dispersal in the California ground squirrel (Spermophilus beecheyi) in which immigration was studied in three colonies, one of which was provided with supplemental food. Immigration to the reference colonies was predominantly male, and to the supplemented colony predominantly female, indicating the importance of young female dispersal in the regulation of density relative to critical resources, and of young male dispersal in the promotion of outcrossing.

The age of the animals that disperse compared with those that do not is also of interest. Howard (1960) and Caughley (1977) cite a number of examples of apparently innate dispersal of young birds and mammals which may lead to the conclusion that 'for the most part, the major dispersal movements are made by virgins about the time they attain puberty' (Howard, 1960). However such age specific dispersal cannot be considered characteristic of an innate response, because individuals that are environmentally forced to disperse frequently include the younger members of the population (Watson and Moss, 1970), because they may be socially subordinate or weaker than their

peers.

- 2 Whether individuals disperse in random directions, or whether the direction is influenced by density gradients, prevailing wind, angle of the sun and so on.

In this study there is no evidence to suggest that the direction of dispersal is anything but random. Passage westwards from the study area into Lesotho is obstructed by the high wall of the Drakensberg escarpment, but one marked animal was nevertheless observed high up the escarpment (2 700 m) below Thadentsonyane (FIG. 6.1), far from suitable 'reedbuck habitat'. However these observations are really too superficial to give much idea as to whether dispersal is 'innate' or 'environmental'.

- 3 Whether dispersing individuals are hounded away from their place of birth or whether they leave of their own volition.

Density dependent 'environmental' dispersal associated with increased aggressive encounters between individuals might normally be expected to affect males preferentially (as in great tits; Greenwood *et al.*, 1979), because the great majority of such encounters occur in social contexts involving competition over 'social resources' such as rank, territory, or access to mating partners. The fact that relatively few male reedbuck dispersed might then be regarded as evidence in support of a hypothesis regarding reedbuck as 'innate' dispersers. However, it is worth noting that social rank, although less obvious amongst females, does occur, and in this regard Lowe (1966) found that the larger/older red deer hinds on Rhum appeared to be dominant to all other classes of either sex within their own home ranges. Dasmann and Taber (1956) attributed a female bias in dispersal of black-tailed deer (*Odocoileus hemionus*) to antagonism among breeding females, which tended to drive out yearling females. I return to pertinent aspects of social behaviour in CHAPTER SEVEN.

- 4 The probability that an individual will disperse, and whether this is a constant or a function of density, rate of increase, food supply or some other influence.

The limited data available from this study provide no evidence in this regard.

- 5 The mean and variance of the distance moved, whether these are constants for a species or vary in response to environmental conditions, and whether the frequency distribution of dispersal distances is multimodal or unimodal; again there is no evidence on

these aspects from this limited study.

- 6 The probability that a dispersing individual will survive to reproduce, as contrasted with this probability for an individual that does not disperse.

Data are again very limited for this study. There is no evidence that any of the dispersing individuals successfully reproduced, but only two of eight confirmed dispersers are known to have died, and three were sighted more than once, apparently 'settled' and presumably with a good chance of subsequently reproducing. The proximity of KwaZulu to the area of study, and the likely fate of the animals dispersing there, has already been mentioned, and it is my belief that the majority of reedbuck dispersing from the extensive study area will be hunted and consumed in these areas.

- 7 The genetic differences between dispersing and sedentary individuals.

Again there is no information on this aspect available for reedbuck. Genetical entomologists were the first to demonstrate the genetic basis of dispersal (Ford, 1964), and little work has been done in this regard on vertebrates. Myers and Krebs (1971) demonstrated that genotypes for two polymorphic plasma proteins differed in frequency between samples of sedentary and dispersing voles, and more recently Bunnell and Harestad (1983) attributed an observed difference in dispersive tendency of black-tailed deer to the existence of two distinct phenotypes - 'dispersers' and 'non-dispersers' - in the population. They suggested that competition for mates was an important force governing the proportion of 'dispersers' and 'non-dispersers' in the population.

It is evident from this consideration of dispersal under Caughley's (1977) information categories that our understanding of the dispersal of reedbuck is far from complete and it is clearly impossible to demonstrate unequivocally that dispersal is either 'innate' or 'environmental'. In any case it is probably not a strictly either/or situation, and elements of both types of dispersal are probably involved. It is, I believe, helpful to consider also the possible adaptive significance of dispersal to reedbuck.

As has been shown in the previous chapter the reedbuck is a denizen of wetlands and other habitats that are characteristic of the early pioneer seres in the plant succession. It occupies a niche in a relatively short-lived seral habitat, that is evolving towards a permanent climax. Horn (1976) and others have stressed that the ecological processes of succession reflect the adaptations of the various species involved; these adaptations

are broadly those of the r-K continuum (MacArthur and Wilson, 1967), r-species being associated with ephemeral habitats, and K-species with those with a long durational stability. As a component of a seral community, one would expect the reedbuck to show adaptations that characterise r-species (TABLE 6.3).

TABLE 6.3 : The contrasting suites of characteristics of the extremes of the r-K selection spectrum (after Southwood, 1977)

r - species	K - species
Short generation time	Long generation time
Small size	Large size
High level of dispersal	Low level of dispersal
Much density independent mortality	High survival rate, especially of reproductive stages
High fecundity	Low fecundity with high parental investment
Panmictic	Territorial
Intraspecific competition - often 'scramble-type'	Intraspecific competition - often 'contest-type'
Low investment in 'defence' and other inter-specific competitive mechanisms	High investment in 'defence' and other inter-specific competitive mechanisms
Time efficient	Food and space - resource efficient
Populations often 'overshoot'	Populations seldom 'overshoot'
Population density very variable - 'boom and bust'	Population density relatively constant from generation to generation

There is some evidence that it does just that: Deane (1966) has demonstrated that as community succession proceeds, with concomitant bush encroachment etc., the reedbuck is unable to adapt and populations decline; reedbuck are clearly able to increase rapidly (e.g. on the Nyika Plateau, Malawi; Bell, pers. comm.; on the Eastern Shores of Lake St. Lucia; Venter, 1979; on farmland in Natal; this study) and may 'overshoot' in a 'boom and bust' fashion (as in Kyle National Park, Zimbabwe; Ferrar and Kerr, 1971). The very high rates of dispersal observed in this study may be considered a further reflection of this r-selection.

From an adaptive point of view the members of any species will evolve those strategies that maximise the numbers of their descendents in their habitats. The reedbuck's habitat is not only relatively ephemeral, but also tends to be well dispersed. To make full use of available wetlands, the reedbuck should, in the course of evolution, adopt methods of exploiting its habitat for as long as it is suitable; high rates of dispersal, and relatively long dispersal distances are required.

Many authors (Howard, 1960; Lidicker, 1962; Greenwood, 1980) have considered the significance of dispersal of offspring away from their natal group or area as a mechanism of avoiding inbreeding. Their reviews will not be repeated here; suffice it to say that inbreeding avoidance is achieved by subadult dispersal, but it is doubtful whether this could alone

account for the very high dispersal rates of reedbuck.

In conclusion, it appears that insufficient is yet known of the dispersal of reedbuck to draw firm conclusions as to whether or not it is a response to population density per se. However, consideration of the reedbuck's ecological role as a successional species favours the belief that dispersal is, at least partly, an innate response, developed as an evolutionary adaptation to the exploitation of the species habitat. If this is so, population regulation must be achieved by means of social interaction which prevents immigrants settling in an area.

This discussion has focussed very much on the mechanisms involved in the dispersal of reedbuck, with little reference to specific management implications. For the most part, the implications are self-evident. The question of possible immigration following excessive animal removal in one area is not a new one to wildlife management (Staines, 1974), and without experimentation we can only guess at the likely outcome of such action. The experimental creation of an artificial reedbuck 'vacuum' was envisaged, but despite the agreed cooperation of a major local landowner, the project was abandoned as politically undesirable for the Natal Parks Board. With regard to immigration into areas where hunting removals exceed net production, Robinette (1966) found that young mule deer apparently filled such voids, and we might anticipate a similar situation for reedbuck.

The natural dispersal of reedbuck has implications for recolonisation programmes, and these are discussed in a separate paper (APPENDIX B).

6.5 CHAPTER SUMMARY

The purpose of studying the spatial organisation of reedbuck was, firstly, to examine the extent of movement between farm properties particularly as this might affect legal protection and harvesting strategies, and secondly, to provide an understanding of the role of animal movement in population regulation.

The results are based on resightings of a sample of 84 known reedbuck; these were mostly captured in nets when feeding at night on winter pastures, and marked with conspicuous coloured collars and/or eartags for individual recognition.

Reedbuck movements are normally restricted to a well defined home range. Seasonal ranges are smaller than lifetime ranges. Considering all age and sex classes the smallest lifetime ranges are those of adult males (74 ha) and the largest those of subadult males (210 ha). Both male and female individual ranges show considerable overlap.

Dispersal affects subadults of both sexes, and to some extent adult males, but not adult females. Approximately 90 % of subadult females were lost by the time they reached two years of age, and 50 % of males were lost by the age of three years; most of these losses could be attributed to dispersal.

It is argued that dispersal is probably largely an innate response, which is considered to be an adaptation to the species' role in community succession. If this is so, population regulation is achieved by preventing immigrants settling in an area.

CHAPTER SEVEN

SOCIAL ORGANISATION AND BEHAVIOUR

7.1 INTRODUCTION

In previous chapters of this thesis reference has been made to certain behavioural attributes of reedbuck which have direct significance to their management. In CHAPTER THREE, for example, I examined the effects of time-related behaviours on animal census, and in CHAPTER FIVE the habitat requirements of reedbuck were largely attributed to the species' characteristic behavioural responses as a 'hider' species. Behaviour affects management in many ways, and in his review, Cowan (1974) considered its management implications under the following headings:

- 1 Strategies of range occupancy
 - (a) Variations on the themes of territoriality, home range and nomadism
 - (b) Special requirements and their influence on distribution
 - (c) Social constraints upon density
- 2 Behaviour of neonates in relation to dam and physical environment
- 3 Feed selection and interspecies compatibility
- 4 Response to physical alteration to the environment by man
- 5 Tameability and controlability
- 6 Social constraints upon harvesting and management
 - (a) The role of the aged in the maintenance of tradition
 - (b) The role of the separate senses in the establishment of critical distance
 - (c) Structure and dependence relationships within groups
 - (d) Sex ratios and reproductive efficiency
- 7 Behaviour and techniques of research
- 8 Behavioural constraints upon non-consumptive use.

Some of these categories have already been considered for reedbuck, at

least in passing (2,3,4 and 7 above) and others (5 and 8) are not of direct relevance to the specific management problems under consideration in this study. It is my purpose in this chapter to consider the reed buck's range occupancy strategy (category 1 above), and social organisation (category 6 above) in relation to management, and with specific reference to population regulation.

Previous work on the social organisation of reed buck has described the species as being, on the one hand, strictly territorial (Jungius, 1971a), and on the other, being organised on a dominance hierarchical system (Venter, 1979). There is plenty of evidence (references in Wynne-Edwards, 1962; Watson and Moss, 1970) to suggest that animal populations may be regulated by a territorial system, but none of limitation by dominance or aggression solely within hierarchies (Watson and Moss, 1970). However, it has been suggested by Davis (1958), and subsequently confirmed for many species (Watson and Moss, 1970) that territorial behaviour and dominance hierarchies are in fact two extremes of a continuum which may be evident for any particular species, and vary with population density, and type of environment. The lack of evidence of population limitation as a result of dominance within hierarchies is, then, surprising, and may simply be the consequence of insufficient work in this field (Watson and Moss, 1970).

Dominance and territoriality are terms which are widely used, yet often poorly understood. Dominance may be defined as 'an attribute that provides its holder with access to certain resources in precedence over other individuals, without actual contest' (Leuthold, 1977). It may be manifest in either of two ways (Leyhausen, 1971). Within an 'absolute social hierarchy' dominance is a fixed attribute of an individual effective wherever it goes within its society, regardless of external circumstances. Within a 'relative social hierarchy' dominance may be tied to some external condition, such as space or time; territoriality is the most important type of 'relative social hierarchy' where an individual is dominant over others in one place, but not in another.

7.2 METHODS

The study of behaviour and social organisation *per se* was considered to be of relatively minor importance in this study, and observations in this regard are largely adventitious.

During regular census (CHAPTER THREE) animals were, whenever possible, classified by age and sex, and group size and type. They were generally regarded as belonging to the same group if they were within 25 m of one another, but a certain amount of discretion was exercised in defining groups in situations of local congregation, or in open, exposed country. Groups were then classified into one of ten group types. These group types

are modified after those used by Attwell (1977), so as to provide more information on adult male associations than would be provided by his classification. The ten recognised group types were:

- 1 Solitary adult male 'group'
- 2 Solitary adult female 'group'; comprising a solitary adult female with or without a juvenile of less than one year
- 3 Solitary subadult 'group'
- 4 Female group; comprising one or more adult females with or without any number of juveniles or subadults of either sex, where the group does not qualify as 2 above
- 5 Bachelor group; comprising two or more males of any age
- 6 Family group; comprising one adult male and one adult female with or without a juvenile of less than one year
- 7 Harem group; comprising one adult male with more than one adult female, with or without their associated juveniles of less than one year
- 8 Subadult group; comprising two or more subadults, which are not all male
- 9 Male mixed group; comprising two or more adult males, with one or more adult females, with or without any number of juveniles and subadults of either sex
- 10 Miscellaneous group; comprising any other association, including pairs with associating subadults older than one year.

Seasonal changes in the proportion of animals sighted in the different group types were examined.

Since resource defence (i.e. territoriality) is more commonly associated with male than female mammals, it was decided to investigate social organisation as it affects the male reedback specifically. All resightings of marked adult males and their associates were classified by group type, and seasonal changes in the proportion of sightings of different social groupings examined. The possibility of permanent pair bonding between reedback was examined by calculating coefficients of association (Leuthold, 1979) between all known adult males and associating known adult females for each two-month period.

The coefficient (a) was calculated as:

$$a = 2N / n_1 + n_2$$

where N was the number of times the two animals were seen together and n_1 and n_2 were the numbers of sightings of the two individuals during the time in which their periods of observation overlapped. Coefficients of association were calculated between all known adult males and all other

known animals except subadult females; these being excluded because most dispersed within a short period of being marked (CHAPTER SIX).

7.3 RESULTS

To avoid confusion over the identification of social groupings at night-time congregation centres, only dawn and dusk census information was used in this analysis. Observations made in 1982 were considered sufficient and 1981 data were ignored. During 1982, 1038 animal sightings were made during dawn and dusk counts, in 566 different groups.

The proportion of animals sighted in different group types each month is illustrated in FIG. 7.1, and mean values are illustrated in FIG. 7.2.

FIG. 7.2 : The mean monthly proportion of the total population of animals in different social groupings

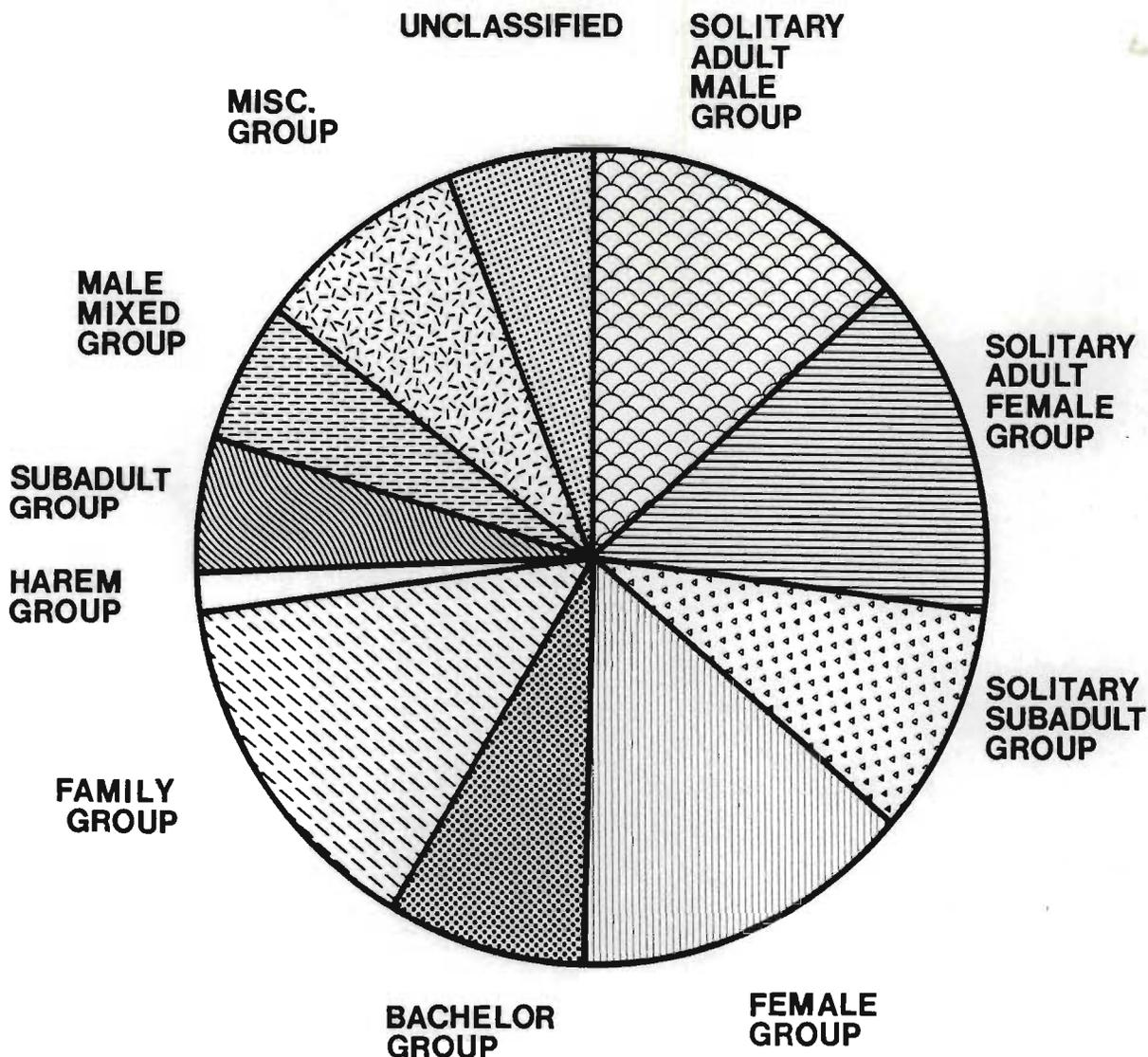
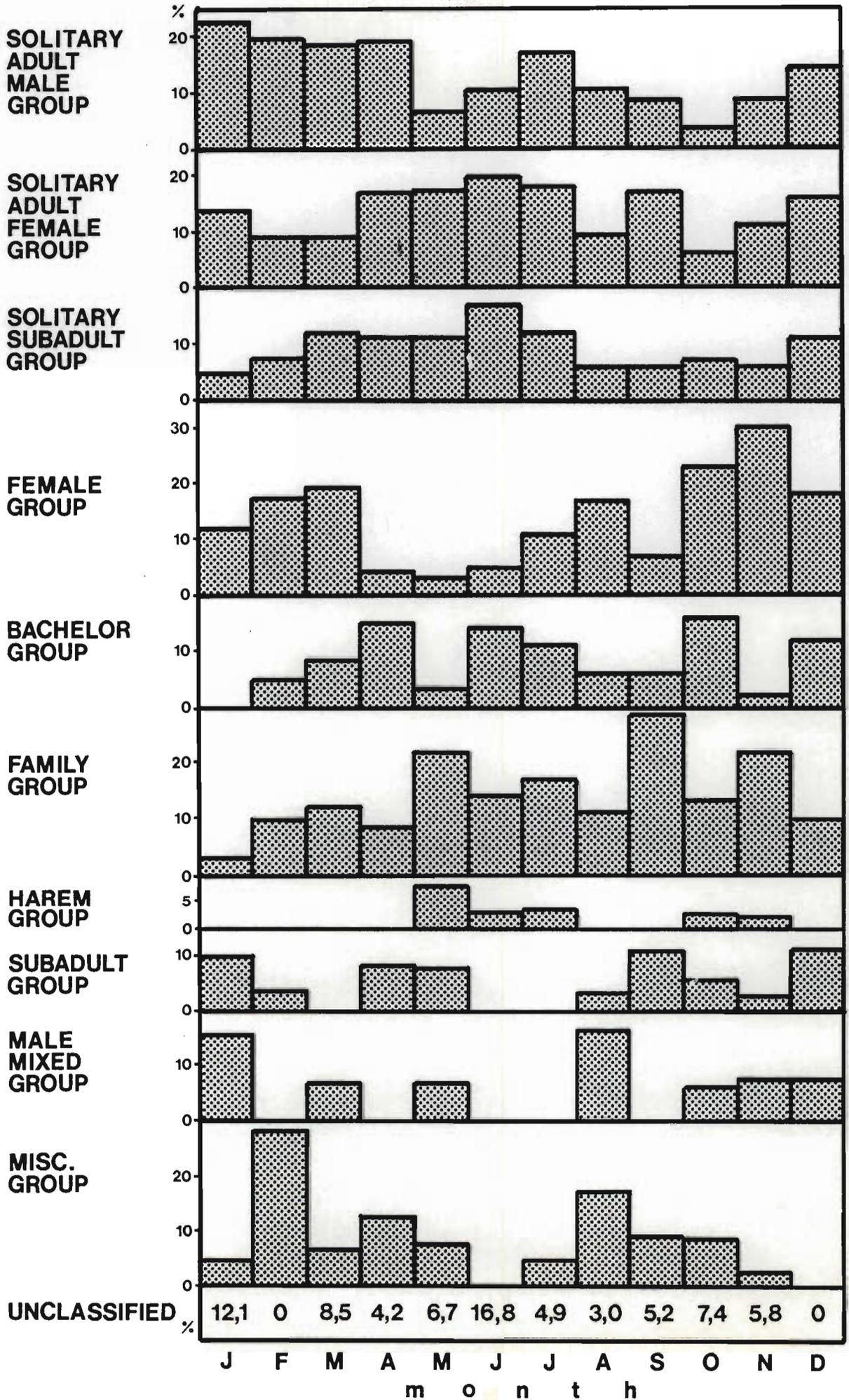


FIG. 7.1 : Monthly changes in the proportion of the total population of animals in different social groupings



The most important social groups, which collectively account for 72,4 % of animal sightings are the solitary adult male group ($13,3 \pm 6,0$ (S.D.) %), the solitary adult female group ($13,5 \pm 4,7$ (S.D.) %), the solitary subadult group ($9,2 \pm 3,6$ (S.D.) %), the female group ($14,0 \pm 8,3$ (S.D.) %), the bachelor group ($8,1 \pm 5,3$ (S.D.) %), and the family group ($14,3 \pm 7,0$ (S.D.) %).

Adult males comprise 28,5 % of the population (CHAPTER THREE), and on average nearly half of these ($13,3 \pm 6,0$ (S.D.) %) occur as solitary adult males. In the late summer and autumn months (January to April), preceding and during 'the rut' (CHAPTER FOUR), the proportion of solitary adult males is higher (range 22,4 % to 18,6 %) than at other times (FIG. 7.1).

Adult females tend to be solitary during winter (especially April to July), or associated with adult males in family groups (May to November). As the adult males become more solitary in summer, these family groups are broken up and females tend to associate together, or with subadults in female groups (FIG. 7.1).

Solitary subadults are seen particularly in autumn and winter. These animals are presumably born mostly during the previous summer's birth peak (CHAPTER FOUR), and are gradually becoming independent of their mothers, yet still 'tied' to artificial winter feed, which prevents them dispersing until spring (CHAPTER SIX).

There were no bachelor groups seen in January, but the proportion of animals seen in this group type rose progressively each month during late summer to a level of 14,9 % in April (FIG. 7.1). The adult males are largely solitary at this time, which coincides with 'the rut', and these bachelor groups probably comprise subordinate, non-breeding males.

Nine known adult males were sighted 331 times in identifiable social groupings. The proportion of these resightings in different social group types is illustrated for each two month period in FIG. 7.3. Again, animals become very much more solitary at the time of the rut, with 81 % of sightings in February/March being of solitary animals, and most of the remainder (16 %) being of family groups, in which the male in question is associating with a single (probably oestrous) female.

Bi-monthly changes in associations between two adult males and their associated adult females are illustrated in FIG. 7.4. Since coefficient values are generally below a value of 0,5, association is clearly the exception rather than the rule. Only adult male 8 was observed for longer than one year, and from observation of its changing associations with adult females it is tempting to suggest that this animal might father successive progeny of several adult females. The strongest associations with each

FIG. 7.3 : Bi-monthly changes in the proportion of resightings of marked adult males in different social groupings

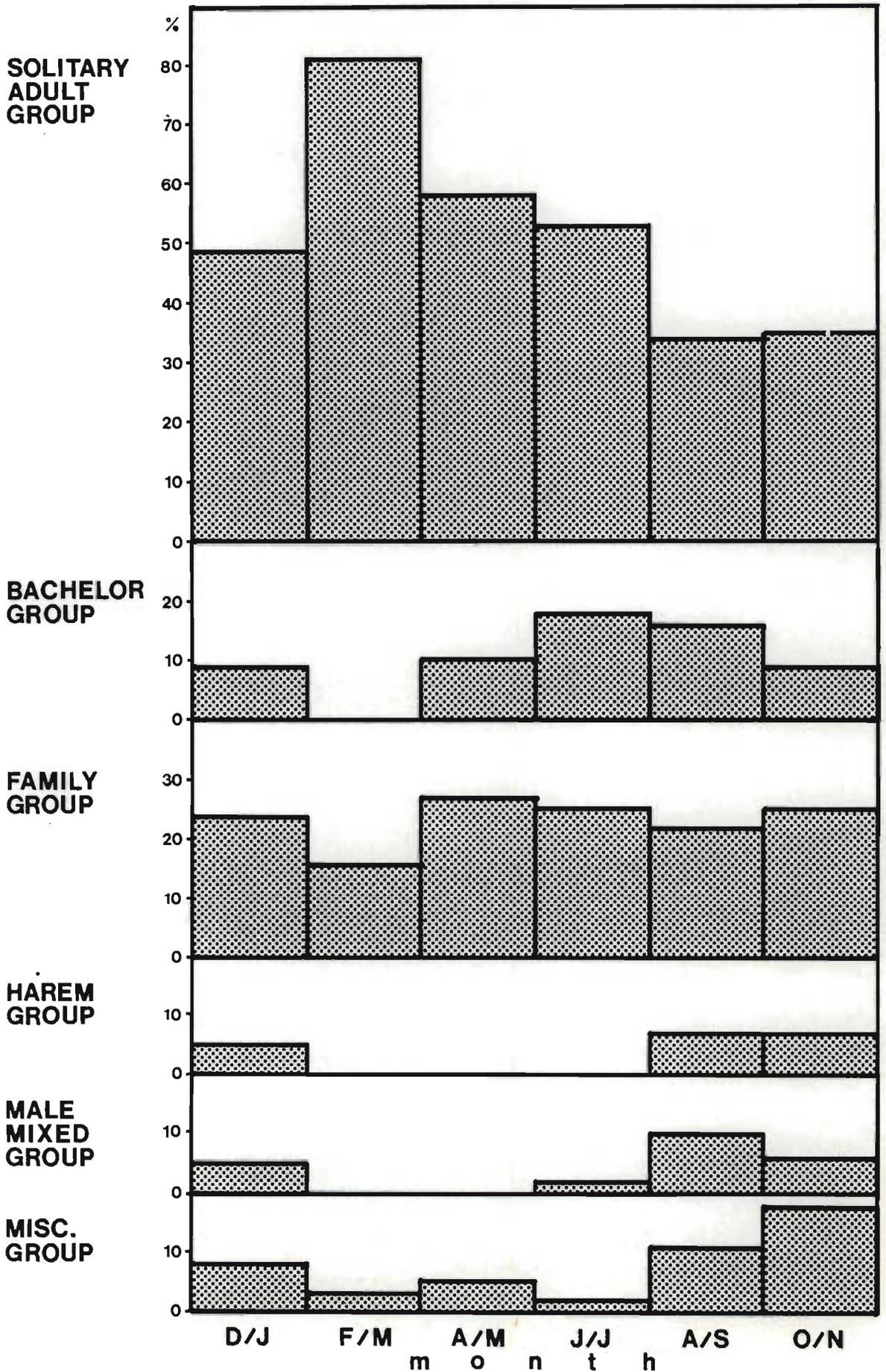
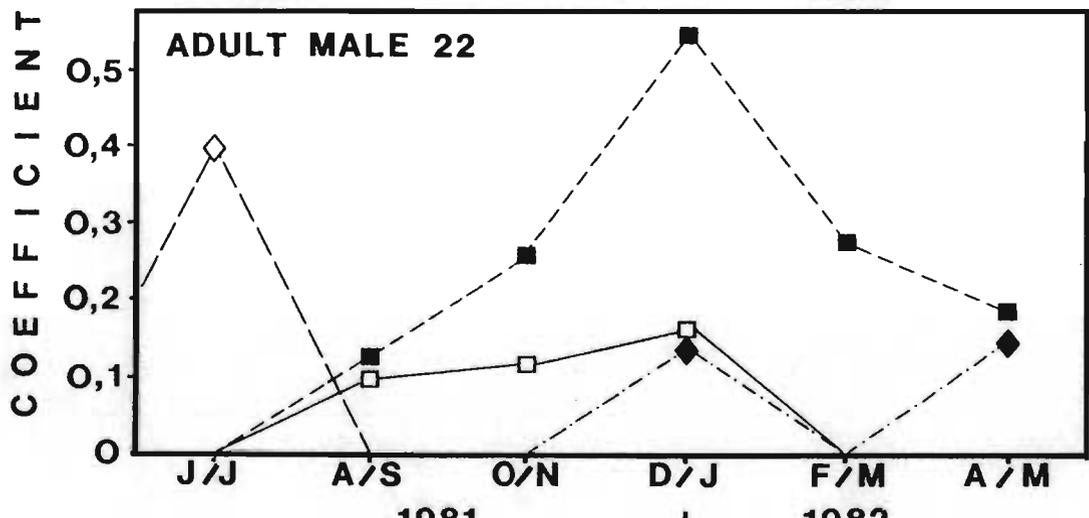
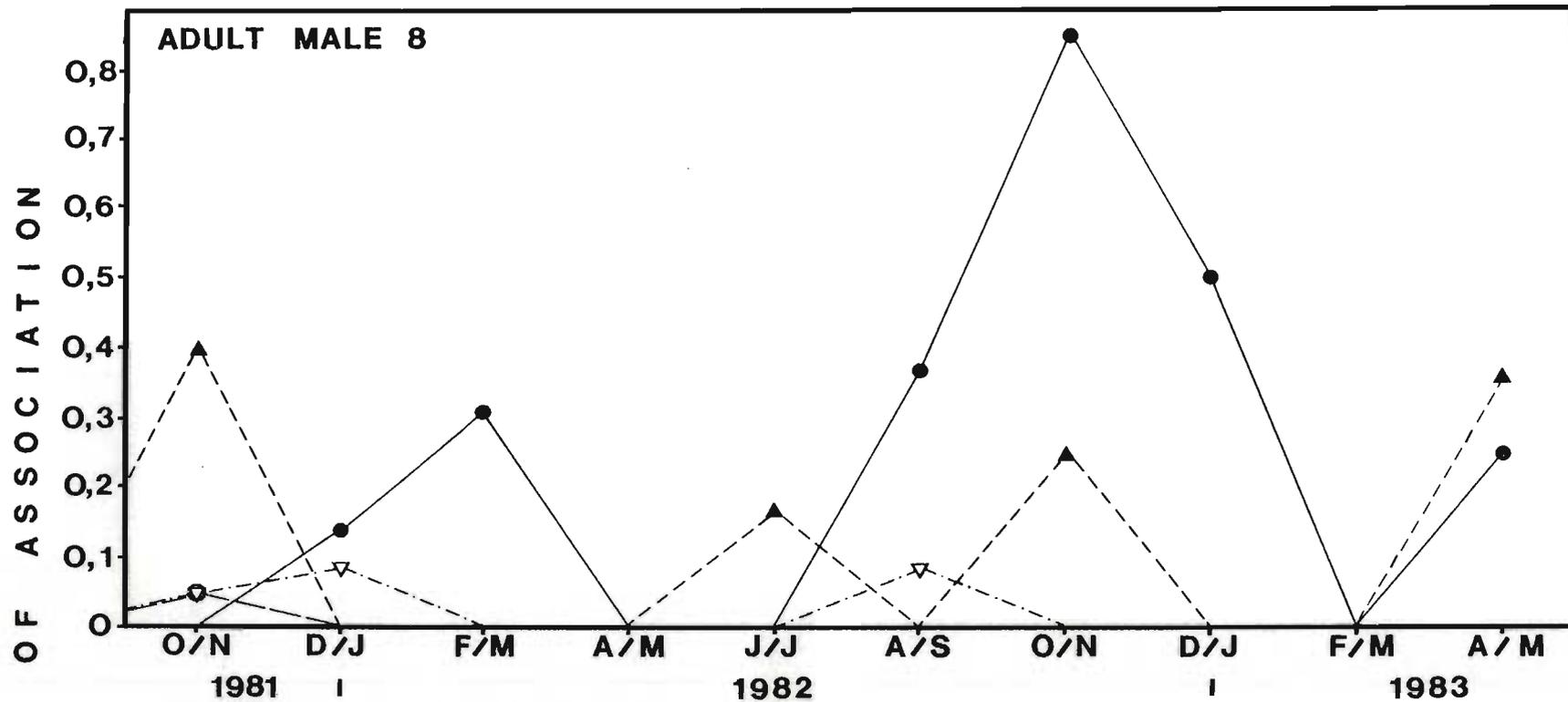


FIG. 7.4 : Bi-monthly changes in the degree of association between marked adult males 8 & 22, and marked adult females



- KEY:**
- Female 11
 - Female 20
 - ▲- Female 16
 - ▽- Female 13
 - Female 39
 - Female 34
 - ◆- Female 23
 - ◇- Female 40

particular adult female recur at approximately eight month intervals, this period almost coinciding with the calculated lambing interval of 8,8 months (CHAPTER THREE).

