

ECOLOGY OF SOME MAMMALS IN RELATION TO CONSERVATION
MANAGEMENT IN GIANT'S CASTLE GAME RESERVE

by

David Treloar Rowe-Rowe

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PREFACE

The field work which formed the basis of this thesis was carried out in Giant's Castle Game Reserve, Natal; and laboratory work was done at the Natal Parks Board headquarters in Queen Elizabeth Park, Pietermaritzburg. Professor J.A.J. Meester supervised the studies.

Unless specifically indicated to the contrary in the text, the whole thesis represents my own original work, and has not been submitted in any form to another university.



D.T. ROWE-ROWE

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ABSTRACT

Key words: abundance relations, antelopes, fire, grassland, habitat preferences, insectivores, jackal, mountains, predation, rodents.

The study was conducted in Giant's Castle Game Reserve, a mountainous, predominantly grassland area, in the Drakensberg of Natal, South Africa. The aims of the study were to provide information on the distribution, status, and biology of small mammals and antelopes, with particular emphasis on their density and distribution in relation to habitat and fire; and to investigate the role of the black-backed jackal (the most common carnivore) in the ecology of the reserve, with particular emphasis on predation on small mammals and antelopes, social organisation, and density.

Small mammal populations were studied by removal trapping, and antelopes were censused along fixed route transects. The jackal's diet was determined mainly from faecal analysis, and radio telemetry was used to study movements, social organisation, and density.

Distribution and habitat preferences of ten small mammal species are dealt with. Numbers, species richness, and diversity in different habitats are compared. Populations in all grassland and scrub habitats are dominated by either a rodent (Rhabdomys pumilio) or a shrew (Myosorex varius) - the former at lower elevations and the latter above 2 200 m. The decrease in R. pumilio numbers was related to grass cover which decreases with increasing altitude. Populations in forests are dominated by an arboreal and rupicolous dormouse (Graphiurus murinus). The influence of fire on populations is dealt with. After fire numbers are initially low and usually only M. varius is present. At about 3 mo R. pumilio recolonises burnt areas, and by 6 to 12 mo small mammal trap success reaches pre-burn figures (earlier in spring-burnt areas than in autumn burns). At low (1 500 m) and intermediate (1 900 m) elevations small mammal numbers and species richness decline during the second year after burning, but at high altitudes (> 2 200 m) numbers remain constant then start to decline during the third year. Differences were related to greater herbage production at lower altitudes. In fire-protected grassland (unburnt for 9 to 16 y) trap success was similar to the peaks recorded in biennially-burnt habitats, but species richness was lower. Population dynamics of the two most-abundantly caught species (M. varius and R. pumilio) are detailed. Breeding coincided with the wet season (spring and summer), starting about a month later at higher altitudes where

temperatures are lower. The annual population cycles are typical of seasonal breeders - there appears to be a die-off of adults towards the end of the breeding season, then a shift in population structure to one which builds up mainly from young individuals. Animals collected at higher elevations were smaller than those collected at lower elevations. The altitude-related differences are discussed in relation to Allen's and Bergmann's rules. Details on diet based on stomach content analysis are given. Condition (assessed from fat deposits and calculated from a mass/length-cubed formula) was lowest at the end of the breeding season, reached a peak at the end of winter, then declined again during the breeding season. The ecological importance of small mammals to the 40 Giant's Castle vertebrates known to include them in their diets is discussed.

Distribution and habitat preferences of eight indigenous and three introduced antelopes are detailed. Coexistence of the antelopes is dependent on niche separation, identified from their specific preferences for vegetation type, physical characteristics of the habitat, food type, and feeding style. Detailed analysis of other aspects of antelope ecology was limited to the five most abundantly-recorded species, viz grey rhebuck, mountain reedbuck, oribi, eland, and blesbok. All of these antelopes showed positive responses to fire, feeding on recently-burnt veld (< 1 y old) in preference to unburnt veld (> 1 y since last burnt). The responses of antelopes and small mammals to fire, and the distribution of the different species, led to the hypothesis that two vegetation climaxes (grassland and forest) and their associated faunas have evolved in the Drakensberg in relation to regularity of burning. Seasonal variation in antelope counted along transects is discussed. Total populations are estimated and compared with past counts and estimates. Density and standing crop are calculated. Details on population structure are given and recruitment and mortality discussed. Most antelope die at the end of winter or early spring (the coldest, driest time of year) when herbage quality is lowest. It is concluded that nutrition during this critical period is the major population limiting factor, and that populations are not limited by jackal predation as was originally claimed.

Jackals are distributed throughout the reserve. Details of population structure are given. Young are born mainly during July and August (when most carrion is available). Litter sizes are 4 to 6 and pup survival is estimated at ca 2/litter. Telemetry studies indicated that mated males and females had overlapping home ranges which did not overlap the home ranges of other mated pairs. Immature (< 1 y old) jackals occupied small

areas within a mated pair's home range, and sub-adults (1 to 2 y old) had home ranges which overlapped those of one or more mated pairs. Density was estimated at ca 1 jackal/2,5 to 2,9 km² . Mean home range size was 18,4 km² . Relative per cent occurrence of items in jackal faeces were: small mammal 55, medium mammal 9, antelope 11, domestic mammal 4, bird 9, reptile 2, insect 4, crab 1, plant food 1, other 3. Significant seasonal differences were observed only in the amounts of antelope and insect material - antelope being highest when most game deaths occur. Diet in relation to availability of prey species is discussed, and so too is the jackal's activity pattern in relation to the activity patterns of its most commonly taken prey. The jackal's feeding strategy is discussed and it is concluded that in Giant's Castle Game Reserve this predator is predominantly a searcher, subsisting on small mammals. Carrion is taken when available, and occasionally the jackal pursues and kills medium-sized prey.

Conclusions are summarised and management recommendations are made.

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INTRODUCTION

For the successful management of a nature conservation area it is necessary to have a thorough knowledge of its fauna and flora. Although ecological studies of some Drakensberg mammals have been undertaken, no overall study has been made. This lack of baseline data has led to the emergence of a number of mammal-related problems in Giant's Castle Game Reserve, viz:

1. Little is known of what small mammals occur in the area, the relative abundance of the different species, and the ecological niches which they occupy.
2. Although fire has long been used as a management tool in the Drakensberg, another pressing question has revolved around the influence of fire on vegetation and its effect on the distribution and density of mammals.
3. During recent years questions have been raised concerning an alleged decline in grassland antelopes, and suggestions have been made that the black-backed jackal (Canis mesomelas) population has increased, and that this, the commonest predator in the reserve, is responsible for decreased antelope numbers. Furthermore, allegations are often made that jackals move out of the reserve, where they are responsible for predation on livestock.

Only two short papers on Drakensberg small mammals (Meester et al. 1979; and Mentis and Rowe-Rowe 1979) have been published, both dealing with recolonisation of grassland after fire.

Grey rhebuck (Pelea capreolus), mountain reedbuck (Redunca fulvorufa), and oribi (Ourebia ourebi) populations were studied at Highmoor, on the Little Berg, by Oliver et al. (1978) where the authors investigated population ecology. In the same area Mentis (1978) censused oribi and grey rhebuck, and measured herbage quality over a 12-month period. Both Highmoor studies were limited to grassland burnt biennially in spring, and neither covered the full altitudinal or habitat range of the Drakensberg.

Publications on the black-backed jackal in the Drakensberg have dealt with the hunting of the animal and have provided some population data and information on diet. Bigalke and Rowe-Rowe (1969) analysed jackal hunting data collected over a five-year period, and Rowe-Rowe (1974) summarised hunting data collected over a 10-year period. The jackal's diet has been

preliminarily investigated by stomach content and faecal analysis (Rowe-Rowe 1976, 1978a), but only 29 of the 165 samples dealt with in these two publications came from Giant's Castle.

The overall objective of this study was therefore to undertake a mammal ecological study of Giant's Castle Game Reserve (GCGR) with the following specific objectives:

1. To provide information on the distribution and status of mammals in the reserve.
2. To provide information on the biology of small mammals and antelope, with particular emphasis on their distribution and abundance in relation to fire.
3. To investigate the role of the black-backed jackal in the mammal ecology of the reserve, with particular emphasis on predation and movements.

At the beginning of 1978 (when the mammal survey commenced) a detailed study of fire and vegetation in GCGR was also started, and an ecological study of eland (Taurotragus oryx) was in progress (Scotcher, in prep.). Information on the history of veld burning in GCGR was collected (Scotcher et al. 1980a), and the effects of fire on plant species composition and basal cover (Scotcher and Clarke 1981) and on herbage production and quality (Scotcher et al. 1980b) in grassland burnt during different seasons, at various altitudes, and on different aspects were quantitatively measured. A final objective will then be the use of information from the mammal study, coupled with data collected by other scientists (Scotcher et al. 1980a, b; Scotcher and Clark 1981; Scotcher, in prep.) to provide guidance for the formulation of management policies which will cater for the best balance between variety of habitats, variety and numbers of mammals, and the management of predator and prey populations, as well as the most suitable burning regime for the area.

THE STUDY AREA

Giant's Castle Game Reserve (29°08' to 29°23'S, 29°23' to 29°37'E) occupies an area of about 36 000 ha between 1 380 and 3 350 m above sea level (Fig 0.1).

TOPOGRAPHY

The Drakensberg escarpment runs approximately south - north along the western boundary of the reserve at an average altitude of 3 000 m, dropping sharply in the east to about 2 200 m. A number of rivers flow approximately west - east from the escarpment, and have incised steep-sided valleys descending from 2 200 m to 1 380 m. Between the river valleys high ridges (the Little Berg) have remained, extending eastwards from 2 200 m to 1 800 m (Fig 0.2).

The main topographic features of the reserve are therefore valley bottoms (1 380 to 2 200 m), valley sides (1 500 to 2 200 m), ridge tops (1 800 to 2 200 m), escarpment (2 200 to 3 000 m), and the summit above the escarpment.

GEOLOGY AND SOILS

The geology of GCGR is made up of four horizontal layers of rock formations. In descending order they are the Basaltic Lavas (between 1 900 and 3 350 m) and the Cave Sandstone between 1 800 and 1 900 m, which has become exposed as an almost continuous band of cliffs at ca 1 800 m. Below the sandstone lie the Red Beds and Molteno Beds which have not been exposed here.

Details of the geological stratification have been given by King (1972).

Two broad soil types occur, viz ferrallitic and acid hydromorphic soils. The ferrallitic soils predominate and are characteristic of the well-drained uplands where they have become severely leached and low in fertility. Acid hydromorphic soils occur on bottomlands, but are also considerably leached. Details on Drakensberg soils are contained in van der Eyk et al. (1969).

CLIMATE

Summers are mild to cool and winters cool to cold. Detailed temperature records have not been maintained in GCGR, but means are probably

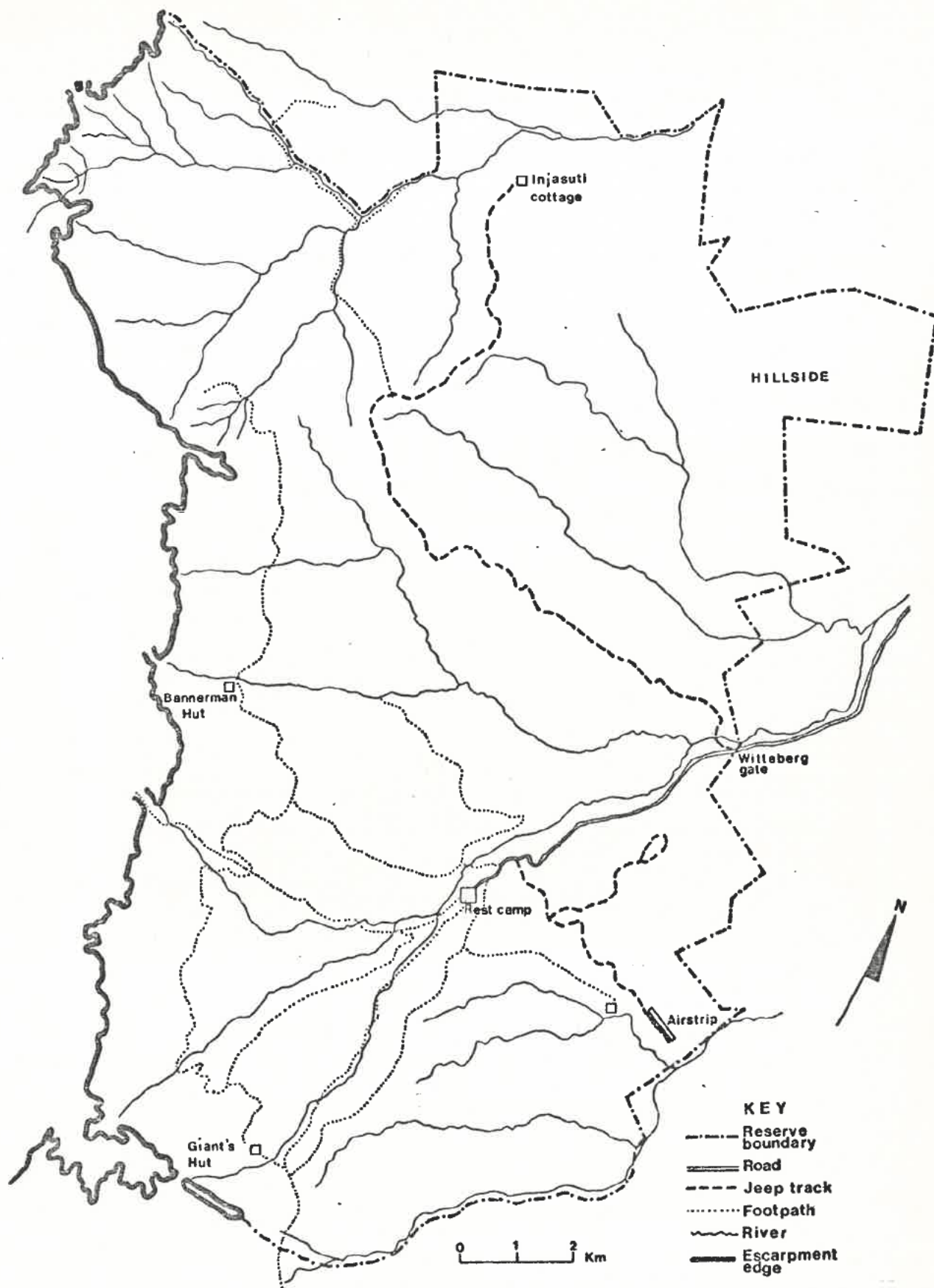


Figure 0.1. Giant's Castle Game Reserve



Figure 0.2 Typical topography of Giant's Castle Game Reserve, showing the escarpment, with deeply incised east-west valleys and ridges.

similar to those recorded at Cathkin Park and Cathedral Peak (Killick 1963; Tyson et al. 1976). The warmest month is January and the coldest is July (mean daily maxima and minima 23° and 13° C; and 14° and 4° C respectively). Minimum temperatures at grass level are much lower than those recorded in the Stevenson screen: at 1 860 m mean minimum daily January and July temperatures are 8° and -8° C respectively (Killick 1963).

The mean annual rainfall measured at the Warden's house at 1 760 m in GCGR is 1 038 mm, which falls on a mean of 101 raindays/annum, mainly from October to April. Actual rainfall during the study period was 1 181 mm, 1 020 mm, and 1 076 mm during 1978, 1979, and 1980 respectively (Fig 0.3). Rainfall at the summit and at the base of the escarpment is higher than that measured at lower altitudes (Killick 1963): at Cathedral Peak 63 % more rain is recorded at 2 200 m than at 1 450 m.

Snow falls mainly between April and September, but can precipitate on the high ground (above 2 500 m) during any month of the year. Fog occurs mainly on the Little Berg and escarpment, sometimes lasting for a few days at a time.

First frosts usually occur in May and the last winter frosts are usually experienced in August or September.

Prevailing winds are rain-bearing easterly to south-easterly during the wet season, and westerly during winter and early spring, when they are dry and often reach high velocities.

Tyson et al. (1976) have described the climate of the Drakensberg in detail.

VEGETATION

GCGR is vegetated predominantly by sub-climax grassland, with patches of forest, woodland, and scrub. There is no published description of the vegetation of the reserve. It is, however, similar to that at Cathedral Peak, described by Killick (1963), where three main vegetation belts were recognised. In GCGR Scotcher (in prep.) has classified and described the woody vegetation. My description of the vegetation of the game reserve is therefore based on Killick (1963) and Scotcher (in prep.). The belts, and the major communities within each are:

1. Montane Belt (up to 1 800 m)

Themeda triandra grassland, tall grassland, Protea woodland, boulder-bed scrub, Greyia-Cussonia grouped-tree woodland/grassland, scrub (Leucosidea, Philippia, or Buddleia-Leucosidea), and climax Olinia forest.

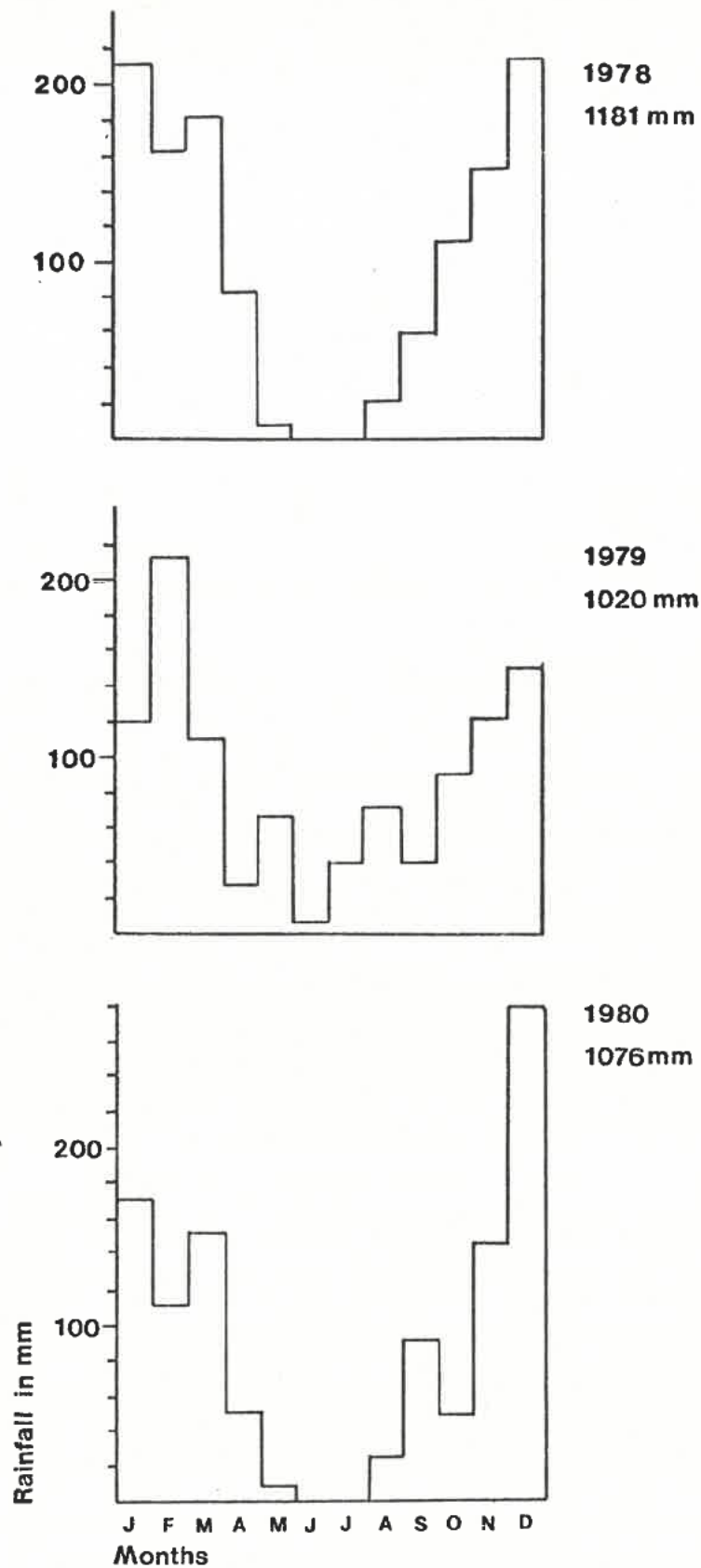


Figure 0.3 Rainfall recorded at 1 760 m during the study period.

2. Sub-alpine Belt (1 800 to 2 750 m)

Themeda triandra grassland, temperate grassland (above 2 200 m), and limited patches of Leucosidea scrub and Leucosidea-Philippia-Cliffortia fynbos as the climax in fire-inaccessible areas.

3. Alpine Belt (above 2 750 m)

Festuca-Pentaschistis-Merxmüllera grassland, and climax Erica-Helichrysum heath.

FIRE

The history of veld burning in GCGR from 1906 to 1979 has been outlined by Scotcher et al. (1980a).

From 1906 to 1965 scheduled burning was done mainly during autumn and winter (either annually or biennially). In 1966 autumn burning was stopped and a spring-burning programme was adopted. Biennial autumn burning was again started in 1976, but was limited to three valleys below the sandstone cliffs. A biennial summer burning trial was started in 1973, but stopped in 1978 when it became obvious that the veld was deteriorating (Scotcher and Clarke 1981). Thirty per cent of the fires recorded in GCGR during the past 74 y were unscheduled (either accidental fires entering from farmland or deliberate burns started by arsonists), mainly during winter or early spring.

The burning policy during the study period (1978 to 1980) was one of biennial spring burning over most of the reserve, limited biennial autumn burning in the Montane Belt, biennial winter burning above 2 200 m, and annual burning of firebreaks during early winter. The reserve is divided into 28 compartments, 14 of which are burnt each year. The firebreaks separating the compartments are 100 to 200 m wide and have a total length of 170 km. Forests are protected from fire, and there are two protection plots on south-east-facing slopes in grassland. One of these plots, ca 200 ha at 1 500 to 1 700 m, has been protected since 1957 and burnt only once (accidentally) during 1969. The other, ca 100 ha at 1 720 to 1 860 m, was protected from 1962 onwards but accidentally burnt in 1978. In addition a grassland area of 600 ha at 1 900 to 2 300 m was left unburnt for 4 y (1976 to 1980).

One unscheduled fire passed through about half of the study area during the second half of August 1978. Areas affected were mainly biennial spring burns (some of which were due to be burnt within about two weeks), portions of the autumn burns, forest margins, and the 100 ha protection plot, which was completely burnt.

Burning compartments in the southern half of GCGR, where all data on small mammals and antelopes in relation to fire were collected, are illustrated in Figure 0.4.

GENERAL APPROACH TO THE STUDY

In this section only the general approach to the study will be outlined. Details of actual methods employed will be elaborated on in the "Methods" sections of Parts 1, 2 and 3 dealing with small mammals, antelopes, and jackals.

Field data were recorded in coded form on data sheets, then transferred to computer cards for final analysis using the SPSS programme (Nie et al. 1970). As much as possible of the following information was recorded for each observation: date, time, locality (using a 500 x 500 m grid on a 1:20 000 contour map), altitude, aspect, degree of slope, vegetation type, fire history, topography, sex and age class (or composition of group), and activity.

Small mammals were sampled between 1 500 and 2 700 m in the southern half of GCGR by trapping with a combination of live and snap traps. Measurements of specimens were taken, reproductive state was determined, and the stomach contents of some were examined. Antelope distribution records were collected throughout the reserve. Game counts, to obtain information on seasonal and annual trends, were done along five fixed routes which traversed most of the vegetation types, burning regimes, and topographic features typical of the reserve. Specific information on antelope numbers in relation to veld burning was collected at two elevations. Black-backed jackal specimens were incidentally obtained, and data were also incorporated on animals killed prior to the start of this study, when jackals were hunted by using foxhounds. The jackal's diet was studied by faecal examination and information on its movements was obtained by live trapping animals and fitting them with radio transmitters.

The study commenced in January 1978 and was intended to be completed by December 1980. Some of the fieldwork was interrupted by the runaway fire during August 1978, therefore sampling of certain small mammal habitats continued until May 1981. Antelope monitoring data collected up to the end of 1981 are included.

PART 1 : SMALL MAMMALS

METHODS

TRAPPING

Sampling was done by removal trapping, using a combination of folding aluminium live traps and plywood-based snap traps. Each trapline consisted of 20 stations ca 15 m apart. A snap trap was set at each station and a live trap, about 1 m from the snap trap, at each alternate station, giving a total of 30 traps. (It was not possible to set equal numbers of snap and live traps as too few of the latter type were available.) A trapping session lasted for four days and four nights, i.e. 120 trap nights.

The snap traps used were 140 x 70 mm plywood-based Museum Mouse Traps (Aidco, Salisbury, Zimbabwe). Two types of folding aluminium live traps were used, viz 230 x 80 x 90 mm Sherman (Sherman Traps, Tallahassee, Florida, USA) and 325 x 95 x 100 mm Elliott (Scientific Equipment, Upwey, Vic., Australia).

Traps were baited with a mixture of peanut butter and rolled oats, and checked once daily.

HABITATS SAMPLED

The habitats sampled and the sampling effort in each area are listed in Table 1.1. It was originally intended that biennial burns and their controls should be sampled four or five times, at approximately 6-mo intervals, to give full 2-y coverage. This was not possible in two of the controls, as a protection plot which included scrub and grassland was burnt in the run-away fire during August 1978, and this same fire upset the burning regime in some biennially burnt grassland habitats, resulting in their being burnt in two consecutive years.

The Alpine Belt was not sampled in GCGR, but data collected at the summit of Sani Pass, outside the reserve, are included.

ESTIMATION OF SPECIES ABUNDANCE RELATIONS

Three measures of abundance relations were used, viz trap success, species richness, and diversity.

Small mammal abundance in each habitat is expressed as the total number of small mammals captured/100 trap nights, and termed per cent success or trap success. Relative abundance of species is compared, both within a

TABLE 1.1 Small mammal habitats sampled in GCGR, arranged approximately in order of ascending altitude.

Vegetation type	Altitude (m)	Aspect	Fire regime	Times sampled	Total trap nights
Montane belt					
<u>Themeda</u> grassland	1 500	N	Biennial autumn	5	600
<u>Themeda</u> grassland	1 540	S	Protected	4	480
Grouped-tree woodland	1 540	W	Biennial autumn	5	600
Protea woodland	1 660	W	Biennial autumn	4	480
Boulder-bed scrub	1 720	NE	Biennial autumn	4	480
<u>Themeda</u> grassland	1 740	E	Annual spring	5	600
Scrub	1 760	NE	Occasional burn	2	240
Scrub	1 760	SE	Protected	1	120
Tall grassland	1 800	NE	Annual spring	3	360
Forest	1 800	S	Protected	4	480
Sub-alpine belt					
<u>Themeda</u> grassland	1 900	NE	Biennial spring	5	600
<u>Themeda</u> grassland	1 860	E	Protected	1	120
<u>Themeda</u> grassland	2 200	NE	Biennial spring	4	480
<u>Themeda</u> grassland	2 200	NE	Protected	4	480
Temperate grass-land boulder-bed	2 300	NE	Biennial winter	6	720
Temperate grass-land	2 300	E	Biennial winter	4	480
Temperate grass-land	2 700	NE	Biennial winter	2	240

habitat and between habitats, by expressing the number of each species caught as number/100 trap nights.

The species richness of a habitat is the number of species collected. As species richness does not give an indication of the evenness of representation of the different species, diversity was also measured.

Diversity was calculated using the Shannon-Wiener index (Poole 1974):

$$H' = - \sum_{i=1}^s p_i \log_e p_i$$

H' is diversity where s is the number of species, and p_i the proportion of the number of individuals belonging to the i th species in the sample.

EXAMINATION OF MATERIAL COLLECTED

The following standard external measurements were taken: mass in g; length of head and body, tail, hind foot (with claw = cu), and ear in mm. Method of measuring followed that described by Smithers (1971), except that head and body and tail were recorded separately, and not as total length.

Reproductive status was determined as follows: males were recorded as having abdominal or scrotal testes (inguinal in shrews), and testis length and diameter were measured. Females were recorded as imperforate, perforate, pregnant, lactating, or post-partum (if placental scars were present). If pregnant the number of fetuses and fetus crown-rump lengths were recorded.

Condition was subjectively assessed in the field based on the amount of subcutaneous fat on the rump, using four categories: 1 = no fat, 2 = little fat present, 3 = medium fat layer, and 4 = very fat. In addition condition factors were calculated using the formula

$$K = \frac{M \times 10^6}{L^3}$$

where K is condition, M mass in grams, and L length in mm (based on the mass/length cubed formula - Lagler 1956).

Diet was determined by microscopically examining stomach contents under low power (10 to 20x). Remains were categorised as white or green plant matter, or insect, and the approximate percentages of each category were estimated.

After the small mammal study in relation to habitats and fire treatment had been completed (May 1981) additional snap-trapping was done to obtain stomach contents for detailed identification of invertebrate remains. Identifications were made by staff and students of the Department of Entomology, University of Natal.