Overall coefficients of association between the known adult males and all other known animals except subadult females are given in TABLE 7.1. In only one case was there a recorded association between two known adult males. Associations between known animals were generally weak with 22 of the 34 associations involving coefficient values of less than 0,1.

TABLE 7.1 : Coefficients of Association (a) between all adult males and all other known animals except subadult females

	I.D. No.	A D U L T M A L E S									
		3	8	22	36	48	49	58	62	65	67
Adult MALES	58	-	-	-	-	-	-	-	0,18	-	-
	11	-	0,17	-	0,02	-	-	-	-	-	-
	13	-	0,03	-	-	-	-	-	-	0,02	-
	15	0,06	-	-	-	-	-	-	-	-	-
	16	-	0,13	-	-	-	-	-	-	-	-
	19	-	-	-	-	-	-	-	-	0,08	-
Adult FEMALES	20	0,31	0,01	-	-	-	-	-	-	0,04	-
	23	0,04	-	0,05	-	-	-	-	-	-	-
	34	-	-	0,32	-	-	-	-	-	-	-
	35	-	0,03	-	0,13	-	-	-	-	-	-
	50	-	-	-	-	-	0,04	-	-	-	-
	53	-	-	-	-	-	-	-	0,45	-	-
	68	-	-	-	-	-	-	-	0,11	-	-
	1	-	-	0,02	-	-	-	-	-	-	-
	4	0,04	-	-	-	-	-	-	-	-	-
	9	0,05	0,01	-	-	-	-	-	0,03	-	-
Subadult MALES	17	-	-	-	-	-	-	-	-	0,03	-
	37	-	-	-	-	-	-	-	-	-	0,11
	38	-	-	-	-	-	-	-	-	0,17	-
	42	0,04	-	-	-	-	-	-	-	-	-
	44	0,08	-	0,02	-	-	-	-	-	-	-
	52	-	-	-	-	-	-	-	-	-	0,22
	57	-	-	-	-	-	-	-	-	0,09	-
	69	-	-	-	-	0,06	-	-	-	-	0,12

7.4 DISCUSSION

As the main purpose of examining social organisation in this study is to evaluate the possible effect it may have on the regulation of population size, this discussion will concentrate specifically on this aspect.

The main issue which apparently deserves clarification is whether or not the reedbeek is territorial. Before turning to the results of this study I will review briefly the evidence cited by Jungius (1971a) in favour of a territorial organisation, and that cited by Venter (1979) in support of his hypothesis of a dominance hierarchy.

Jungius (op. cit.), who undertook prolonged daylight observation of reedbeek in Kruger National Park over a period of one year, described the following evidence from his study population which led him to the conclusion that the species was strictly territorial:

- 1 Young males were predominantly found in sub-optimal habitats (p 41).
- 2 Under intensive observation, a young male was seen to 'displace' an established territorial male (pp 41 - 2). Initially the defendant successfully chased the intruder away for distances up to 600 m, but after some intense fighting, the intruder 'won' part of the territory, and this area was subsequently visited less often by its original occupant.
- 3 If living requirements were no longer provided by an area, as after fire, territories were abandoned: 'evicted' animals tended to congregate in groups of more than three, but these only ever included one male as other males were 'regarded as rivals and driven off' (p 43).
- 4 Optical-acoustic 'marking' of territories was very common; adoption of the 'proud posture', whistling, 'pronking' and exposure of the white undertail at defaecation were common behaviours.
- 5 Olfactory marking of territories was inferred from the observation that reedbeek possess subauricular and inguinal glands. Faeces and urine were regarded as olfactory aids in territory demarkation. A 'stamping ground', covered with droppings, and 'horning sites' were found (pp 44 - 5).

By contrast Venter (1979) described the following evidence in support of his hypothesis of a social organisation based on the dominance hierarchy:

- 1 Although known adult male reedbeek had fixed home ranges, no portion

of them was 'defended'.

- 2 Adult male home ranges overlapped.
- 3 Adult males were often seen together, both in the presence and absence of adult females.
- 4 High intensity fighting was observed between adults, between subadults and between juveniles of apparently equal social status, and was not restricted to adult males.

For a more detailed discussion the reader is referred to the original authors. From the points summarised above it is clear that there are significant differences in social organisation between these two study populations. In particular, adult males at St. Lucia (Venter, 1979) were often seen together while in the presence of adult females, whereas those in the Kruger National Park never associated with one another, except antagonistically, in the presence of females. Such associations between adult males are regarded as 'the main characteristic of a dominance hierarchy' (Leuthold, 1974).

In this study social groupings were analysed specifically with a view to establishing whether or not adult males associated together in the presence of adult females. The fact that 6 % of animals were observed in this kind of group (the 'male mixed group') undeniably suggests the existence of a dominance hierarchy.

At the same time, observations were made during the course of this study which might be justifiably construed as evidence of a territorial system. All concern adult male antagonistic interactions.

The first three observations concern physical damage incurred by known adult males at times when, for some reason, they moved outside their normal home ranges. Adult male 49 is a case in point: during March 1983 the area of low woody scrub that had provided daytime cover for this animal was cleared and ploughed, thus rendering the animal 'homeless'. The sequence of events that followed was not observed, but the animal had obviously been involved in some heavy fighting, as it had a damaged collar and was limping badly when it was sighted a month later in an adjacent area that had not previously been used. It is not known whether this animal survived, as fieldwork on the project finished at about this time. Similarly, adult male 36, which had been consistently observed in a small, fixed home range in the centre of the intensive study area for about a year, suddenly appeared in a rather 'marginal' area some 300 m or so outside its 'normal' home range; it had the tip of one horn missing. It was first seen in this new area on 23/03/82 (i.e. at the height of 'the rut'), and between that

date and 18/05/82 (i.e. the end of 'the rut') was seen five times alternately in the 'new' and 'normal' parts of its range, and each time with progressively worse damage to its horns. It returned permanently to its normal home range as from 05/06/82, and was not 'evicted' over the same ('rutting') period the following year. Finally, Male 1 was a young adult that was never actually seen outside its 'normal' home range, but the sterkolite collar it was wearing was found, torn, several hundred metres outside this area, and it was inferred that this animal had become involved in an abnormally severe fight, as a result of moving outside its 'normal' range.

These three animals have one thing in common, viz. noticeable physical damage, the result of intraspecific conflict, which was associated with a shift in home range area. Whether in the case of male 36 the conflict arose in the animal's 'normal' range or in the 'new' area is immaterial. What matters is that it was clearly relative to space. Where dominance over other animals is contingent upon a piece of land, we call the system territoriality. It should be cautioned, however, that these observations, although apparently indicative of territoriality, might alternatively be the result of attempts by the animals concerned to establish rank relative to new animals that they had not previously met, and these observations alone do not constitute conclusive evidence of territoriality.

There is some other evidence from this study to support the conclusion that this population of reedbuck is, at least temporarily, territorial. On three occasions during regular censusing I observed adult (territorial?) males run after, chase and 'evict' other males from an area. On the first occasion the 'territory holder' ran at an 'intruder' (adult) which was seen approximately 50 m away. The 'intruder' did not resist in any way and was chased for about 100 m before the 'territory holder' turned back and returned to its original location. No females were apparent close by, and the dispute appeared to be over 'territory'. On the second occasion a known subadult male (No. 21), at approximately three years of age, was showing sexual interest in an adult female, and an adult male from about 150 m away approached at speed. The known subadult was apparently submissive, fighting did not follow, but the adult female in question was thereafter accompanied by the adult. The third occasion involved two adult males, again apparently fighting over 'territory' as no females were observed close by: a 'territory holder' ran from about 100 m away towards the 'intruder', and physical contact between the two animals was immediate and intense. Heavy fighting ensued for about ten minutes, until the 'territory holder' began to move slowly back towards the area in which it was originally seen. The 'intruder' did not follow, but carried on walking in the direction in which it was travelling before the incident occurred. The first of these three incidents was observed in March, and the last two in May, which coincides with the 'rutting' peak (CHAPTER FOUR).

Finally with regard to the observed territoriality of this population of reedbuck, the high incidence of solitary adult male 'groups', particularly during the 'rutting' period is perhaps the most convincing evidence. Leuthold (1977) considers the main difference that is outwardly manifest between the two extremes of social organisation to be that, in territorial systems, reproductively active males are usually single and dispersed, whereas with an absolute hierarchy several males of similar status may be found together in one group.

It appears from this discussion that this population of reedbuck shows elements that normally characterise a territorial organisation and others that characterise absolute dominance. Leuthold (1977) has stressed that 'territoriality and rank hierarchy are not radically different forms of organisation, but rather different applications, or manifestations, of one basic phenomenon: dominance.'. He goes on to describe how the two systems might coexist in one population, drawing on the work of Jarman and Jarman (1974) and Gosling (1974) who found that in impala and in Coke's hartebeest high ranking males in a bachelor herd are those most likely to acquire a territory. The argument is worth repeating here, because I believe a very similar system pertains to reedbuck.

While in a bachelor herd, males compete for absolute dominance within the bachelor-male segment of the population. During this time they use a home range much larger than individual territories existing in the same area. They are subordinate to any territorial male whose territory they may enter. A male at the top of the bachelor hierarchy is 'next-in-line' to territory acquisition. Acquiring a territory will give him breeding rights, but the costs are high as he will have to restrict all his activities to a smaller 'resource area', and 'invest' a lot of energy in defence. These changes may influence his physical condition, and in turn his continued ability to occupy a territory in the face of competition from other males. If he loses his territory he will rejoin the bachelor herd, but at a comparatively low rank, and it may take some time for him to recuperate and gradually move upward again in the bachelor hierarchy.

Whilst this population of reedbuck shows elements from either end of the relative - absolute dominance continuum, other populations (Jungius, 1971a; Venter, 1979) apparently fit more neatly into the territorial or dominance hierarchy extremes of it. It is instructive to consider why this should be so. Many behaviours are influenced by local environmental conditions (Leuthold, 1977) and Eisenberg (1966) considers social organisation as 'potentially the most variable structure characterising a given species. It is variable because it reflects the sum total of all the adjustments to the environment in terms of habitat exploitation and energy budget'. We might then reasonably look to differences in environmental conditions

between study areas in a first attempt to explain the observed differences in social organisation.

In my earlier definition of dominance I referred to 'an attribute that provides its holder with access to certain resources ... ', and at that stage the 'resources' involved were not defined. It is possible that the observed differences in social systems of reedbuck reflect differences in these 'limiting resources' in the different areas of study.

Jungius' (1971a) study in the Kruger National Park was not directly management orientated and provides little information on population dynamics. We can only guess that populations under the conditions he describes might be food-limited during the dry season. If this is so, the 'resource' over which dominance may be established could be food. The establishment of territory would enable the exclusive use of the 'static' food resources within an area by the holder of that territory. Incidentally the area would be visited by females because of the attractive food resources there, and this would enhance the territory holder's chances of reproduction. Thus the reedbuck of the Kruger National Park adopt a system of 'resource defence polygyny' (Emlen and Oring, 1977) by which males control access to females indirectly, by monopolising critical resources.

Venter's (1979) study was directly management orientated, and provides more precise information on that population's dynamics. Clearly, on the Eastern Shores of Lake St. Lucia, the reedbuck population was experiencing a superabundance of resources, and exponential population growth was the result. Here, one might suppose, the 'limiting resource' over which dominance would be established would be access to females. Since females are not fixed in space, dominance is not related to space. Furthermore, because of the equitable subtropical climate, seasonal environmental changes are relatively minor, and breeding continues throughout the year without any significant birth peak at any time (Venter, 1979): not only is dominance independent of space, but also of time; it is absolute.

In this study, however, there is a significant summer birth peak between November and February, and a corresponding 'rut' from March to May (CHAPTER FOUR). Oestrous females, as a 'resource', are differentially available at this time, and we would expect competition between males for mating rights to be most obvious during these months. This it appears to be, with males becoming obviously more solitary and 'territorial' at this time.

This explanation is, however, incomplete. Earlier in this thesis it was established that, whilst food is superabundant (CHAPTER FOUR), cover is a limiting resource (CHAPTER FIVE). If cover was limiting in the sense of being 'used up' by the animals concerned we would expect possession of the

'cover resource' (i.e. territoriality) to be most obvious when cover was least abundant after burning in September/October. As this does not appear to be the case, we must look to an alternative explanation for cover limitation. I believe that such an explanation is provided by the observed temporary rise in territorial expression between January and April. With the exception of yearlings, all oestrous females have recently given birth and are nursing juveniles of less than two months of age (CHAPTER FOUR). At this age juvenile reedbuck are totally dependent upon cover for protection, and their mothers are consequently 'tied' to areas where cover is abundant. As a means of enhancing his reproductive success, it follows that the male reedbuck should strive to 'possess' such cover-abundant areas, where oestrous females are 'concentrated'. And since the reason for these females concentrating in these cover-abundant areas is to give birth, it may be beneficial for the male to be present from the time of birth onwards; this would explain why the male reedbuck becomes more solitary as early as January, some two months before the 'rutting peak'. It is almost as if he is establishing his territory early in order to ensure that the female(s) does not leave prematurely, before he has had his chance to mate.

In many ways the situation described above is similar to that of impala where the behavioural mechanism governing and distributing mating rights is invoked only when it is needed (i.e. at rutting time). Under sub-tropical southern African conditions, impala show a marked annual cycle and territories are held only during a short rutting season in April/May, and for the rest of the year the territorial males join bachelor groups and/or female herds (Anderson, 1972; Jarman and Jarman, 1974). In tropical East Africa, where breeding continues throughout the year, male territoriality is apparent throughout the year (Leuthold, 1970; Jarman and Jarman, 1974).

Having established that this population of reedbuck is (perhaps only temporarily) territorial, it is pertinent to consider whether this territoriality can regulate population density. Watson and Moss (1970) have reviewed the role of dominance, spacing behaviour and aggression in the limitation of vertebrate populations, and list four conditions which are both necessary and sufficient to show that social behaviour is an important limiting factor. These are:

- 1 a substantial part of the population does not breed, either because animals die, or because they are inhibited from breeding;
- 2 such non-breeders are physiologically capable of breeding if the dominant or territorial (i.e. breeding) animals are removed;
- 3 the breeding animals are not completely using up some resource such as food, space, or nest sites. If they are, the resource itself is limiting. This condition is met if the breeding animals are only

preventing other animals from using the resource and not completely using it up themselves.

- 4 if social behaviour is limiting, the resultant mortality or depressed recruitment must change at the same rate, and in the opposite sense to other causes of mortality or depressed recruitment.

It is my contention that these four conditions have been met in this study and that social behaviour is an important limiting factor at least for male reedbuck. Under farmland conditions reedbuck rams reach puberty at less than one year of age (CHAPTER FOUR), yet are probably excluded from breeding until they reach about four years of age if they survive the intense fighting that seems to result in so many deaths of young adults (CHAPTER THREE) (conditions 1 and 2 satisfied). There is circumstantial evidence (this chapter) that male reedbuck become territorial at rutting time, and may occupy cover-abundant territories thus preventing access to these areas by their peers; cover is not actually 'used up', but is limiting (CHAPTER FIVE) in-as-much-as only a certain number of territories can be established (condition 3 satisfied). When culling mortality is raised from zero to 20 % population size remains constant (CHAPTER THREE), indicating that 'social losses' have been reduced in a compensatory manner (condition 4 satisfied).

In this chapter I have discussed social organisation particularly as it affects the male. This is because territoriality was most outwardly manifest in the adult male, and a far more detailed examination of social organisation would be required to understand fully the organisation of the female. Nevertheless it is the female that is biologically more active, and which can consequently play the greatest part in population processes.

This study can add little to our knowledge of the social organisation of the female reedbuck, and of social constraints upon population density as is manifest in the female. However, some clue may be provided by the observation that the subauricular glands of females are generally more active than those of males, and seem to 'cycle' with reproductive state (TABLE 7.2). The appearance of these glands was classed as 'hair covered' (inactive), 'bare' (moderately active), or 'bare and greasy' (very active) in a randomly shot sample of 67 reedbuck: they appeared to be least active in subadults, and most active in lactating adult females (TABLE 7.2). Adult females' glands showed a far higher level of activity than those of adult males (χ^2 ; $p < 0.01$). We do not know the function of these glands, but might guess that they could function to strengthen the mother-infant bond and/or act as 'territorial markers' as suggested by Jungius (1971a). If a secretion produced from these glands does act as a territorial marker, it does appear to be secreted most profusely at times when it is most 'needed' for protection of the cover resource by nursing mothers.

TABLE 7.2 : The number of reedbuck shot with subauricular glands at different levels of activity, considered by age and sex class

		Hair covered (inactive)	Bare (moderately active)	Bare & Greasy (very active)
MALES	Subadult	15	2	2
	Adult	17	7	1
FEMALES	Subadult	4	0	0
	Adult: lactating only	0	0	4
	pregnant only	2	5	3
	pregnant and lactating	0	3	2

This can hardly be regarded as conclusive evidence of social constraints upon density in female reedbuck. It may however be a useful clue. Territoriality of the male ungulate is normally very much easier to study than that of the female and has become rather a preoccupation of zoologists'. However, there is some evidence for red deer (Lowe, 1966), black-tailed deer (Taber and Dasmann, 1958), and topi (*Damaliscus lunatus*) (Duncan, 1976) of female dominance relationships that might have a role in population regulation, and the lack of other supportive evidence justifying the conclusion that social factors are important constraints upon density, probably is as much a reflection of our lack of understanding, as of any real absence of such constraints.

7.5 CHAPTER SUMMARY

Evidence from previous chapters of this thesis led to the belief that social organisation could play a role in population regulation, and it was the purpose of this chapter to investigate this possibility.

Most observations in this regard were adventitious, and made in the course of data collection for other aspects of the study. During census, associating animals were considered as members of a group, and groups were later classified into one of ten types. Social organisation was viewed specifically from a male perspective, as it was felt that any evidence of territoriality would be most outwardly manifest in the male. Seasonal

changes in group types were investigated both from census information and from observations of known adult males.

During the months January to April (which includes 'the rut') adult male reedbuck became more solitary and 'territorial behaviour' such as intraspecific conflict was more conspicuous than at other times. Previous studies of reedbuck social organisation have described the species as, on the one hand, strictly territorial, and on the other organised on a system of absolute dominance hierarchy. This population of reedbuck seems to be intermediate, showing elements of both types of organisation. The differences between populations were explained in terms of environmental differences between areas of study. It was concluded that in this population of reedbuck, cover is a limiting resource because it is monopolised by a few territorial males at times of the year when females congregate there to give birth. Soon after birth the female becomes oestrus again, and is mated by the territorial male. In the male, at least, the result of such an organisation is that an upper limit is set to population size.

PART TWO: MANAGEMENT

CHAPTER EIGHT

ECONOMIC IMPLICATIONS AND CONTROL OF CROP DAMAGE

8.1 INTRODUCTION

In view of the study's motivation as a 'problem animal' study, a quantitative assessment of crop damage, its economic implications and possible control is of key importance in formulating management policy.

The principal category of damage attributable to reedbuck results from their grazing of planted annual pastures during the winter months. At this time the quality of natural forage is low (CHAPTER FIVE), and the number of reedbuck feeding on the relatively nutritious pasture grasses increases to more than twice that recorded in summer (CHAPTER THREE). This coincides with the period of shortened daylength, low temperatures, negligible rainfall, and strong desiccating winds which combine to reduce potential primary production of these pastures. This is illustrated in FIG. 8.1, where the potential productivity of annual ryegrass under dryland conditions, and under irrigation is compared with that of natural veld in bioclimatic sub-region 4f (Phillips, 1973): figures are for Italian ryegrass (variety Midmar) and highland sourveld at Kokstad, Natal (Dept. of Agriculture, 1980).

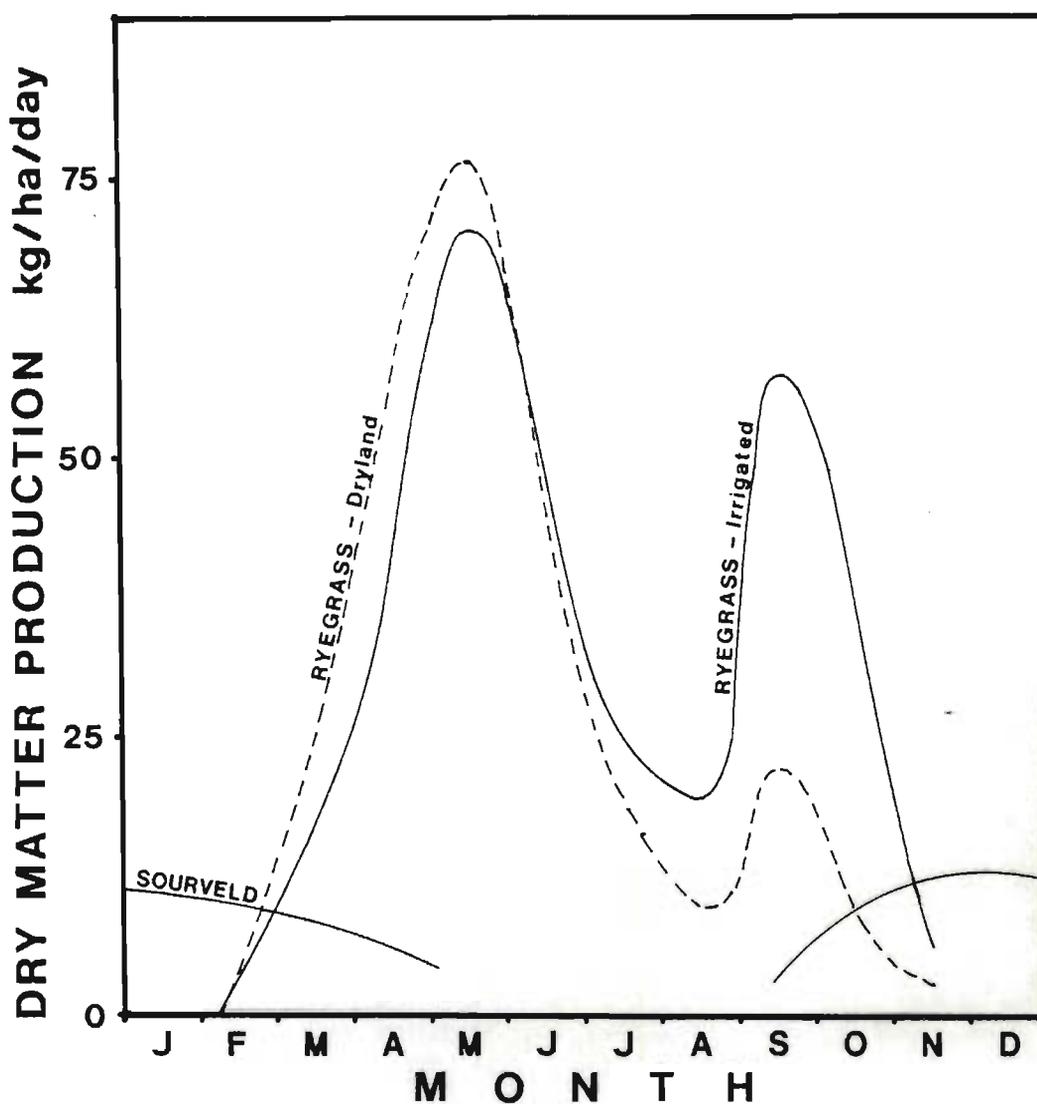
Crop damage assessments depend on the ability to measure the quantity of vegetation standing in a crop before and after any damage has occurred, and the production of the same crop in the absence of damage. The various methods used in measuring the quantity of grassland vegetation are reviewed by 't Mannelje (1978): they include both destructive and non-destructive methods. The value of crop losses depends not only on the quantity involved but also on the type and quality of the crop.

There is a large number of options available in the approach to the control of crop damage which may be broadly classified as follows:

- 1 Lethal control methods, which include shooting, trapping and poisoning.
- 2 Preventative control methods, which include fencing, frightening devices, chemical repellents, and translocation of offending animals.
- 3 Habitat manipulation methods, which make an area less susceptible to damage.

- 4 Physiological control methods, which affect an animal's ability to survive and reproduce in an area.

FIG. 8.1: GRASS PRODUCTION IN BIOCLIMATIC SUBREGION 4f



8.2 EXPERIMENTAL METHODS

8.2.1 Crop damage assessments

8.2.1.1 PASTURE DAMAGE

Pasture damage assessments were made during the winter months from May to September only, using a standard exclusion technique (Brown, 1954; Greig-Smith, 1964; Milner and Hughes, 1968; 't Mannetje, 1978). With this technique small areas of pasture were protected from damage by the erection of exclusion cages on selected pastures, and the productivity of grassland within the cages compared with that of the remainder of the pasture where reedbuck were free to graze.

In selecting particular pastures for exclusion experiments, account was taken of the following:

- 1 the number of reedbuck seen feeding on the pasture at night;
- 2 the area of the pasture;
- 3 the farmer's grazing requirements, and anticipated period before domestic stock would be moved onto the pasture;
- 4 the standing crop of grass;
- 5 the evenness of the grass planting;
- 6 the presence of herbivores other than reedbuck;
- 7 the anticipated production of the pasture during the experimental period.

Because of the amount of work involved, exclusion experiments were set up only on pastures where it was anticipated that significant losses resulting from reedbuck grazing pressure could be measured. The ideal pasture for such experiments therefore had a large number of reedbuck per unit area of pasture, no other herbivores, a small standing crop and low productivity, was evenly planted, and not required for domestic stock grazing for at least three weeks.

Where a pasture was considered likely to yield useful results, up to 60 points were located by random coordinates, and the total standing crop of grass measured by clipping 0,5m² quadrats at these points. These samples were weighed wet, and a curve relating the number of samples to the standard error of the mean plotted. From this it was possible to predict the appropriate level of pasture losses that would be required to reveal significant losses between grazed and ungrazed parts of the pasture, using different numbers of quadrats. These results were considered in relation to anticipated losses from the pasture in question, and a decision taken on the intensity of sampling required.

Choice of quadrat size and shape for all experiments was influenced by the relatively homogeneous nature of planted pasture, the generally short grass sward to be sampled, and the decision to clip quadrats manually for improved precision. These considerations indicated a small quadrat size. Since a large proportion of sampling error arises from edge effects ('t Mannetje, 1978), quadrat shape should attempt to minimise the perimeter : area ratio, and this is best achieved by use of circular quadrats. However, since pasture grasses are generally planted in straight rows, the use of a straight sided quadrat would help in boundary definition, and a square quadrat would therefore be better than a circular one. These theoretical considerations were briefly investigated experimentally by clipping a series of 60 sample 0,5m² square quadrats, and 30 1m

rectangular (proportionally 2x1) quadrats located by random coordinates on a pasture. The rectangular quadrats were placed across the rows. A standard error curve was plotted, and it was found that, for a given area of pasture sampled, the larger number of smaller quadrats gave greater precision. As a result the decision was taken to use $0,5m^2$ square quadrats for all exclusion experiments.

Having established the viability of an exclusion experiment, and the sampling intensity required, the following procedure was adopted in carrying out the experiment:

- 1 The sealed polythene bags containing the initial clipped samples were opened and the contents emptied into perforated paper packets and left to dry. They were subsequently reweighed, to give a (dry matter) standing crop at the start of the experiment.
- 2 The requisite number of excluded plots were located by random coordinates and 5m x 5m areas of pasture fenced off at these points using 1,5m high 'Bonnox' fencing.
- 3 The fenced areas were left in position for a period of some weeks to allow the effects of growth, and of reedbuck grazing pressure to become apparent. Experiments were normally concluded when the farmer indicated that he required the pasture for domestic stock, but in a few cases the 'growing-out' period was sufficiently long, and reedbuck grazing pressure sufficiently high to allow a 'mid-term' clipping.
- 4 During the growing-out period the pasture was visited frequently within three hours of dusk to count the reedbuck feeding there. The pasture was checked during the day and at night for the presence of other herbivores.
- 5 At the conclusion of the experiment four quadrats were located by random coordinates within each fenced area, and the requisite number of 'outside' quadrats were located by the same method over the rest of the pasture. All these quadrats were clipped by hand at ground level, and the grass from each collected separately. Since two people did the clipping, care was taken to ensure that each cut the same number of inside and outside quadrats, and that they were cut alternately to control for operator fatigue.
- 6 Each of the quadrat samples was transferred to a perforated paper packet, and allowed to dry for some weeks.

- 7 When samples had reached constant mass they were weighed, and mean values calculated for standing crop inside and outside the fenced areas. The difference between the two sample means was the loss from that pasture over the experimental period, and the productivity of the pasture was the difference between the crops measured in the initial clipping and in the fenced areas, at the experiment's conclusion.

8.2.1.2 OTHER CROP DAMAGE ASSESSMENTS

Although reedbuck cause damage to many different farm crops, including sugarcane, pineapple, cabbage, lettuce and maize (Gamequest survey results), the levels of damage suffered are probably so case-specific as to limit severely the value of any general observations.

For this reason only one specific assessment of reedbuck damage to crops other than annual planted pastures was made. This was carried out in a field of maize within the intensive study area, and the systematic sampling method adopted was as follows:

- 1 At the end of the growing season, a maize plant was sampled in each tenth row from positions ten paces apart, by walking along the rows, and inspecting the appropriate plant visually.
- 2 The height of each plant was measured, and the degree of damage to the plant recorded on a five point scale:
 - a no damage;
 - b slight damage, affecting leaf ends only;
 - c moderate damage, causing extensive damage to leaves, but flowers and cobs intact;
 - d serious damage, where flower and growing tip were removed, but cobs were present;
 - e severe damage, where flower and growing tip were removed, and no cobs were present.
- 3 A sample of 50 plants in each damage class was destructively sampled, and the individual plants weighed and their heights measured. Undamaged plants were classed as being 'strong' or 'weak' depending on whether they were taller than an arbitrary threshold of 2,25 m, and average statistics calculated for plants in these, and all damage classes.
- 4 The proportion of plants in each class was calculated. The total number of plants in the field was calculated from sample counts of plant numbers per pace, related to the total number of

rows of known length. From this, the proportion of the crop lost and its value were determined.

8.2.2 Experimental evaluation of control methods

The only experimental work carried out in this regard was the construction of a two metre high, five-strand electric fence. This was constructed around half of an annual pasture, and was intended to test whether such a fence would be an effective deterrent in situations where alternative feed was available.

The fence was constructed in mid-winter, and divided an annual oats pasture, which had been subject to particularly high reedbuck grazing pressure during the preceding weeks, into two equal paddocks. Wooden standards were erected at four metre intervals, and polypropylene/wire electric fencing cord was attached to these, secured and insulated with loops of rubber (cut from car tyre inner tubes). The five strands were secured at height intervals of 0,4 m from a level of 0,4 m above the ground to a level of 2,0 m.

8.3 EXPERIMENTAL RESULTS

8.3.1 Crop damage assessments

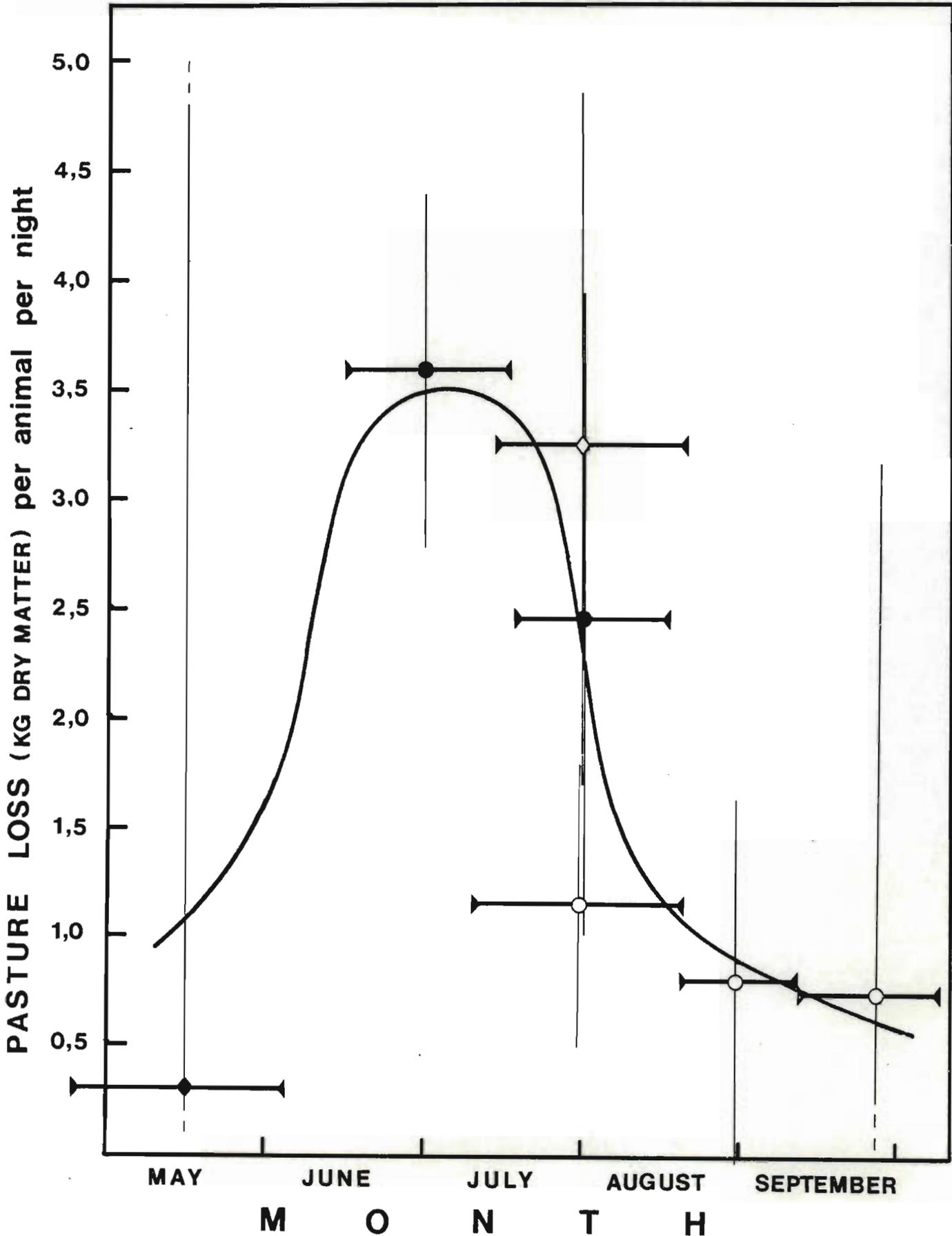
8.3.1.1 PASTURE DAMAGE

During the winter of 1982, between 25 April and 5 October, seven exclusion experiments were performed on four different pastures within the extensive study area. The results of these experiments are presented in FIG. 8.2, in which the measured losses have been expressed as values per animal counted, per night of the experimental period. Although 95 % confidence limits are wide, a peak in pasture losses of about 3,6($\pm 0,8$)kg per animal counted per night is indicated during the first half of July. Losses decline during the second half of the winter, and by September are insignificant. In fact, of the seven exclusion experiments, only the four performed during June, July and August demonstrated significant pasture losses. Since one of the main objectives of this study was to quantify pasture losses, a best estimate of these was made by fitting the illustrated curve (FIG. 8.2) by eye to the data available. It is important to stress that a figure for overall pasture losses per animal, calculated as the area under the curve, can only be regarded as a best estimate, and not a definitive statement. Some of the difficulties and limitations of the method are discussed later.

Considering the period from 15 April to 30 September the per capita

FIG. 8.2: Monthly changes in measured pasture losses from four pastures

Symbols used distinguish pastures. Mean values are shown \pm 95% confidence limits. Horizontal bars represent experimental periods. Curve fitted by eye.



loss is approximately 280 kg. It should be noted, however, that this is probably an overestimate of the loss per animal actually present because, as has been shown (CHAPTER THREE), the number of animals counted represents only about 80 % of those present. As an approximate estimate of the annual loss of pasture grass per reedbuck on the farm, a figure of $280 \times 0,8 = 224$ kg is therefore given. The economic implications of this loss are considered in the discussion section of this chapter.

8.3.1.2 OTHER CROP DAMAGE ASSESSMENTS

The loss of maize from a single field, considered by damage class, is presented in TABLE 8.1. The distribution of damaged plants is shown in FIG. 8.3 in relation to the size of other plants in the field. It is clearly demonstrated that damage is most extensive around the edge of the field, and particularly in regions where maize plant growth is rather poor. This is characteristic of this type of crop damage: edge plants are more vulnerable for obvious reasons, and it is suggested that the weaker plants are more susceptible to damage because they take longer to grow 'out of reach' of the reedbuck, for reedbuck seem to show a preference for the tender new growth at the growing tip (pers. obs.).

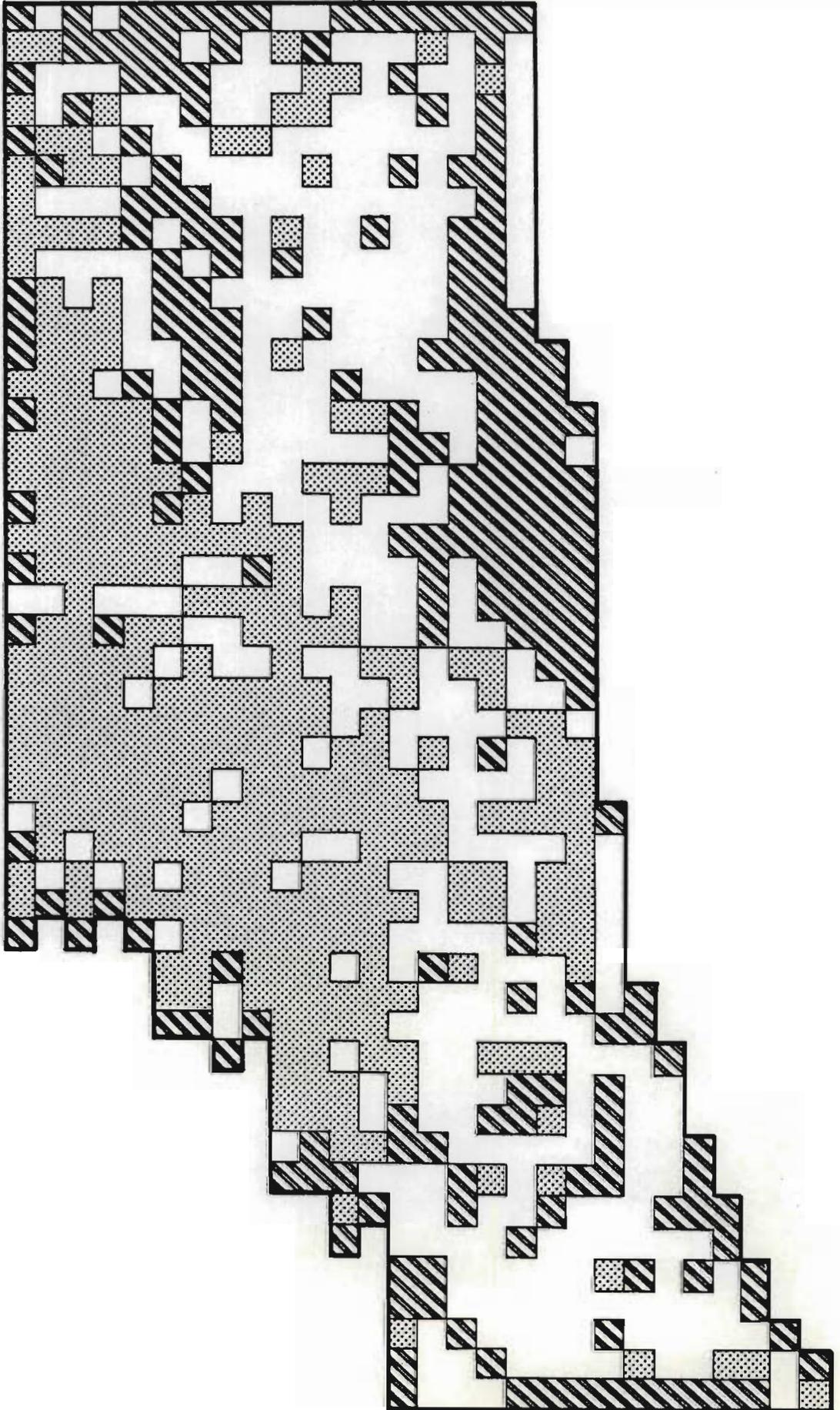
TABLE 8.1 : Reedbuck damage in an eight hectare field of maize

Damage Class	Plant Wet Mass (kg)	Plant Height (m)	Proportion of Plant Population	Anticipated Yield if Undamaged (tonnes)	Actual Yield (tonnes)	Loss (tonnes)
(a) NONE - strong plants	1,10	2,5	0,34	97,8	97,8	0
NONE - weak plants	0,74	1,9	0,40	75,8	75,8	0
(b) SLIGHT	0,71	1,8	0,14	26,4	25,3	1,1
(c) MODERATE	0,42	1,2	0,04	6,9	3,9	3,0
(d) SERIOUS	0,25	0,8	0,03	6,4	2,2	4,2
(e) SEVERE	0,06	0,5	0,05	10,1	0,8	9,3
TOTAL				<u>223,4</u>	<u>205,8</u>	<u>17,6</u>

N.B. Anticipated yields are based on the assumption that damaged plants had potential as 'weak' plants only

In the specific case examined here, 17,6 tonnes of (wet) maize, representing 7,9 % of the total crop (TABLE 8.1) was lost to reedbuck. This evaluation was made just before the crop was harvested for silage, and, although the quality of the plant material was not examined, it is fair to assume that it comprised approximately 30 % dry matter (Arnott and Whitehead, 1982). The economic implications of this loss are discussed below (SECTION 8.4).

FIG. 8.3: Distribution of damaged , strong undamaged  and weak undamaged  plants in a field of maize. Plants were sampled in each tenth row, ten paces apart



8.3.2 Experimental evaluation of control methods

The experimental electric fence was effective in controlling access by reedbuck to the area of pasture it enclosed. However, the same number of animals that were present on the entire pasture before the erection of the fence were counted on the unfenced portion after its erection, and it is doubtful whether per capita pasture grass consumption was any less.

8.4 DISCUSSION

8.4.1 Experimental crop damage assessment

An important consideration in the use of exclusion cages for assessing grazing impact is their possible effect on growth. Several studies (e.g. Cowlishaw, 1951; Owensby, 1969) have reported increased growth under cages, compared with similar ungrazed plots outside, whilst others (e.g. Dobb and Elliot, 1964) reported a reduction in growth. Williams (1951) found that cages resulted in a considerable reduction in wind velocity, an increase in relative humidity, affected temperature and reduced light intensity, and Dobb and Elliot (op.cit.) added that they also reduced vapour pressure deficit. These microclimatic effects influence growth to a degree dependent upon the particular environmental conditions prevailing. For example, Jagtenberg and De Boer (1958) reported an increase in yield of 15 % under cages on clay soils compared with that on sandy or peaty soils. In this study, several exclusion experiments were performed during the winter of 1981 using collapsible 1 m³ exclusion cages, covered on four sides with nylon bird netting, with a mesh size of approximately 2 cm. They were designed primarily for ease of transportation between trials, given the quadrat size requirements discussed earlier (SECTION 8.2.1.1). Apparent per capita grass consumption by reedbuck, assessed with these cages rose to a daily peak of 20 kg (wet) in August, which was clearly unrealistic, and this gave rise to serious doubts concerning the validity of the season's pasture damage assessments. In view of the work of others (reviewed briefly above), there can be little doubt as to the growth stimulatory effect these cages were having, particularly during August when strong 'berg' winds increase vapour pressure deficit differentially between protected and unprotected sites. It was realised that these microclimatic effects could be reduced by increasing both the area enclosed by the cages, and the size of the mesh; so that air flow was less restricted. The most cost efficient way of achieving this was to use 'Bonnox' fencing material, which has a mesh size of 20 cm, and to increase the size of the protected areas to 5m x 5m. An exclusion experiment was run during May 1982 which demonstrated a 52 % increase in yield under the 1m³ cages, to that within the 'Bonnox' fenced area, and an insignificant increase (1 %) within these fenced areas over that achieved outside the enclosures on an ungrazed

pasture. For these reasons, the results presented in this thesis are those arising from the 'Bonnox' fenced exclosures used exclusively during 1982 pasture damage assessments.

The objective of crop damage assessments in this study was to determine the quantity of a farmer's crops that are lost. Several studies have shown that this may not be equivalent to the quantity that is actually removed by the herbivores concerned, because of the effect of removal on the vegetative sward (Dyer and Bokhari, 1976; McNaughton, 1978; Edroma, 1981; Howe *et al.*, 1982). On the one hand, leaf removal may stimulate growth by prolonging the vegetative growth phase and delaying the onset of reproduction and senescence (McNaughton, 1978) in grass plants. Growth may also be stimulated as a result of some biochemical growth promoting agent in the saliva of herbivorous animals (Reardon *et al.*, 1972, 1974; Dyer and Bokhari, 1976; Dettling *et al.*, 1980; Howe *et al.*, 1982), although this has not yet been conclusively demonstrated for mammals. On the other hand, in close-cropping and overgrazing situations, grass growth may be reduced by grazing (Edroma, 1981). Under such conditions the region of cell division at the base of the leaf blades may be damaged or removed so that no further growth can occur. The impact of grazing on grass growth clearly depends on the growth stage of the grazed plants, and the severity of the grazing impact. As far as the crop damage problems reported here are concerned, it is impossible to infer any growth effect, and no general rule-of-thumb is likely to apply. In a well grown irrigated pasture, the effect of grazing could be stimulatory to growth, whereas in a poorer, heavily grazed pasture, the effect is likely to be inhibitory, because the reedbuck is able to bite off grass plants very close to the ground, thus destroying the regions of intercalary growth at the bases of the leaves (*pers. obs.*). With regard to maize damage, reedbuck frequently pull out leaves from the apex of the plant, which can only be detrimental to growth. The possible effect of grazing on plant growth is largely an academic issue in the context of the present study, because, whatever the effect, there is unlikely to be any means of altering it. Growth effect considerations are more applicable to an agricultural situation, where pastures can be grazed in such a way as to minimise possible detrimental effects on their growth. The real issue involved here, is to determine the level of loss suffered as a result of reedbuck grazing, and the results presented fulfil that objective.

A further important consideration in the use of exclosures is the possible grazing effect of herbivores other than those for which the experiment is designed. In the context of this study, the effect of invertebrate herbivores can be ignored because, in the extreme climate of the highland winter, these are inactive. Pastures where exclusion experiments were undertaken were checked irregularly at different times of the day and night for the presence of medium and large sized herbivores. The only

significant ones present were up to six grey rhebuck and three oribi during the course of two experiments: these were converted to a 'reedbuck equivalent', on the basis of their relative size, and treated as if they had been reedbuck in subsequent calculations. A few (never more than two individuals per hectare) scrub hares (Lepus saxatilis) were noted, but their possible effect was considered to be insignificant. Some young heifers broke into one experimental pasture, and the experiment was discontinued as a result. Egyptian geese (Alopochen aegyptiacus) and spur-winged geese (Plectropterus gambensis) are abundant in the study area, but their feeding activity was generally restricted to pastures close to water: they can undoubtedly cause significant losses to newly planted pastures by grazing and trampling, but none of the experimental pastures was affected. The large fence mesh size (20cm x 20cm) would have allowed free movement of the smaller herbivorous vertebrates (e.g. vlei rats, Otomys sp.), but a paucity of their signs (droppings, burrows, nests etc.) indicated that few were, in fact, present.

8.4.2 Economic implications

Recently there has been increasing interest in the justification of wildlife conservation on economic grounds (Mentis, 1978a). This has been enhanced by the belief that wildlife's very survival may depend upon the provision of tangible returns to those who act as its custodians. Revenue from wildlife may be generated from tourism, hunting, or from the sale of animal products, or a combination of these.

In South Africa, the aesthetic value of wildlife provides the strongest incentive for its conservation under existing socio-economic conditions. However, the demands of a rapidly expanding human population on resources are likely to enhance a growing interest in its economic justification in this sub-continent, as elsewhere.

From the point of view of this study economic cost-benefit analysis requires information on the costs of crop damage, and the monetary value of reedbuck.

8.4.2.1 COSTS OF CROP DAMAGE

The costs of crop damage can be evaluated in three different ways. Firstly, in terms of the cost of producing the feed consumed by reedbuck; secondly, in terms of the cost of feed replacement; and finally, in terms of the loss of profit had that same feed been used for the purpose for which it was grown.

The estimated costs of Italian ryegrass pasture production are given in TABLE 8.2, as at June 1982. The figures given are official

TABLE 8.2: Estimated cost of Italian Ryegrass pasture production: June 1982

(extracted from: Document 23863, Department of Agriculture and Fisheries, Natal Region)

	E X P E C T E D	Y I E L D	t / ha	(D. M.)
	5	11,5		16
	<u>Rands</u>	<u>Rands</u>		<u>Rands</u>
Machinery	93,36	96,68		99,99
Labour	80,35	82,37		84,47
Seed	9,00	9,00		9,00
Fertilizer	153,34	280,33		424,89
Delivery charge (on above)	6,97	11,92		17,75
TOTAL COSTS / ha	<u>R 343,02</u>	<u>R 480,30</u>		<u>R 636,10</u>
TOTAL COSTS / t	<u>R 42,88</u>	<u>R 41,76</u>		<u>R 39,76</u>

Notes1. Fertilization

Costs are calculated assuming the following:

- a. Bioclimatic group 3
- b. Red soils - estimated depth of 60 cm
- c. Soil status - P = 2 ppm; K = 83 ppm (0,21 % moisture equivalent)
- d. Minimum application of N - 75 kg/ha: once for yield of 8t/ha, three times for yield of 11,5 t/ha, five times for yield of 16t/ha
- e. P and K applied once only

2. Irrigation

Costs are based on irrigation each month February to September, excluding July, at 50 mm/ha

3. Labour

Costs are based on the following rates:

Tractor driver	80c/hr
Regular labour	70c/hr
Casual labour	60c/hr

4. Delivery charges

Costs are calculated at R0.25/t/km over 30 km

estimates of the Department of Agriculture and Fisheries (as it was then known), which do not include the cost of land, or of a farm's fixed recurrent expenses such as telephone, electricity 'line charge', etc.. Thus the estimates might be considered a valid approximation of the additional cost of producing extra feed on a farm that has been paid for, where extra land is (freely) available

for cultivation, and where the fixed recurrent expenses have been paid. If one drew an analogy to the cost of running a motor vehicle, the costs given in TABLE 8.2 are equivalent to the cost of the petrol alone. On this basis the annual consumption of 224 kg of ryegrass per reedbuck costs approximately R9,40.

On the average farm in Underberg district the total cost of Italian ryegrass pasture production, including a certain amount of interest on land acquisition and production loans, all fixed recurrent expenses etc., is approximately R80 per tonne, or twice the 'official' figures quoted in TABLE 8.2 (Barrow, agricultural financial advisor, pers. comm.). On this basis the reedbuck's annual consumption of ryegrass costs approximately R18.

Costs are clearly variable from place to place, and even between farms in the same locality. The most important variables include soil fertility (as this affects fertilisation costs), ease of access to markets/suppliers (as this affects transportation costs), and the cost of land acquisition. At 1982 prices one hectare of (dry) land in Underberg district cost R25-40 to lease, or approximately R80 in interest to buy, each year; as a percentage of estimated ryegrass production costs (TABLE 8.2) land acquisition thus adds as much as 20 % over the bill paid by a farmer who already owns the land. Reedbuck damage may thus be more financially worrying to a farmer who is trying to acquire land than to one who already owns it.

Viewed from the point of view of feed replacement costs, the most likely replacement for ryegrass lost to reedbuck would be commercially available dry concentrates. At 1982 prices the cost of such concentrates, with a 15 % protein content (approximating to that of lost ryegrass; CHAPTER FIVE), was R210 per tonne. The reedbuck's annual ryegrass consumption would thus cost approximately R47,50 when replaced with concentrates. However, since reedbuck are permanent farm residents, and not occasional visitors making unforeseen crop depredations, it should be possible to 'plan' for reedbuck losses at the time when decisions are made as to how much pasture should be planted in any particular year, in which case the costs per animal would be those of planting extra ryegrass.

Finally, the cost of maintaining reedbuck on farmland can be viewed in terms of lost agricultural production. For the sake of simplicity, I will consider only the dairying alternative, since dairy farmers are those most commonly affected by reedbuck damage. Taking a reedbuck as being equivalent to 0,1 dairy cows, the additional income which could be generated by replacing each reedbuck with dairy stock is summarised in TABLE 8.3. The dairy cow

equivalent is smaller than the direct animal unit equivalent (Mentis and Duke, 1976) because for each productive dairy cow a number of (unproductive) dry cows, heifers and calves have to be supported. The potential income from a dairy cow is based on an annual production per animal of 4 200 litres of milk sold at 34 cents per litre. Only costs directly associated with the additional cow are deducted from revenue to derive profit, as fixed recurrent costs would not change as a result of replacing reedbuck with cows in a real situation. The annual loss of profit amounts to approximately R74 per reedbuck.

TABLE 8.3: The potential annual profit from dairying if reedbuck were replaced with dairy cattle. Figures are quoted per reedbuck equivalent, where 10 reedbuck = 1 cow. (Source: Barrow, pers.comm.)

		Rands
INCOME	420 litres @ 34c	142,80
EXPENSES	Concentrates for milkers	35,70
	Concentrates for heifers	11,70
	Veterinary expenses (dips, AI, milk recording, dairy sundries)	7,00
	Milk transport and levy (@ 3,38c per litre)	14,20
PROFIT		<u>R 74,20</u>

It is possible to express the cost of damage to other crops in a similar way, and with regard to damage to the field of maize (SECTION 8.3.1.2), the 17,6 tonnes lost would cost R228 to produce if land were free and fixed recurrent expenses paid (TABLE 8.4). However, in this case it is difficult to assess how many reedbuck were responsible for the damage because they were very difficult to count within a well grown crop, and such an assessment of damage consequently becomes of very limited value because it has no general application. An estimate of the number of animals involved in this instance is given as 20, making the cost per animal R11,40; this damage was considered exceptionally severe, being far worse than any other maize damage I observed during the course of the study.

TABLE 8.4: Estimated cost of maize silage production: March 1982
 Figures quoted are for an anticipated yield of 30 t (30 % D.M.)
 silage. (extracted from: Natal Agricultural Research Bulletin 12)

	<u>Rands</u>
Machinery	89,19
Labour	23,12
Seed (20kg / ha)	20,00
Fertilizer (N - 115kg/ha; P - 40kg/ha; K - 50kg/ha)	138,94
Pesticide (Dipterex; Thiodan; Volaton)	22,64
Weedicide (Eptan; Atrazine)	50,12
Plastic sheeting	17,28
Insurance (8% of production cost)	28,23
TOTAL COSTS PER HECTARE	<u><u>R 389,52</u></u>
TOTAL COSTS PER TONNE OF 30% D.M. SILAGE	<u><u>R 12,98</u></u>

8.4.2.2 POSSIBLE INCOME FROM REEDBUCK

Reedbuck might be considered as a valuable marketable resource that can, to some extent, offset the cost of their upkeep on farmland. Several interested people have even suggested to me that they could become a competitive form of land-use. There are, in my opinion, only three realistic revenue-generating outlets for reedbuck; sale of venison, sale of live animals for translocation, and sale of hunting trophies.

There are two major constraints upon the sale of venison within Natal. The first of these is that venison is already generally available to local buyers from Natal Parks Board culling operations in the Zululand reserves; this is sold at R2 per kilogram (1982 price), where the buyer collects from the appropriate reserve, and purchases a minimum of ten carcasses. The price is approximately half that of other red meats available from the supermarket shelf. The second constraint is that carcasses are liable for veterinary inspection if they are to be sold (to, for example, a butcher) for the purposes of resale to the public, subject to the regulations of the local health committee or municipal authority. In effect this means that uncertified carcasses cannot be sold for resale within the larger municipal areas, but smaller centres are generally free of

prohibitive legislation. It is perfectly legal to sell uncertified venison directly to a municipal consumer, and herein may lie the greatest potential market.

Of the animals shot during the course of this study, approximately 50 were subsequently sold as dressed carcasses. Some of these were sold to local hotels where they realised as much as R5 per kg, while the majority were marketed direct to members of the public in the major urban centres of Durban and Pietermaritzburg, through advertisements placed in the provincial newspapers. The advertised price was R2,49 per kg for whole carcasses complete with skin and feet, delivered free to the buyer. In total 1705 kg were sold at an average R2,70 per kg. The mean dressed carcass mass was 32 kg, yielding R86 per carcass. Profit would have been considerably less than this had transport costs not been paid by the research project. In view of the venison price set by the Natal Parks Board, it is unlikely that profit from the sale of reedbuck venison could exceed an average R2,00 - 2,50 per kg. Mean dressed carcass mass could be raised from the 32 kg recorded in this study to about 40 kg if selective culling was exercised, and this would result in a mean profit per carcass of R80-100.

Using these figures it is now possible to calculate the proportion of the reedbuck living on a farm that have to be culled in order to recover the cost of their upkeep. In the previous section it was shown that, in the case of the average farm in Underberg district, the annual cost of producing extra grass to feed one reedbuck is approximately R18. Thus, if R80 is profited from the sale of an average carcass, the proportion of the population that would need to be culled to recover costs would be $18/80 = 0,225$, or 22,5%. In CHAPTER THREE it was shown that the study population's potential rate of increase was approximately 20%, from which it is clear that a sustainable yield at about this level would only serve to recover the costs of maintaining a farm's population of reedbuck, and would not yield any financial gain. Obviously, to cull any fewer than 20% of the reedbuck living on a farm would involve some financial loss.