MEASUREMENT OF HERBAGE PRODUCTION

Data on herbage production between 1 500 m and 2 200 m during the first year of growth, and in one fire-protected area, were obtained from Scotcher et al. (1980b). All other herbage data were personally collected at the time that a habitat was being trapped for small mammals. The method employed involved clipping all herbage within a quadrat to a height of ca 30 mm above the ground, oven-drying it, and calculating the above-ground standing crop in g/m^2 .

TRAP EFFICIENCY

The overall success of snap traps was 7,8 % and that of live traps 10,9 %. A t-test for paired samples indicates that the results differ significantly at the 0,1 per cent level ($P < 0,001$).

Actual numbers of each species caught in the two trap types are listed in Table 1.2. Chi-square evaluations were done to test whether numbers caught in snap and live traps differed significantly from the expected 2:1 (i.e. 67:33) ratio that the trapping regime (2 snap traps to 1 live trap) suggested. The efficiency of live over snap traps was significant in the case of R. pumilio and O. irroratus, and non-significant for all other species, although ratios indicate an advantage in favour of live traps (except for M. minutoides).

Data were analysed by months for the two most commonly-caught species. Deviation from expectation was inexplicably significant during October and November ($P < 0,05$ and $< 0,01$) for R. pumilio and during November only ($P < 0,001$) for M. varius. Differences between snap and live trap captures were not significant during all other months.

Comparative efficiencies of snap and live traps have been commented on by a number of authors (Cockrum 1947, Davis 1973, Kern 1977, Nel et al. 1980, Rautenbach and Nel 1980, Wiener and Smith 1972). The results reported make it difficult to decide whether either snap or live traps are superior:- In Wyoming Cockrum (1947) found live traps twice as efficient as snap traps, but Wiener and Smith (1972), working in California and Nevada with a different set of small mammal species, reported the opposite. In the Kruger National Park (Kern 1977) snap and live trap captures were similar in one area (4,7 % snap : 4,5 % live) but differed in another (4,2 % : 1,9 %). Live traps proved to be more successful than snap traps in the Cedarberg (Rautenbach and Nel 1980), but in the Kammanassie Mountains Nel et al. (1980) achieved better results with snap traps. Davis (1973), considering the trap response of O. irroratus only, found that live traps were far superior to snap traps. Over a 10 mo-period at Cathedral Peak, working with the same small mammal species and under similar conditions to those prevailing at GCGR, Rowe-Rowe (1977a) recorded snap and live trap successes of 10,2 % and 8,3 % respectively, which differed significantly at the 0,1 per cent level ($P < 0,001$), the opposite of the situation encountered in GCGR.

TABLE 1.2 Numbers of small mammals captured in snap and live traps which were set in the ratio of 67:33. Chi-square based on actual numbers caught.

Species	Captures		Ratio	Chi-square	P
	Snap	Live			
<u>Rhabdomys pumilio</u>	181	138	57:43	14,18	< 0,001
<u>Myosorex varius</u>	154	89	63:37	1,19	NS
<u>Otomys irroratus</u>	17	19	47:53	6,13	< 0,05
<u>Dendromus melanotis</u>	22	13	63:37	0,22	NS
<u>Graphiurus murinus</u>	15	11	58:42	0,91	NS
<u>Crocidura flavescens</u>	7	5	58:42	0,38	NS
<u>Mus minutoides</u>	8	4	67:33	0,00	NS
<u>Dendromus mesomelas</u>	1	3	25:75	3,29	NS
Total	405	282	59:41	18,40	< 0,001

NS = $P > 0,05$

There are obviously many factors which influence trap efficiency, some of which may be size of trap, the material from which it is made, and the size and behaviour of the species involved: cf. the findings of Wingate and Meester (1977) and Willan (1978) regarding different types of live trap; and results achieved by Nel et al. (1980), Rautenbach and Nel (1980), and Wiener and Smith (1972) who compared snap traps of different sizes.

In considering suitable traps for use in the GCGR study factors taken into account were that they should be efficient, and that they should be light and compact, as equipment often has to be transported over long distances in backpacks. The preliminary work done at Cathedral Peak showed that the equipment selected satisfied both of these demands. The Museum Mouse Traps proved to be efficient in capturing even the smallest species (M. minutoides) and holding the largest (O. irroratus). Although almost the same size as Museum Special snap traps, Museum Mouse Traps were much lighter in overall mass. Size and sensitivity of the folding Elliott and Sherman live traps were very satisfactory. Shermans were preferred, however, because they were the lighter of the two makes.

DISTRIBUTION AND HABITAT PREFERENCES

Two shrews (Mysorex varius and Crocidura flavescens) and eight small rodents (Rhabdomys pumilio, Octomys irroratus, O. sloggetti, Dendromus melanotis, D. mesomelas, Mus minutoides, Graphiurus murinus, and Praomys natalensis) occur in the reserve.

Distribution in relation to vegetation type and altitude is illustrated in Fig 1.1 for all species except P. natalensis, which was captured at only two localities: outside a dwelling in the rest camp and in the ranger's house at Injasuti.

M. varius enjoys the widest distributional range, occurring in all vegetation types and at all altitudes (see Table 1.3).

R. pumilio, the most abundantly caught species, occurs in all habitats from 1 500 to 2 700 m except forest, and is also absent from the Erica-Helichrysum heath on the summit.

O. irroratus occurs in all grassland and scrub habitats from 1 500 to 2 700 m. Although not captured in Themeda grassland at 1 900 m nor in grouped-tree woodland, this rodent's feeding signs were seen in these habitats.

Three other species which were nowhere abundant, but are widely distributed, are D. melanotis, limited to grassland, mainly in the Sub-alpine Belt; M. minutoides, recorded in grassland, scrub, and forest; and C. flavescens which was collected in grassland at all altitudes except 2 700 m.

There are three species which appear to have rather specialised habitat requirements: D. mesomelas was recorded in forest, scrub, temperate grassland boulder-bed, and tall grassland; G. murinus is limited to scrub, forest, and rocky habitats; and O. sloggetti occurs only in the Erica-Helichrysum heath.

All of the small mammal species collected in GCGR fall within the recorded ranges given by Roberts (1951), Ellerman et al. (1953), and Meester and Setzer (1971).

There appears to be very little published information on the habitat preferences of South African small mammals. Concerning the shrews, Roberts (1951) made the broad statements that Mysorex "appears to occur only in moister areas, especially in forests or scrub" and that Crocidura "may occur in any sort of habitat". M. varius has been recorded in a wide variety of habitats (Lynch 1975, Rautenbach 1976 and 1978a, Bond et al. 1980) including grassland and fynbos, and at Cathedral Peak it was trapped

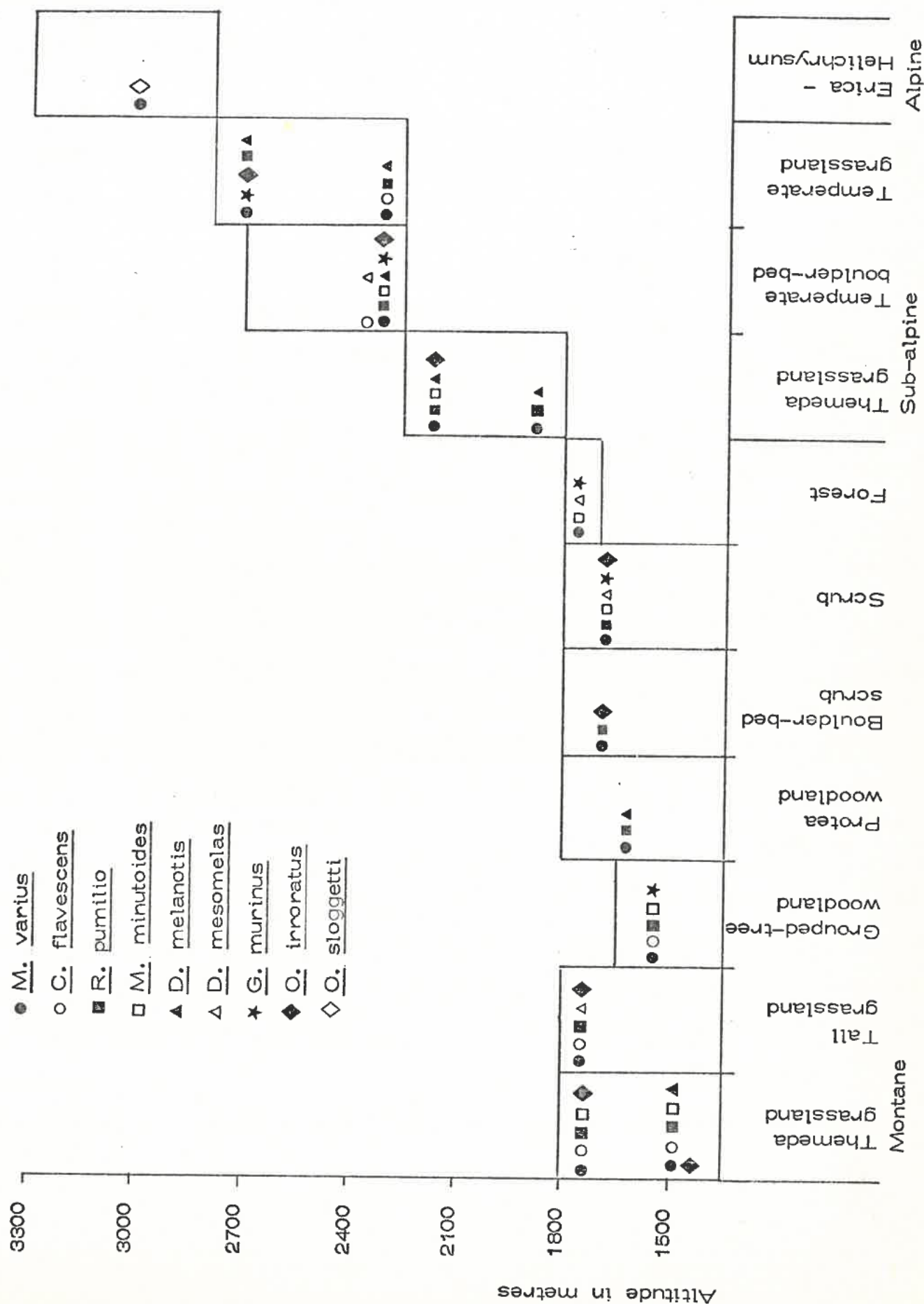


Figure 1.1 Distribution of small mammals in GCGR by altitude and vegetation types. The blocks indicate altitudinal ranges of the vegetation types.

in the same range of habitats as at GCGR (Rowe-Rowe 1977a). C. flavescens was recorded in boulder-bed scrub and grassland from 1 430 to 2 700 m at Cathedral Peak (Rowe-Rowe 1977a) but was not trapped in forest (Appendix 1). Elsewhere it has been recorded in a number of vegetation types (Meester 1963, Rautenbach 1978a). Characteristics of the species' main habitat requirements recognised by Rautenbach (1978a) are dense cover and high rainfall.

Brooks (1974) described R. pumilio as a broad-niche species. In southern Africa it occurs in habitats ranging from moist grassland to Kalahari dune veld (Smithers 1971, Lynch 1975, Nel and Rautenbach 1975, Perrin 1980a, Bond et al. 1980). R. pumilio is essentially a grassland species, and occurs in fynbos or Acacia scrub only where there is good grass cover (Bond et al. 1980, Smithers 1971). Grass cover in woodland and scrub communities in the Drakensberg is good, therefore accounting for the species' almost even distribution over these habitats and grassland.

O. irroratus was generally believed to be a species which occurred in grassy or vleis situations close to water. Davis (1973), however, pointed out that this was not the case, but that the species enjoys a much wider distribution, occurring throughout grassland, although being more abundant in moist habitats. In GCGR, for example, O. irroratus was trapped on ridge tops and on the escarpment at considerable distances from water.

Preferred habitats of the other GCGR species are similar to those described by Roberts (1951): O. sloggetti occurs at high altitudes amongst rocks and forbs; G. murinus is found mainly among rocks and trees; M. minutoides occurs in almost any habitat; D. mesomelas is associated with rank scrub or grass vegetation; and D. melanotis is merely described as being more terrestrial than D. mesomelas.

The two main components in the habitat preference of the arboreal G. murinus appear to be trees or rocks, where it nests either in holes in trees or in rock crevices. In GCGR it was collected in forest; grouped-tree woodland, which although essentially grassland, includes groups of trees around rocks (Fig 1.2); Buddleia-Leucosidea scrub, which included rocks and large shrubs (Fig 1.6); temperate grassland boulder-bed (Fig 1.8 - a rocky drainage line on the escarpment); and at the upper limit of temperate grassland, where one was trapped near large rocks at the base of a basalt cliff. Smithers (1971) found that the species had a wide habitat tolerance ranging from dry to moist in Botswana, but was always associated with trees, and Rautenbach (1976) collected G. murinus from a treeless rocky area.



Figure 1.2 Grouped-tree woodland.

Smithers (1971) was more specific in his description of the preferred habitat of D. melanotis than was Roberts (1951), stating that it preferred thick stands of tall grass. In GCGR the species was recorded in grassland up to 33 mo after fire, but was not found in tall grassland, rank fire-protected grassland, and scrub or forest habitats. D. mesomelas on the other hand was collected in forest, scrub, and tall grassland.

As P. natalensis was collected only near dwellings it is difficult to comment on its habitat preferences in GCGR. At Cathedral Peak the species was collected in Themeda grassland (shortly after fire), tall grassland and scrub, but did not occur above 1 500 m (Rowe-Rowe 1977a, Meester et al. 1979). Small mammal sampling in GCGR was not done below 1 500 m, but Hughes (pers.comm.)* collected P. natalensis in the Hillside section of the reserve at 1 380 m. It is an adaptable species with wide habitat tolerances (Meester et al. 1979), but has so far not been recorded in natural habitats above 1 500 m in the Drakensberg.

* G.R. Hughes, Natal Parks Board, Pietermaritzburg.

RELATIVE ABUNDANCE OF SPECIES

Either one of two species (R. pumilio or M. varius) was dominant in catches from all habitats except forest and protea woodland. In the Montane Belt R. pumilio was the dominant species in grassland, woodland, and scrub but was replaced by G. murinus in forest (Table 1.3, Fig 1.3). At the lower altitudinal limit (1 900 m) of the Sub-alpine Belt R. pumilio was dominant in burnt grassland but not in fire-protected grassland at the same altitude, where M. varius was caught in greater numbers. At all higher altitudes M. varius was dominant, and the numbers of R. pumilio captured decreased along the altitudinal gradient until lowest proportions were recorded at the upper limits of temperate grassland (Fig 1.3).

The decrease in relative importance of R. pumilio with increase in altitude is probably related to the decreasing amount of grass cover with increase in altitude (see Fig 1.4). Decrease in total above-ground standing crop was most marked from 2 200 m onwards and corresponds to the smaller numbers of R. pumilio in the catch. A similar pattern was observed at Cathedral Peak (Rowe-Rowe 1977a): R. pumilio was not recorded in temperate grassland on the escarpment slope, where M. varius was the dominant species, but in almost all grassland and scrub habitats at lower altitudes R. pumilio was dominant (see Appendix 1).

Food abundance possibly contributes to the success of M. varius at higher altitudes. A preliminary survey of arthropods in GCGR has indicated that they are more abundant on the escarpment than at lower altitudes (Miller pers.comm.*, Appendix 2), particularly the prey most commonly eaten by M. varius (cf. Appendix 3). The arthropod survey was done during summer, however, and it is not known whether this situation obtains throughout the year.

R. pumilio is diurnal (Brooks 1974), and although an omnivore, is mainly granivorous (Brooks 1974, and see chapter on "Diet"). It is therefore largely dependent on grass for cover and as a source of food. M. varius on the other hand is nocturnal and insectivorous (Goulden and Meester 1978, Roberts 1951), and does not appear to rely heavily on good grass cover (see chapter on "Influence of fire on populations"), therefore accounting for its ability to exist in habitats which are unsuitable for R. pumilio.

The relative importance of O. irroratus is possibly under-represented in the sample. Davis (1973) commented on the difficulty of trapping the

* R. Miller, Dept of Entomology, University of Natal, Pietermaritzburg.

TABLE 1.3 Relative abundances of small mammals (number/100 trap nights) collected in various habitats in GCGR. Burnt areas are suffixed by B and fire protected areas by P. Arranged in ascending order of altitude.

Vegetation	Altitude (m)	Fire	<u>M. varius</u>	<u>R. pumilio</u>	<u>O. irroratus</u>	<u>D. melanotis</u>	<u>M. minutoides</u>	<u>C. flavescens</u>	<u>D. mesomelas</u>	<u>G. murinus</u>	<u>O. sloggetti</u>	Total
			<u>M.</u>	<u>R.</u>	<u>O.</u>	<u>D.</u>	<u>M.</u>	<u>C.</u>	<u>D.</u>	<u>G.</u>	<u>O.</u>	
Montane Belt												
<u>Themeda</u> grassland	1 500	B	0,3	3,3	0,8	0,2	0,2	0,2	-	-	-	5,0
<u>Themeda</u> grassland	1 540	P	4,2	5,8	-	-	-	0,4	-	-	-	10,4
Grouped-tree woodland	1 540	B	0,8	6,3	-	-	0,2	0,7	-	0,3	-	8,3
Protea woodland	1 660	B	0,2	0,2	-	0,2	-	-	-	-	-	0,6
Boulder-bed scrub	1 720	B	5,8	9,2	1,7	-	-	-	-	-	-	16,7
<u>Themeda</u> grassland	1 740	B	1,0	4,2	0,3	0,2	0,2	0,3	-	-	-	6,2
Scrub	1 760	B	1,7	5,0	0,8	-	0,8	-	0,4	0,8	-	9,6
Scrub	1 760	P	5,8	11,6	-	-	-	-	-	-	-	17,5
Tall grassland	1 800	B	3,6	5,3	2,2	-	-	0,3	0,3	-	-	11,7
Forest	1 800	P	1,5	-	-	-	0,2	-	0,4	3,8	-	5,8
Sub-alpine Belt												
<u>Themeda</u> grassland	1 900	B	2,0	6,7	-	0,3	-	-	-	-	-	9,0
<u>Themeda</u> grassland	1 860	P	5,8	3,3	-	0,8	-	-	-	-	-	10,0
<u>Themeda</u> grassland	2 200	B	6,3	4,0	0,4	2,1	0,4	-	-	-	-	13,1
<u>Themeda</u> grassland	2 200	P	5,8	1,0	0,2	0,6	-	-	-	-	-	7,7
Temp grassland boulder-bed	2 300	B	5,6	3,5	0,8	1,3	0,1	-	-	0,6	-	11,8
Temperate grassland	2 300	B	6,4	2,3	-	0,8	-	0,2	-	-	-	9,8
Temperate grassland	2 700	B	8,8	2,9	0,4	0,8	-	-	-	0,4	-	13,3
Alpine Belt												
<u>Erica-Helichrysum</u> *	3 000	B	10,0	-	-	-	-	-	-	-	1,7	11,7

* Data from top of Sani Pass

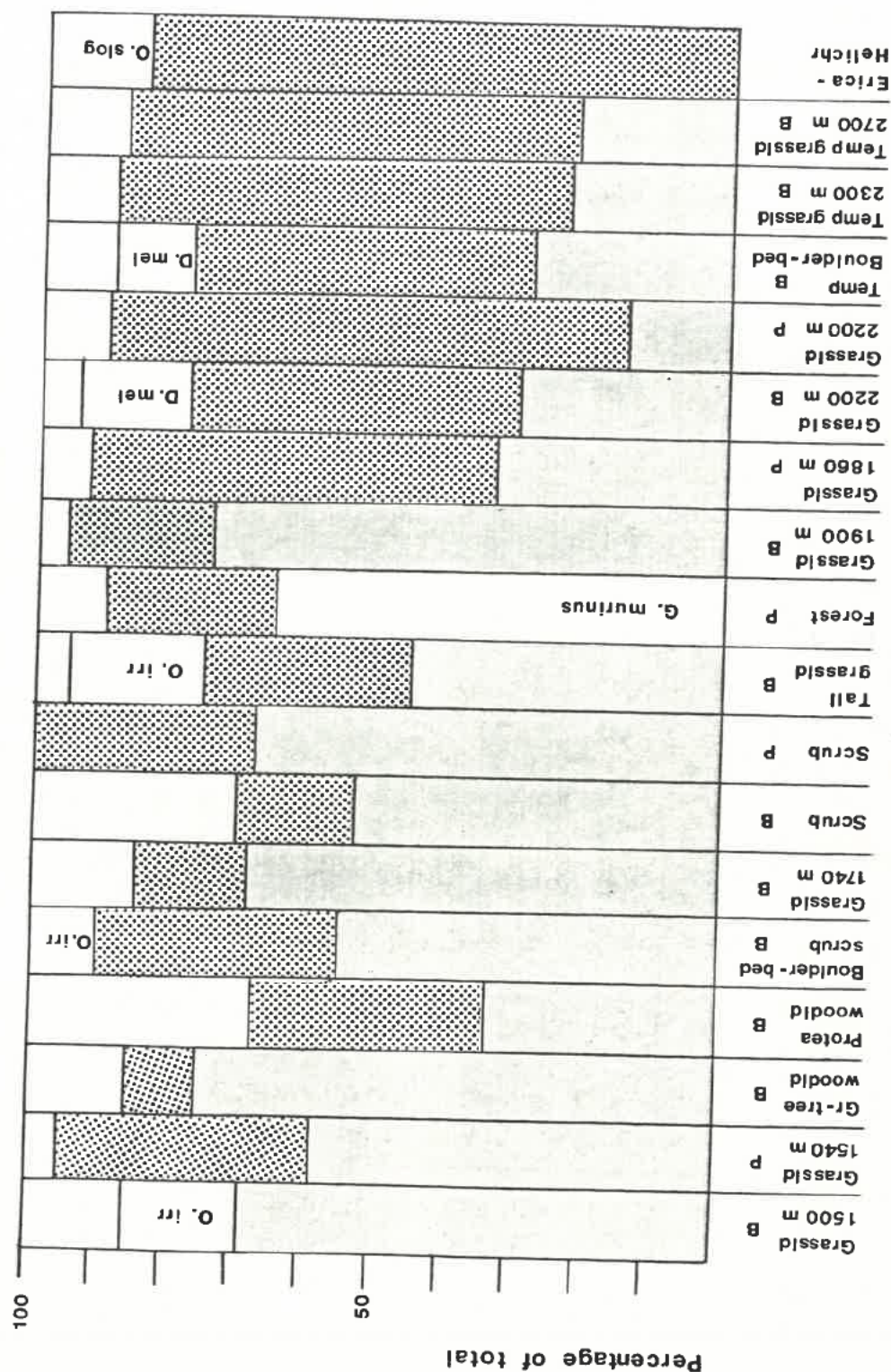


Figure 1.3 Percentage contribution by *R. pumilio* (shaded), *M. varius* (stippled), and other species (open bars) to the total number of small mammals caught. If any one species made a significant contribution to "other species", it is listed in abbreviated form in portion of the open bar. Habitats are arranged in ascending order of altitude from left to right.

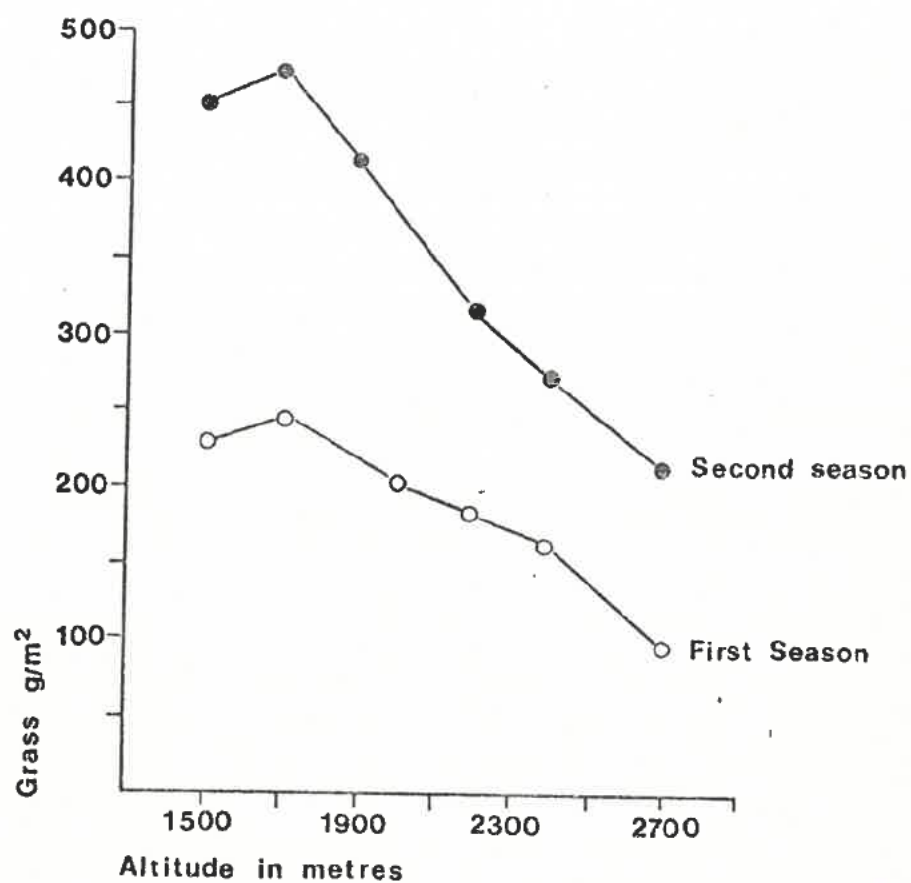


Figure 1.4 Above-ground standing crop of herbage, expressed in g/m² (dry mass) between 1 500 and 2 700 m, at the end of the first and second growing seasons in biennially-burnt grassland. (Incorporating data from Scotcher *et al.* 1980b.)

species and so too do Bond et al. (1980). Signs of O. irroratus (faeces and feeding signs) observed in grassland, woodland, and scrub suggested a higher proportion of the species in small mammal communities than indicated in overall trapping success. Similarly, the relative abundance of O. sloggetti is probably an under-representation of its relative abundance in the Alpine Belt. Numerous individuals were seen on rocks and in the summit vegetation at Sani Pass, and the species has been seen at the top of Bannerman Pass (GCGR), above Organ Pipes Pass (Cathedral Peak), and near the summit of Mont-aux-Sources.

With the exception of D. melanotis in the upper Themeda grassland/lower temperate grassland habitats, other species did not contribute significantly to the overall sample.

At both GCGR and Cathedral Peak R. pumilio made the greatest numerical contribution to the overall sample (Table 1.4), and M. varius was the most ubiquitous and second most abundant. All other species contributed only 17 % to the GCGR total and 24 % to that of the Cathedral Peak sample.

TABLE 1.4 Per cent contribution to total sample and number of habitats in which each species was recorded in two Drakensberg study areas (Cathedral Peak data from Rowe-Rowe 1977a - see Appendix 1).

Species	Per cent contribution		Presence (no. habitats)	
	GCGR	Cathedral Pk	GCGR	Cathedral Pk
<u>M. varius</u>	38,7	27,6	17	14
<u>C. flavescens</u>	1,6	5,4	7	9
<u>R. pumilio</u>	44,1	48,1	16	13
<u>P. natalensis</u>	*	3,5	1	4
<u>O. irroratus</u>	4,9	8,2	9	9
<u>D. melanotis</u>	4,9	-	9	-
<u>D. mesomelas</u>	0,6	1,8	4	4
<u>M. minutoides</u>	1,3	2,1	7	6
<u>T. dolichurus</u>	-	0,5	-	2
<u>G. murinus</u>	3,9	2,6	5	2
<u>O. sloggetti</u>	*	*	1	1

* Present

SMALL MAMMAL TRAP SUCCESS, SPECIES RICHNESS, AND DIVERSITY

The small mammal trap success, species richness, and diversity in all habitats sampled are illustrated in Fig 1.5.

MONTANE BELT HABITATS

In the Montane Belt greater small mammal trap success was recorded in protected grassland than in burnt Themeda grassland, but species richness and diversity were higher in the two burnt grassland habitats. Tall grassland proved to be one of the richest habitats, scoring highly in trap success, species richness, and diversity.

The two woodland habitats differed markedly. Grouped-tree woodland yielded a fairly high trap success (8,3 %) and species richness, whereas protea woodland yielded the lowest trap success of all habitats sampled (0,6 %). Diversity of the protea habitat was higher than that of grouped-tree woodland, but this was because only three animals representing three species were captured, and the diversity index therefore expresses an even representation of species. The importance of protea woodland as a small mammal habitat in GCGR may nevertheless be regarded as low.

Boulder-bed scrub (on river levees) and fire-protected scrub yielded higher trap successes than did occasionally-burnt Buddleia-Leucosidea scrub, but it was in the last-mentioned habitat that greatest species richness and diversity were recorded. The fire-protected scrub developed from grassland which had been protected for 16 y and consisted mainly of a fairly uniform stand of Philippia bushes and grass. The only two mammal species captured were typical of grassland (Table 1.3). The boulder-bed scrub is burnt biennially in autumn and is also a fairly uniform habitat consisting of grass and predominantly Leucosidea bushes. The patch of Buddleia-Leucosidea scrub sampled was more complex. Fire occasionally sweeps throughout it, but usually only the margins are burnt, with the fire penetrating only portions of the habitat. The vegetation is a mixture of grass and scrub (Leucosidea, Philippia, Buddleia, Cliffortia, Euclea), interspersed with fairly large bushes such as Bowkeria and a few forest trees such as Olinia and Podocarpus, and the complexity of the habitat is further increased by the presence of large rocks (Fig 1.6). It is understandable therefore why the small mammal population is the most diverse in GCGR, being a mixture of forest and grassland species.

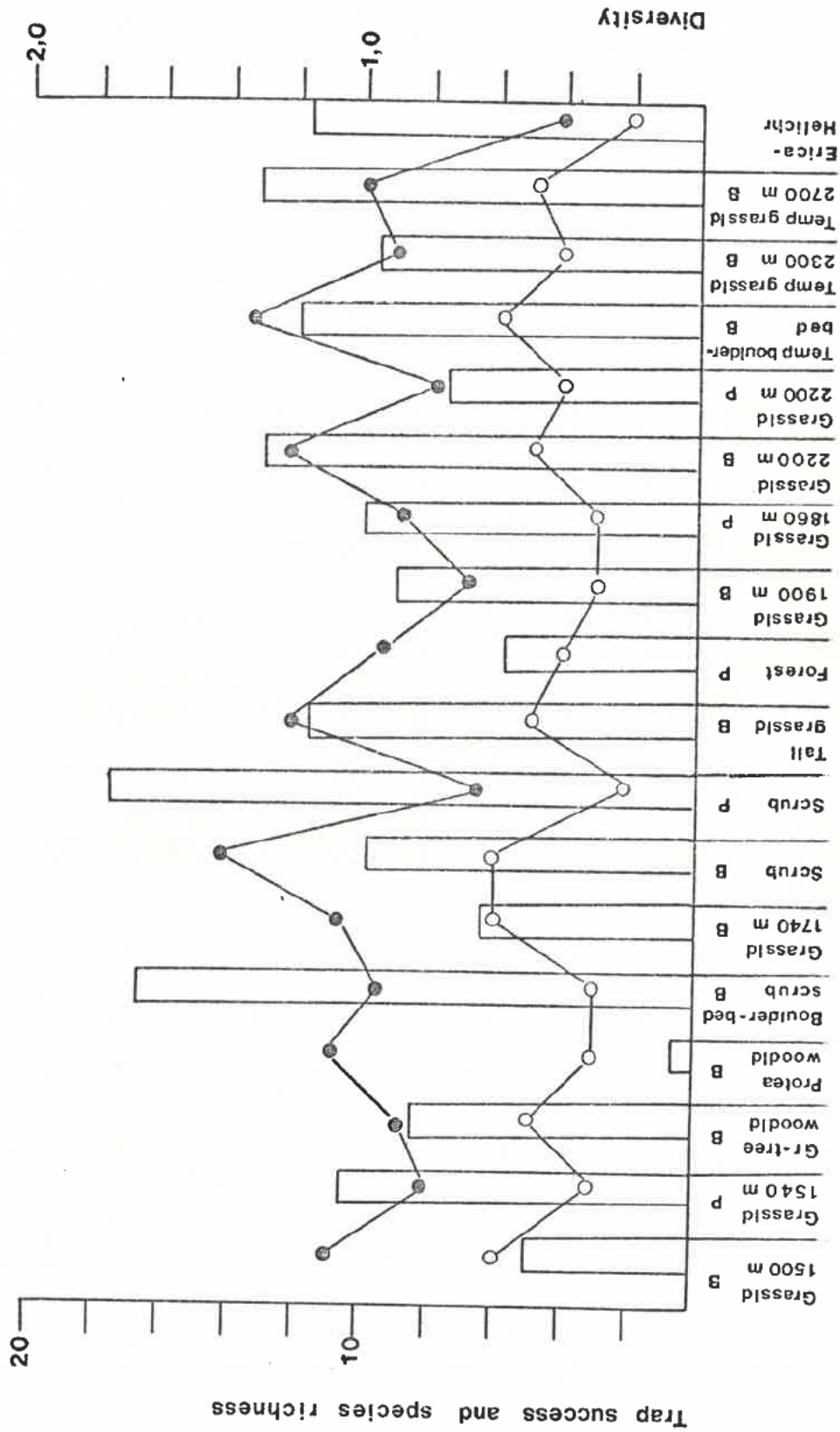


Figure 1.5 Small mammal abundance relations in various habitats in GGR. Abundance (histogram) expressed as captures/100 trap nights, species richness ○, and diversity ● (calculated from number of individuals of each species).



Figure 1.6 Portion of a patch of occasionally-burnt Buddleia-Leucosidea scrub.

Trap success in the forest itself was lower than in any of the scrub habitats, and all but one grassland habitat.

SUB-ALPINE BELT HABITATS

Trap success and species richness of biennially-burnt Themeda grassland and 16 y-old grass at the lower limit of the Sub-alpine Belt were similar. Diversity of the burnt grassland was lower, however, due to the preponderance of R. pumilio, which made up 80 % of the catch. At the upper limit of sub-alpine Themeda grassland the biennially-burnt habitat yielded greater trap success, species richness, and diversity than did the 2 to 4 y-old grass at the same altitude.

In the temperate grassland species richness and diversity were similar at the upper and lower limits, but trap success was greater at the higher altitude. This could be because the higher habitat was sampled only twice, when the veld was 17 and 23 mo old, a stage when trap success tends to be high at this elevation. The boulder-bed habitat in the temperate grassland was richer in trap success, number of species, and diversity than was the open grassland on either side of it. Whereas open temperate grassland (Fig 1.7) is a very homogeneous habitat, the boulder-bed is heterogeneous - it is rocky and, although predominantly grassland, contains a fair number of forbs and some stunted bushes (Fig 1.8).

ALPINE BELT

The proportions of M. varius and O. sloggetti in the Alpine Belt sample are, as already stated, probably not a good representation of these species' proportions in the community, and true diversity is possibly higher than recorded.

DISCUSSION

Trap success, species richness, and diversity of GCGR and Cathedral Peak (Appendix 1) are similar. Overall trap success in GCGR was 9,4 %, nine species were collected (excluding P. natalensis), and diversity was 1,34. At Cathedral Peak trap success was 10,1 %, 10 species were recorded, and diversity was 1,39. Further north in the Drakensberg (Golden Gate National Park) Rautenbach (1976) recorded two shrew and 10 indigenous small rodent species.

Montane small mammal faunas appear to be poorer in species richness (and possibly density and diversity) than those of the ecologically more complex lowveld areas. Compare, for example, the Drakensberg with the



Figure 1.7 Open temperate grassland on the escarpment.



Figure 1.8 Temperate grassland boulder-bed. Compare this more heterogeneous habitat with the open temperate grassland on the right and in Fig 1.7.

Hluhluwe-Umfolozi Game Reserve complex where Bourquin *et al.* (1971) recorded 19 small mammal species (six insectivores and 13 rodents), or Kruger National Park where Pienaar (1964) lists 23 species (eight insectivores and 15 indigenous rodents). It is not possible to calculate diversities from the above-mentioned figures, but in two study areas in the Kruger National Park Kern (1977) recorded nine small mammal species, and the Shannon-Wiener diversity index calculated from his data is 1,97.

A number of authors (e.g. Pianka 1966) have related decreasing species richness to increasing latitude, and Simpson (1966) found that altitude, relief, and rainfall influenced species numbers in North America. Nel (1975) examined South African mammal communities on a longitudinal basis, finding the strongest correlation between species richness and rainfall which increases from west to east. In the Transvaal Rautenbach (1978b) reported declining species richness from north to south and from east to west - the more complex habitats being in the north and the east.

In the mountains of the southern Cape Province species richness is similar to that of the Drakensberg, and abundance is in some cases lower: Bond *et al.* (1980) in two areas recorded seven and six species with trap successes of 6,4 % and 8,9 % respectively, and Nel *et al.* (1980), sampling two areas in the Kammanassie Mountains, recorded 10 and seven species and trap successes of 1,9 % and 2,1 % respectively. In the Cedarberg (Rautenbach and Nel 1980) overall species richness was higher (14 spp.) but trap success was only 3,9 % and most habitats reflected low diversities and species richness.

Both in GCGR and at Cathedral Peak species abundance relations were similar in all grassland habitats (Rowe-Rowe 1977a, Appendix 1). Trap success and species richness of small mammals is lower in montane grassland than that recorded in tropical grassland: on a live-trapping grid in tropical grassland on the equator in Uganda, Cheeseman and Delany (1979) collected 10 small rodent species with a mean monthly trap success of 9,5 % (calculated from the authors' data). Neal (1970), who also did a small rodent study in Uganda at similar latitude and altitude, recorded 11 and 10 species, with trap successes of 13,6 % and 18,2 % in *Themeda triandra* grassland. Diversities were 1,71 and 1,25 respectively. If shrews are excluded from the GCGR grassland data, small rodent trap success is 4,9 %.

Species richness and trap success were lowest in protea woodland in both GCGR and Cathedral Peak. At another locality in the Drakensberg (Royal Natal National Park) Lee (1976) recorded a trap success of 1,7 % in protea woodland and trapped only *R. pumilio*. Protea woodland develops on shallow

soils overlying rock (Edwards 1967). In the protea woodland habitat sampled in GCGR the soil was of a Mispah form (van der Eyk *et al.* 1969) with underlying hard rock. Characteristics of this soil are that it has a shallow A-horizon, and is infertile, lacking in organic matter. The shallow soil is very hard and appears to be unsuitable for small mammals.

Dueser and Brown (1980) concluded that increased habitat complexity promotes increased small mammal species richness. The two most complex habitats sampled in GCGR were the Buddleia-Leucosidea scrub and the temperate grassland boulder-bed, and it was in these habitats that highest small mammal diversity and species richness were recorded.

The forest habitats in GCGR and Cathedral Peak yielded almost identical trap success, species richness, and diversity, but species composition differed (Table 1.3, Appendix 1). In forest at Royal Natal National Park Lee (1976) recorded a trap success of 2.3 % and found that G. murinus was the dominant species. A species collected in the forests of both Cathedral Peak and Royal Natal National Park, but not collected in GCGR, was Thomomys dolichurus. The forest in GCGR differs from that in the other two areas in that it is dominated by Olinia emarginata trees, whereas those at Cathedral Peak and Royal Natal National Park are dominated by Podocarpus spp. and have a denser canopy cover.

In contrast to the poor small mammal faunas of the montane forests are the higher abundance relations recorded in tropical forests in Sierra Leone (Cross 1977). Rodent trap success in two forest habitats was 12 % and 10 %, the samples comprised eight and nine species, and diversities calculated from Cross' data are 1.24 and 1.59.

Small mammal diversity in the Drakensberg appears to be related to succession, increasing from the pioneer stage, reaching an asymptote during an intermediate stage (such as in the Buddleia-Leucosidea scrub in GCGR or forest margin in Cathedral Peak), then declining again in the climax stage.

Although measures of diversity are useful in providing information on evenness of species representation (Pielou 1969, Poole 1974, Routledge 1979), they do not altogether indicate the importance of the habitat in the ecology of the area. Some habitats having low diversities but high densities may, depending on the dominant small mammal species and type of cover, be important to avian and terrestrial predators; whereas some other habitats may have high diversities and play a minor part as a source of prey, but perhaps a major role as a reservoir for a number of species. These aspects will be discussed in more detail in the section on fire.

INFLUENCE OF FIRE ON POPULATIONS

The immediate effects of fire on small mammal populations will be dealt with first, then long-term effects and the recolonisation of different habitats over 1 to 2 y following fire will be discussed in detail.

IMMEDIATE EFFECTS

Three habitats were being sampled at the time that a runaway fire in August 1978 burnt about 50 % of GCGR. Traps had been set in a patch of fire-protected scrub, an area of 1 y-old biennially-burnt grassland, and a firebreak between these two habitats. The firebreak had been burnt during May and cover was poor, the grass having grown to a height of ca 60 mm.

On the first night that the traps were set (the night before the fire) the following small mammals were caught: two R. pumilio and two M. varius in the scrub, three R. pumilio and one M. varius in the grassland, and nothing in the firebreak. The scrub and grassland were completely burnt on the following morning, but the firebreak was not. Trapping continued in all three habitats for the next three nights.

No small mammals were captured in the burnt scrub and one O. irroratus with an empty stomach was caught in the grassland during the night following the fire. Eleven animals were caught in the firebreak during the three-night period, giving a trap success of 12,2 %. The catch comprised 10 R. pumilio and a single D. melanotis. (The same firebreak, which is burnt annually, was sampled during August of the following year for comparison - trap success was 2,5 %, made up of two M. minutoides and one M. varius.)

R. pumilio is a species which occurs in areas with good grass cover, and is usually only present in high numbers about 6 to 12 mo after fire (Meester et al. 1979, this study). The R. pumilio which were trapped on the firebreak were probably animals which escaped burning in the protected scrub and 1 y-old grassland by sheltering in burrows or under rocks, but predators are likely to have taken a high toll of the survivors - a month later only one R. pumilio was caught in 120 trap nights near some large rocks in this same firebreak.

LONG-TERM EFFECTS

Information on recolonisation in relation to time since the veld was last burnt was collected in biennially-burnt Themeda grassland at three elevations, viz 1 500 m, 1 900 m, and 2 200m, and compared with the situa-

tion in unburnt controls at the same elevations. In temperate grassland sampling was done in biennially-burnt open grassland and in a biennially-burnt boulder-bed. Two annually-burnt grassland habitats were sampled in the Montane Belt. A variety of other habitats were sampled in the Montane Belt, viz: biennially-burnt woodland, scrub (biennially-burnt, occasionally-burnt and protected), and forest.

Biennially-burnt and unburnt Themeda grassland

1. Montane Belt Themeda grassland at 1 500 m

When first sampled, 3 mo after it had been burnt during autumn, no small mammals were caught at 1 500 m (Table 1.5). Cover was poor at the time as the burn had benefited from only about two months of growth before the onset of the dormant winter period - herbage was measured at 50 g/m² (Scotcher et al. 1980b). At 7 mo, when herbage had increased to 110 g/m², four animals representing four species were trapped (Table 1.5). Maximum trap success (10 %) was recorded at 12 mo (herbage 240 g/m²) when only R. pumilio and O. irroratus were collected, and had declined to 5,0 % when finally sampled at 23 mo, at a time when herbage was 457 g/m².

Trap success in the control varied between 5,8 % and 15,8 % (Table 1.5), and with the exception of the first occasion sampled, catches were dominated by R. pumilio. No pattern of seasonal fluctuation was apparent: trap success was high during spring, low in autumn and spring, then high again in autumn. An obvious difference in mammal species composition between the two areas is that M. varius was not caught in the burnt area before the grass was 23 mo old, but was present on each occasion that the control was sampled.

2. Sub-alpine Belt Themeda grassland at 1 900 m

The spring-burnt Themeda grassland habitat at 1 900 m was dominated on all occasions sampled by R. pumilio, except at 2 mo when instead D. melanotis and M. varius were caught. Six months after being burnt, herbage was 160 g/m² (Scotcher et al. 1980b), and R. pumilio was the only species caught (Table 1.6), but trap success was almost four times that recorded in the autumn burn after 7 mo (Table 1.5). After 12 mo trap success in the spring burn at 1 900 m was similar to that in the autumn burn. Overall trap success at 1 900 m followed the same pattern as that in the autumn burn at 1 500 m and started to decline during the second year, decreasing from 12,5 % to 8,3 % when herbage measured 430 g/m² at the end of the second growing season.

TABLE 1.5 Small mammal abundance (N/100 trap nights) in biennially autumn-burnt *Themeda* grassland at 1 500 - 1 540 m and in a control plot in similar habitat.

Species	Months since burnt								
	Burnt area					Control			
	3	7	12	19	23	108	114	120	126
<i>M. varius</i>	-	-	-	-	1,7	10,0	1,7	1,7	3,3
<i>R. pumilio</i>	-	0,8	7,5	5,0	3,3	5,0	4,2	4,2	10,0
<i>C. flavescens</i>	-	0,8	-	-	-	0,8	-	-	0,8
<i>D. melanotis</i>	-	0,8	-	-	-	-	-	-	-
<i>M. minutoides</i>	-	0,8	-	-	-	-	-	-	-
<i>O. irroratus</i>	-	-	2,5	1,7	-	-	-	-	-
Total	0	3,3	10,0	6,7	5,0	15,8	5,8	5,8	14,2

TABLE 1.6 Small mammal abundance (N/100 trap nights) in biennially spring-burnt *Themeda* grassland at 1 900 m and in a control plot in similar habitat.

Species	Months since burnt							
	Burnt area					Control		
	2	6	11	15	22	36	42	192
<i>R. pumilio</i>	-	12,5	7,5	7,5	5,8	5,0	1,3	3,3
<i>M. varius</i>	2,5	-	4,2	0,8	2,5	-	2,5	5,8
<i>D. melanotis</i>	0,8	-	0,8	-	-	-	-	0,8
Total	3,3	12,5	12,5	8,3	8,3	5,0	3,8	10,0

The control at 1 900 m, which had remained unburnt for 16 y, was dominated by M. varius, which appears to be more abundant in long-term unburnt grassland than in burnt grassland (Tables 1.5 and 1.6). The runaway fire during August 1978 burnt the entire control area, but it was sampled again 36 and 42 mo later. On both of these occasions trap success was lower than that recorded when the habitat was 16 y old and also lower than that recorded in the biennially-burnt grassland at the same altitude.

3. Sub-alpine Belt Themeda grassland at 2 200 m

At 2 200 m recolonisation took place almost as rapidly in the spring-burnt grassland as at 1 900 m, but more species were present during the first year (Table 1.7). Initially numbers of R. pumilio caught exceeded those of M. varius, but from 17 mo onwards the latter species dominated. On one occasion D. melanotis was the dominant species in the burnt grassland, and at the same time (May) the species was caught also in the unburnt control.

On all occasions that the control at 2 200 m was sampled M. varius dominated the catch. With the exception of one trapping session (41 mo) species richness and trap success were lower than in the burnt area. Herbage was 560 g/m² at the end of the third growing season (Scotcher et al. 1980b) and 680 g/m² at the end of the fourth. In the analyses of all herbage samples from the control (collected monthly 26 to 36 mo after fire) the amount of dry grass exceeded green grass - usually being at least twice as much (Scotcher et al. 1980b).

Biennially-burnt temperate grassland

Winter-burnt temperate grassland was sampled at 2 300 m in open grassland and in a boulder-bed (Tables 1.8 and 1.9). When first sampled 2 mo after being burnt, only M. varius was collected in open grassland and trap success was 5 %. In the boulder-bed, on the other hand, six species were collected and trap success was 12,5 %. In an earlier section I commented on the differences between open grassland and the boulder-bed, particularly the greater amount of cover and more complex habitat of the boulder-bed. Furthermore, herbage growth is more rapid in the boulder-bed: at 2 mo herbage was 27 g/m² in open grassland and 79 g/m² in the boulder-bed. At the end of the growing season the open grassland reached a peak of 171 g/m² whereas herbage in the boulder-bed was 279 g/m².

What appears to happen in the open temperate grassland/boulder-bed habitat is that a nucleus of a variety of small mammals survives in the

TABLE 1.7 Small mammal abundance (N/100 trap nights) in biennially spring-burnt Themeda grassland at 2 200 m and in a control plot in similar habitat.

Species	Months since burnt							
	Burnt area				Control			
	3	9	17	22	27	33	41	46
<u>M. varius</u>	3,3	3,3	5,0	13,3	3,3	9,1	5,8	5,0
<u>R. pumilio</u>	4,2	4,2	2,5	5,0	1,7	-	1,7	0,8
<u>D. melanotis</u>	1,7	6,7	-	-	-	2,5	-	-
<u>M. minutoides</u>	-	1,7	-	-	-	-	-	-
<u>O. irroratus</u>	-	-	-	1,7	0,8	-	-	-
Total	9,2	15,8	7,5	20,0	5,8	11,7	7,5	5,8

TABLE 1.8 Small mammal abundance (N/100 trap nights) in biennially winter-burnt temperate grassland at 2 300 m.

Species	Months since burnt			
	2	8	17	22
<u>M. varius</u>	5,0	10,8	2,5	7,5
<u>R. pumilio</u>	-	2,5	4,2	2,5
<u>D. melanotis</u>	-	1,7	-	1,7
<u>C. flavescens</u>	-	-	-	0,8
Total	5,0	15,0	6,7	12,5

TABLE 1.9 Small mammal abundance (N/100 trap nights) in a winter-burnt temperate grassland boulder-bed at 2 300 m.

Species	Months since burnt					
	2	9	8*	12	17	23
<u>M. varius</u>	7,5	2,5	7,5	4,2	3,3	8,3
<u>R. pumilio</u>	0,8	6,7	4,2	1,7	3,3	4,2
<u>G. murinus</u>	0,8	0,8	0,8	0,8	-	-
<u>D. melanotis</u>	0,8	2,5	-	1,7	-	2,5
<u>O. irroratus</u>	1,7	-	0,8	-	1,7	0,8
<u>M. minutoides</u>	0,8	-	-	-	-	-
Total	12,5	12,5	13,3	8,3	8,3	16,0

* Burnt two years consecutively

TABLE 1.10 Small mammal abundance (N/100 trap nights) in biennially winter-burnt temperate grassland at 2 700 m .

Species	Mo since burnt	
	17	23
<u>M. varius</u>	9,2	8,3
<u>O. irroratus</u>	0,8	-
<u>G. murinus</u>	0,8	-
<u>R. pumilio</u>	-	5,8
<u>D. melanotis</u>	-	1,7
Total	10,8	15,8

boulder-bed where an initial increase in numbers takes place in the presence of good plant growth, followed by emigration to the open grassland when cover there has increased. From about 9 mo onwards small mammal numbers in the two habitats appear to be similar (Tables 1.8 and 1.9).

M. varius was the dominant species in the catch on both occasions that the biennial winter burn at 2 700 m was sampled (Table 1.10).

When first sampled at 17 mo, no R. pumilio were trapped when herbage measured 84 g/m². At 23 mo, however, the species was collected in the upper reaches of drainage lines where there were some dense patches of grass (Themeda and Festuca). At this stage herbage amounted to 230 g/m². Insufficient data were collected to comment further on recolonisation at 2 700 m.

Annually-burnt grassland

1. Themeda grassland

At 1 740 m the pattern of recolonisation (Table 1.11) was initially similar to that observed in the other Montane Belt burnt Themeda grassland habitat (Table 1.5), but trap success was higher. Herbage in the spring burn at 1 740 m, however, was more abundant (180 g/m² at 6 mo) than that in the autumn burn at the same stage (110 g/m²). At 12 mo an inexplicable decrease in trap success was recorded, but when sampled again during the second year a peak of 10 % was recorded after 14 mo of growth.

With the exception of the first occasion sampled (at 1 mo), R. pumilio was dominant in the catch.

2. Tall grassland

An annually spring-burnt tall grassland (Miscanthidium-Cymbopogon grassland) habitat at 1 800 m was sampled three times (Table 1.12). Initially only M. varius was caught. At 6 mo trap success was 10.8 %, made up of five species, and by 11 mo it had more than doubled but only three species were recorded.

Herbage production was not measured in tall grassland. The two dominant grass species grow very rapidly after fire, reaching a height of ca 2 m by the end of the growing season (April). Good cover is therefore present much sooner after a burn than in Themeda grassland.

Woodland

When the autumn-burnt grouped-tree woodland habitat was first sampled 1 mo after burning, grass cover was very poor and only G. murinus was captured (Table 1.13). After 9 mo the catch was dominated by the grassland

TABLE 1.11 Small mammal abundance (N/100 trap nights) in annually spring-burnt Themeda grassland at 1 740 m .

Species	Months since burnt				
	1	6	12	6*	14
<u>D. melanotis</u>	0,8	-	-	-	-
<u>M. varius</u>	1,7	1,7	-	-	1,7
<u>R. pumilio</u>	-	3,3	3,3	5,8	8,3
<u>C. flavescens</u>	-	0,8	-	0,8	-
<u>M. minutoides</u>	-	0,8	-	-	-
<u>O. irroratus</u>	-	-	1,7	-	-
Total	2,5	6,7	5,0	6,7	10,0

* Burnt two years consecutively.

TABLE 1.12 Small mammal abundance (N/100 trap nights) in annually spring-burnt tall grassland.

Species	Months since burnt		
	1	6	11
<u>C. flavescens</u>	-	0,8	-
<u>D. mesomelas</u>	-	0,8	-
<u>O. irroratus</u>	-	1,7	5,0
<u>R. pumilio</u>	-	4,2	11,7
<u>M. varius</u>	1,7	3,3	5,8
Total	1,7	10,8	22,5

TABLE 1.13 Small mammal abundance (N/100 trap nights) in biennially autumn-burnt grouped-tree woodland.

Species	Months since burnt				
	1	9	13	19	23
<u>G. murinus</u>	0,8	0,8	-	-	-
<u>C. flavescens</u>	-	0,8	1,7	0,8	-
<u>M. varius</u>	-	0,8	2,5	0,8	-
<u>R. pumilio</u>	-	5,0	15,0	8,3	3,3
<u>M. minutoides</u>	-	-	0,8	-	-
Total	0,8	7,5	20,0	10,0	3,3

TABLE 1.14 Small mammal abundance (N/100 trap nights) in biennially autumn-burnt protea woodland.

Species	Months since burnt			
	1	7	13	19
<u>M. varius</u>	0,8	-	-	-
<u>D. melanotis</u>	-	-	0,8	-
<u>R. pumilio</u>	-	-	-	0,8
Total	0,8	0	0,8	0,8

species R. pumilio, and this was the case on the other three occasions that the habitat was sampled, a peak of 20 % being reached after 13 mo, when the R. pumilio component was 15/100 trap nights. As was the case in spring- and autumn-burnt grassland at lower altitudes, density decreased during the second year.

Protea woodland, also burnt during autumn, was sampled four times (Table 1.14). At 1 mo one M. varius was caught, and at 7 mo the catch was nil. One D. melanotis was the only animal caught at 13 mo, and at 19 mo one R. pumilio was taken.

Scrub

Autumn-burnt boulder-bed scrub yielded higher trap success from 6 to 24 mo after fire than did most grassland habitats (Table 1.15), reaching a peak at 18 mo. At 6 mo M. varius and R. pumilio were equally represented in the sample, but thereafter R. pumilio was dominant. In boulder-bed scrub there is more cover soon after fire than is the case in open grassland - there are many small rocks and the bushes are usually not completely burnt by the cool autumn burn.

A patch of Buddleia-Leucosidea scrub was sampled 1 mo after an autumn fire had burnt right through it. Despite the fact that all grass and many small shrubs had been burnt, M. varius and two grassland rodents were present (Table 1.16). Although grass cover was minimal 1 mo after the burn, there was good cover in the form of large rocks, and large shrubs and trees. Furthermore, regrowth of grass was progressing fairly rapidly along the banks of the stream that flowed through the scrub. The margins of the area were partly burnt again during autumn 2 y later. It was sampled 6 mo after the marginal fire (i.e. 31 mo after it was completely burnt), at which stage a mixture of grassland and forest small mammals was present (Table 1.16).

In a patch of Philippi-Leucosidea scrub, which had developed as a result of 16 y of protection from fire, only two species were present (Table 1.16) and trap success was similar to that in 2 y-old boulder-bed scrub and the occasionally-burnt Buddleia-Leucosidea scrub. Both burnt and unburnt scrub habitats were dominated by R. pumilio.

Forest

Catches in the forest were dominated by G. murinus (Table 1.17). The numbers taken were similar on three of the four occasions, and no seasonal fluctuations in numbers were apparent. One other scrub/forest species (D. mesomelas) was collected twice, and the two other species recorded (M. varius

TABLE 1.15 Small mammal abundance (N/100 trap nights) in biennially autumn-burnt boulder-bed scrub.

Species	Months since burnt			
	6	12	18	24
<u>R. pumilio</u>	5,0	10,0	12,5	9,2
<u>M. varius</u>	5,0	4,2	7,5	6,7
<u>O. irroratus</u>	-	-	6,7	-
Total	10,0	14,2	26,7	15,8

TABLE 1.16 Small mammal abundance (N/100 trap nights) in burnt and unburnt scrub.

Species	Months since burnt		
	Burnt area		Control
	1	31	192
<u>M. varius</u>	1,7	1,7	5,8
<u>R. pumilio</u>	1,7	8,3	11,7
<u>O. irroratus</u>	0,8	0,8	-
<u>M. minutoides</u>	-	1,7	-
<u>D. mesomelas</u>	-	0,8	-
<u>G. murinus</u>	-	1,7	-
Total	4,2	15,0	17,5

TABLE 1.17 Small mammal abundance (N/100 trap nights) in fire-protected forest.