The alternative to the sale of venison would be to sell animals for live translocation, or as hunter trophies. The cost of live capture in 1982 was approximately R73 per reedbuck (APPENDIX B), which would have to be borne by the seller/buyer. Thus, to yield profit in excess of that obtainable from the sale of the carcass as venison, the charge would have to exceed $R73 + R80 = R153$. The Natal Parks Board's price for live reedbuck in 1982 was R60 to Natal buyers, and R150 to buyers outside the province, and as there is no shortage of animals available from the Natal Parks Board, it is unlikely that a

private seller could realise a significantly higher price for his animals. Thus, on purely economic grounds, there appears to be no advantage to the private landowner in disposing of his excess animals alive, rather than dead.

The carcass value of a hunter's trophy would be around R100 if sold as venison, but a higher price could probably be realised by selling such animals to hunters as trophies. Reedbuck are commonly advertised in the South African hunting press at R200-300; such advertisements are directed at overseas clients, where the reedbuck is only one of many species offered at a particular locality with attractive facilities. Reedbuck on dairy farms in the highlands/midlands of Natal would not attract this type of client, and the local hunter is unlikely to pay more than half that fee. Nevertheless, priced at R120-150, the Natal landowner might find the option of invited hunters attractive, and this option would yield a slightly higher financial return than selling the same animal for venison.

As far as the hunter is concerned, however, reedbuck from the highlands of Natal do not generally make good trophies. The distribution of horn lengths for the Polela study population is shown in FIG. 8.4. To qualify for inclusion in Rowland Ward's records of big game, horn length must exceed 37,5 cm, and in this regard only 2 % of adult males from the study population would qualify for inclusion. A few exceptional trophies have been taken in the highlands/midlands of Natal, including a head of 47 cm that will probably be accepted as the new world record (Daly, pers. comm.), but such trophies are truly exceptional. Since even the largest farm properties in the highlands/midlands of Natal are unlikely to support more than about 30 adult male reedbuck, the chance of a hunter being able to bag a 'book' trophy on any particular property even if the landowner has had no hunters on the property previously, will be well below 1 %. Reedbuck from the Zululand lowveld appear to offer generally better trophies (pers. obs.), and for this and other reasons (CHAPTER NINE), I do not foresee any significant interest in hunting reedbuck in the highlands/midlands of Natal for commercial gain.

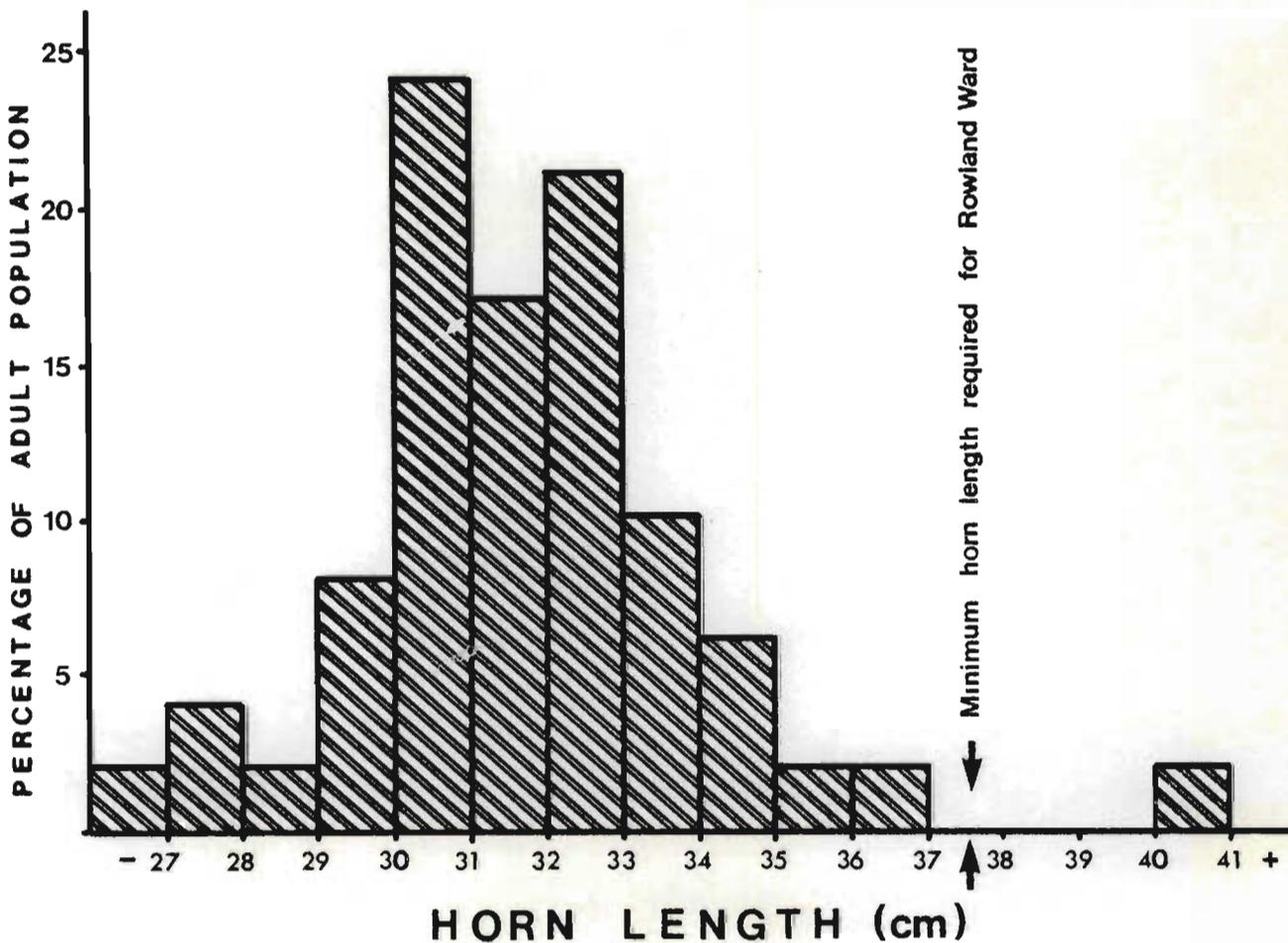
8.4.3 Control of crop damage

8.4.3.1 ANIMAL REMOVAL AS A POSSIBLE CONTROL MEASURE

In CHAPTER THREE it was shown that a 20 % removal of animals has no long-term effect on population size. The explanation for this appears to be that there are a large number of 'floating' subadults

of both sexes that are able to 'fill in' spaces where suitable habitat is left unoccupied by animal removal (CHAPTER SIX). Movement of these subadults occurs in the summer months, and so a cull early in winter is likely to be effective in reducing pasture losses during the remainder of that season, until the 'floaters' become mobile again in spring: only then will available habitat be reoccupied. It is predicted (CHAPTER THREE) that even if culling were implemented at a level significantly higher than the population's potential rate of increase, unoccupied habitat would be quickly resaturated by the 'floating' population. In the long-term, then, animal removal does not appear to offer much hope in reducing reedbeek populations on individual properties where they become a problem in winter. However, animal removal is likely to reduce damage, in proportion to the number of animals removed, for the duration of any particular winter season, when animals are culled at the start of that season.

FIG. 8.4: Horn length distribution of randomly culled adult male reedbeek from the study population



8.4.3.2 HABITAT MANIPULATION AS A POSSIBLE CONTROL MEASURE

In CHAPTER FIVE it was established beyond all doubt that the size of a population of reedbuck that is resident on a farm is directly related to the availability of low woody cover on that property. Removal of such cover reduces population size by as much as two reedbuck for each three hectares of cover. Adopted as a long-term farm management policy, it is my belief that such removal of cover is the most effective way of reedbuck crop damage control. As farming becomes more intensive on any particular farm property, destruction of cover is, in fact, inevitable, such that crop damage by reedbuck is rarely, if ever, a problem on intensively managed properties. Of course, removal of cover has its costs in terms of the loss of other (desirable) farm game, such as guinea-fowl (Numida meleagris).

From the point of view of reducing damage to susceptible crops, it should also be borne in mind that in winter reedbuck remain within about 1,5 km of their food source. The more widely dispersed such food sources are on a farm, the greater the area of potential habitat available to reedbuck, and the higher the population supported will be. Damage can be minimised simply by growing attractive food crops (grasses) within as small an area as possible, and cultivating outlying lands to less attractive crops (roots).

'Decoy' crops might be another useful means of manipulative control, where high value cash crops are involved. The planting of a ryegrass 'buffer' around susceptible crops, such as lettuce and cabbage has proved successful in protecting those crops on a farm in the midlands of Natal (Dawson, pers. comm.).

8.4.3.3 FENCING AS A POSSIBLE CONTROL MEASURE

Fencing is the normal way of controlling domestic stock movements, and has recently become increasingly important in game management. Its more important uses include the containment of game within conserved areas, controlling the spread of the diseases of man and his domestic stock, and the protection of man and his crops from wildlife depredations.

In this study only the last of these is of any importance. Since we can place a monetary value on reedbuck damage, and the likely level of damage on any particular property can be readily predicted by simply counting the number of reedbuck involved (CHAPTER THREE), a cost-benefit analysis for fence construction is straight-forward.

The costs of three types of fence are given in TABLE 8.5. A 2 m high

fence would be required to exclude reedbuck, and could be either of the 'Bonnox wire grid' type, or of an electric type, as was tested in this study. The cost of such fences is compared with that of an ordinary 5-strand cattle fence, which would typically be constructed alternatively along boundaries where access by reedbuck might be undesirable. Since a reedbuck-proof fence will also exclude domestic stock, the difference in fencing costs might be considered equivalent to the cost of excluding reedbuck, at least in situations where new land is being cultivated and a new fence would be required anyway. In such cases the additional cost of excluding reedbuck by means of a Bonnox fence is approximately R1090 per km, and by means of an electric fence, approximately R255 per km. Compared with the costs of producing the grass that would have been eaten had the fence not been constructed (i.e. R18 per animal year), R1090 is equivalent to 60,5 reedbuck-years consumption, and R255 is equivalent to 14 reedbuck-years consumption. On this basis the cost of fencing a squarish pasture of approximately 6 ha, which might otherwise support approximately fifteen reedbuck, would be recovered in one year when fenced electrically, or in approximately four years when fenced with Bonnox fencing.

TABLE 8.5: Fencing costs per kilometre (1982 prices)

Materials	FENCE TYPE		
	5-strand barbed wire cattle fence	2m high 'Bonnox' game fence	2m high permanent 5-strand power fence
	Rands	Rands	Rands
Electric fencing unit*	-	-	247,00
Insulators (500)	-	-	170,00
Accessories	-	-	20,00
Creosoted straining posts (4)	10,64	18,16	18,16
Poles/droppers	213,68	346,56	300,00
Wire	442,00	1452,00	166,50
Labour	180,00	120,00	180,00
TOTAL	<u>R 846,32</u>	<u>R 1936,72</u>	<u>R 1101,66</u>

* Such a unit will power ten kilometres of 5-strand fence, so the cost per km decreases with length of fence

However, the more likely situation is one in which a landowner has existing cattle fences, and reedbuck-proofing involves the full cost of the new fence. In such cases the Bonnox fence, at R1937 per km, would take 108 reedbuck-years to 'pay-off', and the electric fence,

at R1102 per km, 61 reedbuck-years.

The effectiveness of fencing will vary from property to property. If only some of the pastures on a property are fenced off, the likely reduction of pasture loss will be minimal, since the excluded animals will simply move to the next (unfenced) pasture, where worse damage will occur. Fencing must be an 'all' or 'nothing' decision. It will be used to greatest effect where a pasture, or block of pastures is isolated from others (and would thus attract many reedbuck), and has a low perimeter distance : area ratio, thus minimising the length of fence required.

A structural (Bonnox-type) fence is likely to require less maintenance, and be more trouble-free than an electric one. Electric fences, on the other hand, cost only about half that of equivalent structural fences, and are becoming increasingly popular with farmers throughout South Africa. The main disadvantage of electric fences is that each individual animal has to be 'trained' not to attempt to cross them, by receiving a shock. This often results in the breakage of the fence, on initial contact. Each adult reedbuck resident in the area where a fence is to be used will have to be 'trained' in this way, as will 'floating' subadults as they arrive on the farm. The fence will require constant checking and repair, if it is to be an effective deterrent. Breakages can be minimised by hanging beercans containing a little molasses at frequent intervals along the fence, to attract reedbuck to sniff at the fence and receive their first shock (Williamson, pers. comm.).

It is not my intention in this thesis to detail electric fence design and construction methods, because this is dealt with adequately in agricultural literature and commercial sales brochures (e.g. the brochures of Gallagher Electronics Ltd., P.O.Box 5324, Hamilton, New Zealand, which are widely available in South Africa). From the results of this study a 2 m high fence, with five strands spaced equally, appears to be adequate. However, for sociological reasons (CHAPTER NINE) it is unlikely that fencing of any kind will become widely used in the control of reedbuck crop damage.

Fencing, like the removal of cover, has undesirable 'side effects'. In this case, by denying reedbuck access to winter food through fence construction, reedbuck populations would no longer be maintained at artificially high levels, and the resultant loss of animals would affect potential levels of harvest, and the aesthetic benefits of maintaining strong populations of reedbuck on individual properties.

8.4.3.4 REPELLENTS AS A POSSIBLE CONTROL MEASURE

There are a number of ways of making a crop less attractive to wildlife. These include taste repellents, scent repellents and scaring devices. Most of the work in this regard was carried out in the United States of America during the late sixties and early seventies (e.g. Stanton, 1962; Carpenter, 1967; Dietz and Tigner, 1968; Marshall and Whittington, 1969), and the results of a few trials in South Africa later in the seventies (Wright and Bourquin, 1977; Schutz et al., 1978) only served to confirm the limitations of such techniques. If any technique of this nature had been even reasonably successful, one can be sure that it would have had wide appeal and general application.

The main problem seems to be that a repellent's effect is not absolute. It renders a crop only relatively less attractive. If the alternative food source is very inferior, as is highland sourveld to reedbuck in winter (CHAPTER FIVE), the effect of any repellent will be minimal. The only potential use of repellents in the control of crop damage by reedbuck is in situations where the alternative food source is only marginally inferior in the eyes of the reedbuck. Thus a high value cash crop, such as lettuce, might be successfully protected from damage by the use of repellents if, and only if, an alternative attractive foodsource (e.g. ryegrass pasture) is available close by. The repellent will then act to direct the reedbuck's attention away from the lettuce towards the (ryegrass) alternative. However, in my opinion, high value cash crops can best be protected by means of fencing, which gives absolute protection and requires little maintenance. Repellents may be washed away in rain, lose their scent, or in the case of slaughterhouse waste (a commonly-used repellent) be consumed by predators. Thus they typically require a lot of attention and maintenance to be even partially effective. There is no such thing as an inexpensive, 100 % effective, long-lasting repellent.

8.4.3.5 THE CONTROL OF CROP DAMAGE IN THE CONTEXT OF ALTERNATIVE METHODS OF IMPROVED AGRICULTURAL PRODUCTIVITY

This discussion would be incomplete without some further consideration of the primary aim of controlling reedbuck: viz. increased agricultural productivity. Whilst it has been shown that management of reedbuck can improve agricultural productivity, bigger improvements might be possible through efforts in other areas of farm management. This section simply attempts to place reedbuck control in a broader context.

Except in very exceptional circumstances, I do not believe the reedbuck to be a serious economic problem, nor even, in most cases, a cause for concern. Those who shout loudest about crop damage by reedbuck are generally those whose agricultural efficiency is lowest. In many cases the reedbuck is a useful scapegoat for farmers whose basic productivity is low as a result of poor agricultural practice.

If we consider the Polela catchment in which this study was carried out, the reedbuck represents less than 3 % of total animal units (CHAPTER ONE). If the reedbuck were totally removed there would be room for a further 3 % of domestic stock, which by all accounts represents a minimal potential improvement in agricultural productivity. To put this into its proper perspective we might compare it with natural fluctuations in productivity between years, as reflected in milk production totals in Underberg district: during the first year of this study (1981-2) 14 dairy farmers produced an average yield of 4261 litres per cow, compared to 3668 litres per cow on the same farms the following year (Barrow, pers. comm.). This represents a 14 % decline in production between years, brought about largely by differences in weather conditions, especially the availability of water.

Commercial agriculture in South Africa is a relatively new industry, and one which is rapidly improving in efficiency. It is nevertheless true that considerable scope for improvement exists. Barrow (pers. comm.) identifies three key areas of gross inefficiency in dairy farm management in Underberg district, that almost certainly apply elsewhere in Natal:

- (a) inadequate feeding; milk production is closely related to feed consumption, and where 15 kg (D.M.) of roughage per day should be provided per animal, farmers often provide only 12 kg, with a resultant reduction in milk production;
- (b) grazing management; efficient production of feed requires that it is grazed at exactly the correct height, and for the correct time (Tainton, 1981);
- (c) concentrate management; efficiency in the use of dairy concentrates to improve profitability could be improved by specific application at the start of a cow's lactation.

These are alternative methods of improving agricultural productivity that are likely to have a far greater impact on the farm budget than any amount of intensive management of reedbuck. In the context of agricultural productivity, then, it would appear that the control of

crop damage by reedbuck should remain a low priority.

8.5 CHAPTER SUMMARY

The purpose of this chapter was to quantify the damage suffered by farmer's crops that could be directly attributed to reedbuck, and evaluate possible methods of reducing such damage.

The main emphasis of crop damage assessment was the evaluation of pasture losses during the winter months from May to September. Damage was assessed by means of a standard exclusion technique, and significant losses recorded on four occasions. Despite serious limitations in methodology and data quality a best estimate of the total seasonal loss of pasture grass suffered per reedbuck was made. Approximately 0,2 t of grass were lost per animal, which, at 1982 prices cost R 18 to produce, R 47 to replace, or R 74 in lost milk production. To simply recover his costs, a farmer would have to shoot 20 % of the reedbuck on his property annually.

Crop damage can be prevented by the construction of either electric or structural fences, but this is usually not an economic proposition except in the protection of high-value cash crops. Pasture damage is best reduced temporarily by the removal of animals at the start of the winter season, and in the long term by reducing the availability of cover on the farm. Taste and scent repellents and scaring devices do not appear to be useful methods of crop damage control.

Viewed in the context of other potential improvements to agricultural efficiency, the control of reedbuck can give only marginal gains, and there would seem to be little object in pursuing such control exhaustively.

CHAPTER NINE

RESOURCE EVALUATION

9.1 INTRODUCTION

Management must have a goal, which, to be meaningful must be attainable. The formulation of attainable management goals in wildlife management follows the identification of management ideals and assessment of the extent to which a resource can fulfil those ideals. This is the process of resource evaluation.

The object of this chapter is to record the ideals of those who have an interest in the management of reedbuck on farmland in Natal, and from a synthesis of the information gathered and presented in previous chapters of this thesis, assess the extent to which those ideals are, or can be, fulfilled. Recommendations for management, which will be presented in CHAPTER TEN, can then be based on attainable goals.

9.2 MANAGEMENT IDEALS

Those with an interest in the management of reedbuck on farmland in Natal are the owners of the land, and society in general, whose interest is vested in the Natal Parks Board. Ideally, the Natal Parks Board would like to see viable populations of reedbuck throughout the province wherever suitable habitat exists, or could be restored. The ideals of this body are relatively straight-forward, and do not require further examination. Those of the landowners, however, are more complex, and require more detailed analysis.

To this end, the answers to two questionnaire surveys were used to evaluate farmer opinion. Firstly, the GAMEQUEST survey (CHAPTER TWO; APPENDIX A) included some general questions about the attitudes of the participating farmers to antelope on their farms; the relevant sections of the questionnaire are reproduced in TABLE 9.1. Secondly, a farmer opinion survey, conducted by personal interview between myself and 63 landowners in Underberg district, sought information specifically about attitudes to reedbuck in this district (TABLE 9.2). Those interviewed represent the majority of major landowners in the district, and can be considered a random sample, since only those who were not present on their farms when I visited were excluded from the survey.

TABLE 9.2: Questionnaire form used in the Underberg farmer's opinion survey

NAME:

PROPERTY:

1. What is the total area of your property ? acres/hectares.
2. How much annual pasture will you have in 1982 ?

Dryland	<input type="text"/>	Irrigated	<input type="text"/>
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3. What is the farms principle source of income ?

Beef	<input type="text"/>	Dairy	<input type="text"/>	Sheep	<input type="text"/>
Crops	<input type="text"/>	Other	<input type="text"/>		

THE FOLLOWING QUESTIONS REFER SPECIFICALLY TO COMMON REEDBUCK, AND NOT ANY OTHER KIND OF BUCK ON THE ABOVENAMED PROPERTY.

4. What is the maximum number of reedbuck you would like on your farm at any one time ?
5. What is the maximum level of losses to pastures resulting from reedbuck grazing (in terms of a percentage of production during the period 1 June to 30 September) that is tolerable ?

<input type="text"/> 0 % <input type="text"/>	<input type="text"/> 2 % <input type="text"/>	<input type="text"/> 5 % <input type="text"/>	<input type="text"/> 10 % <input type="text"/>	<input type="text"/> 20 % <input type="text"/>	<input type="text"/> 40 % <input type="text"/>
<input type="text"/> 70 % <input type="text"/>	<input type="text"/> 100 % <input type="text"/>				

6. If reedbuck were found to be reproducing at such a rate as to exceed the maximum number desirable for your property, and continued to increase at 15 % per annum, would you be inclined to dispose of this excess ? YES / NO

If yes, which of the following methods would you prefer to use in disposing of the excess. Please indicate first, second and third choice by placing a 1, 2, and 3 respectively in the three boxes you select.

- (a) Shoot them yourself, or allow your friends to shoot them for home consumption.
- (b) Invite paying hunters to shoot.
- (c) Shoot them yourself and sell the carcasses (assuming an easy market).
- (d) Ask a professional culling team to cull the excess, and pay you for the venison.
- (e) Sell them for live capture and translocation to another farmer.
- (f) Give them to the Natal Parks Board for live capture and translocation.
- (g) Fence them off your pastures, to force them elsewhere.
- (h) Apply judicious burning, destroy cover etc. to reduce survival, and encourage emigration from your farm.

7. If numbers are stable on your farm, is a 'harvest' desirable ?

How many animals would you like to 'harvest' annually ?

For what purpose would you like to 'harvest'

TABLE 9.1: Part of the GAMEQUEST survey form used to assess farmer's attitudes to antelope on their farms

<p>10 <i>What is your attitude towards antelope on your farm?</i> Put a cross in appropriate boxes; more than one may apply.</p> <p>10.1 EITHER: You resent the presence of all species on your farm, (a) and you make efforts to control them <input type="checkbox"/> (b) but you do not try to control them <input type="checkbox"/> OR: You resent the presence of certain species which cause problems on your farm, (a) and you make efforts to control them <input type="checkbox"/> (b) but you do not try to control them <input type="checkbox"/></p> <p>10.2. EITHER: You are indifferent – you don't mind their presence on your farm, but you do not value them. <input type="checkbox"/> OR: You value their presence on your farm, (a) because you enjoy having and seeing them on your land <input type="checkbox"/> (b) to provide hunting for yourself and/or your friends <input type="checkbox"/> (c) as a source of game meat for your own use <input type="checkbox"/> (d) as a source of revenue because you entertain fee – paying hunters <input type="checkbox"/> (e) as a source of revenue because you market game dead and/or alive <input type="checkbox"/></p>	<p>11 <i>If you value the presence of antelope on your farm, for whatever reason, list the species you value, in order of preference.</i></p> <table border="1" style="width: 100%; border-collapse: collapse;"> <tr> <td style="width: 50%;">1.</td> <td style="width: 50%;">4.</td> <td style="width: 10%;"></td> <td style="width: 10%;"></td> <td style="width: 10%;">Official Use</td> </tr> <tr> <td>2.</td> <td>5.</td> <td></td> <td></td> <td></td> </tr> <tr> <td>3.</td> <td>6.</td> <td></td> <td></td> <td></td> </tr> </table> <p>12 <i>Are any of the species listed in 6 a problem or potentially so?</i> <input type="checkbox"/> Yes <input type="checkbox"/> No <i>Please list the problem species, and give details of the problem.</i></p> <table border="1" style="width: 100%; border-collapse: collapse;"> <thead> <tr> <th style="width: 30%;">Problem Species</th> <th style="width: 40%;">Problem</th> <th style="width: 10%;"></th> <th style="width: 10%;"></th> <th style="width: 10%;">Official Use</th> </tr> </thead> <tbody> <tr><td>1.</td><td></td><td></td><td></td><td></td></tr> <tr><td>2.</td><td></td><td></td><td></td><td></td></tr> <tr><td>3.</td><td></td><td></td><td></td><td></td></tr> </tbody> </table> <p>13 <i>Which of the species listed in 12 above do you take steps to control, and what control methods do you use? Are these control methods successful, or only partly so?</i></p> <table border="1" style="width: 100%; border-collapse: collapse;"> <thead> <tr> <th rowspan="2" style="width: 20%;">Problem Species</th> <th rowspan="2" style="width: 20%;">Control Method</th> <th colspan="3" style="width: 20%;">Control successful?</th> <th rowspan="2" style="width: 10%;">Official Use</th> </tr> <tr> <th style="width: 5%;">Yes</th> <th style="width: 5%;">No</th> <th style="width: 10%;">Partly</th> </tr> </thead> <tbody> <tr><td>1.</td><td></td><td></td><td></td><td></td><td></td></tr> <tr><td>2.</td><td></td><td></td><td></td><td></td><td></td></tr> <tr><td>3.</td><td></td><td></td><td></td><td></td><td></td></tr> <tr><td>4.</td><td></td><td></td><td></td><td></td><td></td></tr> </tbody> </table>	1.	4.			Official Use	2.	5.				3.	6.				Problem Species	Problem			Official Use	1.					2.					3.					Problem Species	Control Method	Control successful?			Official Use	Yes	No	Partly	1.						2.						3.						4.					
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The results of the Gamequest opinion survey, expressing the opinions of farmers sampled systematically throughout the province, and questioned about attitudes to all antelope on the farm without specific reference to reedbuck, are summarised in TABLE 9.3. From the initial sample of questionnaires distributed, completed forms were returned by 63 % of

TABLE 9.3: The proportion of GAMEQUEST participants expressing different attitudes towards antelope on their farms (n=293)

Attitude	Proportion of respondents (%)
1 The farmer resents the presence of all antelope, and makes efforts to control them	0,3
2 The farmer resents the presence of all antelope, but does not attempt to control them	0,6
3 The farmer resents the presence of certain antelope species, and makes efforts to control these	3,1
4 The farmer resents the presence of certain antelope species, but does not attempt to control them	10,2
5 The farmer is indifferent to antelope on the farm	3,4
6 The farmer values antelope on the farm for aesthetic reasons	94,8
7 ' ' ' ' ' ' ' for private hunting	21,8
8 ' ' ' ' ' ' ' as a source of venison for home consumption	15,7
9 ' ' ' ' ' ' ' as a source of revenue from fee-paying hunters	3,7
10 ' ' ' ' ' ' ' as a source of revenue from game sales	4,4

potential respondents, and it is probably reasonable to assume that these respondents represent those most interested in farm game. The 37 % who did not respond may have died, sold their properties, or been too busy and/or disinterested to reply. Of the respondents, 95 % valued antelope for aesthetic reasons, 22 % for the purposes of private hunting, and 16 % as a source of venison for home consumption. The only other attitude adopted by more than (an arbitrary) 5 % of the sample questioned was one of resentment for certain species which cause problems on 13 % of farms.

With reference to these problems, the proportion of farms supporting a species on which that species is reportedly a problem was calculated. Seven species were recorded as being a problem on more than (an arbitrary) 5 % of the farms on which they occurred, as shown in TABLE 9.4. The most important 'problem' antelope on farms in Natal are, in rank order, grey duiker, common reedbuck, impala and blesbok. Reedbuck are reportedly a problem on 11 % of the farms where they occur, causing damage to planted pastures, sugar cane, maize, cabbage, seed potatoes and pineapples. Of the ten respondents answering the section about control, seven did not attempt to control the problem, one found shooting to be a successful control measure, one found 'shooting to frighten, with permit' successful, and one found chasing with dogs to be partly successful.

TABLE 9.4 : The proportion of farms on which different antelope species are reportedly a problem (GAMEQUEST results)

Species	No. of farmers reporting problems	No. of occurrence records	Problems, as a proportion of occurrences (%)
Grey duiker	29	240	12,1
Common reedbuck	12	106	11,3
Impala	4	36	11,1
Blesbok	4	40	10,0
Bushbuck	5	82	6,1
Kudu	1	17	5,9
Nyala	1	19	5,3

Section 11 of the Gamequest form (FIG. 9.1) requested respondents to list, in order of preference, the antelope species they valued on their farms. The analysis of these data provides some basis for comparing the popularity of different species. Placed in the 1st choice slot a species was given a score of six points, 2nd place a score of five points and so on down to a score of only one point for 6th place and no score for all species placed lower in the list of preferences. The total score was the sum of all

landowner's placings of that species. For each species the maximum number of points possible (the 'potential score') was six times the number of occurrence records of that species. The proportion of the potential score that was achieved by each species was calculated, and in TABLE 9.5 the species are listed in rank order of preference, derived by comparing the proportion of the potential scores realised by each species. This type of analysis clearly favours those species which occupy areas where antelope species diversity is poor; for example, where only two species are recorded on a property, both appreciated by the landowner, the least preferred species gets a score of five points, whereas in a more species rich area the least preferred species might get no score at all. With this limitation in mind, the results seem to indicate that the common reedbuck is one of the most popular antelope on farmland, second only to eland and nyala, and marginally preferable to oribi.

TABLE 9.5: Landowner's preferences for antelope on their farms (GAMEQUEST results - for derivation of scores see text)

Species	Rank position	Preference - Total Score (a)	Preference - Potential Score (b)	a/b (%)
Eland	1	22	24	92
Nyala	2	81	90	90
Common reedbuck	3	456	570	80
Oribi	4	243	306	79
Bushbuck	}	320	420	76
Kudu		64	84	76
Impala		150	198	76
Mountain reedbuck	8	198	264	75
Grey rhebuck	9	191	282	68
Blue duiker	10	80	120	67
Grey duiker	}	632	1068	59
Red duiker		32	54	59
Steenbok	13	200	354	56
Blesbok	14	109	198	55
Springbok	15	7	18	39
Suni	16	1	12	8
Klipspringer	17	0	30	0

The results of the Underberg district farmer opinion survey show that, on average, farmers would not want more than 3,7 reedbuck per km² on their farms. Dairy farmers would be slightly more tolerant than others, and would accommodate 4,6 reedbuck per km² as against 3,3 on non-dairy farms. The maximum harvest required would be 0,74 reedbuck per km² on 65 % of farms. This is equivalent to cropping 20 % of what farmers indicate as a maximum acceptable population for their farms, or, if non-harvest farms are included the required maximum crop would be 13 % of the maximum acceptable population in the district as a whole.