Species	Season			
	Wet	Dry	Wet	Dry
<u>G. murinus</u>	4,2	5,0	1,7	4,2
<u>M. varius</u>	3,3	2,5	-	-
<u>D. mesomelas</u>	-	0,8	-	0,8
<u>M. minutoides</u>	-	-	0,8	-
Total	7,5	8,3	2,5	5,0

and M. minutoides) were ubiquitous and recorded in a variety of other habitats.

DISCUSSION

The overall pattern which emerges from the sampling of the different habitats is that after fire numbers are initially low, and usually only the insectivorous M. varius is present. About 3 mo later grass cover is adequate for R. pumilio, and by 6 to 12 mo small mammal trap success reaches pre-burn figures (earlier in spring-burnt areas than in autumn burns). In grassland at low (1 500 m) and intermediate (1 900 m) altitudes small mammal numbers decline during the second year after burning, but at high altitudes (> 2 200 m) numbers remain fairly constant until the end of the second year, then begin to decline during the third year (Fig 1.9).

In fire-protected areas (unburnt for 9 to 16 y) trap success was similar to the peaks recorded in biennially-burnt habitats, but fewer species were recorded (Fig 1.10).

Possible reasons for the patterns of recolonisation in relation to season of burn, altitude, and habitat structure; and the bimodal peaks in small mammal numbers over the 1 to 16 y-period, are discussed in the sections which follow.

Effects on individual species

1. Myosorex varius

The small mammal most commonly present shortly after fire was the insectivore M. varius. This species is a burrower (Baxter and Meester 1980) which also shelters under rocks. Furthermore, as M. varius is nocturnal (Baxter et al. 1979) and controlled burning takes place during the day, some animals are likely to escape being killed directly by fire.

Fair numbers of insects, particularly those that shelter in the soil or under rocks, survive veld fires (Miller, pers.comm.*). Grass begins to grow within a few days of being burnt and is immediately invaded by herbivorous insects, particularly grasshoppers which occur in great numbers. There is therefore food at an early stage for the M. varius which escape burning.

Rice (1932) found that fire killed invertebrates on the surface, but those under logs or stones survived, and so too did those in the soil where a temperature increase of only 3° C was recorded at a depth of 50 mm. Norton

* Dr R. Miller, Dept of Entomology, University of Natal, Pietermaritzburg.

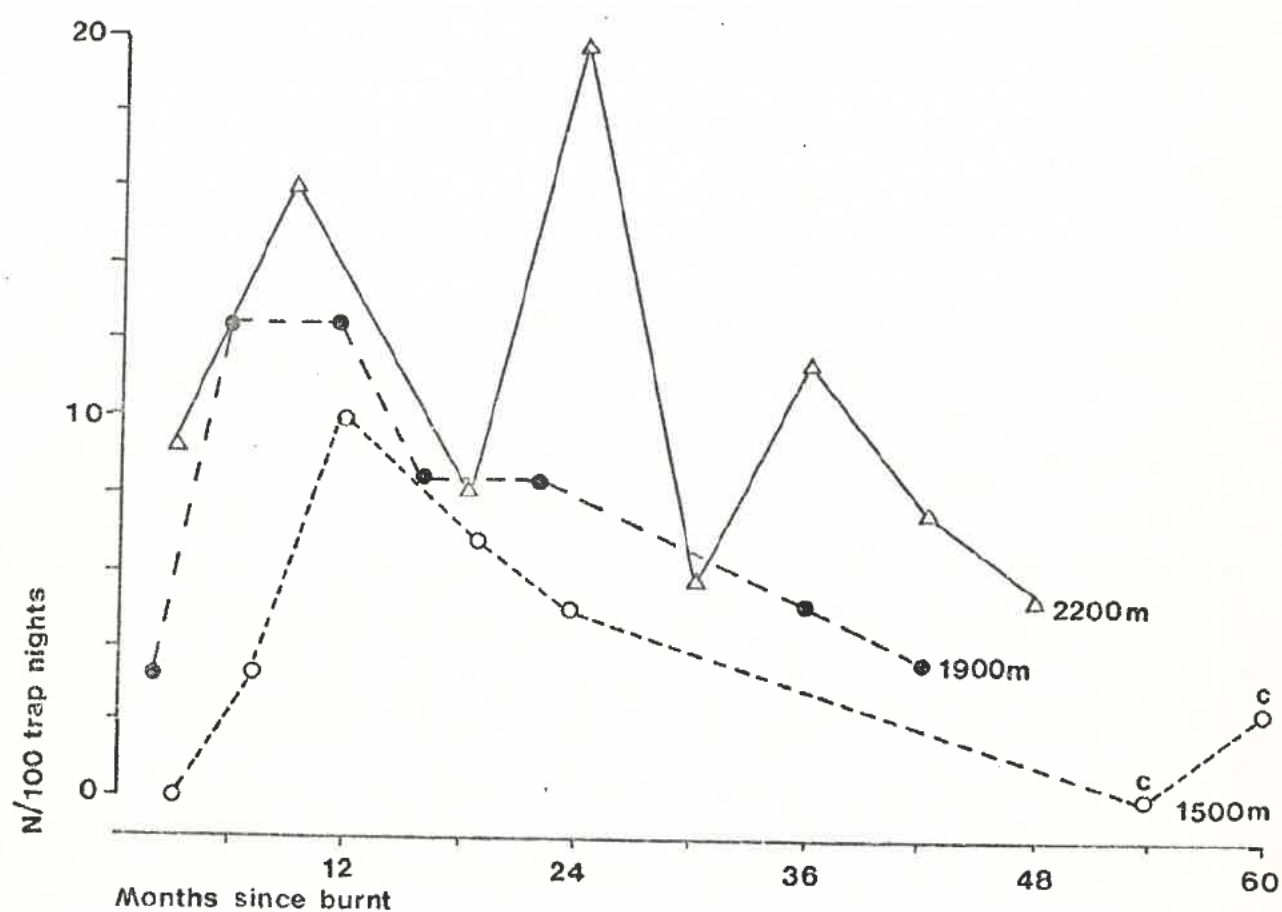


Figure 1.9 Number of small mammals caught (N/100 trap nights) in Themeda grassland at three elevations, in relation to time since the veld was burnt. Points marked c are based on data collected at Cathedral Peak (Mentis and Rowe-Rowe 1979).

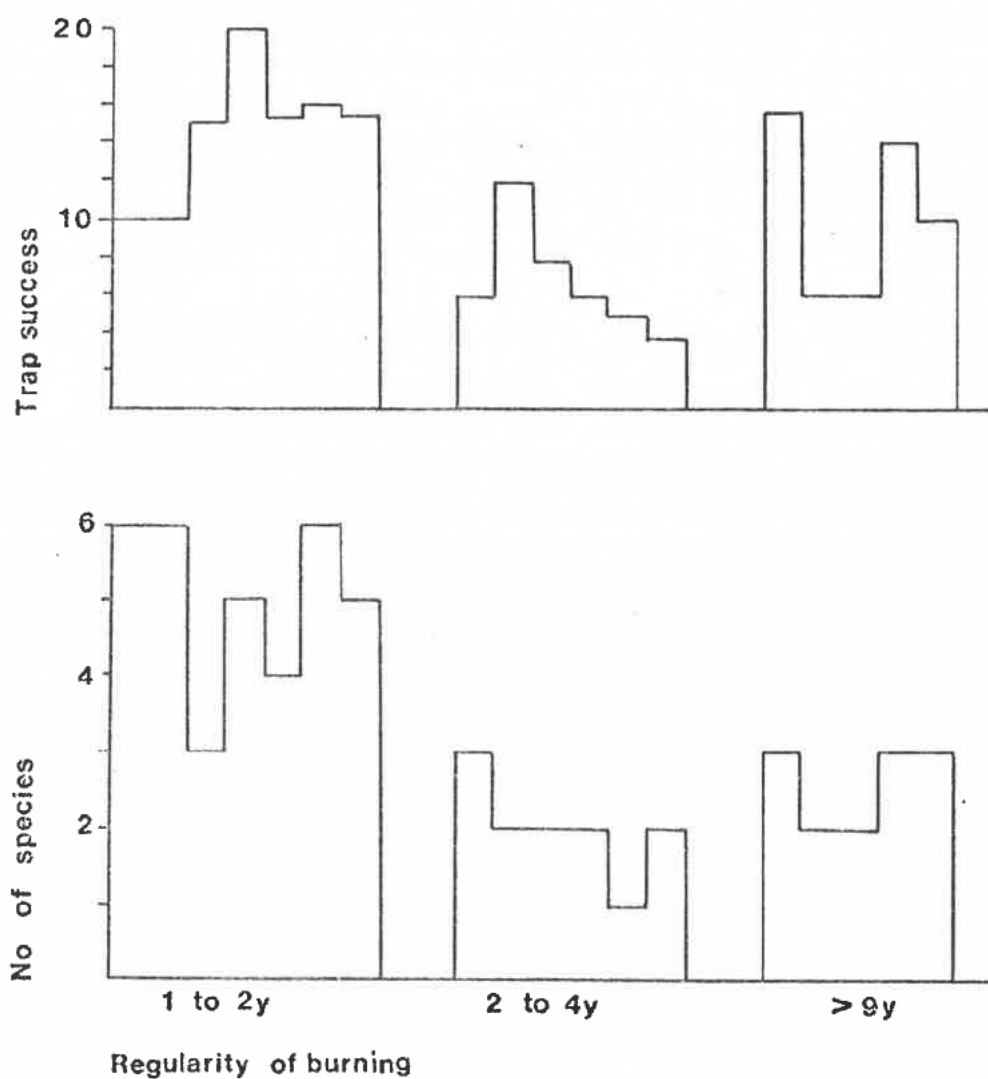


Figure 1.10 Trap success (N/100 trap nights) and species richness of grassland habitats in GCGR in relation to time since burnt.

and McGarity (1965) reported that when native pastures were burnt temperature changes greater than 10° C occurred only in the top 15 mm of soil and concluded that the effects of increased soil temperature on living organisms would be confined to a shallow upper layer.

M. varius is not the only insectivorous animal to recolonise burnt veld. In GCGR insectivorous birds dominate the avifauna of recently-burnt grassland (Brown pers.comm.*) and Manry (in press) noted that the insectivorous bald ibis (Geronticus calvus) was one of the first birds to be recorded after burning.

In GCGR M. varius has emerged as the most adaptable small mammal, occurring in all habitats from 1 500 to 2 700 m (chapter on "Distribution and habitat preferences"). Its wide distribution and ability to exist in both recently-burnt and unburnt areas is probably related mainly to availability of food - arthropods are abundant in both burnt and unburnt habitats over the full altitudinal range (Miller pers.comm.**, Appendix 2).

2. Dendromus melanotis

D. melanotis has been regarded as a grassland species which favours tall, dense grass cover (Smithers 1971, Rautenbach 1978a, Pienaar et al. 1980) but it too was recorded 1 to 3 mo after burning. In one patch of burnt grassland where additional sampling was done to collect distribution records, seven D. melanotis and two M. varius were caught in 120 trap nights, 1 mo after burning. The trapline was, however, only 200 m from an area of unburnt grass.

At least one author has recorded the presence of D. melanotis immediately after fire (Delany 1964), and Cheeseman and Delany (1979) collected two in grassland 1 mo after it had been burnt. As it has been reported utilising burrows (Shortridge 1934, Roberts 1951, Pienaar et al. 1980) it is possible that D. melanotis survives fire. The species is both granivorous and insectivorous (Smithers 1971, this study), therefore being able to exist in recently-burnt veld.

3. Graphiuris murinus

G. murinus, although not caught in significant numbers in any of the burnt habitats, is also apparently able to survive fire and is encountered immediately thereafter (Tables 1.9 and 1.13). In burnt areas it occurs

* C.J. Brown, Dept of Zoology, University of Natal, Pietermaritzburg.

** Dr R. Miller, Dept of Entomology, University of Natal, Pietermaritzburg.

where it can shelter in rock crevices or holes in trees, and as the species feeds on insects and seeds (Smithers 1971, Pienaar *et al.* 1980, this study) which are present in such habitats immediately after fire, the requirements of cover and food are catered for.

4. Rhabdomys pumilio

R. pumilio was absent from all open habitats immediately after fire, but was recorded in low numbers in temperate grassland boulder-bed and burnt scrub 1 to 2 mo after burning (Tables 1.9 and 1.16) where there was still reasonable cover. The general pattern, however, seems to be an absence of the species immediately after fire, then a rapid population recovery coinciding with rapid grass growth, reaching a peak 6 to 12 mo later.

Grass which has been burnt during spring grows continuously until April of the following year (8 mo later) when the green component is highest (Scotcher *et al.* 1980b). A dormant stage then commences during which green matter decreases and dry grass increases until the end of August, when the growing season starts again. In autumn-burnt grassland there is only one month of growth, then a 4-mo dormant period before growth starts again, reaching a peak 12 mo after fire, whereas the peak was reached 4 mo earlier in spring burns (Fig 1.11). The longer growing period on autumn burns probably accounts for the longer recolonisation period after autumn burning by R. pumilio in particular, than was recorded in spring- and winter-burnt grassland.

Spring-burnt grass flowers after *ca* 3 mo and comes into seed at *ca* 5 mo. Although a number of seeds remain on the ground after fire and some food would be available, R. pumilio does not recolonise until there is adequate cover. The species is predominantly granivorous (Brooks 1974, this study) but does also feed on invertebrates and green matter, particularly grass flowers, therefore by the time that cover conditions are ideal, there is abundant food. At 2 200 m the grass began to flower at 2 mo, which might explain why a reasonably high number of R. pumilio were present as soon as 3 mo after burning at this altitude (Table 1.7).

In an area of desert grassland Christian (1977a) recorded R. pumilio before the veld was burnt, but the species was absent after the fire and during the next 12 weeks. Although seeds produced during the previous season were abundant on the ground, the species' absence appeared to be correlated with inadequate cover.

During the second year after the veld had been burnt R. pumilio numbers

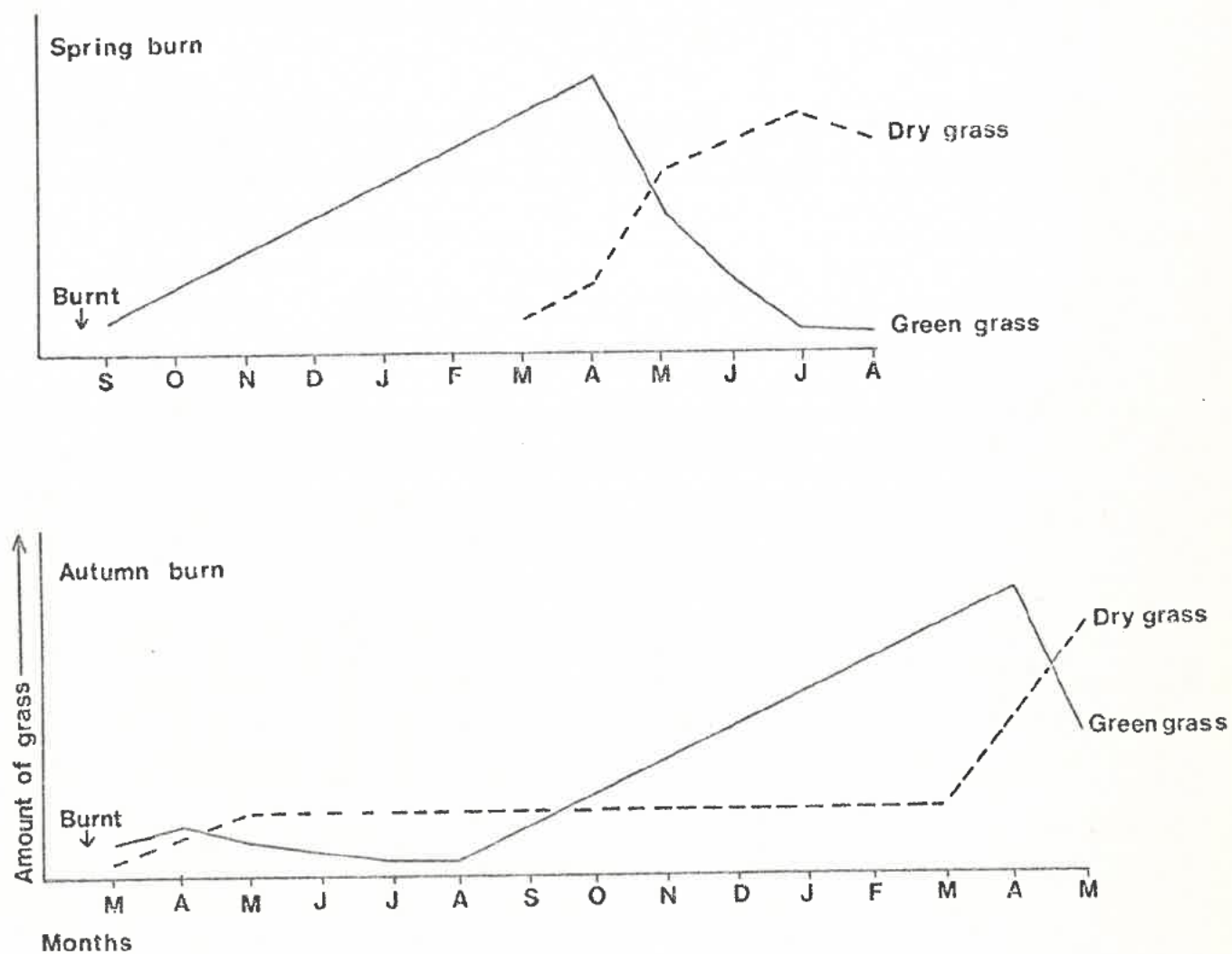


Figure 1.11 Green grass growth and increase in dry grass on a spring burn (above) and an autumn burn (below). Based on data contained in Scotcher et al. (1980b).

decreased in habitats at elevations of 1 900 m and lower. A reason for this may be that at lower elevations herbage production is greater than is the case at higher altitudes, and that there is therefore a greater build-up of moribund grass, and although cover is good, new growth is less accessible. More detail will be given in the sub-section on "Effects of herbage production and composition".

5. Otomys irroratus

O. irroratus was first captured once maximum cover had been established in open Themeda grassland, but at an earlier stage in habitats such as tall grassland, temperate grassland boulder-bed, and scrub, where grass recovery was very rapid or where some forms of cover still remained after a fire.

6. Mus minutoides

M. minutoides was generally first recorded 6 to 12 mo after burning, an exception being temperate grassland boulder-bed, where one animal was caught 2 mo afterwards. M. minutoides is a burrower (Smithers 1971) and is therefore able to survive fire, as was found by Cheeseman and Delany (1979) who trapped the species 1 mo after a Uganda grassland was burnt. The species does not appear to be as successful as M. varius during the few months following fire, which might be dictated by its food preferences. Smithers (1971) has described M. minutoides as graminivorous, which would make it possible for the animal to exist as soon as the grass starts to shoot, a phenomenon which takes place within a day or two of burning, particularly in drainage lines. In this study, however, I found that the species is predominantly granivorous, which agrees with the findings of Pienaar et al. (1980).

7. Crocidura flavescens

Although only 11 C. flavescens were trapped, indications are that the species recolonises only once good cover has been established. Only one specimen was captured in short grass (7 mo after fire on an autumn burn - Table 1.5). In all the other habitats where it was trapped cover was good, viz at the end of the first growing season at altitudes below 1 800 m and at the end of the second growing season at 2 200 m.

8. Dendromus mesomelas

Insufficient data were collected on D. mesomelas for any conclusions to be drawn.

Effects of herbage production and composition

In the Montane Belt small mammal recolonisation in relation to vegetation structure and composition can be compared in four biennial autumn burns (Fig 1.12). Recolonisation followed the same patterns in grouped-tree woodland, boulder-bed scrub, and Themeda grassland, but higher numbers were recorded in the more heterogeneous grouped-tree woodland and boulder-bed scrub than was the case in homogeneous grassland. One would expect small mammal numbers to be higher in protea woodland, but as already discussed (chapter on "Trap success, species richness, and diversity"), this is not a suitable small mammal habitat. Similar low catches were recorded at Cathedral Peak where trap success was 2 % in protea woodland unburnt for 5 y (Rowe-Rowe 1977a, Appendix 1).

In most grassland habitats greatest species richness was recorded during the first year after burning. In burnt grassland at lower altitudes, peaks in trap success were reached approximately 12 mo after fire and decreased during the second year (Fig 1.9), whereas in open grass at 2 200 to 2 300 m, trap success during the second year was as high as or higher than that recorded during the first year. The differences in herbage production and grass species composition along the altitudinal gradient are probably primary causal factors responsible for these differences.

In Montane Belt grassland at the lower limit of the Sub-alpine Belt the veld is dominated by Themeda triandra (27 % and 23 % of species composition - based on data from Scotcher and Clarke 1981), whereas at 2 200 m there is a more even representation of grass species, and twice as many forbs.

Decreasing herbage production with altitude has been illustrated in Fig 1.4. At the end of the second growing season herbage at 2 200 to 2 700 m was usually less than, and at the most 33 % greater than, the amount of herbage at 1 500 to 1 900 m at the end of the first season. Although almost the same amount of green grass is produced during the second growing season as in the first, the build up of dry grass is much greater at the lower than the higher altitudes. During the second year after burning there would therefore be more moribund grass and litter in lower altitude grasslands than at the higher altitudes.

In the long-term protected areas trap success was generally similar to the peak recorded in burnt habitats (Fig 1.10), but species richness was lower. In the grassland habitats which were not burnt for 3 or 4 y (Tables 1.6 and 1.7) trap success and species richness decreased during the third and fourth years, the trap success being lower than that recorded in either biennial burns or long-term protected areas. At Cathedral Peak Rowe-Rowe

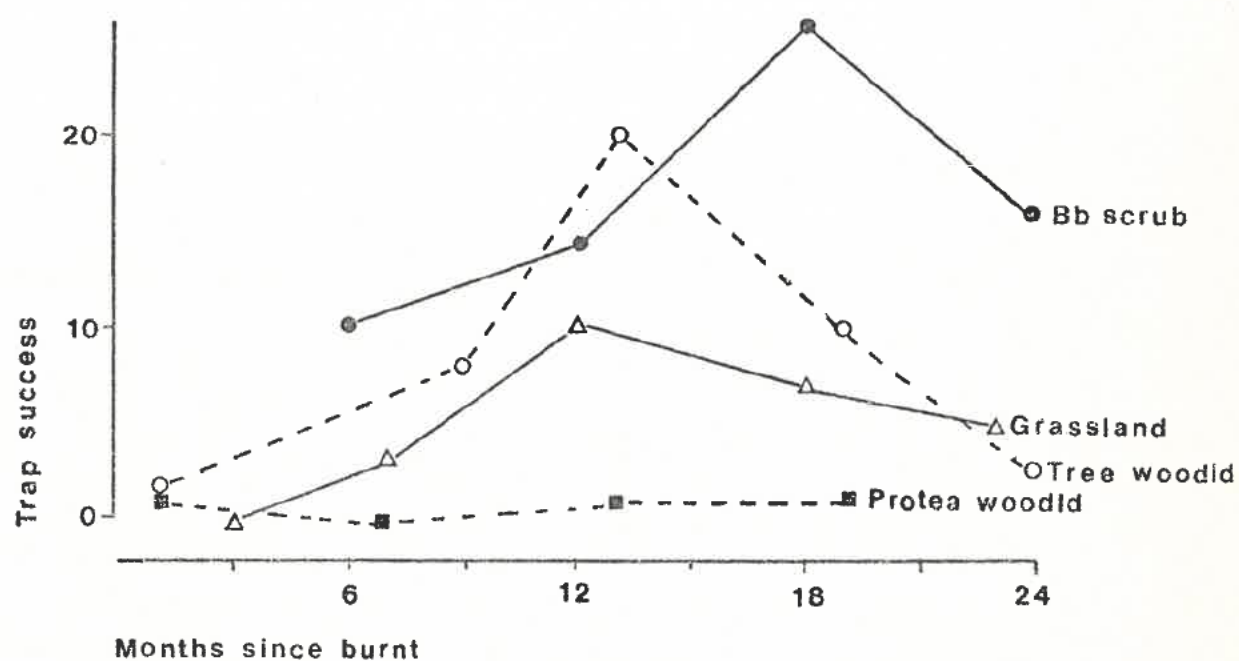


Figure 1.12 Small mammal trap success (N/100 trap nights) in relation to time since burnt in four Montane Belt habitats, burnt biennially during autumn.

(1977a) noted a similar pattern: lowest trap success was recorded in grassland unburnt for 5 y, while catches in biennially-burnt habitats were similar to those recorded in long-term protected areas (protected for 21 y and last burnt 11 y prior to sampling), and species richness in biennial burns was greater.

In Drakensberg grassland, scrub, and woodland habitats there is a continual build-up of dry grass. From the end of the second growing season onwards the amount of dry grass exceeds green grass (Table 1.18). During the third and fourth years the vegetation becomes very rank and the large build-up of dry grass gives it a matted appearance. In long-term protected areas (unburnt for > 10 y) the grass tufts have become very large, but are further apart than is the case in areas unburnt for 4 or 5 y, therefore the vegetation is not as impenetrable, and there is not as dense a layer of moribund grass at ground level as in the ca 4 y-old habitats. The mean distance of 476 mm (SE 17) between tufts in grassland unburnt for 11 y differed significantly from that of 171 mm (SE 6) in an area unburnt for 4 y ($t_{17,29}$; $df\ 78$; $P < 0,001$).

Mentis and Rowe-Rowe (1979) commented on the bimodal distribution in density of francolin and small mammals in Drakensberg grassland where peaks are observed in biennially-burnt and protected areas, and a trough occurs during the period 3 to 10 y after fire. These authors have hypothesised that Drakensberg biota have not been exposed in their evolution to a high incidence of fires of intermediate frequency (3 to 10 y), but that most areas were exposed and accessible to fire and were therefore burnt frequently (ca every 2 or 3 y) and maintained as grassland. Other areas were inaccessible to fire and were burnt very infrequently or not at all, and developed into woody communities with a different faunal structure.

Comparison with other studies

Colonisation of mangrove islands by arthropods (Simberloff and Wilson 1969, 1970) shows some patterns similar to those observed in small mammal colonisation in GCGR. After all arthropods had been eliminated by fumigation (Wilson and Simberloff 1969) rapid colonisation took place and by 8 mo species richness had reached pre-"defaunation" levels (Simberloff and Wilson 1969), although numbers of individuals were low. This initial rapid increase in species richness was followed by a decrease in number of species, than a gradual increase, reaching original levels and a state of equilibrium after 2 y (Simberloff and Wilson 1970). Simberloff and Wilson (1969, 1970) attributed the initial peak in species richness to very little interaction among species. The slump in species richness was attributed to interaction,

TABLE 1.18 Amounts of green grass leaf and dry grass leaf (oven dried mass) in herbage samples collected at approximately the same altitude at the end of different growing seasons.

Growing season	Grass in g/m ²		Proportion
	Green	Dry	Green:Dry
1	160	30	5,3:1,0
2	172	205	1,0:1,2
3	130	330	1,0:2,5
4	140	476	1,0:3,4
12	184	780	1,0:4,2

competition, predation, and physical factors which affected species that were present in low numbers. As population sizes increased, interaction became less important and a state of equilibrium was reached.

The changes in small mammal species richness in burnt grassland in GCGR showed similar patterns: increasing rapidly during the first one or two years after fire (Fig 1.10), then decreasing, and finally stabilising in long-term fire-protected areas. (Although the number of species in such areas was lower than in regularly-burnt grassland.) A major difference between the mangrove islands situation and that in GCGR is that the arthropod populations were eliminated without any drastic habitat change on the islands, whereas fire causes a complete but temporary change. It is possible that a similar situation of species interaction to that observed on the islands prevails in small mammals after fire: while population numbers are low, species richness is high, then it decreases when population levels of the most successful species (*R. pumilio* and/or *M. varius*) increase.

In a number of studies on small mammals and fire, authors have reported a drastic decrease in numbers of individuals immediately after fire, then a fairly rapid recovery with numbers reaching pre-fire (or control) densities in 6 to 15 mo (Cook 1959, Cheeseman and Delany 1979, Kern 1977, Lawrence 1966, Mentis and Rowe-Rowe 1979, Neal 1970, Sims and Buckner 1973). Species richness on burnt and unburnt areas was generally similar (Cook 1959, Cheeseman and Delany 1979, Delany 1964, Kern 1977, Neal 1970, Sims and Buckner 1973). Beck and Vogl (1972), however, recorded more small mammal species in burnt prairie habitats than in a protected control, and so too did Mentis and Rowe-Rowe (1979) in Drakensberg grassland.