The 63 farmers interviewed collectively cultivate 2848 ha of dryland pasture and 1006 ha of irrigated pasture. The mean maximum acceptable level of loss of this pasture is 5,6 % of production during the period 1 June to 30 September. Production of ryegrass pasture under similar conditions at Kokstad, Natal (Bredon and Stewart, 1979) over this period amounts to 4,8 t/ha under irrigation or 3,5 t/ha under dryland conditions. Using these production figures, a maximum tolerable total loss to reedbuck for Underberg district would be $(2848 \times 3,5 \times 0,056) + (1006 \times 4,8 \times 0,056) = 829$ t. If each reedbuck consumes an estimated 0,19 t over this period (CHAPTER EIGHT), then $829/0,19 = 4360$ reedbuck can be fed without undue concern arising from loss of pasture grass on the part of the farming community. This would be equivalent to a reedbuck density of 7,1 animals per km². Comparing this figure with the maximum tolerable number of reedbuck for an average property (3,7 per km²), one might conclude that farmers are more likely to be worried by a knowledge of the number of reedbuck present on their farms than by a knowledge of the quantity of feed they consume.

In the hypothetical instance where reedbuck did become a problem, farmers were asked how they would prefer to dispose of an excess. They were also asked whether they would like to harvest reedbuck if they simply had a harvestable population, and for what purpose such harvesting would be carried out. The acceptability of the various methods of disposal was gauged by deriving an acceptability score, where a 1st choice disposal method received three points, 2nd choice two points and 3rd choice one point. For each disposal method the total number of points obtained by summing the scores given by each interviewed landowner, was taken as the acceptability score for that method. The results are presented in TABLE 9.6.

In the absence of an 'overpopulation' problem, only two methods of harvesting would be of interest to farmers in the district. They are harvesting for home consumption, which 65 % of the farmers interviewed would like to do, and harvesting to sell venison, which 11 % of those interviewed would wish to do. No farmer in the district showed any interest in other methods of disposal except if faced with an

TABLE 9.6: Acceptability of management options for the disposal of excess reedbuck: results of the Underberg farmer's opinion survey. See text for derivation of acceptability score.

Disposal method	Acceptability score	Proportion of farmers wishing to adopt method in routine harvesting (%)
Home consumption	131	65
Sale of venison	62	11
Live donation to NPB	60	0
Live sale	57	0
Trophy hunters	29	0
Professional cull	26	0
Habitat manipulation	4	0
Fencing	2	0

overpopulation problem.

When faced with an overpopulation problem home consumption would be by far the most acceptable method of disposing of an excess. If the disposable excess was too large for home consumption one of three options (sale of venison, or live disposal as a donation to the NPB, or for live sale to other landowners) would generally be taken as a second choice. Trophy hunters were not popular, probably through a 'fear of the unknown' and because of a few bad experiences by farmers in the district of wounded animals involving 'outside' hunters. Disposal of excess animals through the services of a professional culling team, if such a team existed, was equally unpopular. Very few farmers would consider habitat manipulation or fencing as viable options for reedbuck control.

By way of summary, the common reedbuck is a very popular farm game animal, but one which causes more crop damage problems than most. It is considered a problem on 11 % of the farms where it occurs. Farmers in Underberg district would not like to support more than 3,7 animals per km² on their farms, although, in terms of pasture losses, they believe they could afford what 7,1 animals per km² would consume. Even without an overpopulation problem 65 % of farmers would like to harvest 20 % of what they regard as a maximum tolerable reedbuck population on their farms for home consumption annually, and some 11 % of farmers would also sell venison. Only if faced with an overpopulation problem would farmers adopt any other means of

disposing of excess reedbuck.

9.3 STATUS

'Status' is a term that is widely used in wildlife studies, but often poorly defined; here it is used to describe a population's potential for long-term survival.

It is affected by many factors, some of which are properties of the animal itself, some properties of its environment, and some the effects of management. It is my intention in this section to review all these factors, and the effect each has on population status; most have been discussed at length in PART ONE of this thesis. Those that are amenable to management can then become the focus of specific recommendations.

9.3.1 Present distribution and abundance

The reedbuck has reportedly disappeared from 80 % of its previous range in South Africa, and is no longer naturally occurring in the Cape Province or the Orange Free State. My terms of reference were specifically to look at the situation within Natal, where the species is still widespread.

Reedbuck are widely distributed in Zululand as far south as $28^{\circ}45' S$ and as far west as $31^{\circ}15' E$. They appear to be declining in the coastal areas, but are increasing inland. They are also widely distributed throughout the highlands and midlands between $29^{\circ}00' S$ and $30^{\circ}30' S$, and east as far as $31^{\circ}00' E$. Populations in this area appear to be generally stable or increasing. In other parts of Natal there are few records of the occurrence of reedbuck, and those that are present are probably the result of introductions. A distribution map for reedbuck in Natal is given in CHAPTER TWO (FIG. 2.5).

The number of animals that an area can support is closely related to habitat suitability (CHAPTER FIVE), and animal densities throughout the reedbuck's range will vary accordingly. Within the 10 500 ha Polela study area, approximately 650 reedbuck were counted, indicating a total population in this area of about 800 animals, when account is taken of those that were not seen. This gives a density of 7,6 reedbuck per km^2 , which is very much higher than the maximum tolerable density of 4,6 reedbuck per km^2 for dairy farms (SECTION 9.2). In my experience reedbuck densities of this magnitude are not uncommon in the highlands/midlands of Natal, although an average density over the whole region would probably be less than half this because much of the land is (unsuitable) open veld.

9.3.2 Population trend and condition

There is general consensus amongst farmers surveyed by Gamequest that reedbuck populations are increasing or stable on farmland in all areas of occurrence except the Zululand lowveld. To the west of 32° 00' E reedbuck are increasing on 46 % of farms, stable on 48 % and decreasing on just 6 %, whilst to the east of this line, in the Zululand lowveld, reedbuck are increasing on 30 % of farms, stable on 10 % and decreasing on 60 % of farms.

Within the Polela study area reedbuck population size is apparently stable, having reached the area's carrying capacity. Stability is maintained through migration of subadult animals, most of which leave their birth-place, and are not replaced by immigrants.

Population condition in the Polela study area was considered to be representative of that throughout the highlands/midlands of Natal where reedbuck have access to artificial winter feed. This feed enables the animals to maintain artificially high levels of stored body reserves throughout winter, and to breed at all times of the year. Puberty is reached by the age of nine months in the male, and by twelve months in the female, and a lambing interval of just over nine months is indicated. This, together with other reproductive data is considered indicative of a population at, or close to its genetic potential as regards productivity.

9.3.3 Habitat requirements and distribution of suitable habitat

Under natural conditions the reedbuck is a denizen of wetland and early seral habitats. Such habitats provide a supply of relatively nutritious food throughout the year, and an abundance of rank herbaceous cover. These two elements are essential to the reedbuck's survival, and areas where one or other is missing will be unable to support viable populations.

In the highlands and midlands of Natal reedbuck populations probably used to be limited, until recently, by the inadequacy of their winter food supply, provided by a few scattered wetlands. However, as planted winter pastures became more widespread over the past 30 years or so, this limitation was removed and reedbuck populations increased. Today, in areas like the Polela study area, where food is now superabundant, cover has become limiting and reedbuck populations have restabilised at a new (higher) level. If the availability of cover was now increased, as indeed may be happening with the natural spread of the (exotic) bramble, I would predict a corresponding increase in reedbuck populations.

A different situation pertains in the Zululand lowveld. Here, rainfall is less markedly seasonal than in the highlands and midlands of Natal and, as a result, green food is more generally available throughout the year. Reedbuck populations have probably always been strong here. But good

rainfall and flat land also make the area suitable for agriculture, and extensive cultivation is now destroying the reedbuck's habitat and an observed decline in reedbuck numbers has resulted. This decline can be expected to continue as more land comes under cultivation in this area.

As to the future, areas that are unsuitable for extensive cultivation, where winter food is provided either naturally or through artificial planting, and where adequate herbaceous cover is provided, will remain strongholds of the reedbuck. An attempt to summarise the long-term potential for reedbuck in Natal-KwaZulu is provided by FIG. 9.1. Bioclimatic groups 5 (montane) and 8 (dry upland) have no significant long-term potential for reedbuck because winter food is inadequate. Bioclimatic group 1 (coastal lowlands) has very limited long-term potential because of the region's suitability for intensive agriculture. Even if a few reedbuck survive in this region they will be isolated, small, vulnerable populations that are hardly worthwhile to the overall conservation effort. All other bioclimatic groups in Natal have moderate to good long-term potential, and conservation efforts in these areas are most likely to yield results, and should therefore receive priority attention.

9.3.4 The causes of mortality

Little is known about the causes of reedbuck deaths. However, estimates of longevity indicate that male reedbuck live an average four years against the female's five to six years. The shorter longevity of males is attributed to a large number of deaths of young adults arising as a direct result of intraspecific combat.

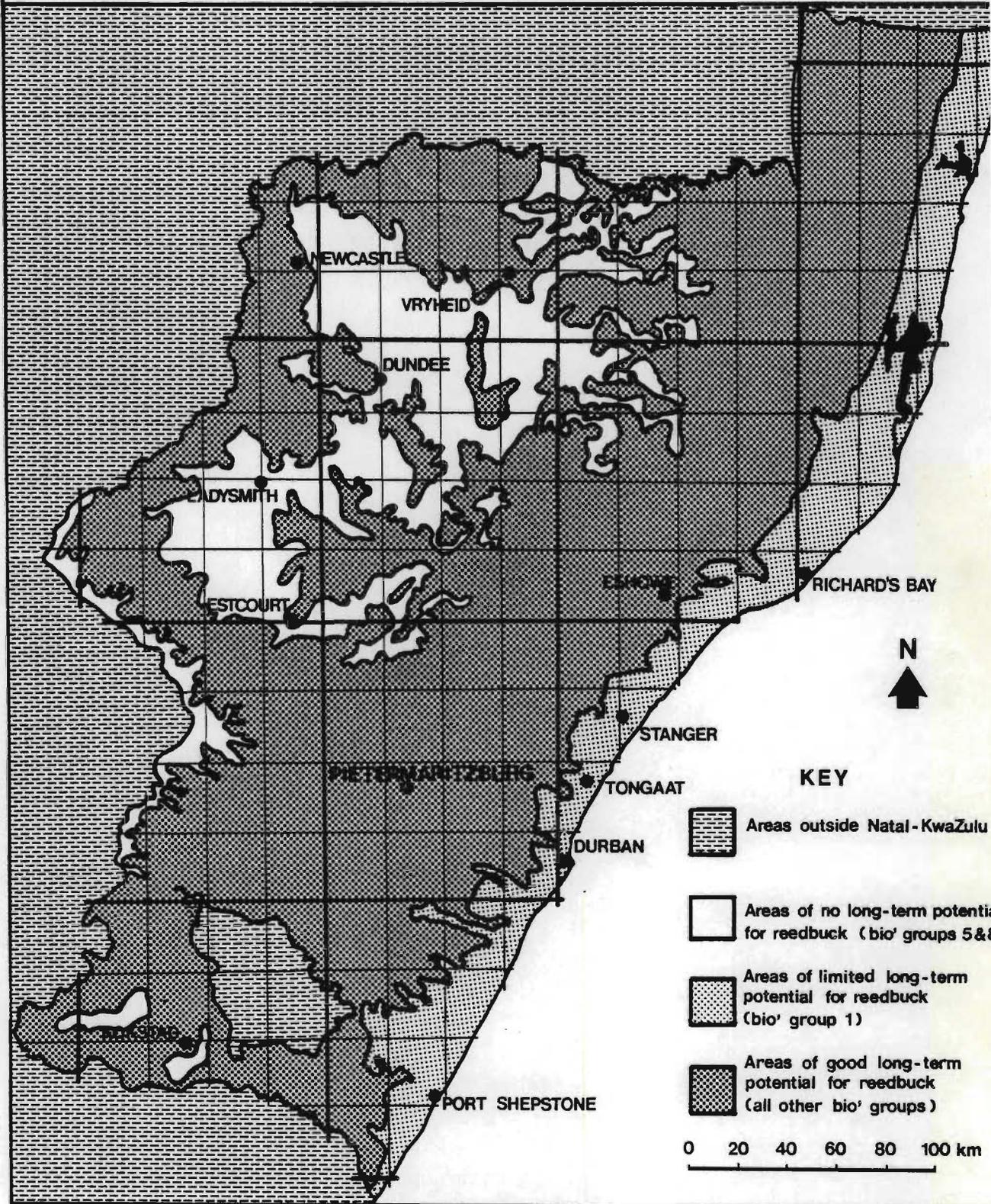
In this study most deaths where the cause was known resulted from man's activities, of which snaring and road accidents were the most important. These deaths were all reported by members of the public and probably overemphasise the importance of such mortality agents because they are obvious and emotional issues. An animal dying of more natural causes in the veld will probably seek cover, and its death go unnoticed.

9.3.5 Behaviour

The reedbuck is a typical 'hider' species, whose first means of defence is to avoid detection. It is usually crepuscular or nocturnal and spends most of each day 'lying-up' in rank herbaceous cover.

Nowhere is the reedbuck's dependence on cover more apparent than in the young animal. During the first three months of life youngsters remain concealed and isolated from conspecifics. They are visited by the mother periodically, not only to suckle, but also to enable the mother to ingest the youngster's urine and faeces, thus minimising local scent that might

FIG. 9.1: The long-term potential status of reedbuck on farmland in Natal-KwaZulu



otherwise attract the attentions of predators. For most of the time the youngster remains motionless, and it is possible for a predator to approach quite close without detecting it.

Within a month or two of giving birth the female reedbuck becomes oestrous again. Since she is nursing a newborn youngster she does not range widely at this time, remaining in the area where the youngster is concealed. The male gains access to her by establishing his territory in the same area. Cover is thus a very important component of a territory, because it is the resource that attracts the oestrous female, and provides the male with the opportunity of mating. This is the situation on farmland in the highlands and midlands of Natal, where food (in the form of artificial pastures) is superabundant, but in other areas where food is scarce, territories might be established around food resources instead of cover resources.

In general terms behavioural responses are mechanisms by which a species is able to maximise its numbers within its habitat. The reedbuck's natural habitat is a cover-abundant one, and the species' behavioural responses are largely cover-orientated. Where cover is scarce, as on farmland, such behaviours may not be advantageous. Indeed one of the greatest threats to the reedbuck's survival on farmland is its inability to escape 'predation' by domestic dogs.

9.3.6 Recolonisation potential

An important aspect to be considered in assessing an animal's status is that animal's ability to recolonise an area where it becomes locally extinct. In this regard the reedbuck can be considered a good recoloniser.

It is estimated that of the young reedbuck born in the intensive study area as many as 90 % of females and 50 % of males emigrate as subadults, and that they commonly move at least 35 km from their birth-place. This is probably an innate response, genetically programmed into a reedbuck, that naturally ensures utilisation of widely scattered 'pockets' of suitable wetland habitat.

This natural ability for recolonisation is a useful 'management tool' that can contribute greatly to the species' long-term survival on farmland. There are no areas of farmland south of 29°00'S in Natal with long-term potential for reedbuck (FIG. 9.1) that are not 'within reach' of a recolonisation source (CHAPTER TWO, FIG.2.5).

Parts of Natal to the north of 29°00'S and west of 31° 00' E have only scattered (introduced) populations of reedbuck and yet potentially suitable habitat. These areas are 'out of reach' as far as natural recolonisation from existing populations is concerned, and a need is apparent for

artificial translocation of animals to these areas.

9.3.7 Effect of crop damage control measures

The most likely crop damage control measures to be implemented in future will be a certain amount of animal removal, some habitat management, and very limited fencing operations. None of these will, in my opinion, significantly affect the status of reedbuck on farmland.

It is apparent from this study that a 20 % annual 'surplus' of animals is produced on farmland, and these animals, which would normally be displaced from suitable habitat and probably die early, will act to 'absorb' the population losses that might result from crop damage control operations. At present only 11 % of farmers consider the reedbuck to be a problem on their farms, and even if they culled significantly more than 20 % of their animals, the majority of landowners (who require a maximum average crop of 13 % p.a. (SECTION 9.2)), would continue to 'make good' the difference.

Fencing and habitat management are control options that will be adopted by only a relatively few landowners, and the effect such measures have on reedbuck numbers will thus be localised. They will serve to return reedbuck populations to more natural conditions under which fewer animals will be supported, but there is no reason to believe that a reduced population would be any less viable.

9.4 CONCLUSION

From the evidence presented in this thesis there appear to be no real areas of unresolvable conflict, either between different bodies of people with an interest in reedbuck on farmland, or between farmers and the reedbuck they support on their land.

Reedbuck populations do not increase indefinitely when provided with artificial feed on farmland, but stabilise at a level set by the availability of cover. On most farms that level is well within the farmer's tolerance. In the Polela study area, for example, 1615 ha of pasture yield 6460 tonnes of feed during the winter months June to September, while approximately 800 reedbuck in the area consume 152 tonnes, or 2,4 % of that crop. Farmers over the district as a whole say that they are prepared to lose 5,6 % of production over this period to reedbuck, and so the losses are well within their tolerance. The reedbuck is, in fact, a very popular animal on farmland, and, in the Gamequest survey ranked first in preference over all other antelope species that occur widely on farmland throughout the province.

Farmers do not require more than an average 13 % annual harvest from the

reedbuck population they say they are prepared to support, and since a 20 % 'surplus' is produced each year, this level of harvest should be readily sustainable.

These mean figures, that have led me to the conclusion that no real conflict exists, obviously reduce the legitimate views of many individual farmers to single statistics, and obscure the inherent variability in farm conditions between properties. They tell us nothing of the (real) Polela farmer whose reedbuck make up 12,5 % of animal units (AU) on his property, or of another Polela farmer who would like to harvest 50 reedbuck annually from a maximum tolerable population of 100 individuals. These are specific cases which we must be equipped to tackle, where extraordinary crop damage control measures, or harvesting strategies will be required. Some management recommendations are given in CHAPTER TEN.

CHAPTER TEN

MANAGEMENT RECOMMENDATIONS

10.1 INTRODUCTION

It is clear from preceding chapters of this thesis that the local status of reedbuck on farmland in different parts of Natal is widely different and this will call for the local application of quite diverse management strategies. In some areas the primary objective of management will be to preserve small or declining populations of reedbuck, whilst in others management will be directed at controlling populations that are considered a liability to agriculture. The recommendations that follow are made with a view to meeting the demands of all those potentially interested in reedbuck management.

10.2 MANAGEMENT GOALS

The recommended management goals for reedbuck on farmland in Natal are:

- 1 to maintain or re-establish viable populations wherever this is acceptable to the landowner;
- 2 to maximise long-term utilisation of the resource;
- 3 to minimise any conflict between reedbuck and landowner using the most cost-effective method or combination of methods.

10.3 PROPOSED PRESERVATION MEASURES

The following recommendations are made with the aim of maintaining or re-establishing viable populations of reedbuck wherever this is acceptable to the landowner, throughout Natal.

10.3.1 Legal protection

The reedbuck should remain on the statute books as a protected game species, whereby animals can only be shot legally with the Natal Parks Board's permission. The purpose of such protection is to facilitate in re-establishing reedbuck, or maintaining existing small populations in areas where their occurrence is 'threatened'. It will do little to enhance the

status of reedbuck throughout a large area of the highlands/midlands of Natal, where landowners are generally responsible custodians of wildlife and where legal protection of a 'problem' species might be seen as being 'obstructive'. In these areas permission to shoot reedbuck should be freely given (SECTION 10.4.2).

10.3.2 Translocation

If, in the future, public funds continue to be used for reedbuck translocation, I recommend that the Natal Parks Board should adopt a positive role in identifying possible sites for their reintroduction. The Board would do well to concentrate initially on establishing viable populations in northern Natal west of 31° E and north of 29° S. The following policy recommendations are made:

- 1 The Natal Parks Board should work towards establishing a network of reintroduction centres which should:
 - (a) provide the main emphasis of the reintroduction programme, and attract the highest level of subsidy;
 - (b) be established no closer than 50 km from one another, as intervening areas will be recolonised naturally by animal dispersal;
 - (c) be initiated with an input of at least 30, but not more than 100 reedbuck;
 - (d) comprise an initial introduction of adult animals only, as subadults are likely to scatter before they have a chance to breed;
 - (e) be carefully selected areas able to provide adequate natural herbaceous cover, and winter forage in the form of natural wetland vegetation and/or cultivated pastures;
 - (f) be centrally situated in an intended area of recolonisation.

In purely practical terms, farm conservancies could provide the requirements of a reintroduction centre. The landowners would share the cost of purchasing the (subsidised) breeding stock, and hence be able to buy more animals than would any individual. To encourage the establishment of effective recolonisation centres, the Natal Parks Board might consider donating one reedbuck for each one that is purchased.

- 2 Animals should not be provided at subsidised rates simply because the recipient lives in Natal. A more worthwhile criterion for subsidisation would be the animal's contribution to the extension of the species' range. Thus game-fenced properties would not qualify for subsidy, and nor would farms offering isolated pockets of

suitable habitat in areas of extensive cultivation.

- 3 To allow for initial mortalities, no translocation of fewer than 14 animals should be attempted to unfenced properties, or of fewer than seven animals to fenced properties.
- 4 Adults only should be moved, with preference shown for females, which have an 86 % chance of being pregnant (if they are moved from Lake St. Lucia), and which are unlikely to move away from the site of reintroduction. A sex ratio of 2 : 1 in favour of females is recommended.
- 5 No introductions should be made to properties with existing populations of reedbuck, or to areas within 50 km of such populations. Principles of genetic conservation should be adhered to, and where possible animals should be moved from the closest source.

10.3.3 Habitat protection

Over much of the reedbuck's range there is no need to protect wetland habitats in order to preserve populations of reedbuck because modern farming practice generally provides adequate alternative habitat opportunities for this species. The essential components of a reedbuck's habitat are year-round high quality food, and cover. Where one or other is missing, there is a need for remedial action before reedbuck can be expected to survive in an area. My recommendations for the optimisation of reedbuck habitat on farmland are:

- 1 Ensure that all parts of a property are within 1,5 km of a year-round, nutritious food supply, such as a major vlei or planted winter pasture.
- 2 Maximise the availability of cover between feeding areas, and try to ensure that no part of the farm is far from such cover. It is preferable to provide numerous small blocks of suitable cover, widely scattered around a farm, than to provide a similar area of cover in one block.
- 3 Cover is best provided by permanent rank herbaceous vegetation, approximately 1,5 m tall, with a few woody shrubs present. Maximum visibility through this vegetation at a height 0,8 to 1,0 m above the ground should not be more than 5 m, but at the same time the vegetation should not be so dense as to obstruct the reedbuck's free passage. Forest and mature plantation do not provide suitable cover for reedbuck, because little or no herbaceous understorey exists.

- 4 Try to ensure that plenty of cover is available at all times of the year. Different patches of cover should be burnt on a two-year rotation to create a mosaic of alternate burnt and unburnt habitat blocks.

10.4 PROPOSED HARVESTING MEASURES

10.4.1 Animal census technique

In the mistbelt (bioclimatic region 3; Phillips, 1973) and highland (bioclimatic region 4) regions of Natal the most reliable method of estimating reedbuck numbers is to conduct a spotlight count soon after dark in mid-winter. The recommended procedure and counting conditions are:

- 1 The count should be conducted at a time of year when naturally occurring grasses are dormant (i.e. in mid-winter), and artificially planted frost-tolerant pastures are serving as 'congregation centres' for reedbuck. June and July are good months for such counts throughout the region, but in upland areas where climatic conditions are more extreme, counts can be conducted at any time after the first frosts in May, until early September.
- 2 From a vehicle, equipped with a hand-held spotlight of at least 200 000 candlepower, search all the likely feeding areas and their surrounds. 'Likely feeding areas' are normally only pastures, but might include wetlands and firebreaks if these are green at the time of the count. Count all the reedbuck seen, and if an age and sex classification is required for harvesting (SECTION 10.4.3) use binoculars to help classify animals according to the field classification chart provided in APPENDIX D.
- 3 Ensure that all feeding areas have been searched within three hours of nightfall, or before the grass is frosted, whichever is the earlier. The count can be started half an hour after sunset, or as soon as it is completely dark.
- 4 Avoid counting on especially cold and/or windy nights when many reedbuck will seek cover, and may go unnoticed. If pastures become frosted before the count is completed, abandon the count, and try again another night.
- 5 The brightness of the moon will not affect the results of a count, and there is no need to plan a count to coincide with dark phases.
- 6 For management purposes there is no real benefit in repeating the

count in order to obtain an average figure. The single count will give an estimate of numbers that lies between two-thirds and all of those present. If an average of twelve counts were taken (at considerable extra effort), we would still only have an estimate lying between three-quarters and all of those present. In my recommendations on harvesting quotas (SECTION 10.4.3), the percentage of animals to be cropped is based on the actual number counted by this method.

There may be situations where a farmer has no spotlamp, or has no inclination to make a night pasture count as detailed above. He may prefer to rely on a reedbuck population estimate made by his farm conservancy game guards or other employees, in which case the following 'dusk count' procedure could be adopted. It should be stressed, however, that there is no real substitute for a properly conducted night pasture count, and the results of a dusk count are not very reliable. To conduct a dusk count adopt the following procedure:

- 1 The count should be made after veld burning in spring, and before regrowth becomes too rank. September, October and November are recommended months.
- 2 In planning the counts, divide the property into different 'blocks', each of which can be comfortably covered on foot in about two hours. The different blocks should be searched on consecutive days during the two hours immediately preceding nightfall, by patrolling the entire area on foot, and thoroughly searching it by scanning with binoculars from hilltops and other suitable view sites. Most of the animals counted will probably be sighted at a distance of 300 m to 1 000 m from the observer, and the best vantage point should be taken to scan the entire area at the time of sunset, when the animals are emerging from their 'lying-up' places. Counts should not be finished until it becomes too dark to see; the last minutes before dark will reveal the most animals.
- 3 Avoid counting under extreme weather conditions.
- 4 The total number of reedbuck seen in all blocks will probably represent between 40 % and 60 % of those present. In my recommendations on harvesting quotas (SECTION 10.4.3), the proportion of animals to be cropped is based on an estimate of population size derived as twice the number counted by this method. There is a lot of natural variation in the number of reedbuck that can be seen in the same area on different days, and it would therefore be advantageous to make several counts and take an average figure as the estimate. If the object of counting is to see whether there is a

change in the number of reedbuck present on a farm over a period of years, an average of eight counts each year would enable one to detect any change in numbers exceeding about 25 % of the original population. If only one count is made each year, however, the change in numbers would have to exceed 40 % before one could be reasonably certain that the difference between the two counts was not due to the inexactitudes of the counting method. This level of accuracy may be adequate for long-term monitoring purposes, as it would enable an annual increase of 15 % over three years to be detected by simply making an appropriate dusk count at three-year intervals.

10.4.2 Harvesting quotas

Harvesting quotas must be decided upon according to particular local conditions in an intended area of animal removal. The decision of how many animals to shoot will normally rest with the Natal Parks Board zone officer. His decision should be based on the following recommendations:

- 1 All farmland to the east of 31°20'E in northeastern Natal, between 29°00'S and 30°15'S in the midland/highland regions, and throughout Ixopo and Unzinto magisterial districts should be considered as a 'safe utilisation zone'. Here, the following recommendations pertain to harvesting:
 - (a) Harvesting should be encouraged, so as to enhance the value of the reedbuck resource on farmland.
 - (b) On receipt of an application to shoot reedbuck the zone officer should not make a farm visit (as he frequently does under present policy); this serves only to waste his time and the Board's money.
 - (c) In situations where a count has been made by the landowner, an annual quota equivalent to 20 % of the estimated number of reedbuck present should be routinely made.
 - (d) In situations where no count has been made, an annual quota should be set at 20 % of the population size estimated by the zone officer. In the midland/highland regions he will not go far wrong by estimating population densities of five reedbuck/km² on farms where dairying is the principal income, and three reedbuck/km² on other farms. This is a very rough guide, and if a landowner feels the quota derived for his property in this way is too small, he should be encouraged to make a count of his animals so that a more realistic one can be set.
 - (e) In situations where a landowner is interested in maximising his yield, and is prepared to count and classify his animals by means of a night pasture count (SECTION 10.4.1), an annual

harvesting quota of 30 % of the number of reedback counted should be made. The quota permit should specify that animals are to be removed in the ratio of two males to each female (SECTION 10.4.3).

- (f) In situations where a landowner has a genuine 'overpopulation' problem, a 40 % harvesting quota should be granted (SECTION 10.5.1). A genuine problem exists only if one or both of the following applies:
- (i) the estimated number of reedback animal units (AU) exceeds 5 % of the total domestic stock complement of the farm. To make the necessary calculation consider seven sheep or five reedback as equivalent to one animal unit.
 - (ii) the estimated number of reedback is likely to consume more than 5 % of the total amount of pasture grass produced on a farm during the months June to September inclusive. To aid in this assessment use a figure of 0,8 reedback per hectare of pasture as the maximum tolerable, or refer to TABLE 10.1 which lists the number of reedback that should be tolerable on farms with given areas of planted ryegrass pastures.

TABLE 10.1: The maximum number of reedback that should be tolerable to farmers with given areas of ryegrass pasture. Figures are based on a maximum tolerable loss of 5 % of production over the period June to September inclusive.

Pasture area (ha)	Maximum tolerable reedback population
2	2
5	4
10	8
25	20
50	40
100	80

- 2 The remainder of the province (i.e. all areas except those stated in 1 above) should be considered a 'preservation zone'. Harvesting should be discouraged, and where applications to shoot are made the zone officer should visit the property, conduct a night (or dusk) count, and set a quota representing 10 % of the estimated population. In the case of reintroduced animals, no permission to shoot should be

granted within a minimum period of five years from the date of reintroduction.

10.4.3 Animal removal procedure

Unlike many bushveld animals that are often difficult to harvest because they occupy terrain that is largely inaccessible, the reedbuck is very easily exploited on farmland. The most cost and time-efficient way of removing animals is to shoot them from a truck at night, with the aid of a powerful spotlight and medium calibre rifle. The procedure adopted is, however, largely a matter of personal preference. Many people derive great pleasure from a daytime hunt, whereby the reedbuck provides recreational as well as material benefit, and in such cases, this method of removal should obviously be encouraged.