Studies involving small mammals and fire which resemble the Giant's Castle study in duration and methods include those done by Cook (1959), Neal (1970), Kern (1977), and Cheeseman and Delany (1979). Cook (1959) studied burnt and unburnt grassland and brush in California over a 30-mo period and concluded that increasing cover was the most important factor related to small mammal population recovery. The studies by Neal (1970) and Cheeseman and Delany (1979) were undertaken in Uganda. Neal (1970) collected information on recolonisation of various grassland and one scrub community for 11 mo after burning. The four species most adversely affected by fire were diurnal. Neal concluded that the fire itself was not directly responsible for the disappearance of these species, but that some emigrated to unburnt areas and others were taken by predators. With increasing cover the affected species either reappeared in the burnt area or increased in numbers. In

their 9-mo monitoring study following fire Cheeseman and Delany (1979) reported similar results to those of Neal (1970). They found that two diurnal species were adversely affected, and that two nocturnal species actually increased immediately after fire. In contrast to the findings of Neal (1970), however, a diurnal species (Lemniscomys striatus) was not seriously affected.

The only other detailed South African study involving the effects of fire on small mammals was undertaken in the Kruger National Park by Kern (1977), who collected information in mixed veld (Pretoriuskop) and sweetveld (Satara) over a 10-mo period.

Most of Kern's fieldwork was done in the Pretoriuskop area where each burning treatment was sampled four or five times, whereas the Satara treatments were each sampled twice, and as the grass cover of the Terminalia-Dichrostachys veld of the Pretoriuskop area comprises predominantly sourveld species (van Wyk 1972), it makes a more suitable comparison with the sourveld of GCGR than does the Satara sweetveld.

The highest trap success which Kern (1977) recorded on the Pretoriuskop control (unburnt for 22 y) was 9,4 % comprising six species. Maximum trap success and species richness of the other burning treatments in the Pretoriuskop area were: annual spring burn 5,4 % (4 spp.) at 6 mo; triennial spring burn 9,7 % (7 spp.) at 30 mo; and triennial autumn burn 6 % (5 spp.) at 35 mo. Altogether Kern (1977) recorded nine small mammal species in the Pretoriuskop area. Taking all trapping sessions into account, all nine species were collected on the triennial burn treatments and seven species each were recorded on the control and annual burn.

Kern's overall conclusion was that the fire regime most beneficial to small mammals was that of no burning at all. His trap success and species richness figures do not provide convincing evidence in support of the statement - cf. the triennial spring burn with the control. Species diversity in the triennial burns was at times lower than that in the control, but this can be expected in a recolonisation situation.

The only marked difference between the control and the burns was that the small mammal biomass of the control was greater than that on the burns on all occasions sampled.

Small mammal population differences in burnt and unburnt habitats at Pretoriuskop were not as marked as was the case in GCGR where, although maximum densities in burnt areas were similar to those in controls, the burnt areas were generally richer in number of species.

There are a number of factors which may contribute to the differences

in effects of fire on small mammal populations in the Kruger National Park and GCGR, such as altitude, temperature, rainfall (ca 50 % higher in GCGR), soils, vegetation composition, cover, and grazing pressure by large herbivores.

The Pretoriuskop veld is characterised by a mixture of tall and short grass species with basal cover of 3,1 % to 4,3 % (van Wyk 1972). In GCGR the grassland is characterised by species with short to medium stature and basal cover of 9 % to 12 % in the areas where small mammals were trapped (Scotcher and Clarke 1981). At Pretoriuskop recovery of the burnt veld is slow and the new grass is heavily grazed by large herbivores (van Wyk 1972). In GCGR recovery, particularly of spring burns, is rapid (Scotcher et al. 1980b) and grazing pressure is minimal. At the end of the growing season in GCGR, which coincides with the onset of the harsh winter, there is a sudden decline in green matter and an increase in dry material (Fig 1.11). The dry grass never recovers, therefore there is a continual build-up with more being added each winter (Table 1.18), and consequently an ever-increasing build-up of litter. It is unlikely that the milder winters of the Kruger National Park would have as drastic an effect on green grass and that there would be as great a build-up of litter in triennial burns and the control.

Ecological importance of fire in the Drakensberg

One of the important functions of successful small mammal populations is that they provide a source of food for a number of predators. In GCGR there are at least 10 carnivores, 22 avian predators, and eight snakes which include small mammals in their diet (details in chapter on predation).

Protected grassland probably inhibits avian predators as the canopy cover is too dense to allow effective hunting. Some carnivores might make limited use of such an area, but the vegetation is generally too dense for anything but the smallest mammalian predator to penetrate and pursue prey. The predators least hampered by these conditions are probably snakes. The inhibition of hunting allows small mammal numbers to build up. As a reservoir for the recolonisation of burnt areas protected grassland therefore performs an important function, although basically only R. pumilio and M. varius are involved.

Spring-burnt grassland provides the physically most suitable hunting ground for predators, although initially small mammal populations are low and only nocturnal species are present. Once populations of the diurnal R. pumilio become established (which takes place rapidly) both avian and

terrestrial predators benefit from the not yet too dense cover and the medium-sized rodents. In most burnt habitats the small mammal variety includes species with a range of activity patterns and varying sizes which become established during the first year, therefore catering to a wide variety of predators. During the second year after fire biennially-burnt grassland acts as a reservoir for adjacent burnt areas, and remains a hunting ground for terrestrial and avian predators.

Recolonisation of autumn-burnt grassland takes place less rapidly than is the case in spring-burnt areas. The importance of an autumn burn to predators would therefore come into being later than that of a spring burn.

The two habitats which had greatest small mammal species diversity and fairly high densities were biennially-burnt temperate grassland boulder-bed, and Buddleia-Leucosidea scrub which was occasionally or partly burnt. These habitats contained the greatest variety of small mammals, including both forest and grassland species. They are obviously important to predators and are good reservoirs for the recolonisation of adjacent open areas once the correct type of cover has been established. Furthermore, when these habitats are burnt, their complexity ensures that small mammals are not decimated and population nuclei remain.

Forest, the climax stage of areas inaccessible to fire, supports entirely different faunas. Small mammal numbers are lower than in grassland and scrub habitats, but are dominated by an arboreal and rupicolous species, G. murinus. Forest margin (sampled at Cathedral Peak - Appendix 1) is similar to forest in that density is fairly low, but species richness and diversity are high and the small mammal community is a mixture of forest and grassland species. The policy of protecting or only partly burning forest margins ensures a grassland recolonisation nucleus and protects the forest from unscheduled fires by reducing the full load adjacent to it.

The current fire programme in GCGR provides a mosaic of habitats burnt at different times (Fig 0.4). Within the burning compartments there are scrub patches, cliff bases, and rocky drainage lines, which do not always burn cleanly and provide small areas in which small mammals can continue to exist. Ideally smaller burning compartments would provide for faster recolonisation. This, however, might not be entirely practicable due to the added effort of burning additional firebreaks and the restricted time of year at which this can be effectively and safely done. The only fire regime which is at present of doubtful ecological benefit is that of autumn burning in grassland. As already pointed out in this study, recolonisation takes

place slowly. Scotcher and Clarke (1981) expressed the opinion that autumn-burning of grassland in GCGR needed detailed examination and closer monitoring, as the system had been in practice only since 1976, and they were unable to make final assessments of veld condition. Scotcher *et al.* (1980b) did find, however, that the nutritional value of autumn-burnt grassland remained higher than that of a spring-burnt grassland during winter. This may be an important consideration in antelope management.

In the more complex autumn-burnt grouped-tree woodland and boulder-bed scrub small mammals built up to greater numbers than was the case in the more homogeneous autumn-burnt grassland (Fig 1.12).

As an autumn fire spreads more slowly and burns at lower heat than does an early spring fire (when the vegetation is dry), less damage is done to fire-sensitive woody plants. There is therefore a case in favour of continuing to burn such areas during autumn, a practice which would be least harmful to woody vegetation and at the same time maintaining satisfactory small mammal populations.

POPULATION DYNAMICS

SEX RATIOS

Sex ratios of trapped small mammals are listed in Table 1.19. Deviation from parity was significant only in the two shrew species, in which a preponderance of females was recorded.

Detailed analyses of data on the two most abundantly-caught species were done to test for significant differences in the sex ratios of adults, sub-adults, snap-trapped and live-trapped animals overall, snap- and live-trapped adults, and snap- and live-trapped sub-adults. No significant departure from a 1:1 ratio was observed for any of the different categories of R. pumilio. The adult male:female ratio of live-trapped M. varius did not differ significantly from parity, but in all other categories there was a significant preponderance of females ($P < 0,05$). Greatest differences were observed amongst sub-adults (Chi-square 14,36; $P < 0,001$) and in the overall snap-trapped sample (Chi-square 12,91; $P < 0,001$).

Brooks (1974) pointed out that trap-based sex ratios do not necessarily reflect the true composition of the population, as they may result from differential trap response or movement patterns. In his study on R. pumilio Brooks recorded a non-significant preponderance of males in live-trapped animals but a highly significant 1,7:1 ratio in snap-trapped mice, while a significant 0,8:1 ratio in favour of females was recorded at birth in a laboratory colony.

The 1,2:1 ratio of R. pumilio collected in GCGR is similar to the ratios reported by de Wit (1972), Hanney (1965), Perrin (1980a), and Smithers (1971), all of whom recorded a non-significant preponderance of males. The total collection of 435:336 made by Rautenbach (1978a) departs significantly from 1:1 ($P < 0,01$).

In a study of the activity patterns of the European common shrew (Sorex araneus) Vlasák (1980) recorded sexual differences in the activity of immature animals only, but found that males were more active than females. A similar situation may have prevailed amongst M. varius in GCGR, but with young females being more active. In at least two other instances (Rautenbach 1976, 1978a) females exceeded males in M. varius collections, but differences were not significant.

Similar sex ratios to those recorded for two other species collected in GCGR have been reported, viz for O. irroratus (Davis 1973, Perrin 1980a,

TABLE 1.19 Sex ratios of small mammals trapped in GCGR and Chi-square evaluation for deviation from parity.

Species	Males	Females	Ratio	Chi-square	P
<u>R. pumilio</u>	172	138	1,2:1	3,73	NS
<u>M. varius</u>	82	150	0,5:1	19,93	<0,001
<u>O. irroratus</u>	17	16	1,1:1	0,03	NS
<u>D. melanotis</u>	14	19	0,7:1	0,76	NS
<u>G. murinus</u>	7	11	0,6:1	0,89	NS
<u>M. minutoides</u>	8	4	2,0:1	1,33	NS
<u>C. flavescens</u>	1	10	0,1:1	7,36	< 0,01
<u>D. mesomelas</u>	3	0	-	-	-

NS = $P > 0,05$

Rautenbach 1978a) in which the ratios were ca 1:1, and G. murinus (Rautenbach 1978a, Smithers 1971) in which a preponderance of females was recorded. Rautenbach (1978a) and Smithers (1971) recorded ratios in favour of males in D. melanotis, but the non-significant departures from parity do not differ greatly from the GCGR ratio which favoured females. Sample sizes of other species collected are too small for consideration.

POPULATION STRUCTURE

It was possible to examine the population structure of M. varius and R. pumilio only, as insufficient data were collected on the other species.

The monthly catch of each of the two species was divided into mass classes, using 2 g intervals for M. varius and 5 g intervals for R. pumilio. The number of animals in each mass class was then expressed as a percentage of the total monthly catch and presented diagrammatically (Figs 1.13 and 1.14).

From November to April there was a wide representation of mass classes in the M. varius samples, but from May to September fewer mass classes were present. During May and June the catches were made up almost entirely of small animals and no large adults were caught. The pattern strongly suggests that a die-off in adult shrews takes place at the end of the breeding season and that during the next season the population builds up from young animals. From July to September it is obvious that the small May - June animals grow and reach full adult size. The first young animals appear to enter the trappable population in about October.

Baxter (1977) quoted a record of M. varius living for as long as two years in captivity, but Meester (pers.comm.)* does not believe that these shrews live longer than 16 to 18 mo in the wild. The GCGR data suggest that some of the animals do survive for 12 to 16 mo, but that there is a big die-off amongst adults by the end of the breeding season.

The population dynamics of M. varius have features in common with those previously recorded in some other shrews. It has been shown that European and North American shrews in the wild have a lifespan which does not exceed 18 mo (Vogel 1980). Buckner (1966) found that only 20 % of the new generation of Sorex cinereus and S. arcticus reached sexual maturity and that almost all surviving animals die before the age of 15 mo. Churchfield (1980) observed similar dynamics in S. araneus - 20 to 30 % survived to breed and maximum life expectancy was 13 mo.

* Prof J.A.J. Meester, Dept Biological Sciences, Univ. of Natal, Durban.

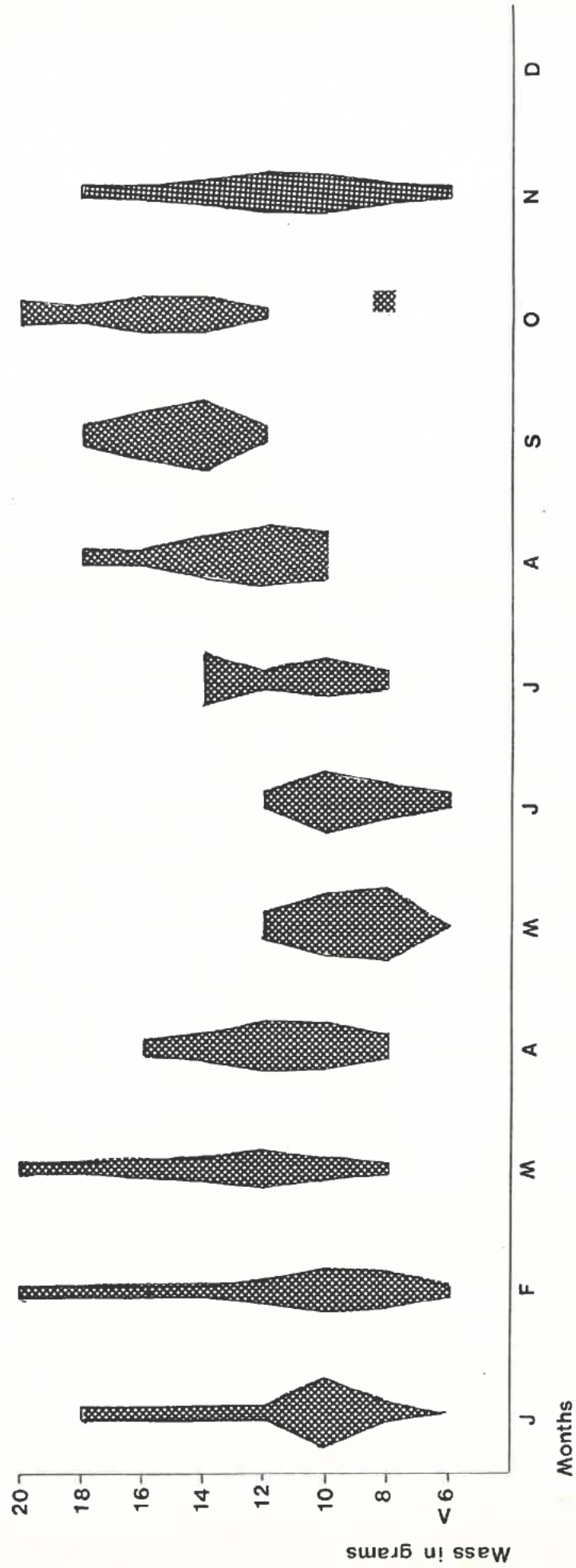


Figure 1.13 Mass classes of *M. varius* trapped during each month in GCCR. The width of the histogram represents the percentage of the total monthly sample which falls into that mass class.

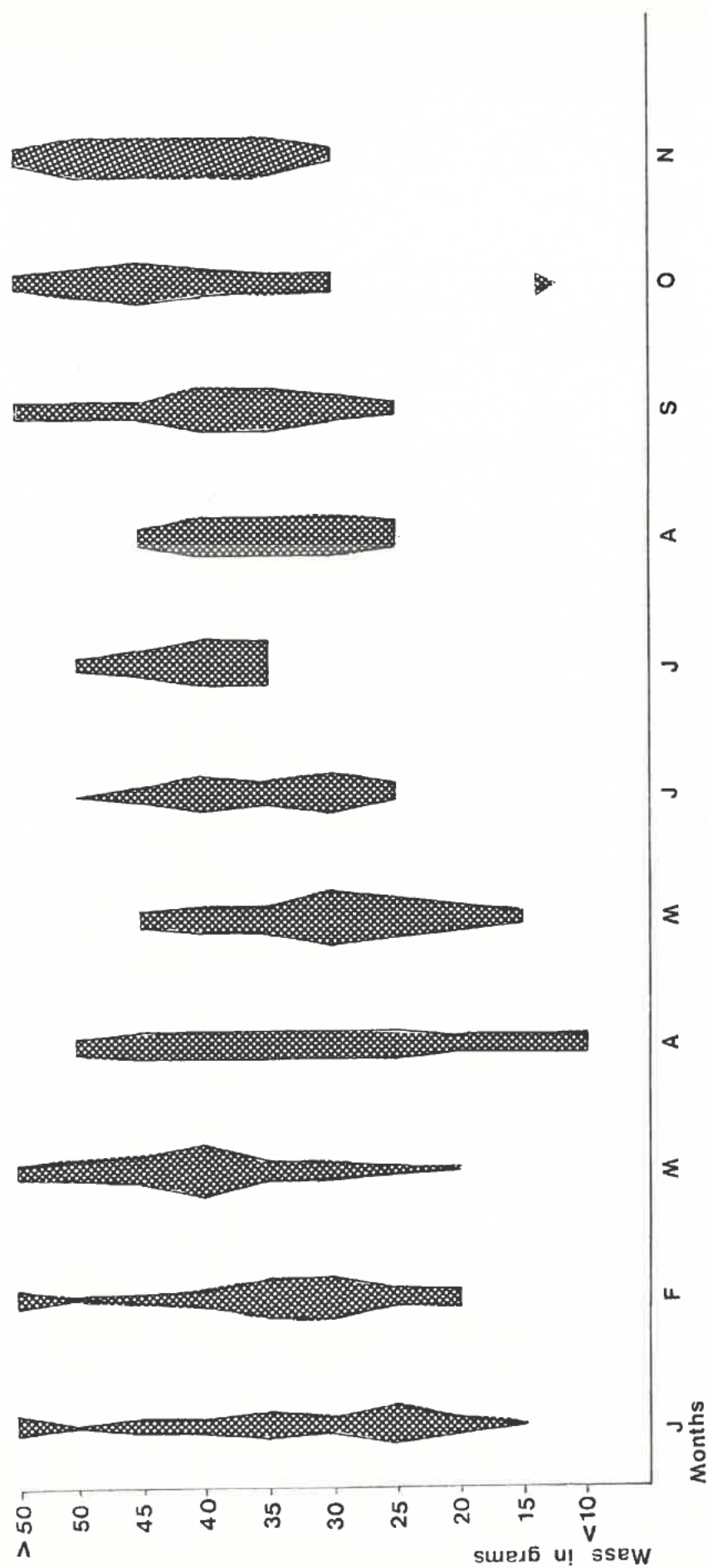


Figure 1.14 Mass classes of *R. pumilio* trapped during each month in GCGR. The width of the histogram represents the percentage of the total monthly sample which falls into that mass class.

In the R. pumilio samples there was a wide range of mass classes from January to April (Fig 1.14). From May to September the catches were made up of what appeared to be some adults and young animals from the last breeding season. The first young of the season entered the trappable population in October, but no small animals were captured during November. It was during November each year that wet season sampling of the high altitude habitats (2 200 to 2 700 m) was done, and the absence of young from these samples may mean that at the higher altitudes the breeding season commences later than at the lower altitudes (see "Reproduction").

The population structure cycle of R. pumilio in GCGR is similar to what Brooks (1974) found near Pretoria and that reported by Perrin (1979) from a study area near Grahamstown, in that the greatest range of age classes was recorded in months following the breeding season, and the smallest range was observed in the non-breeding season, followed by an upward shift in population age structure. Perrin (1979), working in an area which experiences erratic rainfall, recorded the greatest range of age classes in R. pumilio during April and May, following a breeding peak in February. In GCGR the wide size range of animals collected from January to April indicates that the breeding peak occurred earlier and extended over a longer period, probably related to the high regular rainfall and the long wet season. (See also "Reproduction".)

In captivity Brooks (1974) found that R. pumilio had a lifespan which just exceeds two years, but he believed this to be considerably less in the wild, where the oldest individual in his study population was 16 mo old and only 2,3 % of the animals were older than 12 mo. De Wit (1972) also estimated a similar longevity for R. pumilio (17 mo for males and 12 mo for females) but was unable to indicate what proportion of the population lived longer than 12 mo. In the population studied by Perrin (1979) the age structure suggests that the lifespan exceeds 12 mo in only a small percentage of the mice.

The population structure cycles of M. varius and R. pumilio are similar in that they exhibit the patterns typical of seasonal breeders. A difference between the two is that a greater range of mass classes was recorded earlier in the season in M. varius than was the case in R. pumilio, a phenomenon which is related to the onset of breeding at an earlier date in M. varius. (See also "Reproduction".)

REPRODUCTION

M. varius

Breeding season in the Drakensberg extended from August to March: pregnant females were collected during these months and lactating females from September to April, and an increase in mean testis length was observed in July with a decrease in April (Fig 1.15). The percentage of animals in breeding condition (Fig 1.15) was highest from September to November (no data for December) and lowest during April to August. Although the percentage of males with inguinal testes examined during August was low there was an increase in mean testis length even in males with abdominal testes.

Mean number of fetuses was 2,8 (N = 19, range 1 to 4).

Rautenbach (1978a) reported a similar breeding season in the Transvaal where pregnant females were collected from September to March, and similar litter sizes to those from GCGR were recorded by Baxter and Lloyd (1980): 3,0 in captivity and 2,9 in trapped animals.

C. flavescens

Pregnant females were collected during October and February. Each of the three pregnant females contained five fetuses. The only adult male collected had abdominal testes during December.

In Uganda Delany (1964) recorded an average of three fetuses (N = 6, range 2 to 4) in animals trapped just prior to the start of the wet season. Baxter (1977) observed a breeding season from August to April and a litter size of 3,7 in captive animals.

R. pumilio

Pregnant females were collected during all months from September to March, and no lactating animals were recorded outside of this period. Testes began to increase in length during July and decreased during April (Fig 1.16). The percentage of animals in breeding condition was lowest from April to June and reached a peak during November (Fig 1.16). The data suggest that males become reproductively active about a month earlier than do females. As the breeding season is determined by the female, however, it may be described as extending from August, when mating takes place, to March.

Mean number of fetuses was 4,6 (N = 22, range 3 to 7).

Breeding in R. pumilio appears to coincide with the wet season (Brooks 1974, Hanney 1965, Perrin 1980a, Rautenbach 1978a, Taylor and Green 1976).

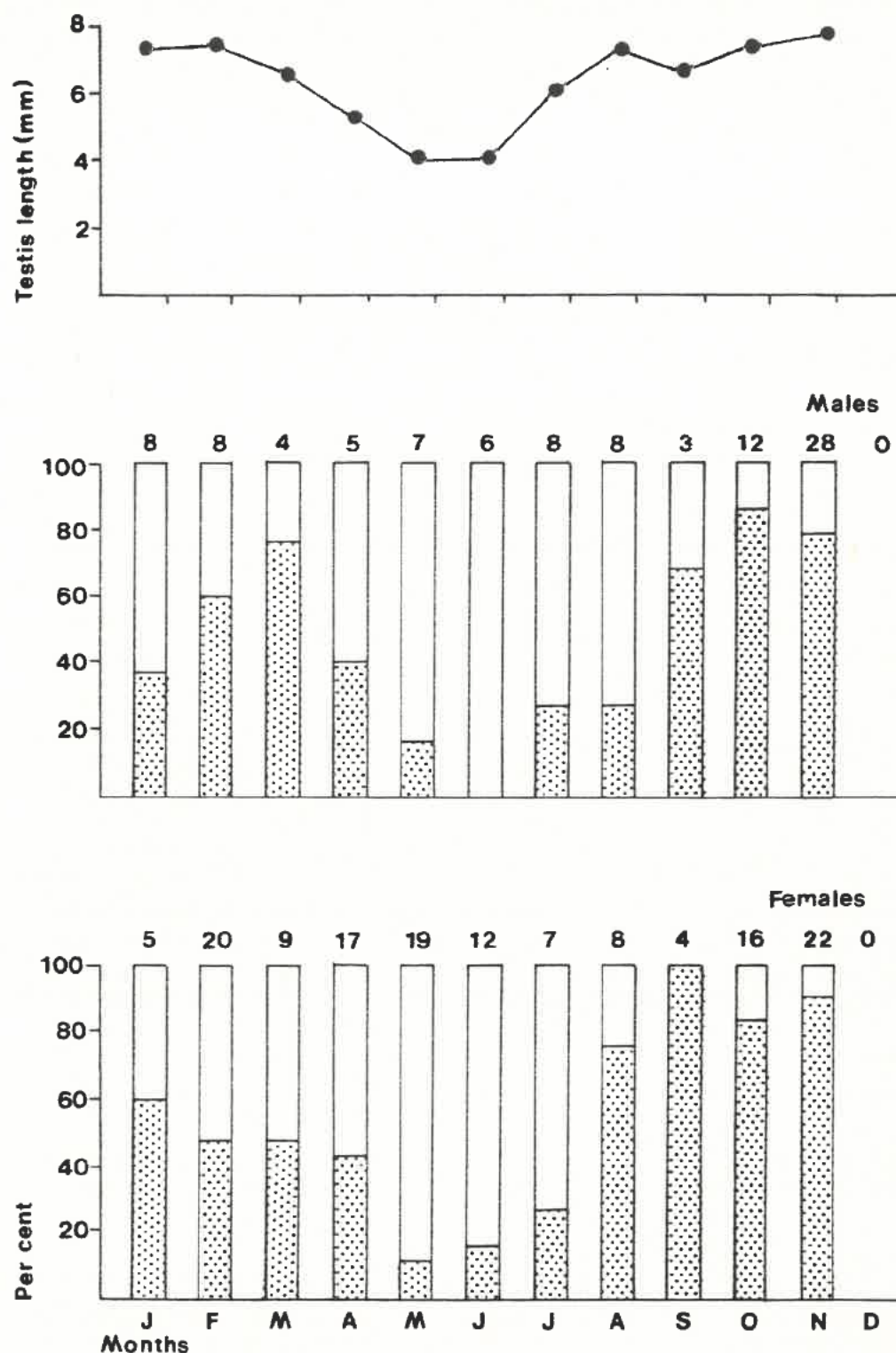


Figure 1.15 Reproductive condition of *M. varius*, showing mean testis length (graph), percentage males with inguinal testes (shaded bars, upper histogram), and percentage perforate females (shaded bars, lower histogram). Unshaded portions represent males with abdominal testes and imperforate females. Sample sizes are indicated above the bars.

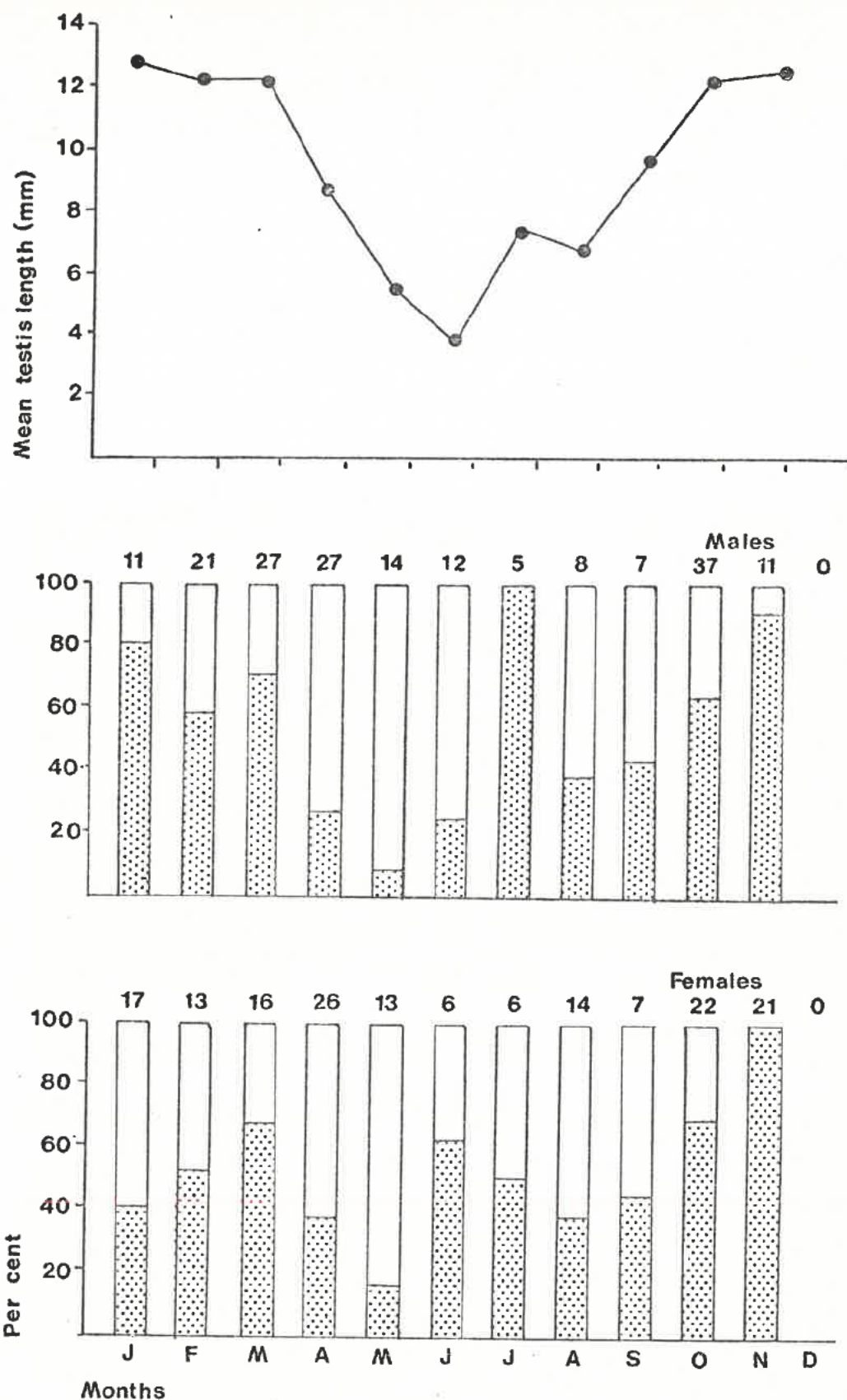


Figure 1.16 Reproductive condition of *R. pumilio*, showing mean testis length (graph), percentage males with scrotal testes (shaded bars, upper histogram), and percentage perforate females (shaded bars, lower histogram). Unshaded portions represent males with abdominal testes and imperforate females. Sample sizes are indicated above the bars.