The best time of year to remove reedbuck is probably in late May or June. Shooting at this time will not only reduce the size of the population that has to be fed over winter, but also minimise the chance of shooting a ewe leaving a dependent lamb. Weather conditions at this time of year are also right for making biltong (dried meat).

In deciding which animals to shoot, the landowner must decide whether he is trying to maximise his yield, or simply remove a small surplus of animals. If the latter applies, shooting animals at random will be least disruptive to normal social inter-relations, and provided the sustainable yield is not exceeded, will not permanently affect population size. Under most circumstances a random cull is recommended.

Where a farmer wishes to maximise his yield, however, a selective cull will be necessary. In principal, maximising a population's yield involves culling as many unproductive animals as possible, and minimising the number of natural deaths suffered by a population. In order to achieve this for reedbuck, the following recommendations are made:

- 1 Cull subadults of both sexes heavily; most would otherwise be lost through emigration. A 50 % cull of this age class is recommended.
- 2 Cull young adult males heavily; about half the three year old males in a population would otherwise die (mostly as a result of fighting) before they reached four years of age. A 50 % cull of this age and sex class is recommended.
- 3 Cull adult males and adult females moderately, so that few animals reach old age and die of natural causes. A 20 % annual crop of these age and sex classes is recommended.

- 4 Adjust the adult sex ratio to one male to two females. In doing this avoid over-shooting solitary adult males which are probably the fittest, most reproductively active, territorial animals. Remember that an adult male's home range is only about 80 ha, and ensure that enough males remain to cover receptive females wherever they happen to be on the property.

A model population, yielding a 32 % annual crop is described in TABLE 10.2. By increasing the proportion of adult females in the population to 40 %, a theoretical annual crop of lambs (using the observed lambing rate of 1,3 lambs per annum) would be 52 % the size of the 'parent' population. Thus a 32 % yield provides for considerable 'natural wastage'.

TABLE 10.2 : The number of animals in different age and sex classes of a reedback population managed to maximise yield. Pre and post-harvest numbers in each class are given, as are the numbers of animals to be removed from each class to give a 32 % annual yield.

Age and sex class	Pre-harvest numbers (assuming previous sex ratio adjustment)	Cull Numbers	(%)	Post-harvest numbers
Adult female (> 1 yr)	40	8	(20)	32
Adult male (> 4 yrs)	20	4	(20)	16
Subadult male (1-4 yrs)	10	5	(50)	5
Youngsters (< 1 yr)	30	15	(50)	15
TOTAL	<u>100</u>	<u>32</u>		<u>68</u>

10.4.4 Marketing

Farms that support reedback are generally relatively small landholdings, supporting low populations of reedback with potential to produce only modest surpluses of animals for marketing. Marketing must therefore be carried out locally, and my recommendations are that individual landowners should explore the following possible markets:

- 1 hotels and restaurants (such markets offer the best available prices);
- 2 members of the public (through press advertisements);

- 3 local butchers (subject to the regulations of the local health committee or municipal authority).

Venison is a very marketable commodity, and it should be possible to sell it at prices no lower than the current 'floor price' for beef or mutton. A cooperative marketing system between neighbouring farmers and/or members of the same game conservancy might be beneficial, as it would enable that cooperative to enter into contract with local hotels etc. to supply a regular quota which a single landowner would be unable to do by virtue of the large quantity of venison that may be required.

10.5 PROPOSED CONTROL MEASURES

If a genuine crop damage problem exists, as defined in SECTION 10.4.2, the following control measures are recommended:

10.5.1 Control of animal numbers

As a short-term ameliorative procedure to control pasture damage, up to 40 % of the estimated reedbuck population should be removed at the start of winter. Although this exceeds the population's sustainable yield, it is unlikely to have a long-term effect on a farm's population size, since increased immigration will probably result. The high yield of animals from such a control programme would provide the farmer with a 100 % profit on the cost of producing grass to feed his population of reedbuck, and this is seen as adequate compensation. The immigrants that come to 'fill in' during the following summer will be surplus subadult animals from other farms, and there would be no cause for concern at repeating a 40 % removal each year, providing census demonstrates that reedbuck remain a problem on the farm, as defined in SECTION 10.4.2.

Damage to cash crops can be effectively controlled with fencing, and excessive animal removal as described above is not recommended in this case. Rather, a sustainable yield should be taken.

10.5.2 Fencing

Fencing is recommended only where its cost is justified. This will normally apply to the protection of high value cash crops, but it may also be economic to protect isolated pastures that would otherwise attract large numbers of reedbuck. Each specific problem must be evaluated by considering the costs of the crop damage suffered in the absence of fencing, and the costs of preventing such damage. In the case of pasture protection, fencing is not recommended unless each kilometre of electric fence prevents a minimum 60 reedbuck-years of damage, and each kilometre of 'bonnox' fence, 110 reedbuck-years of damage.

10.5.3 Habitat manipulation

The following are recommended procedures for minimising crop damage:

- 1 Destroy cover - each three hectares may support two reedbuck.
- 2 Concentrate attractive crops (such as pastures) into the smallest possible area of the farm - thus minimising the 'catchment area' from which reedbuck are drawn.
- 3 Grow crops that are unpalatable to reedbuck (such as root crops), in the most vulnerable lands.
- 4 Graze the most vulnerable pastures (those next to cover) first, and if possible prolong the presence of domestic stock in these lands - reedbuck prefer not to feed on 'disturbed' pastures.
- 5 In the case of a valuable crop that suffers some damage, but not enough to warrant the construction of a fence, plant a 5 m wide strip of ryegrass around it, to divert the reedbucks' attention.

10.6 PROPOSED RESEARCH AND EXTENSION WORK

Although our knowledge of the biology of the reedbuck is far from complete, sufficient is now known to permit sound, informed management. Faced with limited financial resources, it would seem unwise to embark on further reedbuck research at this stage, when other conservation priorities require attention. However, I see two areas of research that would be beneficial to the long term status of reedbuck on farmland in Natal:

- 1 The identification of suitable sites for the establishment of reintroduction centres. This research would preferably be undertaken by somebody with a thorough knowledge of the province, using the criteria listed in SECTION 10.3.2 as a guide.
- 2 Ongoing monitoring of progress with the reintroduction programme, enabling a frequent review of priorities. This should be an integral part of zone officer duties, involving at least one farm visit every other year to count and classify the introduced animals and their progeny.

The importance of extension work to promote and publicise the recommendations embodied in this thesis cannot be over-emphasised because they are of direct relevance to approximately 8 700 landowners, who collectively control 60 % of the province's land area. The impact of such extension work could be enhanced by:

- 1 Equipping each zone in the highlands/midlands of Natal with two spotlamps, one for the exclusive use of the zone officer, and the other specifically for loan to farmers wishing to count their reedbuck at night. This is a good way of promoting interest, as was demonstrated in the Polela study area where several farmers bought their own lamps after going out to count reedbuck with me.
- 2 Printing a short guide to reedbuck management to be made widely available to farmers.
- 3 Promoting the reedbuck as a 'model' game conservancy animal that can flourish under correct management, and yield good aesthetic, recreational and material returns. The reedbuck is an ideal candidate for such promotion because a good deal is now known about it, it is indigenous and widespread, popular, easily seen, provides excellent eating and is easily managed. Furthermore the habitat requirements of reedbuck are shared by many other farm game species which would benefit from farm management aimed at improving conditions for reedbuck.

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APPENDIX A :

**Questionnaire form used in the GAMEQUEST
postal survey**

10

Wat is u houding teenoor wildsbokke op u plaas?
Trek kruisies in die toepaslike blokkies; meer as een kan van toepassing wees.

- 10.1. ÒF:
U is teen die aanwesigheid van alle spesies op u plaas gekant,
(a) en u wend pogings aan om hulle te bekamp, of
(b) u probeer nie om hulle te bekamp nie.
ÒF:
U is gekant teen die aanwesigheid van sekere spesies wat probleme op u plaas veroorsaak (sien 8 hieronder)
(a) en u wend pogings aan om dié wildsoorte te bekamp, of
(b) u probeer nie om hulle te bekamp nie.
- 10.2. ÒF:
Dit traak u nie – u gee nie om dat hulle op u plaas is nie maar u waardeer hulle nie.
ÒF:
U waardeer hul aanwesigheid op u plaas
(a) omdat u dit geniet om hulle op u grond te hê en te sien
(b) om jag vir u en/of vriende te voorsien
(c) as 'n bron van wildsvleis vir u eie gebruik
(d) as 'n bron van inkomste omdat u betalende jagters onthaal
(e) as 'n bron van inkomste omdat u dooie en/of lewende wild verkoop.

11

Indien u die aanwesigheid van wildsbokke op u plaas om watter rede ook al waardeer, noem die spesies wat u waardeer in volgorde van voorkeur.

		Vir Ampelike Gebruik
1.	4.	<input type="checkbox"/>
2.	5.	<input type="checkbox"/>
3.	6.	<input type="checkbox"/>

12

Lewer van die spesies wat in 6 ingelys is, 'n probleem of 'n moontlike probleem op? Noem asseblief die probleemspesie en verstrekk besonderhede van die probleem.

J A N E E

Probleemspesie	Probleem	Vir Ampelike Gebruik
1.		<input type="checkbox"/>
2.		<input type="checkbox"/>
3.		<input type="checkbox"/>

13

Watter van die spesies in 12 hierbo genoem, probeer u om te bekamp en watter bestrydingsmetodes gebruik u? Is hierdie bestrydingsmetodes suksesvol, of net gedeeltelik suksesvol?

Probleemspesie	Bestrydingsmetode	Bestryding suksesvol?			Vir Ampelike Gebruik
		Ja	Nee	Gedeeltelik	
1.		<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
2.		<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
3.		<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
4.		<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

14

Lees die lys habitatoorte hieronder, meld naastenby hoe groot elke tipe op u plaas is en die getal 'blokkie' van elke habitatoort. 'n Blok is 'n ononderbroke stuk grond wat in een van die habitatsklasse val: 'habitatsblokke' word nie deur heinings afgemerk nie, want daar kan, byvoorbeeld, landerye weerskante van 'n heining wees en dus kan een 'blok' landerye in 'n aantal verskillende kampe onderverdeel wees.

Habitatoort	Definisie	Oppervlakte	Getal 'blokke'
101 Landerye	Gebiede wat jaarliks of meer dikwels bebou word, en permanente weivelde.	<input type="checkbox"/>	<input type="checkbox"/>
102 Ou landerye	Gebiede wat binne die afgelope tien jaar geploeg is maar minstens twee jaar lank nie bebou is nie, met uitsluiting van permanente weivelde.	<input type="checkbox"/>	<input type="checkbox"/>
103 Plantasies	Uitheimse bome (bv. wattelbome, gombome, pynbome, populierbome) wat opsetlik geplant is.	<input type="checkbox"/>	<input type="checkbox"/>
104 Vrywilligers	Stukke uitheimse plante (bv. wattelbome, gombome, pynbome, populierbome) wat nie opsetlik geplant is nie.	<input type="checkbox"/>	<input type="checkbox"/>
105 Uitheimse ruigtes	Kolle doringrige uitheimse onkruid (bv. braambos).	<input type="checkbox"/>	<input type="checkbox"/>
106 Water (damme, riviere)	Oop waters.	<input type="checkbox"/>	<input type="checkbox"/>
107 Waterige streke (vleie)	Nat grond of grond met seisoensoorstromings; gras, riete en waterbiesies is opvallend.	<input type="checkbox"/>	<input type="checkbox"/>
108 Oewerstruikgewas	Inheimse bome en struik van minder as 4 m hoog wat langs riviere en spruite groei, met gras daar onder.	<input type="checkbox"/>	<input type="checkbox"/>
109 Rivierwoud	Hoë bome in 'n smal strook langs groot riviere.	<input type="checkbox"/>	<input type="checkbox"/>
110 Inheimse woud	Geil groot blaarryke bome met blaardakke wat oormekaar gryp en/of mekaar raak. Grasdekking swak of afwesig.	<input type="checkbox"/>	<input type="checkbox"/>
111 Doringveld-bosland	Talryke inheimse bome met gras daar onder, wat in die gebiede met laer reënval voorkom.	<input type="checkbox"/>	<input type="checkbox"/>
112 Doringveldruigte	Ruie, ondeurdringbare, dikwels, doringrige plantegroei, minder as 4 m hoog.	<input type="checkbox"/>	<input type="checkbox"/>
113 Bos- (doringveld-) grasveld	Grasveld met inheimse bome en struik hier en daar	<input type="checkbox"/>	<input type="checkbox"/>
114 Veldhooi-grasveld	Onbeweide gebiede waar veldhooi jaarliks gesny word.	<input type="checkbox"/>	<input type="checkbox"/>
115 Plat droë grasveld	Plat of sag golwende natuurlike grasveld.	<input type="checkbox"/>	<input type="checkbox"/>
116 Skuins droë grasveld	Skielik golwende of steil natuurlike grasveld.	<input type="checkbox"/>	<input type="checkbox"/>
117 Geboue, paaie, ens. Ander (Noem asseblief)		<input type="checkbox"/>	<input type="checkbox"/>
TOTAAL	MAAK ASSEBLIEF SEKER DAT DIE GEBIEDE OP DIE TOTAAL IN DEEL 4 UITKOM	<input type="checkbox"/>	<input type="checkbox"/>

15

Dui die brandstelsel aan wat op u plaas gebruik word, deur 'n kruisie in die toepaslike blokkie te trek.

- Algehele afbrand van natuurlike grasveld,
 Algehele jaarlikse afbrand, met een of meer gebiede van minstens 1 hektaar natuurlike grasveld wat elke jaar onafgebrand gelaat word.
 Algehele afbrand elke tweede of derde jaar.
 Beurtelinge afbrand waar minstens 1/2 van die natuurlike grasveld elke jaar onafgebrand gelaat word.
 Ander; noem asseblief

Beskerm u u vleie teen brand?

J a N ee

10 What is your attitude towards antelope on your farm?
Put a cross in appropriate boxes; more than one may apply.

10.1 EITHER:
You resent the presence of **all** species on your farm,
(a) and you make efforts to control them
(b) but you do not try to control them
OR:
You resent the presence of **certain** species which cause problems on your farm,
(a) and you make efforts to control them
(b) but you do not try to control them

10.2. EITHER:
You are indifferent – you don't mind their presence on your farm, but you do not value them.
OR:
You value their presence on your farm,
(a) because you enjoy having and seeing them on your land
(b) to provide hunting for yourself and/or your friends
(c) as a source of game meat for your own use
(d) as a source of revenue because you entertain fee – paying hunters
(e) as a source of revenue because you market game dead and/or alive

11 If you value the presence of antelope on your farm, for whatever reason, list the species you value, in order of preference.

		Official	Use
1.	4.		
2.	5.		
3.	6.		

12 Are any of the species listed in 6 a problem or potentially so? Yes No
Please list the problem species, and give details of the problem.

Problem Species	Problem	Official	Use
1.			
2.			
3.			

13 Which of the species listed in 12 above do you take steps to control, and what control methods do you use? Are these control methods successful, or only partly so?

Problem Species	Control Method	Control successful?			Official	Use
		Yes	No	Partly		
1.						
2.						
3.						
4.						

14 Check through the list of habitat types below, give the approximate area of each type on your farm, and the number of 'blocks' of each habitat type. A block is any unbroken area of land that falls into one of the habitat categories: fences do not delineate habitat 'blocks' because, for example, there may be cultivated land on both sides of a fence and so one 'block' of cultivated land may be subdivided into a number of different fields.

	Habitat type	Definition	Area	No. of 'blocks'
101	Cultivation	Areas under annual or more frequent cultivation, and permanent pastures	<input type="checkbox"/>	<input type="checkbox"/>
102	Old cultivated lands	Areas ploughed within the last ten years but not cultivated for at least two years, excluding permanent pastures.	<input type="checkbox"/>	<input type="checkbox"/>
103	Plantation	Deliberately planted exotic trees (e.g. wattles, gums, pines, poplars)	<input type="checkbox"/>	<input type="checkbox"/>
104	Volunteers	Stands of exotic plants (e.g. wattles, gums, pines, poplars), not deliberately planted.	<input type="checkbox"/>	<input type="checkbox"/>
105	Exotic thickets	Patches of thorny exotic weeds (e.g. bramble)	<input type="checkbox"/>	<input type="checkbox"/>
106	Aquatic (Dams, Rivers)	Areas of open water.	<input type="checkbox"/>	<input type="checkbox"/>
107	Wetlands (Vleis)	Moist or seasonally flooded ground; grass, reed and sedge sp. prominent.	<input type="checkbox"/>	<input type="checkbox"/>
108	Riverine scrub	Indigenous trees and shrubs less than 4m high occurring along rivers and streams, with a grass understorey.	<input type="checkbox"/>	<input type="checkbox"/>
109	Riverine forest	Tall trees occurring in a narrow belt along major rivers.	<input type="checkbox"/>	<input type="checkbox"/>
110	Indigenous forest	Luxuriant, tall leafy trees with canopies overlapping and/or touching. Grass cover poor or absent.	<input type="checkbox"/>	<input type="checkbox"/>
111	Thomveld woodland	Numerous indigenous trees with a grass understorey, occurring in the lower rainfall areas.	<input type="checkbox"/>	<input type="checkbox"/>
112	Thomveld thicket	Dense, impenetrable, often thorny, growth, less than 4m high.	<input type="checkbox"/>	<input type="checkbox"/>
113	Wooded (Thomveld) Grassland	Grassland with occasional scattered indigenous trees and shrubs	<input type="checkbox"/>	<input type="checkbox"/>
114	Veld hay grassland	Areas ungrazed and mown annually for veld hay.	<input type="checkbox"/>	<input type="checkbox"/>
115	Flat dry grassland	Flat or gently undulating natural grasslands.	<input type="checkbox"/>	<input type="checkbox"/>
116	Sloping dry grassland	Abruptly undulating or steeply sloping natural grasslands.	<input type="checkbox"/>	<input type="checkbox"/>
117	Buildings, Roads, etc.		<input type="checkbox"/>	<input type="checkbox"/>
	OTHER (Please specify)		<input type="checkbox"/>	<input type="checkbox"/>
	TOTAL	PLEASE CHECK THAT THE AREAS ADD TO THE TOTAL GIVEN IN SECTION 4.	<input type="checkbox"/>	<input type="checkbox"/>

15 Indicate with a cross in the appropriate box the burning regime adopted on your farm.

Total annual burn of natural grasslands.

Total annual burn, with one or more areas of at least 1 hectare of natural grasslands left unburnt each year

Total burn every second or third year

Rotational burn where at least 1/3 of natural grasslands are left unburnt each year

Other (please specify)

Do you protect your vleis from fire?

Yes No

APPENDIX B: Paper submitted to Lammergeyer

RATIONALISING THE TRANSLOCATION OF REEDBUCK

P C Howard
Institute of Natural Resources

INTRODUCTION

During the decade of the nineteen seventies, there was a rapid increase in the number of common reedbuck Redunca arundinum on the Eastern Shores of Lake St Lucia in the Zululand lowveld. Fears were expressed that, in the absence of intervention, a population crash such as occurred in the Kyle National Park (Ferrar and Kerr, 1971) could occur here as carrying capacity was exceeded. Accordingly, a research project was initiated in 1976 to investigate the problem and make recommendations for subsequent management. Intervention was considered desirable, and recommendations made (Venter, 1979) that animals should in the first case, be removed live for translocation, and that any further excess be culled.

Reedbuck were first moved live from the Eastern Shores in 1978, and more have been translocated each year subsequently (Fig. 1). By the end of 1982, a total of 1500 reedbuck had been moved live to other conservation areas (23 % of the total), or private land (77 %) in all four provinces of South Africa and Swaziland (Fig. 2 and Fig. 3).

The purpose of this paper is to review what has already been achieved by this programme, and consider what future direction it should take, with specific reference to the following:

- 1 Is the translocation programme creating viable breeding nuclei of reedbuck at the point of introduction ?
- 2 Is the translocation programme being carried out in the most efficient way ?
- 3 What are the short and long-term goals of the programme and to what extent are these goals best achieved by the present translocation programme ?
- 4 Is the cost of the programme justified by the results achieved ?

METHODS

The level of success achieved in the translocation of reedbuck was assessed by means of a questionnaire survey mailed to 74 recipient land owners/managers. These represented all recipients of breeding stock, but excluded recipients of trophy males. A limited number of farm visits, including spotlight searches of each property at night, was carried out by the author in August 1982, as a check against the answers given in the questionnaire.

The questionnaire requested the following information:

- 1 the number of reedbuck of each sex received each year, and the number of these that were still alive two weeks after their introduction;
- 2 whether there were any reedbuck on the farm before the introduction;
- 3 details of any subsequent mortalities;
- 4 an estimate of present population size;
- 5 details of any infants seen, or other evidence of breeding;
- 6 details of any of the introduced reedbuck scattering to neighbouring farms.

This sub-project formed part of a broader study of reedbuck management on farmland, and reference is made to some of the findings of this research (Howard, in prep.).

RESULTS

A total of 48 questionnaires was completed, 27 from Natal respondents, and 21 from outside the Province. Seven follow-up farm visits were made by the author. Of the 48 properties surveyed, 19 % had populations of reedbuck present before the translocation of stock from St Lucia. Forty six percent of respondents volunteered the information that their properties were game-fenced, and of the remaining 54 %, 46 % cited evidence that at least some of the introduced reedbuck had scattered.

Initial mortality, suffered within two weeks of the animals being offloaded, averaged 24 % for males and 26 % for females: the difference between the sexes being insignificant ($p > 0,1$; student's t-test). Average mortality rates appeared to vary between years (Table 1), but the differences were not statistically significant, because of the high level of variability. The apparent trend was for progressively higher initial loss of animals in translocations made progressively later in the winter.

For each property a mean annual rate of population increase was calculated,

expressed as a percentage of the breeding nucleus remaining after the initial two week-period, using the respondents estimate of present population size. Rate of increase was then examined in relation to the size of the nucleus, and the results are illustrated in FIG. 4. No clear relationship exists, either for fenced or unfenced properties, but the following observations are of value:

- 1 the mean rate of population increase on fenced properties was 6 % p.a., compared with a value of -2,1 % on unfenced properties (variation is considerable and these rates are not significantly different: student's t-test, $p > 0,1$);
- 2 in cases where ten or fewer animals were introduced, the population declined on six out of nine unfenced properties, but on only three of nine fenced properties;
- 3 where the introduced nucleus comprised more than ten, but fewer than 25 animals, seven of the eight introductions resulted in an increasing population;
- 4 with an established nucleus of 25 or more animals, all five introductions declined to some extent.

DISCUSSION

Because the first translocations of reedbuck were made only five years ago, and only 48 respondents participated in the questionnaire survey, the results of this investigation must be considered preliminary. However, the results do give some indication of the level of success achieved by the translocation programme so far, and cognizance should be taken of these in future conservation planning. In this discussion, I return to the four questions posed in the introduction.

- 1 Is the translocation programme creating viable breeding nuclei of reedbuck at the points of introduction ?

It is really too early to answer this question with any degree of confidence. The success achieved by any particular introduction depends on a multitude of factors, the more important of which include the number of animals moved, their age and sex, and the suitability of the habitat to which they are moved. Because the number of introductions monitored is small it has been impossible to isolate the effects of particular variables. However, the survey has revealed that:

- (a) The number of animals introduced to an unfenced property should exceed ten, if the introduction is to stand a reasonable chance of success. Since, on average 25 % of the animals will die as a result of being moved,

this effectively means that a minimum number of 14 reedbuck should be offloaded at any particular site of introduction.

- (b) Almost half the unfenced properties surveyed lost some of their introduced reedbuck when the animals moved away from the site of introduction. Research (Howard, in prep.) indicates that this 'scattering' is a common behaviour in young non-breeding animals, especially prevalent amongst females. It is suggested that this loss of animals could be largely avoided if only sexually mature animals were moved. In this regard, it is also worth noting that 86 % of adult female reedbuck from St. Lucia are pregnant (Venter, 1979) and that when these animals are introduced they should give birth within the 233 day gestation period, to enhance further the possibility of an introduction being successful.
- (c) The suitability of the habitat at the site of introduction is obviously important to the success of a translocation. The reedbuck, as its name implies, is commonly associated with wetlands, since here it is able to find, amongst other things, a supply of adequate food even in the driest months of the year. For logistical reasons, reedbuck have to be captured at St Lucia during the dry months, and it is therefore essential that an adequate supply of green food is available at the site of introduction. If none is naturally available, it might be supplied artificially by planting ryegrass or similar pastures. Several questionnaire respondents noted that many of their introduced reedbuck had died as a direct result of 'the drought'.

It is not possible at this stage to answer the question of whether viable breeding nuclei are being established, further than making the above remarks. It is my opinion, based on the seven farm visits, that landowners tend to be over-optimistic about the success of the introductions. There were several cases of introduced (pregnant) animals giving birth the year after their introduction, but not subsequently, and only time will tell whether the progeny of these pregnant animals will create a viable nucleus.

- 2 Is the translocation programme being carried out in the most efficient way ?

This question is concerned with the logistics of capture and transportation. An average 25 % initial mortality has been noted, and my purpose is to consider whether this figure can be reduced. Little can be done to reduce capture trauma, and transportation injuries have been minimised by individual crating of animals. We might predict that the number of animals that are able to withstand these physical injuries, psychological trauma and the change of habitat and diet will be related to their general condition as defined by Hanks (1981). If we assume a decline in condition during winter, then there is some evidence to suggest that mortality is indeed higher amongst animals that are

moved in poor condition, at the end of winter. Translocations made in April (1980 and 1981) suffered an average 18-19 % mortality, compared to those made in June (1978) with 26 % mortality, July/August (1982) with 30 % and September (1979) with 36 % mortality. To support this further, two post-translocation mortalities were examined by the author on a farm in Natal in August 1982, and in both cases the animals concerned were in a weakened condition with very low visceral and bone marrow fat reserves.

Where possible, then, translocations should be undertaken when the animals have their greatest chance of survival, which appears to be at the end of summer.

- 3 What are the short and long-term goals of the programme, and to what extent are these goals best achieved by the present translocation programme ?

Zaloumis and Cross (1974) point out that the reedbuck has recently disappeared from 80 % of its range in southern Africa (Fig. 5), and our short-term goal should be to restore the species to all suitable areas that it previously inhabited. For long-term direction, we must turn to The World Conservation Strategy (IUCN, 1980) which identifies one of the primary objectives of conservation as the maintenance of genetic diversity. Genetic diversity is clearly manifest between species, but the existence of quite distinct genetic stock within a species is commonly ignored. Greig (1979) has reviewed some principles of genetic conservation in relation to wildlife management in southern Africa, and Osterhoff *et al.* (in prep.) have demonstrated the existence of quite distinct genetic differences in the blood proteins of reedbuck from the Eastern Shores of Lake St. Lucia compared to those of the Natal highlands, some 400 km distant. If we are genuinely concerned for the maintenance of genetic diversity, our translocation programmes should avoid the mixing of genetically distinct stocks.

Given that our goals are to restore the species to its former range without mixing existing (genetically distinct) stock, we have two options. The first is a non-interventionist policy where the species is left to recolonise suitable areas of its own accord. Such a policy would ensure the maintenance of genetically distinct stock. Its success would depend to a large extent on the rate at which reedbuck are able to disperse, and in this regard there is some evidence that the species is a 'good disperser'. Howard (in prep.) has shown that 90 % of subadult female and 50 % of subadult male reedbuck dispersed away from their birthplace on farmland in the Natal highlands, and that they commonly covered distances of 35 - 40 km. This may be regarded as an adaptation to a life associated with wetlands which tend to be scattered, relatively temporary habitats. This innate dispersal can undoubtedly be of great value in the conservation of local populations, but on a regional basis, there would appear to be little hope of natural recolonisation of the vast areas of the Cape Province, Orange Free State and the Transvaal that are

currently devoid of reedbuck.

The second option is that of translocation. This has obvious advantages over the natural dispersal of animals in that the restoration of range is achieved almost instantaneously. We certainly cannot afford to ignore the political uncertainties of the region which preclude long-term planning of any kind. The pragmatist might argue that these issues completely over-ride considerations of genetic conservation and that if introduced animals, regardless of origin, can survive and breed in an area, that is sufficient reason for their re-introduction there.

However whilst translocation has immediate and obvious advantages in achieving short-term recolonisation, there are many examples where it has been used to treat the symptoms of a problem, rather than its cause. If the habitat has gone, any number of introductions will, in the long-term, fail. Where translocations are made to areas that already support dwindling populations of reedbuck, we must surely consider the cause of the problem, before proceeding to treat the symptoms?

If we consider what has been achieved by the translocation programme to date, some observations can be made:

- (a) many of the introductions were too small to create viable nuclei after initial mortalities, and losses through dispersal;
- (b) almost half the properties receiving reedbuck were fenced off from the outside world. Game farms and zoos perform a valuable function in the preservation of species, but in terms of the restoration of species to its former range, the animals might as well have gone to a zoo on another continent. In my opinion the plight of the reedbuck is not yet sufficiently grave to consider investing conservation funds into this kind of project.
- (c) principles of genetic conservation have been generally followed within Natal, but in the Transvaal several introductions have been made to farms already supporting local populations of reedbuck.

4 Is the cost of the programme justified by the results achieved?

This is not a question that can be easily answered as it depends upon value judgements. The results of the programme have been reviewed, and the cost is summarised in Table 2. Including the loss of revenue from the sale of venison that would have been derived from culling the translocated animals if they were not moved alive, the cost of supply, before transportation, is approximately R130 per animal (1982 figures). This compares with the charge made to a Natal

buyer of R60, and to a buyer from outside the province of R150.

POLICY RECOMMENDATIONS

Until now the translocation of reedbuck to private land has been largely dependent upon the initiative of landowners in requesting animals from the Natal Parks Board. Within Natal less than half the cost of these animals has, however, been borne by the buyers, with a high level of subsidy provided by the Natal Parks Board.

If, in the future, public funds continue to be available for reedbuck translocation, it is my contention that sufficient is now known to allow more discriminatory use of those funds. In particular, I believe that the Natal Parks Board should adopt a positive role in identifying possible sites for the reintroduction of reedbuck, and might consider following these policy recommendations:

- 1 Conservation authorities should work towards establishing a network of reintroduction centres. These centres should:
 - (a) provide the main emphasis of the reintroduction programme, and attract the highest level of subsidy;
 - (b) be established no closer than 50 km from one another, as intervening areas will be recolonised naturally by animal dispersal;
 - (c) be initiated with an input of at least 30, but not more than 100 reedbuck;
 - (d) comprise an initial introduction of adult animals only, as subadults are likely to scatter before they have a chance to breed;
 - (e) be carefully selected areas able to provide adequate natural herbaceous cover, and winter forage in the form of natural wetland vegetation and/or cultivated pastures;
 - (f) be centrally situated in an intended area of recolonisation.