Smithers (1971) is the only author to report some winter pregnancies in animals collected in an arid region (Botswana). Brooks (1974), Perrin (1980a), and Taylor and Green (1976) found too that males became reproductively active about a month prior to females. The onset of reproductive activity in females usually coincides with the first significant rains of the season (cf. GCGR data, Brooks 1974, Perrin 1980a, Taylor and Green 1976).

Mean litter size has been given as between 4,5 and 5,9 in studies of wild populations (Brooks 1974, de Wit 1972, Hanney 1965, Perrin 1980a, Smithers 1971, Taylor and Green 1976) and 6,5 to 7,0 in captive animals (Brooks 1974, Meester and Hallett 1970).

O. irroratus

Although the sample size is small the data suggest that breeding extends over a longer period than was the case for R. pumilio: a lactating female was collected in May, pregnant females were recorded during October, November, and January; and males with scrotal testes were recorded during July, September to November, and January.

Mean number of foetuses was 1,6 (N = 5, range 1 to 2).

Both Davis (1973) and Rautenbach (1978a) concluded that O. irroratus bred during the warm wet season in the Transvaal, but in the eastern Cape Province Perrin (1980a) found that the species bred throughout the year and that rainfall did not have a significant effect on reproduction. Perrin (1980a) reported a mean litter size of 1,48 which is similar to the mean for the GCGR litters, but the mean litter sizes of 2,3 and 3,2 recorded in the Transvaal by Davis (1973) and Rautenbach (1978a) respectively were greater.

D. melanotis

No pregnant females were recorded and the only lactating animal was collected during January. Perforate females were collected during May and November, and males with scrotal testes during April, October, and November. Most immature animals were collected during April and May, which suggests that the young are born during summer.

Very little has been published on the reproduction of D. melanotis. Smithers (1971) collected a female containing four foetuses during December in Botswana and recorded pregnancies from December to March in Rhodesia. Delany (1964) recorded a pregnant female with three foetuses during the wet season (July) in Uganda.

D. mesomelas

Males with abdominal testes were collected during September. A lactating female and a male with scrotal testes were recorded during November at Cathedral Peak.

In Malawi Hanney (1965) took two pregnant females at the end of the wet season (March and May) and one at the beginning of the dry season (June). Foetuses numbered two to six.

G. murinus

No pregnant or lactating animals were collected. Perforate females were collected during October and November, and from March to May; males with scrotal testes during September to November; and immature animals during March.

Neither Rautenbach (1978a) nor Smithers (1971) recorded any breeding data. Pienaar et al. (1980) reported one pregnant female taken during February. The times at which adults in breeding condition and immature animals were taken in GCGR suggest that this species too breeds during summer.

M. minutoides

As the sample size is small and as no pregnant or lactating animals were collected, interpretation of the data is difficult. Perforate females were collected during May and June, males with scrotal testes during March, October and November, and immature animals during January, August, and October.

Smithers (1971) suggested that the species breeds throughout the year, and in Malawi Hanney (1965) collected pregnant or lactating females during summer, autumn, and winter.

The overall pattern which emerges from the reproductive data collected in GCGR is that most small mammals breed during the wet season. In the Kenya Highlands Taylor and Green (1976) concluded that food was the primary factor regulating rodent reproduction, and rainfall the ultimate factor controlling food supply. A similar situation occurred in GCGR. Good rains fell during early spring each year (Fig 0.3), herbage growth following the rains was rapid (Fig 1.11), and the nutritional value of the veld (particularly green grass, inflorescences, and forbs) was highest during spring and summer (Scotcher et al. 1980b). Crude protein content, for example, is as high as 15 % during spring but drops to 2 or 3 % in winter (Scotcher et al. 1980b).

A number of other authors have reported small mammal reproduction coinciding with rainfall in regions having a distinct wet season (Brambell and Davis 1941, Chapman et al. 1959, Cheeseman and Delany 1979, Coetzee 1975, Delany 1964, de Wit 1972).

Perrin (1980a) observed a bimodal pattern in the breeding of R. pumilio, with a recession in mid-summer, which he positively correlated with the erratic rainfall of the study area. Peaks in the number of births were recorded in February or March, following months of high rainfall. In areas in which rainfall is more predictable and even, R. pumilio breeds throughout spring and summer, e.g. in GCGR, study areas near Pretoria (Brooks 1974, de Wit 1972), and in the Kenya Highlands (Taylor and Green 1976).

M. varius reached a breeding peak (Fig 1.15) about a month earlier than did R. pumilio (Fig 1.16). The differences are probably related to the availability of nutritious food: M. varius lives entirely on invertebrates (this study), high in nutritive value, which might be available earlier in the season than is suitable plant material, which forms the bulk of the diet of R. pumilio in GCGR.

Perrin (1980b) reported seasonal changes in the nutrient content of the diet of R. pumilio. Breeding in the species followed peaks in nutrient content of the diet. Reproduction of O. irroratus in the eastern Cape Province, however, was not influenced by rainfall (Perrin 1980b). The species produces small litters throughout the year (Perrin 1979), and as it lives on large quantities of poor quality herbage during all seasons, Perrin (1980a) concluded that reproduction in O. irroratus is independent of rainfall and food with high nutritive value, and is therefore K-selected (Pianka 1970). R. pumilio on the other hand produces large litters seasonally, being dependent on rainfall and nutritious food, and may be considered r-selected.

Brooks (1974) stated that the breeding season of R. pumilio was restricted to the wet season, but in considering the factors which controlled reproduction, he rejected rainfall and photoperiod, and stated that only temperature and nutritive value of the diet could be involved - temperature being the most likely factor. I do not see, however, how Brooks (1974) could have completely eliminated rainfall from his consideration, as new growth in plants and seed production (i.e. increase in nutritive value of the food) are dependent on rainfall in the known range of R. pumilio.

Data relating to all female M. varius and R. pumilio collected in GCGR during October and November were examined to see whether there were any differences in the pregnancy rates of animals caught at lower altitudes

(< 1 900 m) and those trapped at high altitudes (> 2 200 m). In M. varius (N = 38) 83 % of the low altitude females were pregnant or lactating whereas only 35 % of those from above 2 200 m were. Of the R. pumilio (N = 35) pregnant or lactating females comprised 45 % of the low altitude sample and a mere 8 % at the high altitudes. These percentages not only illustrate the phenomenon that the breeding season starts later at higher altitudes, but further emphasises the conclusion that onset of breeding occurs earlier in the season in M. varius than in R. pumilio.

Rainfall at the higher altitudes is greater than at the lower altitudes in the Drakensberg (Killick 1963, and see "Study area: climate"), but temperature decreases with altitude (Killick 1963, Tyson et al. 1976). The later onset of breeding amongst the two small mammal species at higher altitudes in GCGR is therefore probably due to the effect of lower temperatures.

In considering the findings of Perrin (1980a, b), Brooks (1974) and this study, it appears that rainfall, food, and temperature all play a part in determining the start of the breeding season. Rainfall and food are closely linked, and provided these two factors are present, temperature can further influence the timing of reproduction.

MEASUREMENTS

Field measurements were obtained of nine species of small mammals which occur in GCGR (Table 1.20). The primary value of these measurements is that they provide data on Drakensberg small mammals for comparison with material from other localities. Although the sample sizes in some instances are small, the data collected in GCGR supplement the rather meagre existing records for species such as D. melanotis and G. murinus which are not well represented in museum collections.

M. varius and R. pumilio were collected in sufficiently large numbers to consider sexual dimorphism in these two species, and to allow investigation of the effect of altitude on size. The usual expectation is that with increase in altitude, decrease in temperature is associated with increase in body size (Bergmann's "rule") and decrease in size of appendages (Allen's "rule").

There were no significant differences between R. pumilio males and females ($P > 0,05$), but in M. varius males were significantly larger than females in mass and head and body length ($P < 0,01$). It is generally accepted that males are larger than females in species in which males compete with each other for females, or that sexual dimorphism has evolved to reduce food competition between the sexes (Brown and Lasiewski 1972, Erlinge 1979). It is not known whether M. varius is territorial and whether males do compete with each other. In the trapped sample, however, females significantly outnumbered males by 150 : 82. A possible explanation for this preponderance might be that the males and females feed on different size ranges of prey and consequently have different hunting patterns which may account for the larger number of females trapped, or that during the breeding season the females need to forage further afield to cater for the additional energy demands imposed during reproduction.

Means of the measurements of all M. varius and R. pumilio collected between 1 500 and 1 900 m were calculated and tested against the means of those animals collected from the base of the escarpment (2 200 m) upwards (Table 1.21).

The high altitude M. varius did not conform to Bergmann's "rule" by being larger and therefore experiencing less heat loss in the colder environment. In actual fact the opposite was recorded with high altitude animals being significantly smaller than those at lower altitudes. The most likely explanation for these smaller-sized shrews is that Dehnel's phenomenon operates - Mezhzherin (1964) reported that with increasing latitude the

TABLE 1.20 Body Measurements of small mammals collected in GCGR, listed in the order mean \pm SE, range, and sample size. Mass in g and other measurements in mm.

Species	Sex	Mass	Head & body	Tail	Hind foot	Ear
<u>M. varius</u>	M	13 \pm 0,4	78 \pm 0,6	34 \pm 0,4	13 \pm 0,1	8 \pm 0,1
		6 - 20	62 - 91	28 - 40	12 - 15	7 - 10
		77	76	75	76	73
	F	10 \pm 0,2	76 \pm 0,4	36 \pm 0,4	13 \pm 0,1	8 \pm 0,1
		6 - 19	65 - 90	28 - 45	11 - 16	6 - 10
		146	145	145	143	132
<u>C. flavescens</u>	M	25	102	57	16	11
		-	-	-	-	-
		1	1	1	1	1
	F	21 \pm 3,2	96 \pm 5,9	53 \pm 1,4	16 \pm 0,8	10 \pm 0,4
		7 - 33	69 - 125	49 - 63	12 - 18	8 - 11
		10	10	10	10	10
<u>R. pumilio</u>	M	36 \pm 0,8	105 \pm 0,9	83 \pm 0,7	21 \pm 0,1	13 \pm 0,1
		9 - 71	69 - 141	53 - 110	16 - 24	9 - 16
		155	154	145	150	149
	F	34 \pm 0,9	102 \pm 1,0	82 \pm 0,7	21 \pm 0,1	13 \pm 0,1
		12 - 63	72 - 130	60 - 100	18 - 25	10 - 15
		128	126	120	124	123
<u>O. irroratus</u>	M	109 \pm 8,7	158 \pm 5,0	83 \pm 3,3	28 \pm 0,4	21 \pm 0,5
		47 - 165	125 - 185	54 - 105	26 - 31	19 - 23
		16	16	16	16	16
	F	90 \pm 6,1	149 \pm 3,9	78 \pm 2,3	28 \pm 0,3	22 \pm 0,6
		50 - 136	123 - 178	61 - 101	25 - 30	18 - 26
		16	16	15	16	16

Continued overleaf

Species	Sex	Mass	Head & body	Tail	Hind foot	Ear
<u>O. sloggetti</u> *	M	86 - 1	149 - 1	45 - 1	25 - 1	10 - 1
<u>D. melanotis</u>	M	10 $\pm 0,6$ 6 - 13 14	71 $\pm 1,4$ 63 - 79 14	73 $\pm 1,2$ 65 - 79 14	17 $\pm 0,2$ 16 - 18 14	16 $\pm 0,3$ 15 - 17 13
	F	10 $\pm 0,8$ 6 - 19 19	71 $\pm 1,2$ 64 - 88 19	74 $\pm 1,3$ 68 - 88 19	18 $\pm 0,3$ 15 - 19 19	16 $\pm 0,3$ 14 - 19 18
<u>D. mesomelas</u>	M	11 10 - 14 3	73 69 - 81 3	107 104 - 112 3	20 18 - 22 3	13 11 - 16 3
	** F	14 - 1	71 - 1	104 - 1	20 - 1	11 - 1
<u>G. murinus</u>	M	27 $\pm 1,5$ 23 - 34 7	96 $\pm 1,8$ 91 - 103 7	76 $\pm 1,4$ 72 - 80 5	16 $\pm 0,5$ 14 - 18 7	14 $\pm 0,6$ 13 - 17 6
	F	26 $\pm 2,9$ 12 - 34 10	92 $\pm 3,4$ 75 - 108 10	74 $\pm 1,5$ 64 - 80 10	17 $\pm 0,1$ 17 - 18 10	15 $\pm 0,5$ 13 - 17 10
<u>M. minutoides</u>	M	10 $\pm 0,7$ 6 - 12 8	65 $\pm 3,2$ 47 - 74 8	52 $\pm 1,2$ 48 - 56 6	13 $\pm 0,4$ 12 - 14 8	9 $\pm 0,4$ 8 - 12 8
	F	7 6 - 8 4	58 52 - 65 4	47 42 - 49 4	12 12 - 13 4	10 9 - 11 4

* Collected at summit of Sani Pass.

** Collected at Cathedral Peak.

the dimensions of representatives of the genus Sorex decreased. The reduction in body mass in shrews with decreasing temperatures is accompanied by reduction in head and body length, size of internal organs, smaller skull measurements and consequently smaller brain size, and reduced endocrine activity. The size of the stomach does not decrease (Pucek 1970) therefore the absolute amount of food eaten by a smaller shrew is high relative to body mass. Furthermore, with decreased body size there would be more hairs per unit area, therefore providing better insulation. It is assumed that in the colder conditions on the Drakensberg escarpment slope a small M. varius would have as much opportunity of finding food as would a large one, and because it has a smaller body to feed its chances of survival would be greater.

There were no significant differences between the means of the measurements of R. pumilio at high and low altitudes, therefore this rodent also does not conform to Bergmann's "rule" in GCGR.

To test whether Allen's "rule" applied to M. varius and R. pumilio means of the proportions (expressed as percentages) of appendages to head and body length were calculated for high and low altitude specimens (Table 1.22). M. varius did not conform to Allen's "rule" - hind foot and ear length are proportionally almost the same at high and low altitudes, and while high altitude animals have proportionately longer tails, neither these nor any other differences in proportions are significant ($P > 0,05$).

There were no proportional differences in hind foot or ear length of R. pumilio, but tail length was proportionally significantly shorter in high altitude animals ($P < 0,05$). In respect of this appendage R. pumilio therefore conforms to Allen's "rule".

Coetzee (1970) examined relative tail length of R. pumilio in relation to climate and concluded that tails exceeded head and body length in hot arid areas but that they were shorter than head and body length in cold wet regions. The shortest proportional tail lengths which Coetzee (1970) reported were from Lesotho, being 80,4 % of head and body length. In GCGR the proportion is similar, being 79,5 %, lending support to Coetzee's (1970) hypothesis that R. pumilio conforms to Allen's "rule". At least four other small mammals from GCGR have proportionately shorter tails than their relatives collected in warmer areas of southern Africa (Table 1.23).

It is concluded that in GCGR M. varius does not conform to either Bergmann's or Allen's "rules", but that Dehnel's phenomenon obtains, whereby the shrews decrease in size with increase in altitude, an adaptation to reducing absolute food requirements. R. pumilio does not conform to Bergmann's

TABLE 1.21 Altitude-related size differences of M. varius and R. pumilio in Giant's Castle Game Reserve. Means of mass in g and linear measurements in mm.

Species	Measurements	Altitude		Value of t	Degrees of freedom	P
		< 1 900 m	> 2 200 m			
<u>M. varius</u>	Mass	13,0	10,2	3,79	222	< 0,001
	Head and body	78,4	74,9	4,78	218	< 0,001
	Tail	35,4	35,2	0,34	217	NS
	Hind foot	13,7	12,9	2,73	217	< 0,01
	Ear	8,5	8,2	3,66	202	< 0,001
<u>R. pumilio</u>	Mass	35,7	33,9	1,10	281	NS
	Head and body	103,8	104,1	0,15	278	NS
	Tail	83,0	80,6	1,83	263	NS
	Hind foot	20,8	20,5	1,48	272	NS
	Ear	12,6	12,9	1,44	270	NS

NS = $P > 0,05$

TABLE 1.22 Appendages of M. varius and R. pumilio as percentages of head and body length at low (< 1 900 m) and high (> 2 200 m) altitudes in Giant's Castle Game Reserve.

Species	Appendage	Altitude		Value of t	Degrees of freedom	P
		< 1 900 m	> 2 200 m			
<u>M. varius</u>	Tail	45,5	47,2	1,78	217	NS
	Hind foot	17,6	17,3	0,60	217	NS
	Ear	10,9	10,9	0,48	202	NS
<u>R. pumilio</u>	Tail	80,8	77,7	2,49	263	< 0,05
	Hind foot	20,3	19,8	1,45	272	NS
	Ear	12,3	12,4	0,62	270	NS

NS = P > 0,05

TABLE 1.23 Small mammal tail length as a percentage of head and body length in specimens from three different regions.

Species	Region	Tail %	Source
<u>M. varius</u>	GCGR	45	This study
	Transvaal	48	Rautenbach (1978a)
<u>R. pumilio</u>	GCGR	80	This study
	Transvaal	84	Rautenbach (1978a)
	Botswana	100	Smithers (1971)
<u>O. irroratus</u>	GCGR	52	This study
	Transvaal	59	Rautenbach (1978a)
	Pretoria	61	Davis (1973)
<u>D. melanotis</u>	GCGR	104	This study
	Transvaal	123	Rautenbach (1978a)
	Botswana	123	Smithers (1971)
<u>G. murinus</u>	GCGR	81	This study
	Transvaal	82	Rautenbach (1978a)
	Botswana	87	Smithers (1971)
<u>M. minutoides</u>	Transvaal	72	Rautenbach (1978a)
	Botswana	76	Smithers (1971)
	GCGR	81	This study

"rule", being of similar size at high and low altitudes, but conforms to Allen's "rule" in that high altitude animals have proportionately shorter tails which may be advantageous in minimising heat loss.

DIET

The contents of 186 stomachs from nine small mammal species were examined (Table 1.23). The purpose of the examination was to determine the main types of food that the small mammals were eating and not to identify individual plant and invertebrate species eaten, which in addition to being very time-consuming and requiring specialised techniques, is not always possible due to the degree of mastication.

After the small mammal survey had been completed additional snap trapping was done. Invertebrate remains in the stomachs of the small mammals collected were identified by staff and students in the Department of Entomology, University of Natal. Details of the identifications are given in Appendix 3.

The two shrew species took only invertebrates. Only the two *Otomys* spp. were strictly herbivorous; *R. pumilio* and *M. minutoides* were omnivorous but predominantly granivorous and also took insects, and *G. murinus* was equally granivorous and insectivorous.

Both of the shrew species have previously been described as insectivorous (Rautenbach 1978a, Roberts 1951). At GCGR *M. varius* did not live entirely on insects, but fed also on other arthropods (Appendix 3). In captivity Baxter (1977) fed *M. varius* and *C. flavescens* on a prepared diet with ox heart as the main ingredient. In addition they were given insects, snails, and earthworms. *C. flavescens* has also been recorded feeding on the carcasses of small mammals and birds (Baxter 1977, Rautenbach 1978a). One of the *C. flavescens* stomachs from an animal trapped at Cathedral Peak contained *R. pumilio* remains which were undoubtedly present as a result of the shrew having eaten part of a snap-trapped animal.

The wide variety of arthropods recorded in the shrew's stomach contents (Appendix 3) suggests that *M. varius* is an opportunistic feeder. Insect occurred more frequently than did other classes, and Coleoptera (both larvae and adults) were the most commonly recorded order, being present in almost two thirds of the stomachs. Incidence of Coleoptera is probably highest as they are abundant (Appendix 2), of a convenient size, come to ground when laying eggs, and the larvae develop in the soil and litter. Coleoptera were also the most frequently recorded arthropod taxon in *R. pumilio* stomachs (Appendix 3).

O. irroratus has been recognised as being entirely graminivorous (Davis

TABLE 1.24 Stomach contents of small mammals collected in GCGR.

Species	N	Per cent contents			Invertebrate
		Plant material			
		White	Green	Bark	
<u>M. varius</u>	37	-	-	-	100
<u>C. flavescens</u>	5	-	-	-	100
<u>R. pumilio</u>	89	74	11	-	15
<u>O. irroratus</u>	17	-	96	4	-
<u>O. sloggetti*</u>	1	-	100	-	-
<u>D. melanotis</u>	14	95	-	-	5
<u>D. mesomelas</u>	4	65	-	-	35
<u>G. murinus</u>	11	49	-	-	51
<u>M. minutoides</u>	8	86	13	-	1

* Collected at the summit of Sani Pass.

1973, Perrin 1980b, Rautenbach 1978a), living mainly on leaves and stems of grasses. Brown plant material, believed to be bark, was present in small quantities in four of the stomachs, and signs of the animal having fed on bark were occasionally noted at the bases of Leucosidea sericea bushes. Davis (1973) commented on the species' habit of feeding on bark and cited a number of instances in which damage had been caused to plantations of young Pinus spp.

Although only one O. sloggetti stomach was examined, the rodent was seen eating leaves, young stems, and flowers of Helichrysum plants on a number of occasions.

Roberts (1951) stated that R. pumilio fed mainly on green vegetable matter and sometimes took seeds, but the species has since been recognised as an omnivorous rodent (Brooks 1974, Choate 1971, Hanney 1965, Perrin 1980b, Taylor and Green 1976). Smithers (1971) described the mouse as granivorous, having only recorded seeds in its diet, and Brooks (1974), Choate (1971), and Taylor and Green (1976) described it as predominantly granivorous. Hanney (1965), in a sample of twelve stomachs, recorded slightly more green material than seed remains. Perrin (1980b) concluded that R. pumilio is an unspecialised omnivore which exploits transient but nutritious foods.

In GCGR seasonal variation was observed in the diet of R. pumilio, particularly in the amounts of white and green plant material (Fig 1.17). Least white material and most green material was present during spring, which coincides with the period of new green growth. White material then increased, reaching a peak in autumn, and green material decreased, being lowest during autumn, the season during which seeds are most abundant. During winter a slight decrease in white matter was recorded with a concurrent slight increase in green matter. The observed increase in green matter was probably partly due to the fact that the tall grassland habitat was sampled during July. In this moist valley-bottom habitat there was more green growth than in other grassland habitats at that time, and higher percentages than normal of green matter were recorded in R. pumilio stomachs.

Brooks (1974) observed similar seasonal variation in the amounts of white and green plant material in the diet of R. pumilio near Pretoria. Differences between the Pretoria and GCGR samples were that Brooks (1974) recorded a higher overall percentage of green material than was the case at GCGR, and a marked increase in insect intake during spring.

The other rodent, M. minutoides, found to be omnivorous in GCGR has previously been described as granivorous (Pienaar et al. 1980), graminivorous (Smithers 1971), granivorous and insectivorous (Hanney 1965), and

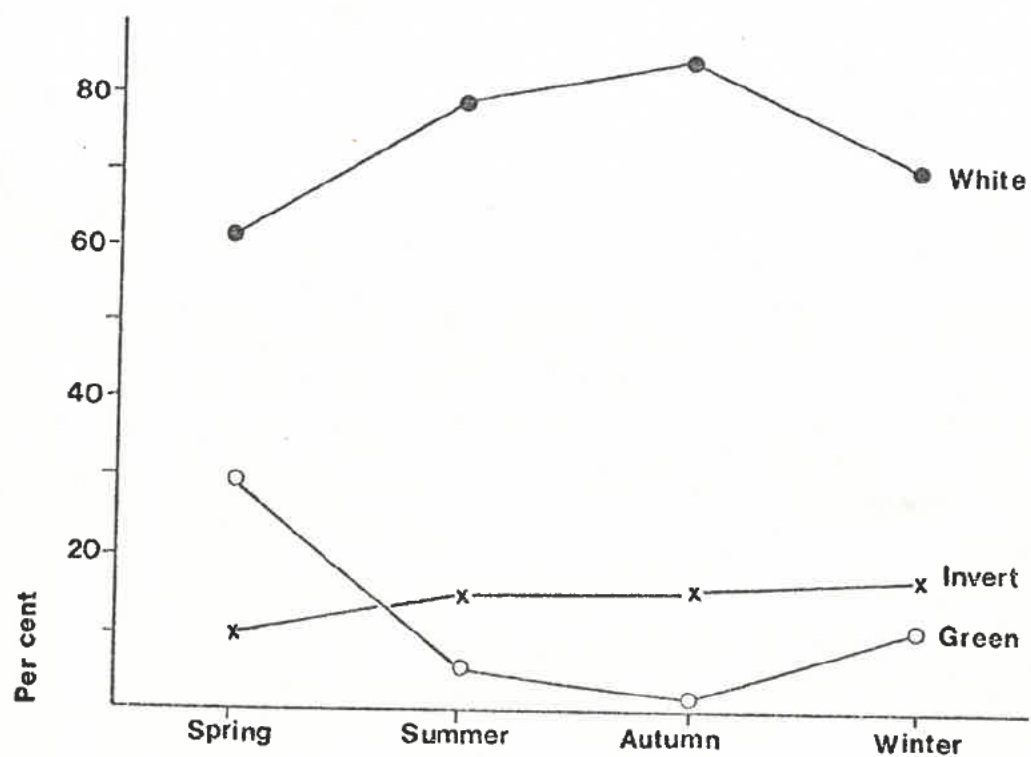


Figure 1.17 Seasonal variation in the percentages of white and green plant material and invertebrates in the stomach contents of *R. pumilio*.

omnivorous (Delany 1964). Like most omnivorous animals, M. minutoides is probably an opportunistic feeder. To establish the complete food spectrum of the species and the proportions of each category in the diet, it would be necessary to examine a larger number of stomachs collected throughout the year.

The stomach contents of the other three GCGR rodents (D. melanotis, D. mesomelas, G. murinus) which indicated granivorous and insectivorous diets do not differ greatly from what has been found in other areas. Smithers (1971) and Hanney (1965) recorded seed and insect remains in the stomachs of D. melanotis and D. mesomelas respectively, and both Rautenbach (1978a) and Smithers (1971) found that G. murinus took seeds and insects. In captivity these rodents were given a staple diet of seeds, but all three took insects (Coleoptera and Isoptera) in preference to seeds whenever they were offered.

If the diets of the small mammals of GCGR as indicated in Table 1.23 are considered, the first impression is that the community is dominated by species which are predominantly granivorous. If the relative abundance of the different species (see Table 1.4) is considered the combined granivorous impact on food resources is approximately equal to the insectivorous impact. Species with graminivorous feeding habits appear to be less than those which are either granivorous or insectivorous, but as has already been mentioned (chapter on relative abundance) O. irroratus is probably under-represented in the trapped sample. Furthermore, O. irroratus is by far the largest of the small mammals encountered in GCGR.

CONDITION

Physical condition of rodents has been determined by extraction of fat from the entire carcass (Batzli and Pitelka 1971, Perrin 1981a), dissecting out fat deposits on the testicular mesenteries and expressing this fat as a percentage of body mass (Brooks 1974), visually assessing the amount of subcutaneous or kidney fat (Sheppe 1972, Taylor and Green 1976), or expressing the ratio of body mass:length (Lawrence 1966).