In purely practical terms farm conservancies, which are groups of farms collectively patrolled by a number of guards, could provide the requirements of a reintroduction centre. The landowners would share the costs of purchasing the (subsidised) breeding stock, and hence be able to buy more animals. To encourage the establishment of effective

recolonisation centres, the Natal Parks Board might consider donating one reeduck for each one that is purchased.

- 2 Animals should not be provided at subsidised rates simply because the recipient lives in Natal. A more worthwhile criterion for subsidisation would be the animal's contribution to the extension of the species range. Thus game-fenced properties would not qualify for subsidy, and nor would farms offering isolated pockets of suitable habitat in areas of extensive cultivation.
- 3 To allow for initial mortalities, no translocation of fewer than 14 animals should be attempted to unfenced properties, or of fewer than seven animals to fenced properties.
- 4 Adults only should be moved, with preference shown for females, which have an 86 % chance of being pregnant, and which are unlikely to move away from the site of reintroduction. A sex ratio of 2:1 in favour of females is recommended.
- 5 No introductions should be made to properties with existing populations of reeduck, or to areas within 50 km of such populations. Principles of genetic conservation should be adhered to, and where possible animals should be moved from the closest source.

SUMMARY

Since 1978, 1500 reeduck have been moved from the Eastern Shores of Lake St Lucia to reserves and private land in all four provinces of South Africa. A postal questionnaire was used to monitor the success of these translocations. Together with observations made on selected recipient farms in Natal, and evidence of the reeduck's ability for natural dispersal, the replies indicate that the present programme could be improved. Some policy recommendations are made in the belief that the establishment of a few major reintroduction centres would achieve the desired goals more effectively than the present programme where animals are scattered far and wide.

ACKNOWLEDGEMENTS

I thank all those who replied to the questionnaire survey and the Natal landowners whose hospitality I enjoyed during my visits to their farms. This work was made possible by financial support from the University of Natal/Natal Parks Board Research Fund, the BP Education Trust and the Institute of Natural Resources, for which I am extremely grateful. Mrs B Smit is thanked for typing

the manuscript.

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Table 1. The proportion of translocated animals dying within two weeks of offloading. (Means are shown ± 1 standard error. The number of translocations considered is given in parentheses)

Year	Mortality (%)	Month of Translocation
1978	26 \pm 6 (n = 4)	June
1979	36 \pm 9 (n = 13)	September
1980	19 \pm 4 (n = 19)	April
1981	18 \pm 6 (n = 11)	April
1982	30 \pm 10 (n = 13)	July/August

Table 2. Approximate costs per capture in South African rands, with equivalents in United States dollars (1982 figures)

Helicopter	R16,40	(\$20,00)
Vehicle running expenses	R 3,50	(\$ 4,30)
Staff	R50,65	(\$61,80)
Depreciation on equipment	R 2,30	(\$ 2,80)
Lost revenue from sale of venison	R58,00	(\$70,80)
TOTAL	R130,85	(\$159,70)

FIG.1: The number of reedbuck moved live each year from the E. Shores of Lake St Lucia

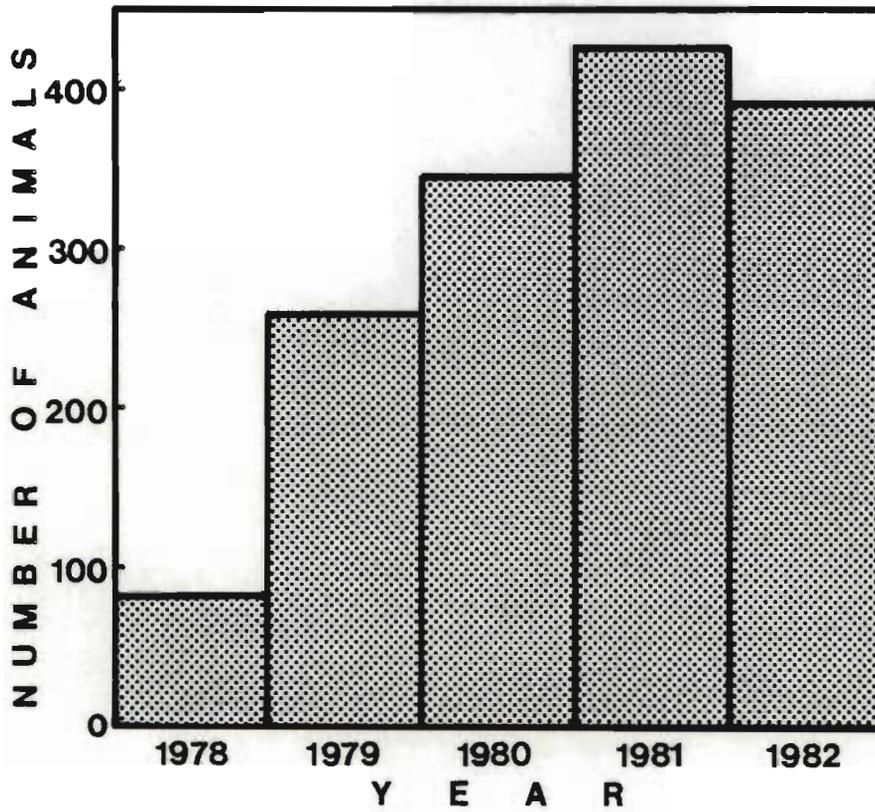


FIG. 2. : Translocations from the Eastern Shores of Lake St Lucia to destinations within Natal, for the period 1978 to 1982

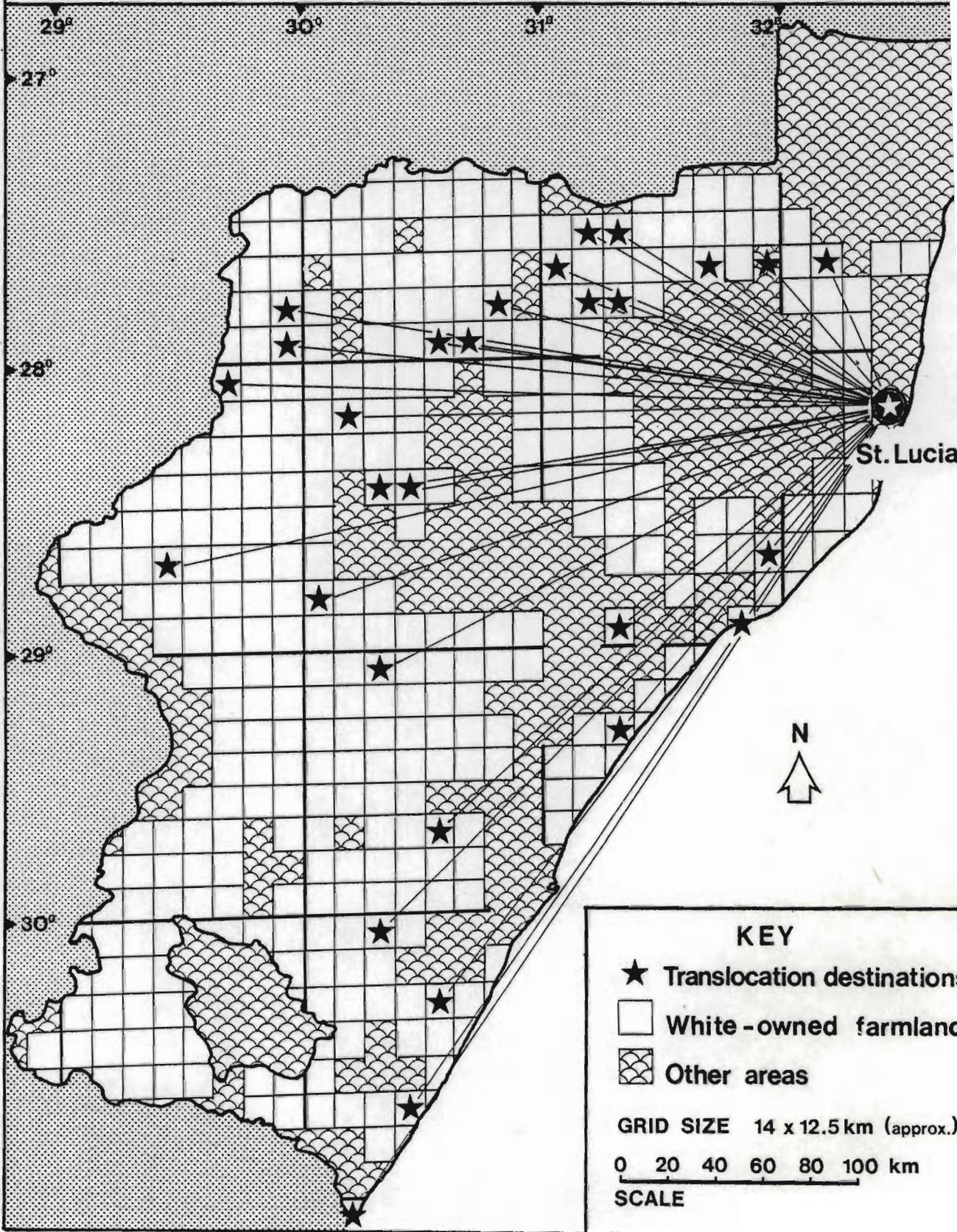


FIG. 3 : Translocations from the Eastern Shores of Lake St. Lucia to destinations outside Natal, for the period 1978 to 1982

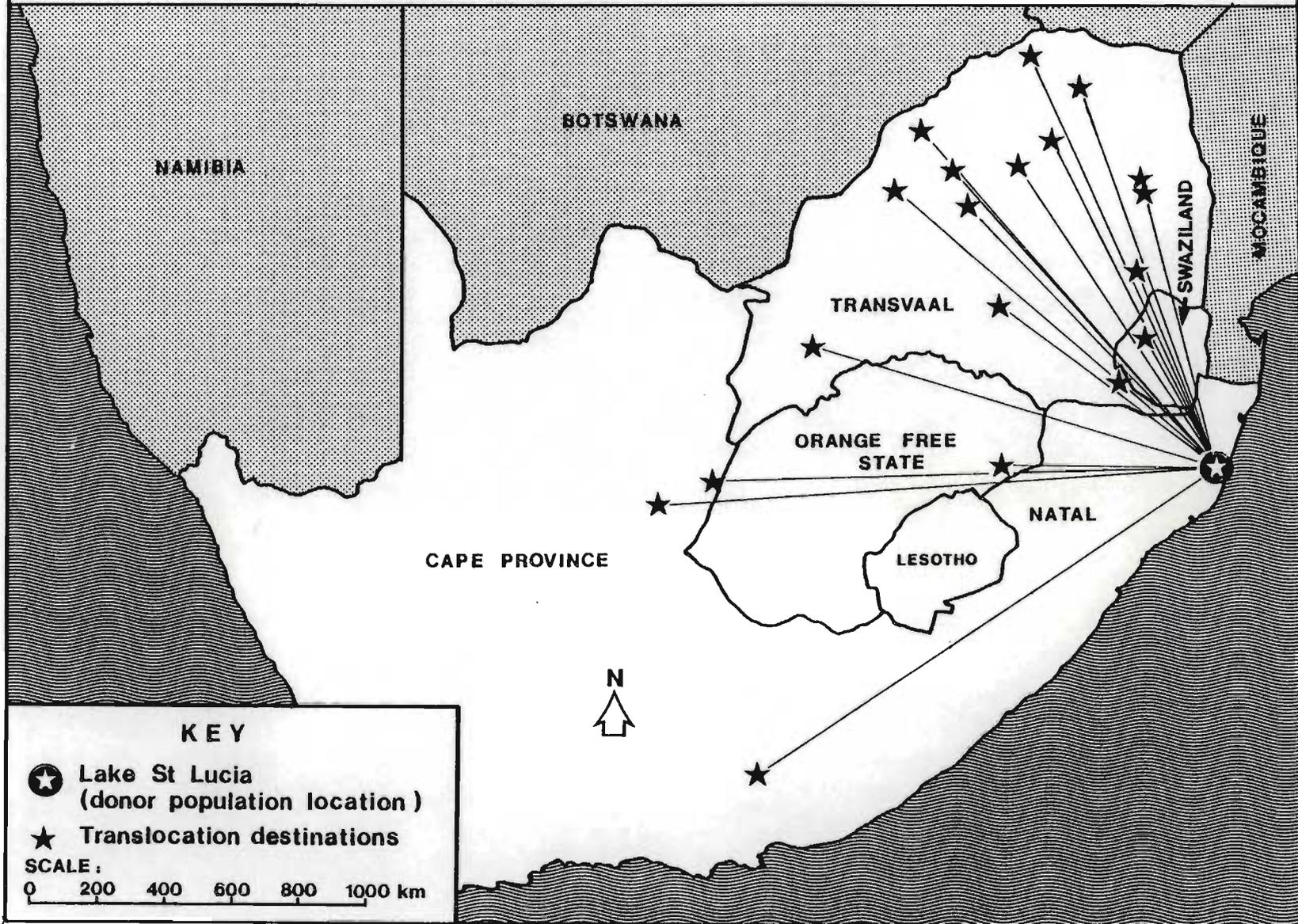


FIG. 4 : The relationship between the number of reedbeek successfully relocated, and their annual rate of population increase

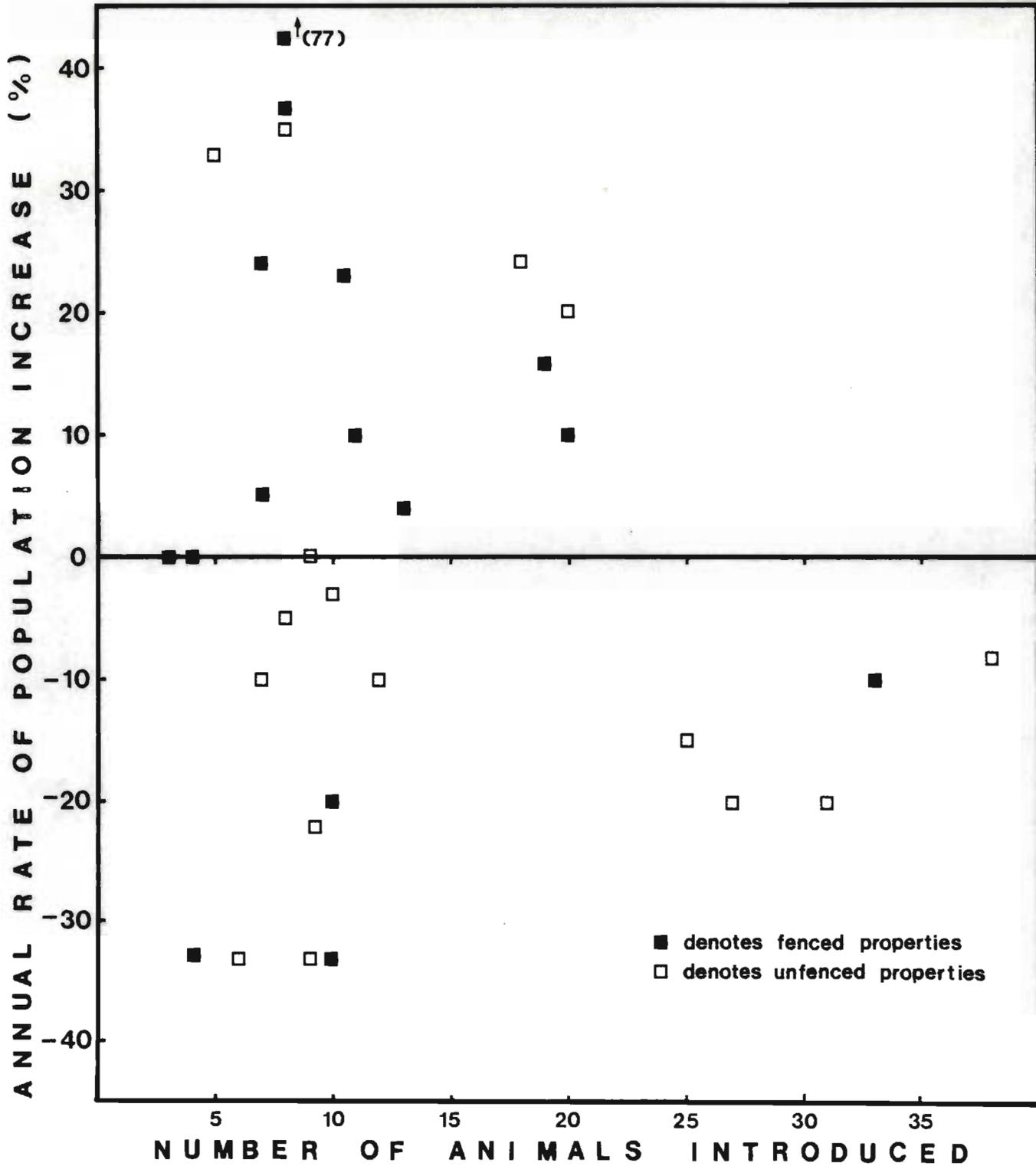
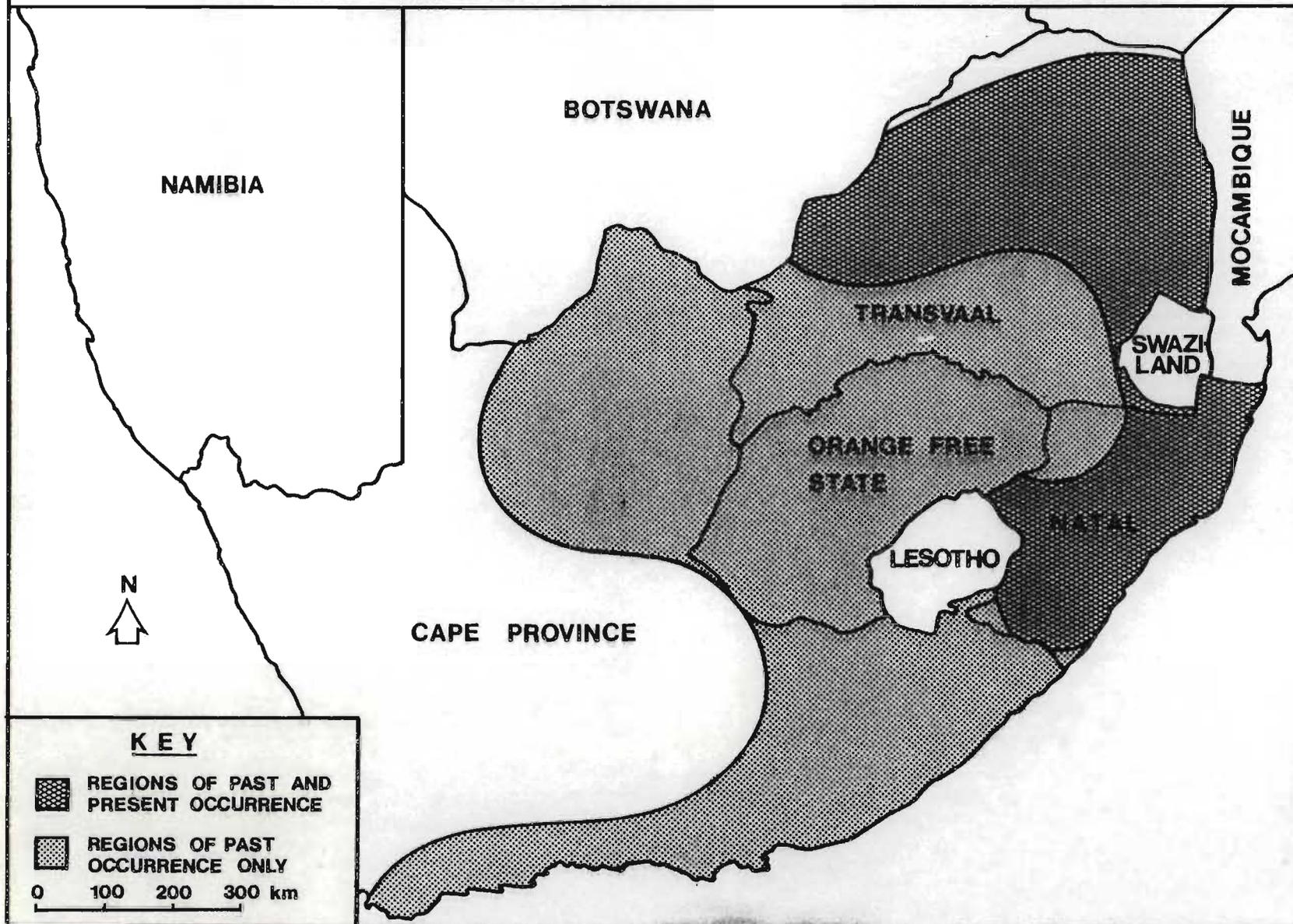


FIG. 5 : Past and present distribution in South Africa (after Du Plessis, 1969 ;
Rautenbach, 1982 ; Howard and Marchant, In prep.)



APPENDIX C : Paper in preparation (incomplete results)

GENETIC VARIABILITY OF REEDBUCK AND ITS IMPLICATIONS FOR MANAGEMENT

D.R. OSTERHOFF, J.C. GROENEWALD and P.C. HOWARD

INTRODUCTION

In recent years naturally occurring populations of common reedbuck (Redunca arundinum) have disappeared from the Cape Province (Stuart, 1982), and the Orange Free State (L van Zyl, cited by Venter, 1979), and have been declining on farmland in the Transvaal (du Plessis, 1976). Zaloumis and Cross (1974) point out that the species has disappeared from 80 % of its former range in the region (FIG. 2.2; CHAPTER TWO).

In Natal, however, the situation is very different. A rapid increase in reedbuck numbers on the Natal Parks Board controlled Eastern Shores of Lake St. Lucia during the 1970's prompted a research project, the outcome of which was a recommendation to dispose of an apparent excess of animals (Venter, 1979). Simultaneously, the Board was receiving an increasing number of complaints from farmers in the highlands and midlands of the province who were concerned by crop damage pressures resulting from increasing populations of reedbuck on their farms. Although in this case populations appear to be self-regulatory (Howard, in prep.), there is an abundance of animals available for translocations.

The Natal Parks Board has adopted a policy of live disposal in preference to culling, wherever practicable, in an attempt to restore the species to as much as possible of its previous range. In order to rationalize this translocation programme, it was considered pertinent to investigate levels of genetic variability and adaptation within and between the potential 'donor' populations. If, it is argued, genetically distinct sub-populations exist all necessary precautions should be taken to maintain their integrity, by avoiding the mixing of stock from different areas. This is in accord with the principles of genetic conservation, as reviewed by Greig (1979), and the philosophy of the World Conservation Strategy (IUCN, 1980) which identifies one of the primary objectives of conservation as the maintenance of genetic diversity, as is manifest both between and within species.

Until comparatively recently, studies of genetic variability and adaptation relied heavily on comparisons of gross morphological features. This has now been largely superseded by comparisons of genetic markers in the form of electrophoretically distinguishable blood proteins. Such techniques

have proved of inestimable value in mammalian systematics studies (e.g. Selander et al. 1971; Robinson and Osterhoff, in press) helping to clarify the taxonomic relationship between closely related species. They have also proved useful in distinguishing local differences in the genetic make-up of many species including rabbits (Richardson, 1980), Scandinavian moose (Ryman, et al. 1980) and impala (Osterhoff et al. 1972).

The purpose of the work described in this paper is to examine genetic variability and the possibility of genetically distinct stock between populations of reedbuck from different parts of Natal. Translocation policy could then be formulated to conform to the principles of genetic conservation.

METHODS

Fresh whole blood samples were collected from the jugular vein of a random sample of culled reedbuck from two locations in Natal. From each population between 50 and 60 animals were sampled during 1982 from an area of land not exceeding 10 000 ha. The first collection site was the Natal Parks Board controlled Eastern Shores of Lake St. Lucia in the Zululand lowveld (32°30' E, 28°10' S). This is a subtropical coastal area, falling within the coastal lowlands bioclimatic subregion (Phillips, 1973) which naturally supports dune forest and hygrophilous grassland communities. The second collection site was an area of semi-intensive farmland in the Underberg district of the Natal highlands (centred on 29°20' E, 20°45' S). Approximately 400 km from St. Lucia, this area lies 1 750 metres above sea level, and falls within Phillips' (1973) highland sourveld bioclimatic subregion. The natural vegetation is predominantly fire-maintained sub-climax grassland, and the region experiences a long harsh winter.

The fresh blood samples from each collection site were sent, chilled, to the Department of Zootechnology of the University of Pretoria, Onderstepoort, for examination of selected blood proteins, using a starch gel electrophoretic technique. A detailed description of the laboratory methods used has been given elsewhere by Osterhoff (1968), and an abridged version will be included in the published paper describing this work.

RESULTS

At the time of writing, results are available from electrophoretic analysis of 24 blood samples collected from animals in the highlands population, and from 30 samples from animals in the St Lucia population. The results are presented in TABLE Cl. Two of the seven blood proteins tested (Transferrin and nucleoside phosphorylase) were polymorphic, with significant differences in phenotype frequencies between the two populations.

TABLE C1 : Frequencies of blood protein types in populations of reedbuck from the highland and St Lucia regions of Natal.

PROTEIN	PHENOTYPE	HIGHLANDS POP'N (n=24)	St LUCIA POP'N (n=30)	SIGNIFICANCE OF DIFFERENCE (χ^2)
Albumin	AB	24	30	-
Haemoglobin (typing technique 1)	A	24	30	-
Haemoglobin (typing technique 2)	Rr	24	30	-
phospho-glucomutase	S	24	30	-
6-phospho-glucose dehydrogenase	1	24	30	-
X - protein	+	24	30	-
nucleoside phosphorylase	{ 1 2 3 }	{ 10 7 7 }	{ 5 17 8 }	0,05 < p < 0,10
Transferrin	{ C CD CH DD DF DH DO DR FH RR }	{ 1 7 1 0 14 0 0 0 1 0 }	{ 0 5 0 5 1 2 14 2 0 1 }	p < 0,05

DISCUSSION

Even without the full results, this investigation has demonstrated significant differences in the genetic make-up of reedbuck from these two regions of Natal. Although the causes of these differences are not understood, their implications for management are clear. In the interests of genetic conservation (Greig, 1979), it is important not only to preserve existing reedbuck populations, but also to maintain their genetic integrity. This means that translocations of reedbuck should not be made to areas where reedbuck already exist, or which stand a good chance of being recolonised naturally by better adapted local immigrants.

Osterhoff and Op't Hof (1974) have suggested that the less genetic

variation found in a population of animals, the greater the possibility of its having reached a dead end in specialisation, and thus of local extinctions. Thus, in cases where translocation appears to be the best option available to wildlife managers in the restoration of a species to parts of its previous range, the donor population should ideally be one chosen for its genetic diversity which is able to provide those animals most capable of adaptation to a new environment. It is impossible to infer from the results of this limited investigation, that one or other of the reedbuck populations studied is more genetically diverse, although the seven transferrin phenotypes of the St Lucia population (compared with only five in the highlands) could be indicative of this.

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APPENDIX D: Age determination

INTRODUCTION

Many aspects of animal population ecology depend upon an ability to determine the age of individuals within a population. Amongst these the more important include the age at which puberty, sexual senescence and the fertility peak occur, rates of growth, the determination of life-span, and understanding of social behaviour and organisation. Because of its importance in so many fields of population ecology, age determination methodology has been the subject of many studies and a copious literature (reviewed by Morris, 1972; Spinage, 1973). Nevertheless it is still true that 'no wholly reliable method for African mammals has yet been demonstrated' (Spinage, 1973). And even if it had, it is generally accepted that extreme precision in age determination is often more of academic than of practical interest (Spinage, op.cit.)

There are two stages in age determination. The first is a comparative process whereby the individuals within a population are categorised by age relative to one another. The second is the process of determining the absolute ages of these categories, and this is normally achieved by reference to known age material.

METHODS

The choice of methods adopted in this study was determined by two overriding considerations. Firstly, as only two known age reedback over the age of nine months are available, the potential for determining precise age determination criteria is severely limited. Secondly, the objectives of the study do not justify exhaustive efforts in the field of age determination, as, for the pragmatic purposes of management, no high level of precision is required. Accordingly the methods adopted attempt to determine the age of the material available to within reasonable limits of accuracy, with economy of effort, at the same time providing an adequate description of the criteria used to enable possible recalibration of relative age classes for age distribution comparisons with other populations of reedback. The laboratory methods used are based on the sequence of eruption of the permanent teeth (in juveniles) and on tooth attrition (in adults).

(a) Field age classification

Within the intensive study area the ages of animals sighted in the field were classified as adult, subadult, juvenile, and infant (FIG. D1). The

infant was capable of passing underneath the stomach of the adult female; the juvenile had a shoulder height less than the mid-shoulder height of the adult female, and in subadult females the shoulder height was lower than the asymptotic height. Subadult males were further subdivided according to the length of their horns in relation to their ears, and subadult females were classified by shoulder height recorded in tenths of that reached at maturity. By this classification, a juvenile female thus enters the subadult class at 5/10ths of adult shoulder height. Marked individuals were used to determine rates of growth over known periods of time under farmland conditions.

(b) Source of post-mortem material

The skulls of 199 reedbuck were collected from a randomly shot sample of subadult and adult reedbuck. The majority of these animals (about 90 %) were shot within the extensive study area, and the remainder came from farms elsewhere in Underberg magisterial district.

In addition 54 skulls were collected of animals that had died of 'natural causes', all of which were found in Underberg district.

(c) Age determination by tooth eruption

Where possible the maxillary tooth row was examined, and in all cases where the permanent teeth were not fully erupted, the animal was classified into one of the ten eruption classes, following Venter (1979) (TABLE D1).