In the GCGR small mammal study subcutaneous fat was rated visually and allocated a score from 1 to 4, and a mass:length cubed ratio (generally used by fishery biologists) was employed to calculate a condition factor (K). The sample sizes of only M. varius and R. pumilio were large enough for analysis.

It is important to calculate K from a mass:length cubed ratio, and not from a direct mass:length ratio as did Lawrence (1966). The basic assumption is that mass is directly proportional to volume. To correlate linear growth with increase in mass (= volume), it is essential to consider the cube of a linear measurement unless using a log-log plot (Crass, pers.comm.*). If a mass-linear relationship is plotted on an arithmetic scale, a curvilinear relationship results (see Lawrence, 1966). It was found, however, that females in advanced stages of pregnancy had to be excluded from the data as the additional body mass resulting from pregnancy tended to exaggerate K.

The results achieved by using both methods revealed similar patterns (Figs 1.18 and 1.19). In the M. varius sample (Fig 1.18) fat deposits and K were lowest during autumn (the end of the breeding season) and early winter. At the end of winter (just prior to the start of the breeding season) fat deposits and K were highest, but declined again during the breeding season (spring and summer). The R. pumilio data (Fig 1.19) showed similar troughs in fat and K during autumn. Both fat and K reached peaks during winter, and although fat decreased markedly during spring, K did not reflect a similar drop, but did decrease to levels parallel to those of fat during summer.

Fluctuations in condition of both species appear to be related to breeding. During the rainy season energy resources are channelled into reproducing and fat is not laid down. When breeding stops at the end of the wet

* R.S. Crass, Natal Parks Board, Pietermaritzburg.

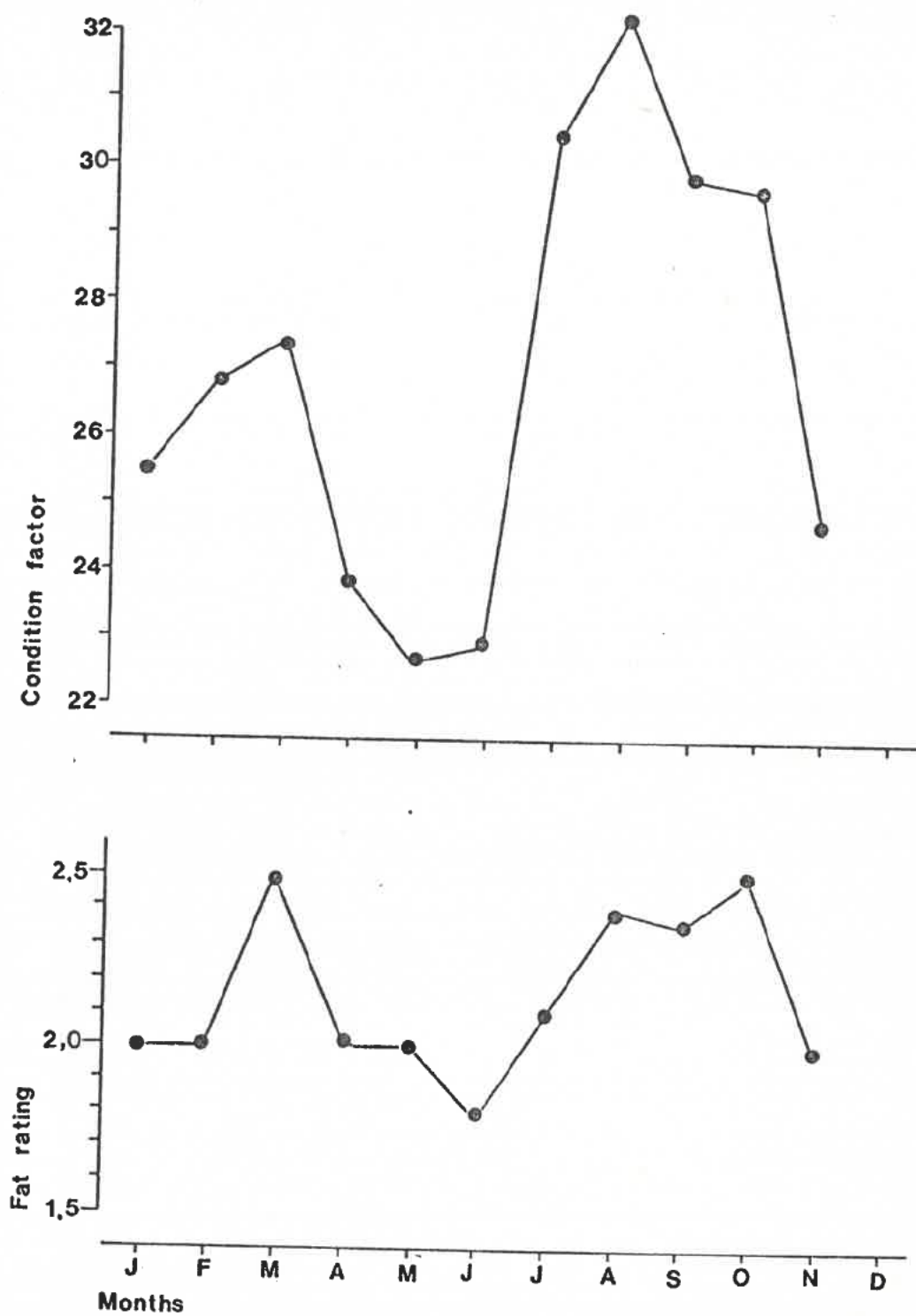


Figure 1.18 Mean condition factor (above) and mean fat rating (below) of *M. varius*, by months.

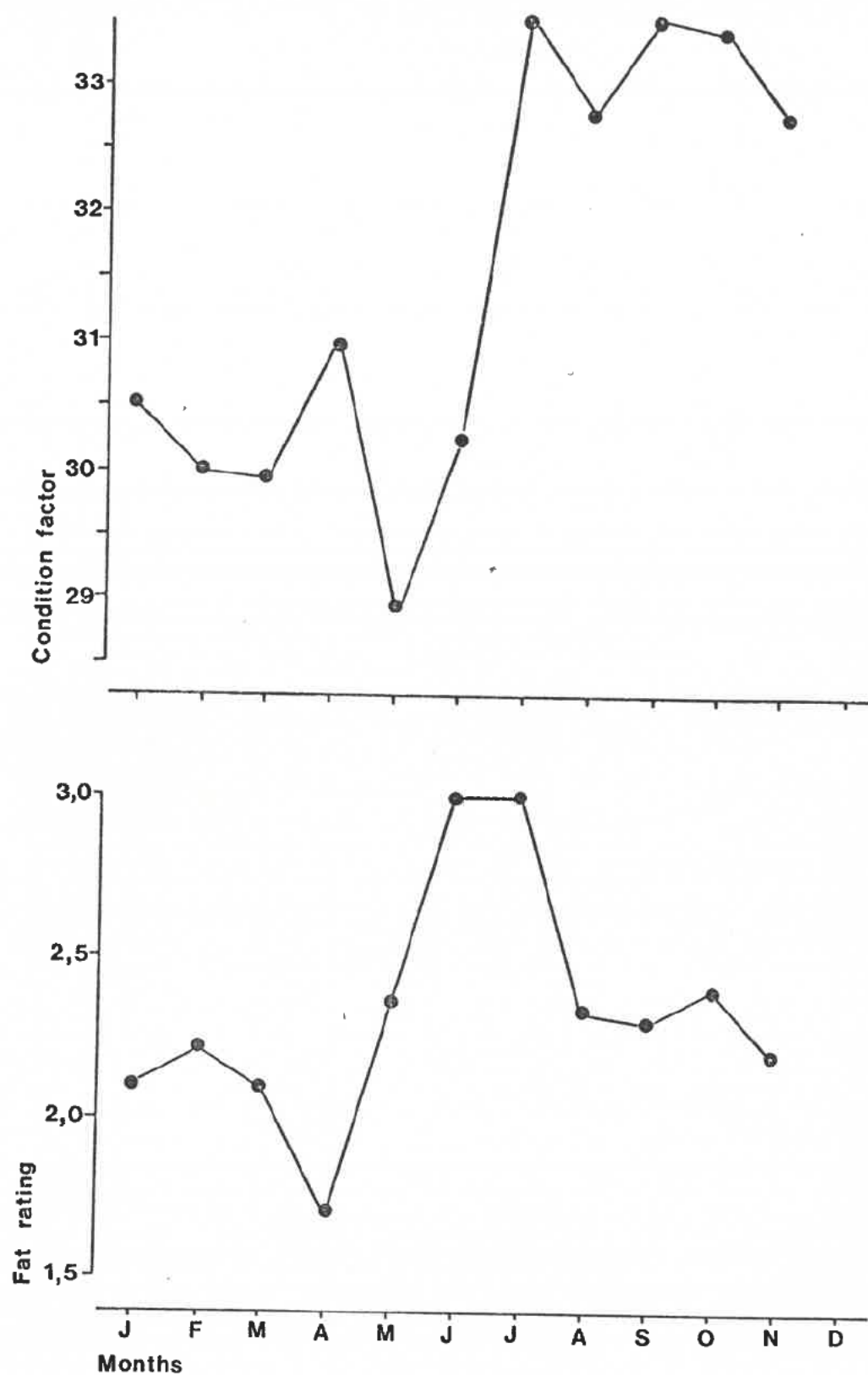


Figure 1.19 Mean condition factor (above) and mean fat rating (below) of *R. pumilio*, by months.

season nourishment is diverted from reproduction to building up fat reserves during the dry season, which then decrease again once breeding starts.

Seasonal fluctuations in the fat deposits of R. pumilio, similar to those observed at GCGR, were recorded by Brooks (1974) near Pretoria, Perrin (1981a) in the eastern Cape Province, and Taylor and Green (1976) in Kenya. In two other African rodents, Arvicanthus niloticus and Praomys natalensis (Taylor and Green 1976), and in one North American species, Microtus californicus (Batzli and Pitelka 1971), similar relationships between condition and reproduction were observed. Perrin (1981a) has suggested that certain fat levels are essential before wild rodents can breed successfully. A different situation was reported from Zambia by Sheppe (1972), who stated that there was a decrease in fat in Praomys natalensis during the dry season. His results show that animals had more fat in the middle of the dry season (June, July) than was the case at the end of the wet season (March), but that fat decreased during the rest of the dry season which extended until November or December. There is one major difference between the Zambian situation and that in the other four areas considered (GCGR, Pretoria, E. Cape, Kenya): the Zambian dry season was much longer than that in the other areas, and animals must therefore have deteriorated in condition later in the dry season due to food and water shortages.

The similar patterns resultant from the two methods of assessing condition suggest that K may well be used as a rapid and objective means of condition assessment in small mammals.

PREDATION

In GCGR there are at least 40 vertebrates known to include small mammals in their diets. These comprise 10 carnivores, 22 birds, and eight snakes (Tables 1.25, 1.26, 1.27).

The relative abundance of each predator has been rated as very rare, rare, fairly common, common, or very common, based on assessments from this study for carnivores, Brown (pers.comm.)* for birds, and Bourquin and Channing (1980) for snakes. The importance of small mammals in the carnivores' diets is based on their occurrence in faeces or stomachs (Rowe-Rowe 1978a, this study). For birds and reptiles small mammal importance in each predator's diet is rated as very minor, minor, medium, or major, based on information contained in McLachlan and Liversidge (1975) and FitzSimons (1970), or supplied by Brown (pers.comm.). In Table 1.28 the relative abundance, size range and activity patterns of prey species are listed.

Small mammals feature prominently in the diets of almost all of the carnivores listed in Table 1.25. Nocturnal carnivores did not feed exclusively on nocturnal small mammals, and neither did diurnal carnivores feed entirely on diurnal prey, a situation which can be expected in predators which hunt much of their prey by scent. Furthermore, the small mammal remains identified in stomachs and scats were not present in the same proportions as species trapped. In 477 jackal and 32 genet scats, for example, more O. irroratus than R. pumilio or shrew remains were recorded. This disproportionate representation will be discussed in the chapter on jackal diet. The entire size spectrum of all small mammals occurring in GCGR is available to all of the carnivores listed, including the very small African weasel (Rowe-Rowe, 1978b), therefore preference and not body size limits the selection of prey.

In addition to the species listed in Table 1.25 two other carnivores occur in GCGR viz spotted-necked otter (Lutra maculicollis) and clawless otter (Aonyx capensis). The spotted-necked otter has not been recorded feeding on mammals and the small mammal component in the clawless otter's diet was < 1 % (Rowe-Rowe 1977b).

Seven of the birds listed in Table 1.26 are terrestrial hunters and the remaining 15 are aerial hunters. The terrestrial hunters all have catholic diets in which the importance of small mammals is minor or very minor, and

* C.J. Brown, Zoology Dept, University of Natal, Pietermaritzburg.

TABLE 1.25 Carnivores preying on small mammals in GCGR. Sources of information: Rowe-Rowe (1978a) and this study.

Species	Abundance	Activity	Small mammal importance in diet
Black-backed jackal <u>Canis mesomelas</u>	Very common	Nocturnal & crepuscular	Major
Zorilla <u>Ictonyx striatus</u>	Rare	Nocturnal	Medium
African weasel <u>Poecilogale albinucha</u>	Very rare	Nocturnal	Major
Large-spotted genet <u>Genetta tigrina</u>	Common	Nocturnal	Medium
Egyptian mongoose <u>Herpestes ichneumon</u>	Fairly common	Diurnal	Medium
White-tailed mongoose <u>Ichneumia albicauda</u>	Fairly common	Nocturnal	Minor
Water mongoose <u>Atilax paludinosus</u>	Common	Crepuscular	Minor
Caracal <u>Felis caracal</u>	Rare	Nocturnal	Medium
Grey wild cat <u>F. lybica</u>	Common	Nocturnal	Major
Serval <u>F. serval</u>	Fairly common	Nocturnal & diurnal	Major

TABLE 1.26 Birds preying on small mammals in GCGR. Sources of information: McLachlan and Liversidge (1975) and Brown (pers. comm.)*.

Species	Abundance	Activity	Small mammal importance	Hunting method
Grey heron <u>Ardea cinerea</u>	Very rare	Diurnal	Minor	Terrestrial
Black-head heron <u>Ardea melanocephala</u>	Rare	Diurnal	Minor	Terrestrial
Cattle egret <u>Bubulcus ibis</u>	Rare	Diurnal	Very minor	Terrestrial
Hamerkop <u>Scopus unbretta</u>	Rare	Diurnal	Very minor	Terrestrial
White stork <u>Ciconia ciconia</u>	Rare	Diurnal	Minor	Terrestrial
Secretary bird <u>Sagittarius serpentarius</u>	Fairly common	Diurnal	Minor	Terrestrial
Stanley bustard <u>Neotis denhami</u>	Rare	Diurnal	Minor	Terrestrial
E. red-footed kestrel <u>Falco amurensis</u>	Fairly common	Diurnal	Minor	Aerial
Rock kestrel <u>Falco tinninculus</u>	Common	Diurnal	Major	Aerial
Yellow-billed kite <u>Milvus aegyptius</u>	Rare	Diurnal	Medium	Aerial
Black-shouldered kite <u>Elanus caeruleus</u>	Common	Diurnal	Major	Aerial

Continued overleaf

Species	Abundance	Activity	Small mammal importance	Hunting method
Martial eagle <u>Polemaëtus bellicosus</u>	Rare	Diurnal	Minor	Aerial
Jackal buzzard <u>Buteo rufofuscus</u>	Common	Diurnal	Major	Aerial
Steppe buzzard <u>Buteo buteo</u>	Rare	Diurnal	Medium	Aerial
African goshawk <u>Accipter tachiro</u>	Rare	Diurnal	Minor	Aerial
African marsh harrier <u>Circus ranivorus</u>	Rare	Diurnal	Medium	Aerial
Black harrier <u>Circus maurus</u>	Fairly common	Diurnal	Medium	Aerial
Gymnogene <u>Polyboroides typus</u>	Rare	Diurnal	Minor	Aerial
Barn owl <u>Tyto alba</u>	Rare	Nocturnal	Major	Aerial
Grass owl <u>Tyto capensis</u>	Fairly common	Crepus- cular	Major	Aerial
Marsh owl <u>Asio capensis</u>	Rare	Crepus- cular	Minor	Aerial
Spotted eagle owl <u>Bubo africanus</u>	Fairly common	Nocturnal	Major	Aerial

* C.J. Brown, Zoology Department, University of Natal, Pietermaritzburg.

TABLE 1.27 Snakes preying on small mammals in GCGR. Sources of information: Bourquin and Channing (1980) and FitzSimons (1970).

Species	Abundance	Activity	Small mammal importance in diet
Berg adder <u>Bitis atropos</u>	Common	Diurnal	Medium
Puff adder <u>Bitis arietans</u>	Fairly common	Diurnal & nocturnal	Major
Mole snake <u>Pseudaspis cana</u>	Rare	Nocturnal	Major
Rinkals <u>Hemachatus haemachatus</u>	Fairly common	Diurnal & nocturnal	Medium
Red-lipped snake <u>Crotaphopeltis hotamboeia</u>	Rare	Nocturnal	Minor
Skaapsteker <u>Psammophylax rhombeatus</u>	Fairly common	Diurnal	Minor
Black house snake <u>Lamprophis inornatus</u>	Rare	Nocturnal	Major
Brown house snake <u>Boaedon fuliginosus</u>	Rare	Nocturnal	Major

TABLE 1.28 Relative abundance, mean mass, and activity patterns of small mammals in GCGR. (Relative abundance = % contribution to total collected.)

Species	Abundance (%)	Mass (g)	Activity
<u>R. pumilio</u>	44,1	35	Diurnal
<u>M. varius</u>	38,7	11	Nocturnal
<u>O. irroratus</u>	4,9	99	Crepuscular
<u>G. murinus</u>	3,9	26	Nocturnal
<u>D. melanotis</u>	4,9	10	Nocturnal
<u>C. flavescens</u>	1,6	21	Nocturnal
<u>M. minutoides</u>	1,3	9	Nocturnal
<u>D. mesomelas</u>	0,6	14	Nocturnal

they probably feed on them only opportunistically. The aerial hunters on the other hand appear to rely more on small mammals as a source of food. Of primary importance to the aerial hunters is that the veld should support good small mammal populations, but that cover should not be so dense as to impair hunting or make it impossible.

In aerial-hunting raptors activity patterns of predator and prey are likely to be similar. Siegfried (1965), for example, reported 84 % incidence of R. pumilio in the diet of the diurnal black-shouldered kite, and Tarbotan (1978) recorded 43 % R. pumilio and 30 % Otomys sp. in its diet. On the other hand the nocturnal barn owl fed on only 1 to 2 % R. pumilio, 5 to 10 % O. irroratus, and over 80 % nocturnal small mammals in Natal (Vernon 1972). In the diet of the crepuscular grass owl the R. pumilio component was higher, viz 8 to 24 % (Vernon 1972).

R. pumilio and O. irroratus are the two species most likely to be taken by the 11 diurnal aerial hunters listed in Table 1.26, whereas nocturnal and crepuscular hunters would have a wider range of species and sizes of animals available to them.

Because of its ability to pursue and hunt prey in burrows or other secluded places it is unlikely that the activity patterns of the small mammals will affect a snake's choice of prey. Not all of the snakes will be able to feed on the entire size range of small mammals. Berg adder, red-lipped snake, and skaapsteker will be limited to taking smaller specimens or species.

CONCLUSIONS

The overall trapping effort of 7 560 trap nights in 17 habitats in Giant's Castle Game Reserve defines the distribution, relative abundance, and species diversity of the small mammals of the reserve. Sampling effort in some of the habitats was low, however, and additional trapping in these areas might have revealed the presence of more species.

The large sample sizes of Myosorex varius and Rhabdomys pumilio provided sufficient information on which to draw definite conclusions on the ecological relationships of these two species in GCGR. M. varius was the most adaptable small mammal in the reserve, occurring in all habitats from 1 500 m to 3 000 m, irrespective of vegetation type, burning regime, or stage of growth of the vegetation. Unlike the other two southern African species in the genus Myosorex (M. cafer and M. longicaudatus), M. varius exhibits wide habitat tolerances which allow it to exist in both forest and grassland. M. cafer and M. longicaudatus are specialised and restricted to forest habitat (Meester and Dippenaar 1978).

In GCGR, M. varius, with its wide habitat tolerances, was usually the first species to become established after veld burning, therefore adopting a role as a pioneer parallel with that reported in Praomys natalensis elsewhere (Meester et al. 1979). P. natalensis is also a species with wide habitat tolerances and one of the first to recolonise after fire.

R. pumilio, similarly, has wide habitat tolerances, although not as wide as those of M. varius, occurring in all grassland, woodland, and scrub habitats, but is absent from forest. The key factor affecting its presence is adequate grass cover, which is emphasised by its absence from recently-burnt grassland, woodland, and scrub, and its recolonisation of such areas once herbage had reached at least 100 g/m² (oven dried mass). At lower altitudes where herbage production was greatest, R. pumilio was the most abundant species. With increasing altitude and the corresponding decrease in herbage production, the relative abundance of R. pumilio in trapped samples decreased, while the proportion of M. varius increased.

Forest was dominated by Graphiurus murinus which was caught in other habitats only where trees or large rocks were present. The small sample sizes of all other small mammals collected permitted no more than brief speculation on their particular habitat preferences and in most instances they can be associated only with certain vegetation types.

Diversity indices for small mammal communities in Giant's Castle were

generally low, which was attributed to the simplicity of the vegetation and the numerical dominance by the two broad-niche species, M. varius and R. pumilio. Highest diversities were recorded in the most complex habitats, a phenomenon which conforms to accepted theories of diversity.

The major shortcoming of the small mammal trapping study in relation to fire was that too many habitats were sampled with the result that the sampling effort in each was inadequate. This was the consequence, unfortunately, of the small mammal study being conducted simultaneous with studies of antelopes and the black-backed jackal. In evaluating data on the responses of small mammals to burning, the low numbers caught at some of the stages during recolonisation made statistical comparisons difficult. A more detailed study, with more frequent sampling, using a large number of live traps would have provided more suitable sample sizes.

Despite the shortcoming referred to above, the phenomena recognised in the responses of the small mammals to fire were similar to those recognised in grassland francolins (Mentis and Bigalke 1979) as well as those in small mammals elsewhere in the Drakensberg (Mentis and Rowe-Rowe 1979), and fit the hypothesis proposed by Mentis and Rowe-Rowe (1979) that two vegetation climaxes exist (viz fire-maintained climax grassland, and climax forest maintained by climate and the exclusion of fire) and that Drakensberg animals have adapted either to a system of regular burning or to one in which fire is excluded (in which faunas different from those in grassland occur). No francolin species, small mammals, or antelopes are known to favour a fire regime intermediate between regular burning and long-term protection from fire. (See also pages 59, 136, and 233.)

Herbage production in relation to time since burning was the proximal factor affecting recolonisation, with habitat structure, the degree of cover, and amount and availability of food being ultimate factors. Herbage production, in turn, was affected by season of burn and altitude. Herbage grew more rapidly in spring-burnt than in autumn-burnt areas, and above ground standing crop of herbage decreased with increase in altitude. After fire small mammal numbers were initially low on biennial burns, but recolonisation was rapid, and trap success reached pre-burn figures 6 to 12 months after burning. Lowest numbers were recorded in grassland unburnt for three or four years, where only one or two species were present compared with five or six in biennially-burnt areas. In fire-protected habitats, burnt once only in 16 to 20 y, trap success was similar to the peaks recorded in biennially-burnt habitats, but fewer species were present.

It is concluded that biennially-burnt areas support highest small

mammal numbers and most species, due to the presence of adequate cover and accessible nutritious food. If herbage is left unburnt for three or four years the build-up of moribund grass at ground level results in an unsuitable small mammal habitat in which mobility, food accessibility, and food quality deteriorate. In long-term fire-protected grassland and scrub, changes have taken place in the basal cover and species composition of the vegetation. In these more stable habitats stabilisation of small mammal numbers and equilibrium of species is reached. This is unlike the situation in biennially-burnt areas, where the first two years after fire may be regarded as dynamic, with changes in small mammal species richness and composition taking place due to colonisation and extinction.

The decline in number and diversity of small mammals, reaching a trough some years after burning, may have implications in forest plantation management. In view of the prevalence of rodent damage to seedlings in pine plantations it would be worthwhile to establish when the troughs in rodent numbers occur (they may be different in different areas) and therefore the most suitable time for planting pine seedlings, which are apparently most vulnerable to rodent damage during the first two years.

Except in M. varius and R. pumilio, insufficient data were collected on resident species to analyse population structure and reproduction.

The 1,2 : 1 preponderance of males in the 310 R. pumilio sampled did not differ significantly from parity. In the total sample of 232 M. varius, however, females significantly outnumbered males by 1,8 : 1. This does not necessarily reflect the true composition of the population but possibly results from differential trap responses and/or activity patterns of the sexes. Female M. varius are significantly smaller than males, may therefore feed on a different size range of prey, and may consequently have different hunting patterns. It is not known whether M. varius males or females are territorial therefore it is impossible to speculate whether this aspect of their behaviour accounted for the greater number of females trapped. Alternatively, females with young may need to forage more extensively. During the breeding season the male : female ratio shows a significant preponderance of females, whereas in the non-breeding season the sex ratio is even (see Fig 1.15 on page 73 for monthly sample sizes). The energy demands of the female shrews are likely to be higher than those in males because of their smaller size and their particular role in reproduction, therefore they may be more active than the males and range further. The sample size during the non-breeding season, however, was small and more data are required to establish the validity of this suggestion.

Changes in the sex ratio may take place with age, as appears to be the case in at least four antelopes studied in GCGR. As far as is known the sex ratio at birth in grey rhebuck, mountain reedbuck, eland, and blesbok was 1 : 1, but amongst adults there were preponderances of females. If this applies also to M. varius then the shrew may be categorised as an r-strategist, and assist in explaining its role as a generalist and pioneer.

A final possibility in accounting for the significant preponderance of M. varius females in the trapped sample may be that there actually are more females in the population. In wolves it has been found that the sex ratio at birth was correlated with population density (Mech 1975). In areas where wolf population densities were highest the sex ratio at birth was in favour of males, but where population densities were low, significantly more females than males were born, therefore ensuring greater productivity. The sex ratio at birth may similarly be in favour of females in the GCGR M. varius population. In support of this it may again be noted that from February to May, when there are most young animals in the trapped sample, the preponderance of females was most significant (Fig 1.15).

Reproduction in M. varius and R. pumilio coincided with the wet season (spring and summer). Differences in the time of onset of breeding were observed between the two species, and within each breeding commenced later in the season at higher than lower altitudes. It is concluded that breeding probably commences earlier in M. varius than in R. pumilio as more insects are available earlier in the season than is abundant suitable food (ripe seeds) for R. pumilio. Although precipitation is greater at higher than lower altitudes, temperatures are lower, therefore the later onset of breeding at the higher altitudes was probably related to lower temperatures. The lower temperatures presumably have an effect on the growing season, which is shorter at higher than lower altitudes (cf. differences in herbage production, Fig 1.4 on page 27). There is therefore less time for reproduction at higher altitudes, which may have an effect on litter size or the number of litters produced per season. Insufficient data on altitude-related litter sizes are available from this study, further underlining the need for additional research on the influence of altitude on the reproduction and year-round population structure of both species.

The population age structures of M. varius and R. pumilio were similar in that they were typical of seasonal breeders, viz that the greatest range of size classes was recorded in the months following the breeding season, and the smallest range was observed in the non-breeding season, followed by

an upward shift in size classes.

The seasonal change in population age structure of R. pumilio reveals nothing new and follows patterns previously reported for the species (Brooks 1974, Perrin 1979) whereas the data on M. varius are the first to have emanated from a field study of this shrew. The population dynamics of M. varius has features in common with those recorded in some European and North American shrews. During winter the catches comprised entirely small shrews, suggesting that a die-off in adults takes place at the end of the breeding season, leaving mainly young animals. The possibility of body size reduction in shrews during winter (Dehnel's phenomenon) should not be ruled out, however, as this has been found to take place seasonally in cold northern hemisphere climates (Pucek 1970).

Mezhzherin (1964) and Pucek (1970) have attributed reduced body size in shrews during winter (or with increase in latitude) to a decrease in the size of the braincase, changes in size and shape of intervertebral discs, reduced endocrine activity, tissue dehydration, and reduced size of internal organs (except the stomach). Coupled with the reduced body size is increased amount of hair per unit area, therefore providing better insulation. While the relative amount of food eaten by a smaller shrew, which has a proportionately large stomach, and proportionately greater surface/volume ratio, is therefore high relative to body mass, in absolute terms it is less than that needed to maintain a larger animal, and therefore relatively more efficient.

It is unfortunate that, in the GCGR study, the ages of the shrews were not determined, perhaps from the amount of toothwear, as this would have given an indication of whether the body had in fact decreased in size or whether the population was dominated by young animals. This matter deserves further study.