(d) Age determination by tooth wear

In cases where the full permanent dentition was present, animals were classified into tooth wear classes, based on the general appearance of the teeth (i.e. separation of the entostyles, disappearance of infundibula, etc.). Initially, Venter's (1979) classification was used but this proved inadequate because the distinguishing criteria were too specific to allow a general appraisal of the state of wear of the entire tooth row. Grimsdell and Bell (1975) produced a series of tooth wear photographs for the closely related black lechwe in Zambia, and because they had access to known age material they were able to determine the absolute age of adult lechwe to within one year. Their photographic record was used in this study to allocate relative age classes to each reedbuck skull. Because of the similarity between reedbuck and lechwe, a similar pattern of tooth wear was assumed, but whereas the lechwe's life-span is in the region of twelve years, that of the reedbuck is probably closer to ten (Mentis, 1972). Accordingly, the series of reedbuck skulls, classified by this method into twelve age classes, was now adjusted by shifting a proportion of the skulls down one (or two) classes until the entire series of skulls was

TABLE D1 : Tooth eruption and replacement in the maxillary tooth row (after Venter, 1979)

Tooth eruption class	Approximate age (mths)	Premolars			Molars		
		2	3	4	1	2	3
1	0 - 6	d	d	d	e		
2		d	d	d	E		
3		d	d	d	E	e	
4	6 - 12	d	d	d	P	E	
5		d	d	d	P	E	e
6	12 - 18	d/e	d	d	P	E	E
7		e	d/e	d/e	P	P	E
8	18 - 24	e	e	e	P	P	E
9		P	E	e	P	P	P
10	24 - 30	P	P	P	P	P	P

Explanation of symbols:

d = deciduous tooth

d/e = deciduous tooth still present, with permanent tooth erupting below

e = permanent tooth just erupting: only cusps or tips visible above bone

E = erupting permanent tooth: all four cusps well above bone, but not fully erupted

P = fully erupted permanent tooth

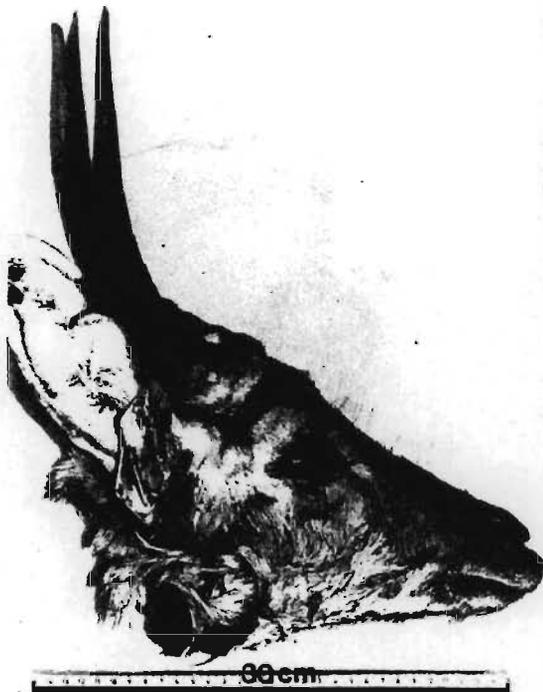
reclassified into ten chronological age classes, equivalent to ten years of life.

The approximate age-at-death of two subadult male reedbuck was known, and the state of tooth wear in these animals was compared with the derived tooth wear series. As the agreement between the two was good, no further adjustment was made. Known-age specimen 1 (PLATE D1) was captured and marked as a 14,5 kg lamb in April 1981 and shot in September 1983, while specimen 2 was marked in August 1981 at an estimated age of 10,5 months (based on horn length - FIG. D1) and found freshly dead in March 1983.

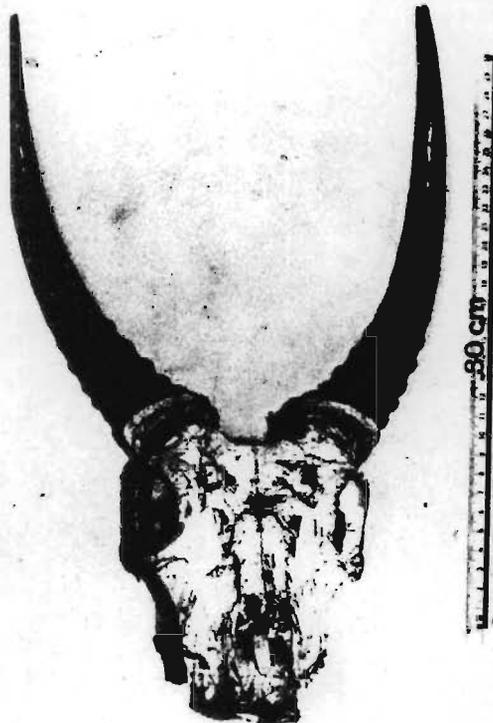
To further examine the validity of this (rather subjective) method of age determination, the crown height of the first molar in the maxillary row was measured with Vernier slide calipers. The measurement was made on the buccal side, vertically above the saddle, following Spinage (1971). Mean crown heights for each age class were calculated and examined in relation

PLATE D1: Horn growth and tooth wear in two known age rams

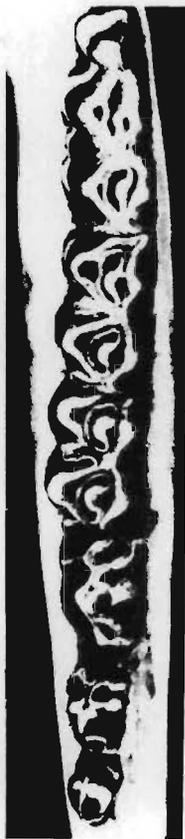
SPECIMEN 1: 2,7 ($\pm 0,1$) years



SPECIMEN 2: 2,5 ($\pm 0,2$) years



MAXILLARY TOOTH ROW



MANDIBULAR TOOTH ROW



MAXILLARY TOOTH ROW



MANDIBULAR TOOTH ROW

to the supposed age of the class and the mean crown heights of other classes, to determine whether realistic rates of tooth attrition occurred between the allocated age classes.

(e) Age determination by cementum line counts

A sample of maxillary first molars was extracted, one from a representative skull from each age class. These were then bisected vertically and transversely through the saddle with a miniature hacksaw, and the cut surface of cementum pad underlying the crown of the tooth was polished with 'wet and dry' paper. The polished surface was dampened with laboratory alcohol and examined for cementum lines under reflected light using a dissecting microscope (Grimsdell and Bell, 1975; Williamson, 1979). An attempt was made to count the number of incremental lines in the cementum.

The same sample of teeth was then used to examine cementum lines in stained decalcified root sections by the method of Stoneberg and Jonkel (1966). Teeth were sectioned sagittally, fixed in buffered neutral formalin, decalcified in 5 % nitric acid, embedded, sectioned at 10 μ m, and stained with Harris' haematoxylin (Steenkamp, 1975; Ludbrook, 1978). The mounted sections were examined under a low power light microscope, and the number of darkly staining bands in the cementum counted. The results were examined in relation to the supposed age of the teeth.

(f) Age determination by horn growth

Horn length was measured along the front edge of the horn, around the curve from the base to the extreme tip, excluding the boss of hardened skin at the base. Mean values were calculated within each of the age classes determined by tooth eruption and wear. In addition 24 marked juvenile and subadult males were field age classified according to their horn length relative to the length of their ears on each sighting occasion over periods of six months to two years.

(g) Age determination by body growth

Changes in body mass and dimensions with age are considered elsewhere (CHAPTER FOUR) for all animals examined post-mortem. Marked immature animals were also classified in the field according to size at regular intervals to examine obvious changes in body dimensions.

RESULTS

(a) Field age classification

Nineteen marked subadult males were observed over periods in excess of six

between five to six months of age, and for a period of about a year grow by about one quarter the ear length each three months. Thus, at 18 months of age the horns are approximately the same length as the ears. Thereafter, horn growth begins to slow down, reaching close to the maximum size by 36 months of age. A useful field age criterion for males between three and four years of age is neck girth which continues to broaden as the animal reaches social maturity.

(b) Sequence of tooth eruption

Tooth eruption and replacement in the maxillary tooth row is summarised in TABLE D1 (after Venter, 1979). Full adult dentition is present from 24 - 30 months of age.

(c) Tooth wear

Tooth eruption and wear classes are photographically illustrated in PLATE D2 for the maxillary tooth row, and in PLATE D3 for the mandibular molariform teeth. FIG. D2 illustrates the decline in crown height of the maxillary first molar, with estimated age.

FIG. D2 : Change in Maxillary M¹ Crown Height with Estimated Age
(mean values are shown \pm standard deviation)

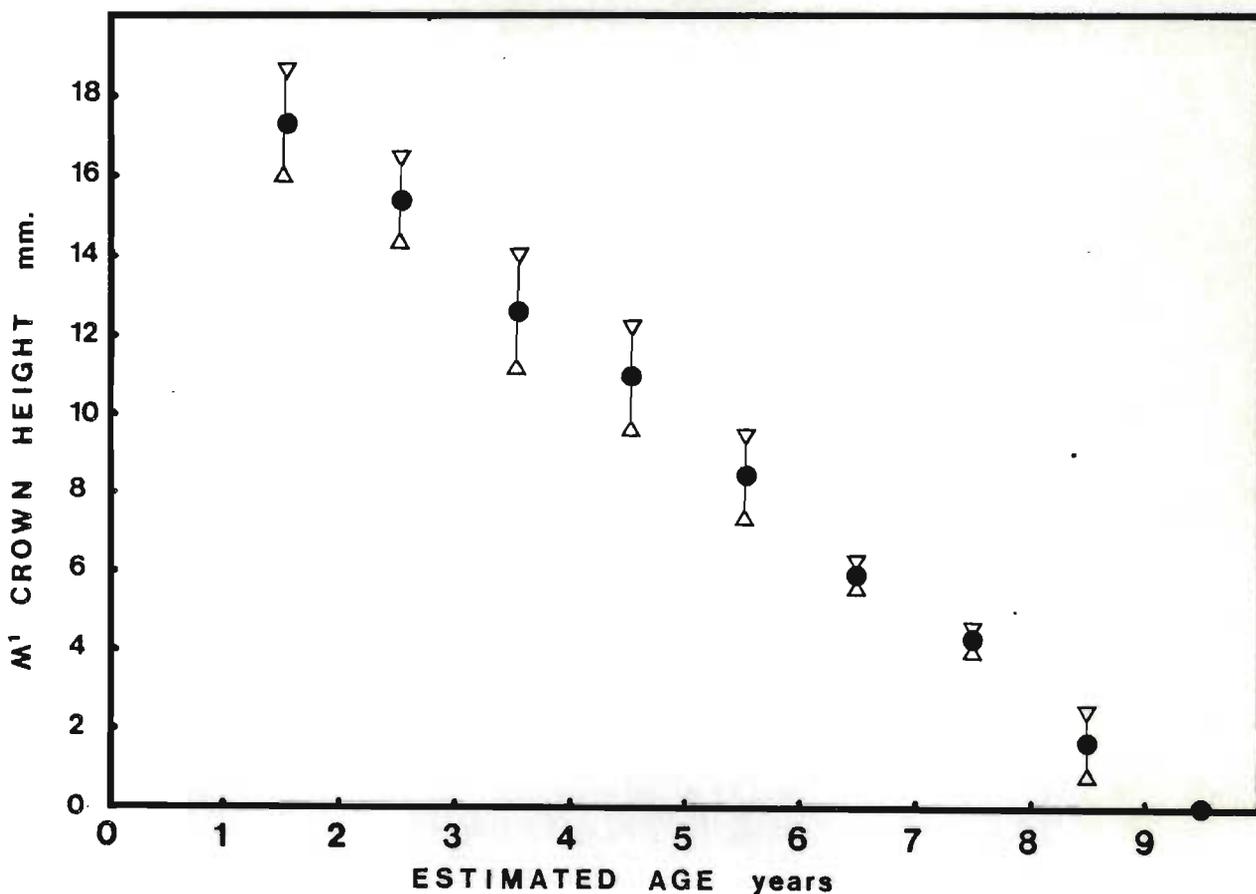


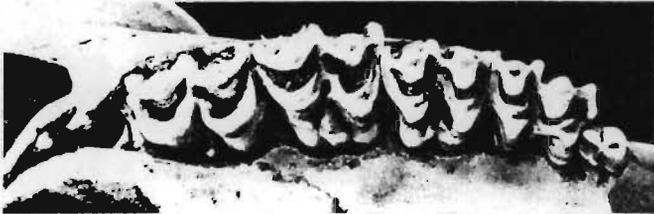
PLATE D2 : Maxillary tooth row eruption and wear groups. Ages are indicated in years



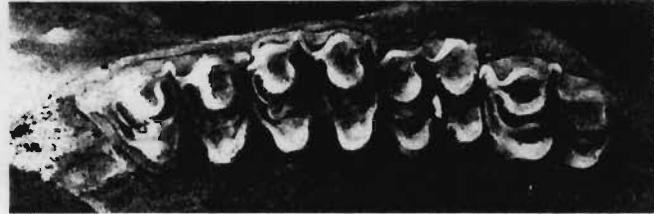
0-0,5



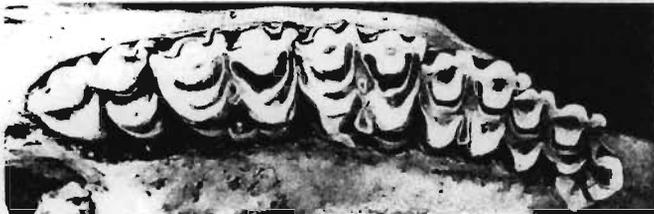
3,1-4,0



0,6-1,0



4,1-5,0



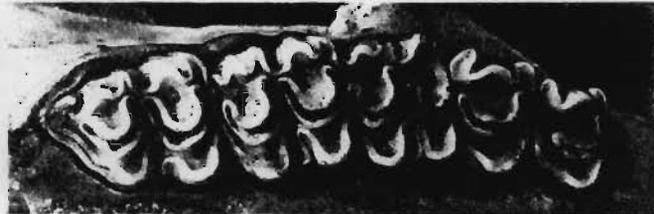
1,1-1,5



5,1-6,0



1,6-2,0



6,1-7,0



2,1-2,5



7,1-8,0



2,6-3,0

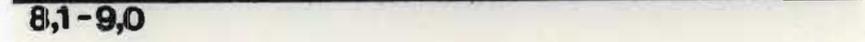
(No representative specimen available)

8,1-9,0

PLATE D3: Mandibular tooth row eruption and wear groups. Ages are indicated in years



(No representative specimen available)



(d) Cementum line counts

Under reflected light bisected teeth revealed only very indistinct layering, which was difficult to interpret. Stained decalcified tooth sections were only slightly better, and although about 50 % of the teeth examined did show some layering, the lines were often indistinct, with merging and diverging lines causing considerable confusion. Where lines were present the number counted seemed to be about twice the estimated age of the animal in years. However, as this time-consuming technique did not appear to offer any marked improvement in age estimation in this study, it was abandoned.

DISCUSSION

Accuracy in age determination depends upon access to material of known age, against which to compare the collected material under study. So little known age material was available in this study that the age determination criteria described in this section are necessarily of limited value.

One very commonly used technique of determining the absolute age of mammals is that of counting incremental (growth) lines in dentine, cementum or bone. This technique can be of application even where known age material is unavailable, and it has been used widely in temperate zones because one dark line, corresponding to a period of reduced growth during winter, is reliably laid down each year. However, in Africa the dominant physiological rhythm seems to be one of two main lines of reduced growth each year, not only in regions of bimodal rainfall (Spinage, 1967), but also in areas of unimodal rainfall (Simpson and Elder, 1969). Implicit in the very limited results of this study is the same physiological rhythm, which seems to persist even under the extreme climatic conditions of the Natal Drakensberg. It is unfortunate that the incremental lines were not more reliably present and distinct, thus justifying further effort in this field.

In the absence of sufficient known age material, or clearly visible cementum lines, crown height measurements were taken to assess the validity of the derived tooth wear classes. Spinage (1971, 1973) notes that the overall pattern of attrition should tend to follow a negative exponential rate of decay, whereas the crown height measurements taken in this study suggest a more nearly linear rate of decay. In other words, the crown height data suggest that the estimated ages of younger animals are too high, and those of older animals too low. This type of error is not uncommon in visual assessments of tooth wear (Spinage, 1973), and arises because the rapid rate of wear in the young age classes makes them look older than they really are, whilst slower tooth wear in the older classes makes them difficult to separate from the younger ones.

This simple 'objective' assessment of tooth wear highlights one source of error in the criteria used for age determination in this study. A number of workers (Gilbert and Stolt, 1970; Erickson *et al.*, 1970; Kerwin and Mitchell, 1971; Thomas and Bandy, 1975; Attwell and Jeffery, 1981) have examined the validity of visual tooth wear assessment as an age determination technique, by comparing ages estimated in this way with those estimated from counts of cementum lines in the same individuals. The level of agreement between the two techniques in these studies has been in the region of only 50 - 60 %, reflecting the high degree of subjectivity involved in visual tooth wear assessments. There are other sources of error, too, not least of which is the inherent variability of tooth eruption and wear between individuals within the population. This sort of error can only be objectively evaluated with a moderately large collection of known-age skulls, as has been done for the common duiker (Wilson *et al.*, in press). In their study, Wilson *et al.* found one case where the incisiform teeth of a 26 month old duiker were at the same state of development as those of a 48 month old individual. This, however, is exceptional, and others (e.g. Hemming, 1969; Miller, 1972) have reported far greater consistency in tooth replacement timing.

Clearly, then, a high level of precision in age determination is difficult to achieve, even with known age material. In this study the decision was taken not to pursue age determination studies exhaustively, although some improvement in the results obtained might be expected had a more thorough investigation been undertaken. The most appropriate method would be a 'combination' technique where the individuals are age determined independently by a number of different techniques, and a combination age score derived from a consideration of the results of each of the independent assessments. This sort of approach was used as long ago as 1950 (Gustafson) to determine the age of single human teeth, but there is no reason why such assessments should be restricted to ageing criteria in teeth, and might be further improved by use of horn growth phenomena (Simpson, 1971), incremental lines in bone (Grobler, 1979), measurement of eye lens mass (Friend, 1968, cited by Morris, 1972), accumulation of insoluble lens proteins (Otero and Dapson, 1972), and changes in bone marrow and fusion of epiphyses.

Given the recognised limitations of the age determination technique adopted, it is instructive to consider, firstly, how accurate the described age classes are likely to be and, secondly, how any inaccuracy might affect the study's overall conclusions. With respect to the first consideration, the principal assumption made is that maximum longevity is nine to ten years. This is based on three records of longevity given by Mentis (1972), all of which fell between nine and ten years. Allometric laws, which scale numerous biomechanical and physiological processes to size in mammals have long been recognised (Western, 1979), and would seem to support this as

being a realistic life-span for an animal the size of a reedbuck. Spinage (1976), however, used a figure of 14 years for the age at which the M1 crown height would be worn to zero in a study of the Grant's gazelle (*Gazella granti*), an animal of similar size to the reedbuck. The farmland conditions under which this study was undertaken undoubtedly enhance survival, and the nutritious pasture grasses that contribute much to the reedbuck's diet are likely to be less abrasive to the teeth than natural forage; these two factors would tend to increase longevity, and the figure of 9.5 years that is used in this study is consequently more likely to be an underestimate than an overestimate. If the estimated age of the older animals were underestimates, a more realistic inversely exponential rate of M1 crown height decay would follow recalibration of estimated age within a longer life-span. The recalibration would mostly affect animals in the older age classes, and as these are in the minority (CHAPTER THREE), the practical implications of such recalibration are negligible. The bulk of animals are in the younger age classes, where recalibration would have little effect.

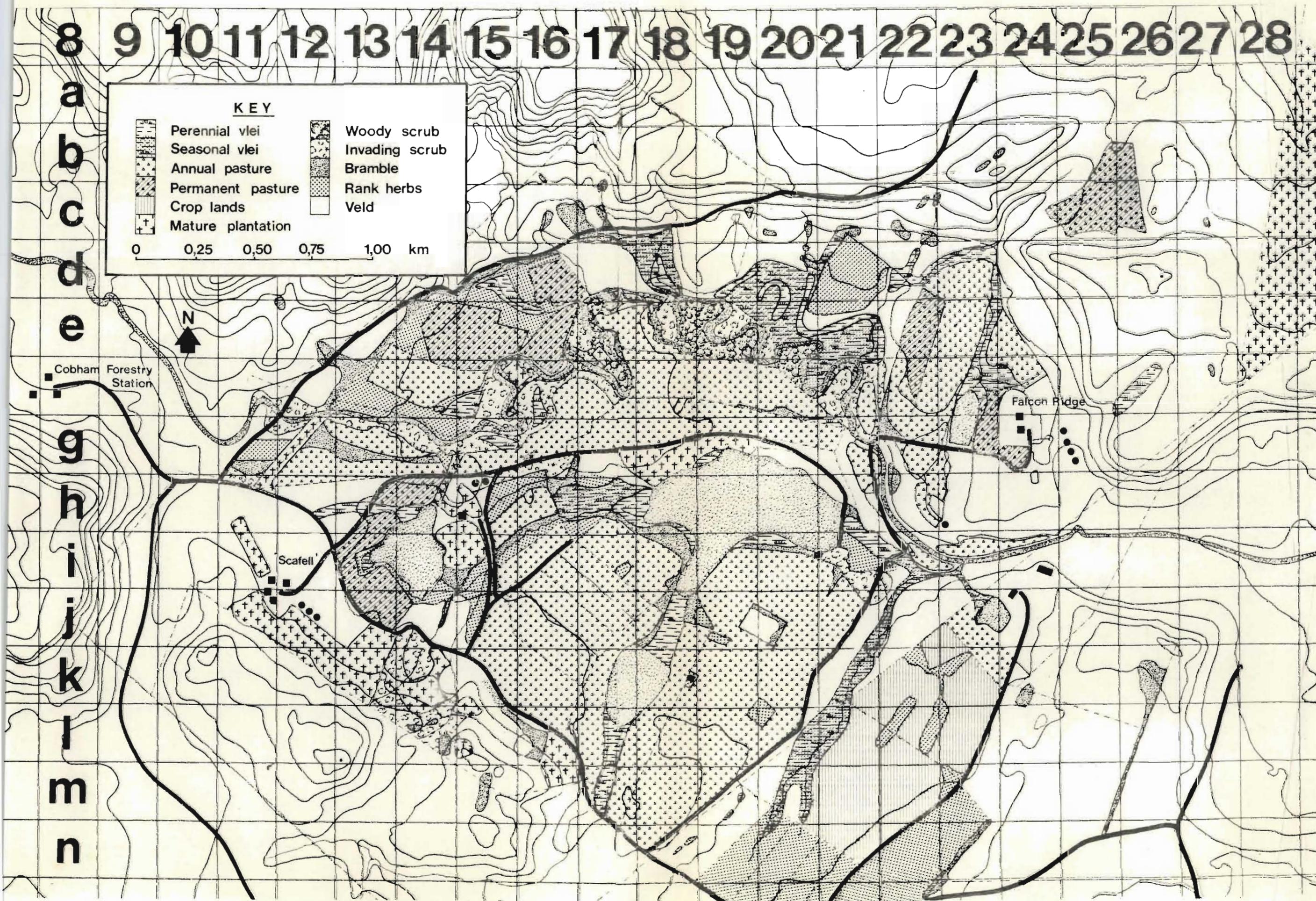
To understand how any inaccuracy might affect the study's overall conclusions, we must consider which conclusions depend on this technology. The most important of these obviously relate to our understanding of population demography, which is governed to a large extent by the age at which females start breeding, and the age at which they stop. Since no decline in fertility with age was detected (CHAPTER FOUR), the latter consideration is equivalent to the calculation of longevity. In CHAPTER THREE some considerable discrepancy was demonstrated between female longevities calculated by three different methods, and in this regard sample sizes were obviously too small to reach firm conclusions. Even if age determination had been perfected, this would have made little difference to overall conclusions because, in the final analysis, sample size, and not age determination technology, is limiting.

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PHYSIOLOGICAL CONDITION OF COMMON REEDBUCK
UNDER DIFFERENT ENVIRONMENTAL CONDITIONS
IN THE NATAL DRAKENSBERG

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INTRODUCTION

In recent years there has been a marked increase in the numbers of common reedbuck (Redunca arundinum Boddaert, 1785) on farmland in the Natal highlands. This may be the result of an increasing trend by farmers to plant and irrigate pasture grasses on these lands for winter stock feed. It is postulated that by taking advantage of such pastures, common reedbuck populations are no longer limited by winter forage quality, and survive and reproduce much better than would be the case in a natural system.

To test this hypothesis rigorously would require considerable research effort. However, as the 'physiological condition' of an animal is closely related to that animal's chance of surviving and reproducing (Hanks, 1981), it was felt that a comparison of the condition of animals in a natural system with those living on farmland at a time of the year when they are most likely to be under nutritional stress would go a long way towards testing this hypothesis. If it is validated we can offer some explanation for the apparent demographic success of farmland populations, and justify management actions.

MATERIALS AND METHODS

Ten adult male common reedbuck were ~~shot~~ between 8 August and 10 September, and examined post mortem. Five were taken from farmlands on the Polela river near Himeville, and five from the nearby Natal Parks Board's Loteni and Giant's Castle reserves in the Natal Drakensberg. The three areas lie between 28'35' and 29'15' S and 28'50' and 29'10' E, where the dominant vegetation is fire maintained sub-climax grassland, falling within the highland sourveld bioclimatic subregion (Phillips, 1973). The reserve areas are maintained in as near to a natural state as possible whereas frost-tolerant pasture grasses are planted on farmland, and thus provide nutritious food during the winter.

For each animal shot the following condition indices were evaluated:

(a) Indices of stored protein status

- (i) Dressed mass/total body length (Taber and Dasman, 1958; Grimsdell and Bell, 1975), being the total mass of the bled carcass less the entire contents of the body cavity and the head, divided by its skeletal length from the tip of the snout around the body curves to the tip of the tail.
- (ii) Liver mass/total body length (Williamson, 1979).

(b) Indices of stored fat status

- (i) Kidney Fat Index, being the mass of fat associated with the kidney expressed as a percentage of the kidney's mass; using Riney's (1955) standardised technique.
- (ii) Percentage of fat in the marrow of the femur, tibia and metatarsus (Neiland, 1970; Sinclair and Duncan, 1972; Brooks et al., 1977).

(c) Indices of reproductive condition

- (i) Testes mass/total body length (Robinette and Child, 1964).
- (ii) Seminiferous tubule diameter (Chapman, 1970), taken as the mean of 30 diameters measured from histological preparations.

(d) Indices of pathological condition

- (i) Packed cell volume (P C V) (Wilson and Hirst, 1977), being the proportion of the blood made up of cells when separated from the serum in a centrifuge.

RESULTS AND DISCUSSION

Comparative data on the physiological condition of adult male common reedbuck culled in late winter on farmland, and in reserve areas are presented in Table 1. In five cases the condition indices used indicate that animals in the reserve areas are in significantly worse condition than those on farmland.

Stored protein status

Protein reserves, stored in the body musculature and in the liver, and assessed by use of the dressed mass and liver mass indices, are significantly higher in the farmland population. From these results it appears that by the end of winter reedbuck living under natural conditions, in the marginal habitat offered by the Drakensberg reserves, have severely depleted protein reserves.

Stored fat status

The results of this study show that kidney fat is low in both populations, and mobilization of fat from the bone marrows is underway. There are however significantly higher fat reserves in the marrows of the femur in animals from the farmland population, and fat reserves in the marrows of the tibia and metatarsus are high in this group. In the reserve population, marrow fat is low in both femur and tibia, with mobilization also clearly underway in the metatarsus.

In wild ungulates stored fat is mobilized in a definite sequence (Riney, 1955), beginning with that in the body cavity, and only after that is largely depleted, moving to the bone marrow. In the bones of the legs, fat is first mobilized in the femur and humerus, later in the tibia and radius and finally in the metatarsus and metacarpus (Brooks *et al.*, 1977). An animal in which stored fat has been mobilized from the metatarsus and metacarpus, is thus in very poor condition.

With only a little stored fat remaining in the femur and tibia, and mobilization well underway in the metatarsus the animals from the reserve population are thus in poor condition.

Reproductive condition

Histological examination of testes material from both populations revealed that spermatogenesis was in progress in all animals. Although there was no significant difference in testes mass index, the seminiferous tubule diameters of reedbuck from the farmland population were significantly greater than those of animals taken from the reserve population.

Considered in isolation, the interpretation of these results is somewhat difficult. The observed differences in tubule diameters

need not imply any strict seasonality in the sexual cycle of male reedbuck in the reserve population, since spermatogenesis was evident. As with the other condition indices, it probably does reflect some degree of seasonal nutritional stress amongst animals living under natural conditions, which may affect their demographic success.

Pathological condition

The condition of the two populations, as expressed by blood packed cell volume (P C V), is very significantly different, but as Hanks (1981) points out the physiological basis for such differences is poorly understood, and the results should thus be interpreted cautiously.

CONCLUSION

The highlands of Natal offer only marginal habitat for common reedbuck, where the end of winter is a time of severe nutritional stress and animals are in poor condition. Under natural conditions a disproportionate number of reedbuck deaths occur at this time of the year (C. Albertyn, pers. comm.). It is likely that forage quality is a limiting factor for animals in the natural system, but that the provision of highly nutritious food in winter on farmland enables improved survival and may also affect reproductive success. The data presented in this paper support the view that common reedbuck living on farmland in the highlands owe their demographic success largely to the artificial provision of winter feed that enables them to survive the critical late-winter bottle-neck.

SUMMARY

The physiological condition of common reedbuck in late winter, was found to differ significantly between animals in natural areas and those on farmland, which have access to artificial feed. This provides some explanation for the demographic success of this species on farmland.

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TABLE 1: Comparative data on the physiological condition of adult male common reedbuck, shot in late winter on farmland and nearby reserves. Means are shown ± 1 standard error

Condition index	Farmland populations	Reserve populations	% difference between populations	Significance levels (using student t-test)
Dressed mass (kg)/total body length (m)	27,6 \pm 2,0 (n=4)	22,9 \pm 0,5 (n=5)	20,5	p<0,05
Liver mass (kg)/total body length (m)	0,60 \pm 0,05 (n=4)	0,37 \pm 0,01 (n=5)	62,2	p<0,01
Kidney Fat Index	13,2 \pm 3,8 (n=5)	8,0 \pm 1,6 (n=5)	65,0	p< 0,1
Femur marrow fat %	49,5 \pm 16,4 (n=2)	6,5 \pm 5,4 (n=5)	663,9	p<0,05
Tibia marrow fat %	56,0 \pm 26,6 (n=2)	18,1 \pm 9,1 (n=4)	209,4	p> 0,1
Metatarsus marrow fat %	71,9 \pm 13,8 (n=2)	47,9 \pm 11,8 (n=5)	50,1	p> 0,1
Testes mass (kg)/total body length (m)	0,036 \pm 0,004 (n=4)	0,029 \pm 0,003 (n=5)	24,1	p> 0,1
Seminiferous tubule diameter (μ)	229 \pm 18 (n=5)	174 \pm 5 (n=5)	24,0	p<0,05
Packed Cell Volume (PCV) (%)	58 \pm 1,0 (n=3)	44,2 \pm 1,4 (n=4)	31,2	p<0,01