Measurements of both M. varius and R. pumilio collected at low (< 1 900 m) and high (> 2 200 m) altitudes were compared. No significant size differences in the absolute measurements of R. pumilio were observed, but high altitude animals had proportionately shorter tails. It was therefore concluded that in overall size this rodent does not conform to Bergmann's "rule", but that it does conform to Allen's "rule" in respect of tail length.

Contrary to Bergmann's "rule", the higher altitude M. varius were significantly smaller than those at lower altitudes, and contrary to Allen's "rule", there were no significant proportional differences in length of appendages. The smaller high altitude shrews are likely to be the result

instead of the effect of Dehnel's phenomenon (Mezhzherin 1964) in which smaller, not larger, body size is correlated with decreasing temperatures.

Data collected on the diet of the small mammals of GCGR revealed very little new information, and corroborate previous studies. R. pumilio, as has been found elsewhere, emerged as a mixed feeder, in this instance living mainly on white plant matter (seeds). M. varius has always been recognised as feeding on invertebrates, and the only new information obtained in this study concerned the details of the invertebrates eaten. The species took a wide variety of arthropods but mainly Coleoptera, which were most abundant in the area, of a convenient size, and could be captured on the ground, suggesting that the shrew is an opportunistic feeder. This observation assists in explaining its role as the most successful pioneer species in GCGR.

Condition was assessed by visually rating subcutaneous fat deposits, and by calculating the condition factor (K) from a mass : length cubed ratio. These two methods revealed similar patterns in M. varius and R. pumilio, which followed the conventional patterns associated with breeding, i.e. condition was lowest at the end of the breeding season (autumn and early winter), and highest at the end of winter, but declined again during the breeding season (spring and summer).

The mathematical principle behind the comparison of the relative "fatness" of bodies using the condition factor lies in the comparison of cylinders and has been used by fishery biologists. If two cylinders, made of the same material, with equal diameters but unequal lengths, are compared the relation between mass (= volume) upon length indicates the degree of "fatness" of each cylinder. Although mice and shrews are not true cylinders, the similarity of the patterns obtained from rating condition on the basis of fat deposits and from calculating the condition factor, suggest that K may well be used as a rapid and objective means of assessing condition in small mammals.

As small mammals are important in the diets of a number of predators greater numbers and diversity of small mammals will contribute to the numbers and diversity of predators. Management of the habitat can therefore aim at producing the desired diversity. On the basis of information collected during this study a mosaic of biennial burns, providing burnt and unburnt veld each year, and interspersed with areas protected from fire, caters optimally for both small mammals and their prey.

The synoptic picture resulting from the small mammal study in Giant's Castle Game Reserve is that the altitudinal gradient, increasing from

1 500 m to over 3 000 m above sea level, with resultant differences in vegetation and climate, plays an important part in influencing the distribution, relative abundance, reproduction and size of at least two of the small mammals (M. varius and R. pumilio) which occur in the reserve. With increase in altitude and decrease in herbage production, the cover-dependent R. pumilio gives way to the more generally-adapted M. varius; breeding commenced later in the season at higher than lower altitudes; and at the higher altitude M. varius were smaller, a possible adaptation to decrease absolute energy requirements.

Further important influential factors are the seasonal, highly predictable, high rainfall of the area, and the management practice of controlled burning. The high, predictable rainfall results in a marked growing season with which is correlated a marked small mammal breeding season. The high rainfall is responsible also for high herbage production and the necessity of periodic defoliation by fire. Habitat destruction by fire results in drastically reduced small mammal populations, but the predictable high rainfall assures rapid recovery with which is associated rapid small mammal recolonisation.

PART 2 : ANTELOPES

METHODS

DISTRIBUTION AND HABITAT PREFERENCES

Data were randomly collected throughout the study period. The following details relating to the habitat were recorded for each observation : altitude; aspect in degrees east of north; slope in degrees, by 5° intervals; topography, described as valley bottom, valley side, ridge top, plateau, main escarpment slope, or summit; and vegetation type and its fire history, indicating regularity of burn, and season and year burnt. Data were analysed using the SPSS programme (Nie *et al.* 1970) and an attempt was made to identify ecological separation of the species by using Biplot analyses (Gabriel 1971).

RESPONSES TO FIRE

Information on antelope numbers in relation to veld burning was collected in grassland at two elevations, viz 1 900 m and 2 200 m.

At 1 900 m antelope were counted from a vehicle travelling along a 7 km-long track, running approximately west to east, from the main reserve road to the airstrip (= Airstrip route, Fig 2.1). Under the normal burning programme grass on alternate sides of the track was burnt every second year, and areas of visible grassland on either side of the track were approximately equal. Counts were repeated five times per month.

At 2 200 m an area of approximately 6 km² near Bannerman hut (Fig 2.1), normally burnt every second spring, was not burnt when 24 mo old and was left until 48 mo old. Areas on either side of it received normal biennial treatments. Comparative antelope counts were done on foot in the burnt and unburnt grassland (= Bannerman route). As the burnt and unburnt areas differed in size, and distances walked could not be measured accurately, the index of abundance was expressed as antelope counted/hour of walking.

Randomly-collected data on the distribution of antelope in relation to the time since the veld was last burnt were analysed separately.

POPULATION TREND MONITORING

Antelope were counted three times a month by observers on horseback or on foot along each of five fixed routes. The routes, identified by the num-

bers given to them in the following descriptions, are indicated in Figure 2.1:

Route 1

Route 1, which covers a distance of 19 km, starts at the main camp (1 760 m), goes along a ridge top to the contour path at 2 300 m, along the contour path for 9 km, then down another ridge and back to the starting point. Vegetation along the entire route is grassland, burnt biennially in spring, except for that above the contour path which is burnt biennially during winter.

Route 2

Route 2 starts at the Pines game guard camp. The first 5 km of the route traverses biennially autumn-burnt grassland at ca 1 660 m, then enters biennially spring-burnt grassland, running up a ridge to 2 000 m, across a number of ridges and the upper reaches of streams, then back to the main camp at 1 760 m. Total length of the route is 13 km .

Route 3

Route 3 covers a distance of 18 km . The entire route traverses biennially spring-burnt grassland on ridge tops and plateaux, starting from Injasuti cottage at 1 900 m, ascending to 2 220 m, then ending at 1 800 m .

Route 4

Route 4, which is 15 km long, starts at Ketelaki game guard camp (1 420 m) and runs along a river valley for its entire length to 1 720 m . Vegetation is predominantly woodland, burnt biennially during autumn.

Route 5

Route 5 starts at Hillside house (1 700 m), runs up to the top of a ridge at 2 080 m, then into a river valley and finally across a large plateau and back to the starting point. The 12 km-long route traverses biennially spring-burnt grassland along its entire length.

PAST GAME COUNTS

Records were available of some game counts done as early as 1962. Antelope were then counted along certain firebreaks in the reserve during August, when the veld on either side of the green firebreak was unburnt. It was possible to repeat one of these counts, viz along the jeep track from Witteberg

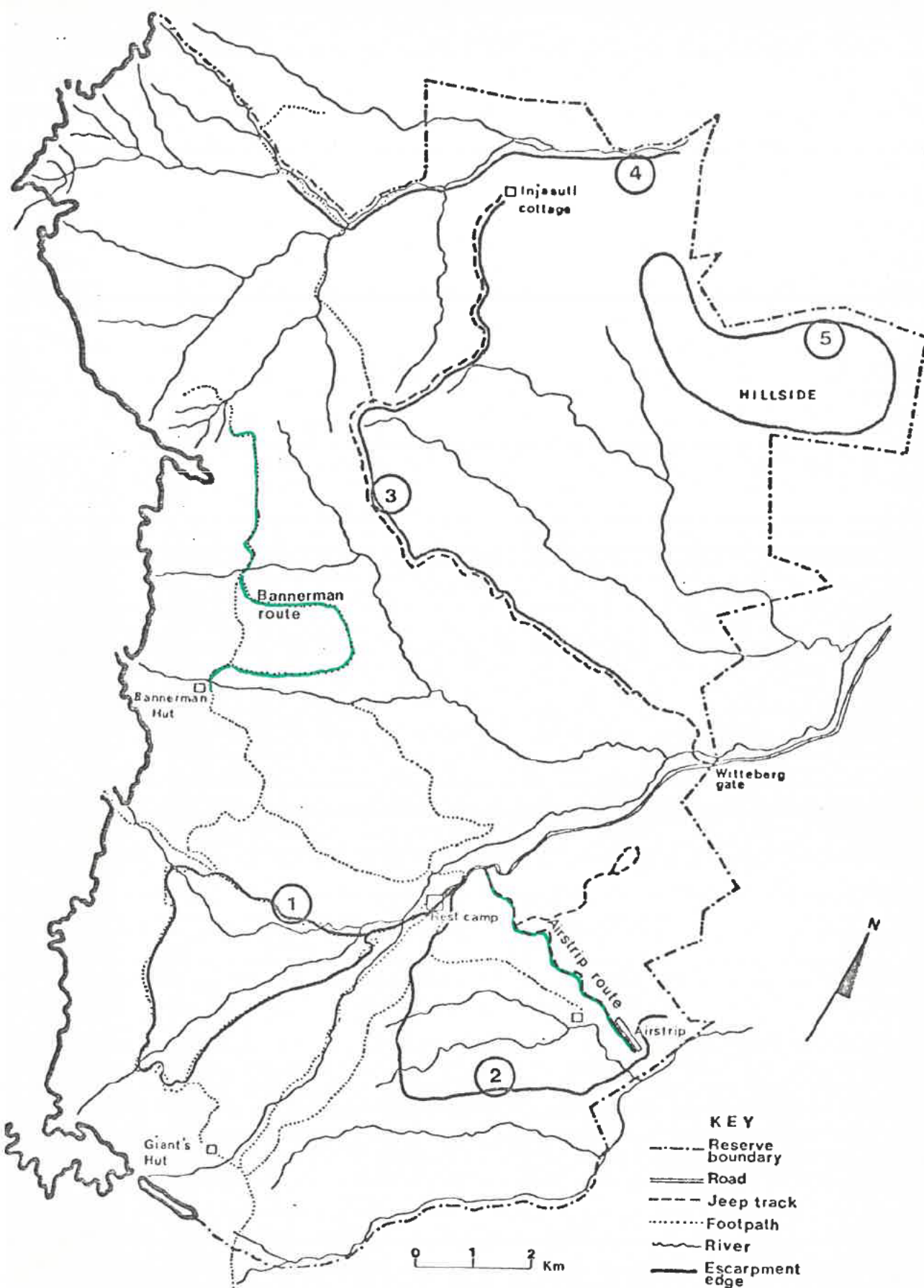


Figure 2.1 Game count routes in GCGR, indicating fixed routes (1 to 5), and Airstrip and Bannerman routes.

to Injasuti cottage (Fig 2.1).

Records were also available of aerial counts of eland and ground counts of all antelope species for the entire reserve, made during 1972 and 1973.

POPULATION AND STANDING CROP ESTIMATES

Population estimates of grey rhebuck, mountain reedbuck, and oribi were made from numbers of these antelopes counted along fixed routes in relation to eland counted along the same routes at the same time, and the known population of eland, using the index and control formula proposed by Caughley (1977), viz

$$N_x = \frac{N_y n_x}{n_y}$$

where N_y is the known population of species y and n_x and n_y the numbers counted along the transect. Eland were selected as the control, as they are large and conspicuous, and can be accurately counted from the air (Scotcher in prep.).

Standing crop is expressed as ha/animal unit (AU). An animal unit is defined as that biomass consuming energy at the same rate as an average steer of 455 kg. The number of antelope making up an AU was calculated from the formula used by Mentis and Duke (1976), viz

$$\frac{455^{0,75}}{(\text{Mean mass of species } y)^{0,75}}$$

The per cent contribution of each species to the total biomass was calculated as follows:

$$\frac{\text{Total AU for species } y}{\text{Total AU for all species}} \times 100$$

and termed per cent metabolic biomass.

DISTRIBUTION AND HABITAT PREFERENCES

Eight antelope species have occurred in GCGR since its proclamation in 1903, viz grey rhebuck (*Pelea capreolus*), mountain reedbuck (*Redunca fulvorufula*), common reedbuck (*R. arundinum*), oribi (*Ourebia ourebi*), klipspringer (*Oreotragus oreotragus*), eland (*Taurotragus oryx*), bushbuck (*Tragelaphus scriptus*), and grey duiker (*Sylvicapra grimmia*). As it was believed that blesbok (*Damaliscus dorcas phillipsi*), red hartebeest (*Alcelaphus buselaphus*), and black wildebeest (*Connochaetes gnou*) occurred in the reserve prior to its proclamation, numbers of these animals were reintroduced, mainly between 1955 and 1966. Blesbok became well-established and increased in number. The black wildebeest introduction was not successful, and because of habitat destruction due to severe over-grazing and a lack of evidence that the species had ever occurred in the mountains almost all of the animals have been removed. The introduced hartebeest have not flourished. Many died shortly after their introduction and the rate of increase of the surviving animals has been slow. The species has not, however, been responsible for any habitat destruction.

With the exception of bushbuck and grey duiker, which were recorded in scrub and forest; klipspringer, which occur only on steep dwarf-scrub-covered slopes and ledges on the main escarpment; and eland, which utilise grassland, scrub and forest; all other species were recorded only in grassland (Table 2.1) or open vegetation.

The most commonly-encountered antelopes in GCGR were grey rhebuck, mountain reedbuck, eland, oribi, and blesbok. The physical habitat preferences of these species have been compared in relation to altitude, aspect, slope, and topography in Figures 2.2 to 2.5. Responses of the five species to burning will be dealt with in the next chapter.

Grey rhebuck were recorded over the full altitudinal range of the study area, but mainly from the Sub-alpine Belt above the sandstone cliffs (Fig 2.2). Altitudinal distribution of eland was similar to that of grey rhebuck, but did not extend to the summit. Mountain reedbuck were recorded mainly below and just above the sandstone cliffs (96 % of the observations were made at 1 900 m and lower). Oribi and blesbok were encountered mainly at 1 800 m to 1 900 m, which is the altitude of most plateaux and gentle-sloping broad ridge tops.

In GCGR there are almost equal numbers of north, south, and east slopes, and very few west slopes. North, north-east, or east slopes were favoured

TABLE 2.1 Habitat preferences of antelopes in GCGR.

Antelope	Vegetation	Altitude	Aspect	Slope	Topography
Grey rhebuck	Recorded mainly in open grassland. Never in forest. Occasionally in all other open vegetation including summit	At all altitudes, but mainly above cave sandstone, 1 800 to 2 300 m	Mainly N, NE, E	Up to 35°. Mainly < 20°	All topographic types. Few records from summit. Valley bottoms not favoured
Mountain reedbuck	Mainly in grassland, protea woodland, and occasionally tall grassland	Mainly at 1 900 m and lower (below sandstone)	Almost equal utilisation of all available aspects	Steep slopes of 20° to 30°	Mainly valley sides
Eland	Recorded mainly in grassland. Also in all other types, excluding the summit	At all altitudes up to 2 700 m, but mainly 1 800 to 2 300 m	Mainly N, NE, E	Up to 35°. Mainly < 20°	Not recorded on summit. No single type favoured
Oribi	Grassland. Only in tall grassland after fire	Up to 2 200 m, but mainly at 1 800 and 1 900 m	Mainly N, NE, E	< 10°	Not recorded on escarpment or summit. Gentle slopes in all other types favoured
Blesbok	Grassland. Only in tall grassland after fire	1 800 to 1 900 m	Mainly N, NE, E	< 10°	As for oribi
Common reedbuck	Mainly tall grassland. Also open grassland	Mainly 1 800 m and lower	N to E	< 10°	Valley bottom
Klip-springer	Swarf scrub in the upper Sub-alpine/lower Alpine Belts	Above 2 500 m	N to E	25° to 35°	Escarpment
Bushbuck	Forest, thicket and scrub	Mainly up to 1 800 m. Sometimes higher	N to S	?	Valley sides and bottoms
Grey duiker	Forest, thicket and scrub	Mainly up to 1 800 m. Recorded up to 2 200 m	?	?	Valley sides and bottoms
Red hartebeest	Grassland	Up to 2 300 m. Mainly 1 800 to 2 000 m	?	< 10°	Any gentle slope
Black wildebeest	Grassland	Up to 2 200 m. Mainly 1 800 to 1 900 m	N to E	Mainly < 5°	Plateaux and flat ridge tops

by all species (Fig 2.3) in preference to south-east and south slopes. Only mountain reedbuck displayed almost equal utilisation of all slopes from north to south.

Oribi and blesbok showed distinct preferences for more gentle slopes - more than 50 % of the observations were on slopes of $< 5^\circ$ and almost all the rest on $< 10^\circ$ (Fig 2.4). Mountain reedbuck on the other hand favoured the steepest slopes, 70 % of the observations being on slopes of above 20° . Grey rhebuck and eland were recorded over the full range of slopes, but showed a preference for those of 20° and less.

Grey rhebuck and eland utilised the greatest ranges of topographical features (Fig 2.5). Mountain reedbuck showed a marked preference for valley sides, and oribi and blesbok preferred ridge tops and plateaux.

In the Biplot analysis, vectors based on the values of the variates altitude, aspect, slope, and topography, were computed for all observations in which data for the four variates were recorded, and plotted for each of the five antelopes (Fig 2.6)*.

Eland and grey rhebuck displayed the widest usage of the variates, that of grey rhebuck actually being somewhat wider than indicated in Figure 2.6, which does not include data from the summit (omitted so that all species could be plotted on a more convenient scale). For all vectors of the observations on both species up to 2 700 m there is almost complete overlap.

The vectors of the variates for oribi and blesbok overlap almost completely, with blesbok showing a slightly narrower use of the four habitat parameters. Mountain reedbuck, similarly, displayed a specialised usage of the parameters, and least overlap with the other four antelopes.

The Biplot shows the spread of grey rhebuck and eland over a wide range of altitudes, blesbok and oribi concentrated at intermediate altitudes, and mountain reedbuck at low to intermediate altitudes. The correlations between altitude, topography, and slope are high (0,90 to 0,99), therefore the influence of the variates topography and slope on these vectors closely follows the pattern of altitude. Mountain reedbuck is the only species which shows a fairly even distribution of values along the range of aspects (0° to 345°), while the plots for the other species illustrate their preference for north to east (0° to 90°) aspects.

Aspect was not strongly correlated with the other three physical parameters (correlations of 0,04 to 0,47).

* Notes on the interpretation of the Biplot are given in Appendix 4.

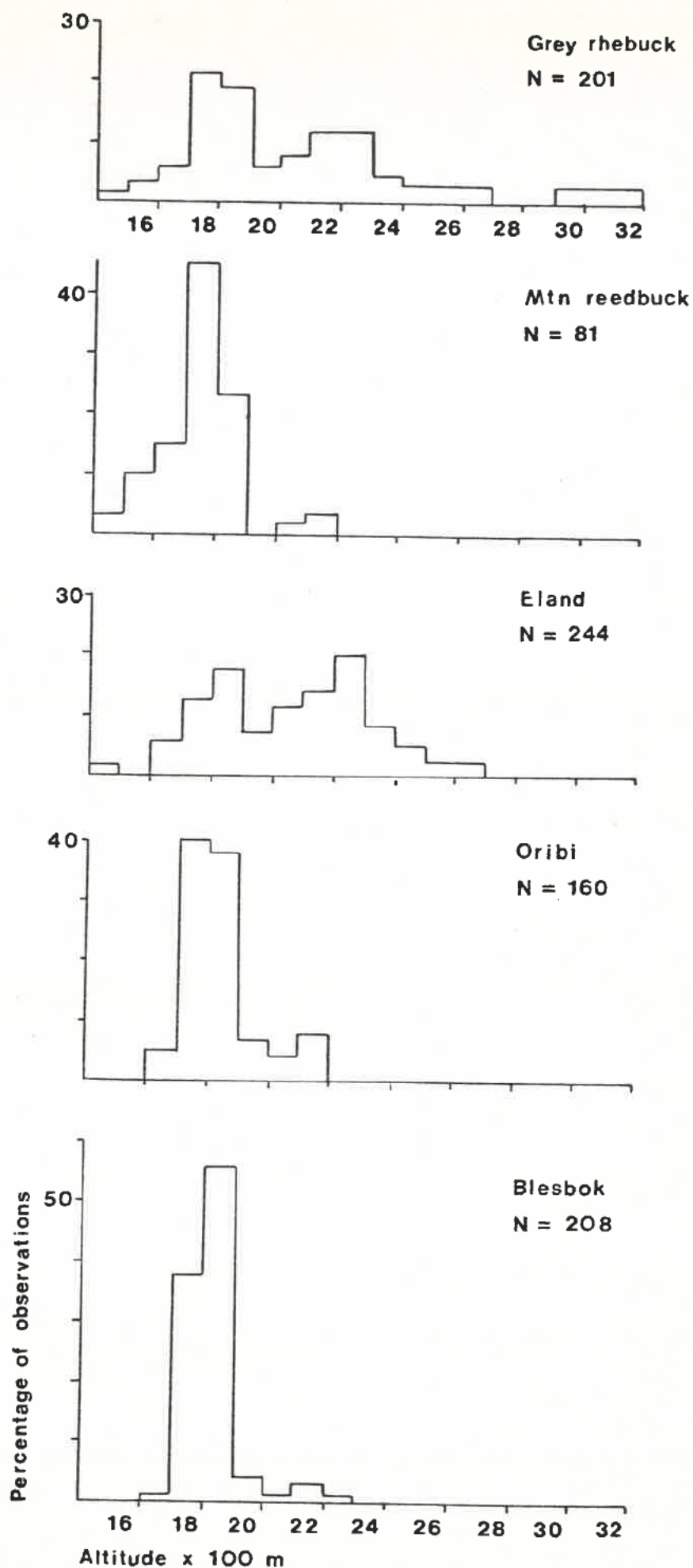


Figure 2.2 Altitudinal distribution of the five most commonly-recorded antelopes in GCGR.

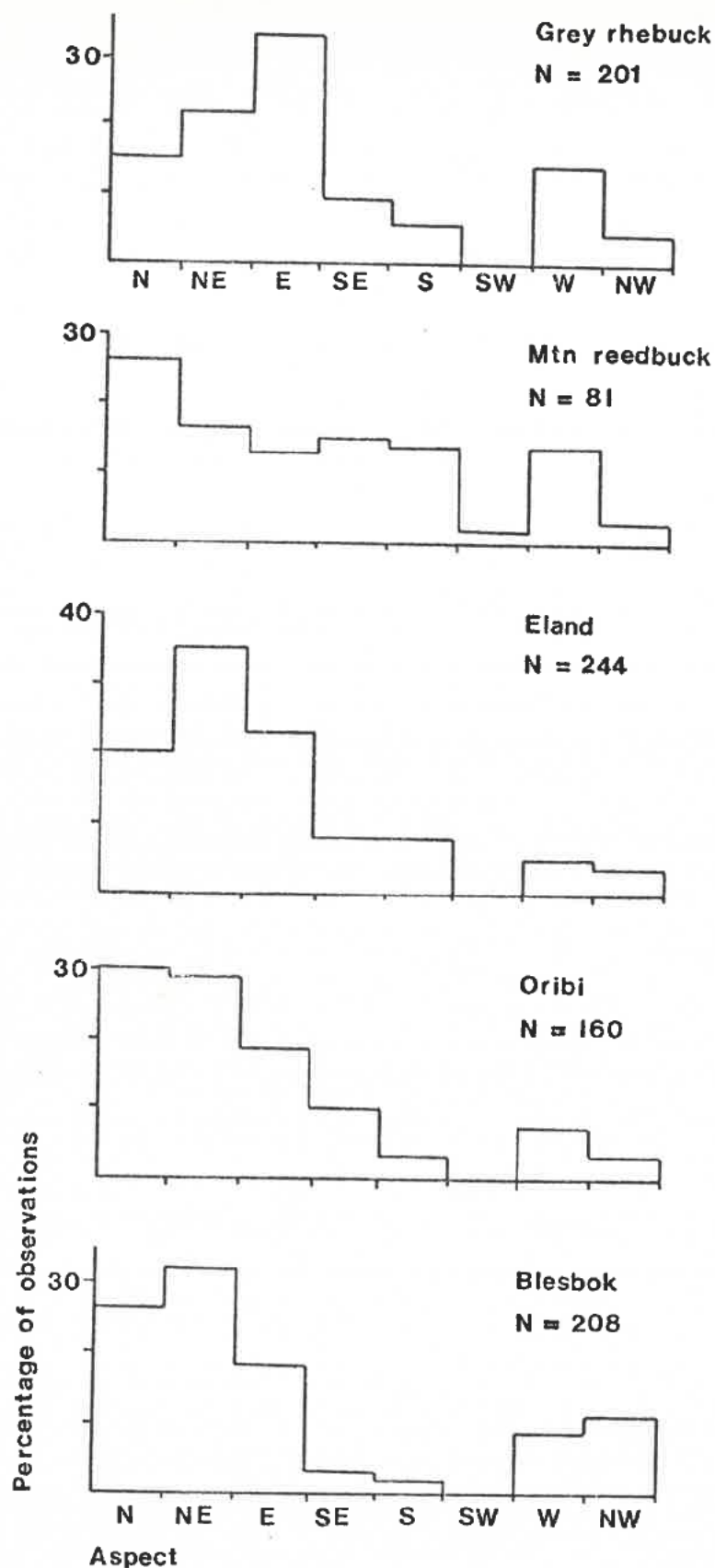


Figure 2.3 Distribution of five GCGR antelopes in relation to aspect. (N, NE, SE, and S slopes occur in approximately equal numbers in GCGR, but there are very few SW, W, and NW slopes.)

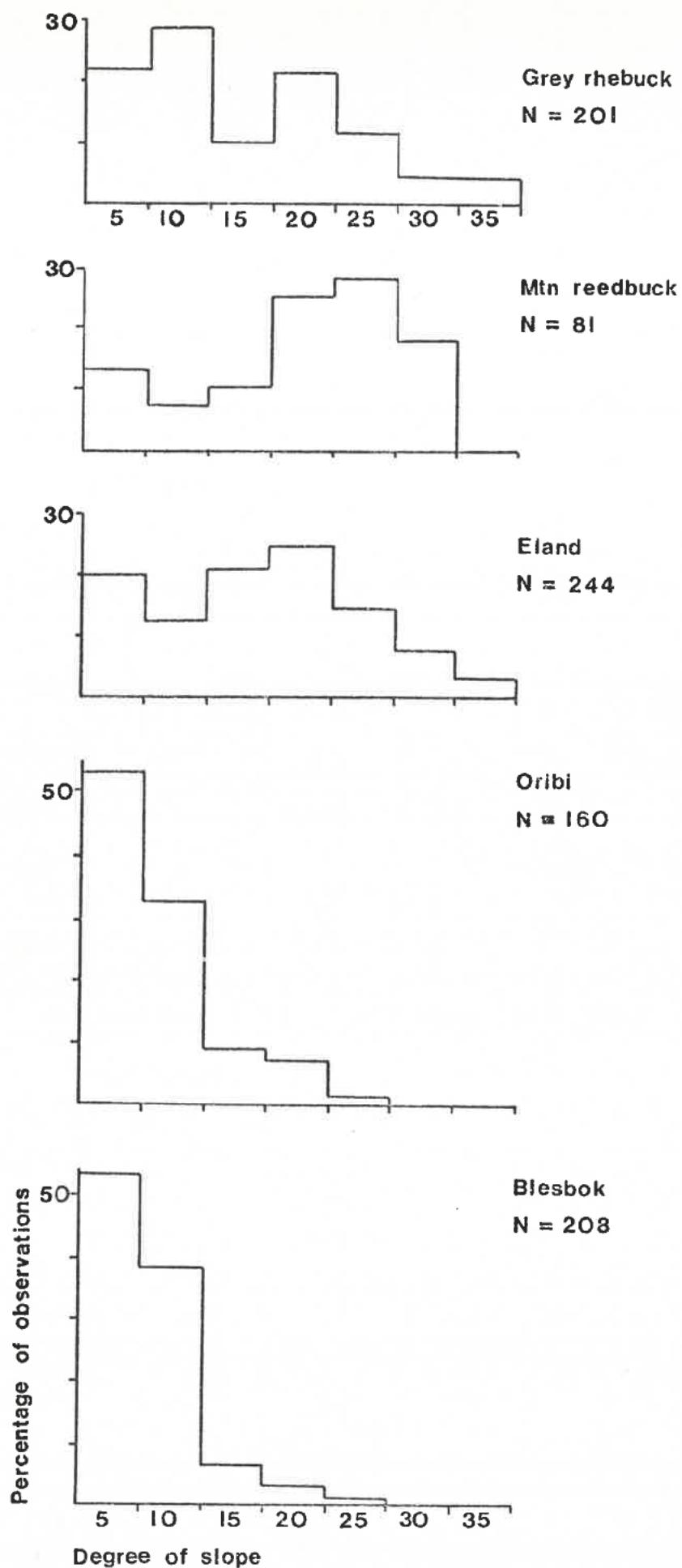


Figure 2.4 Distribution of five GCGR antelopes in relation to degree of slope.

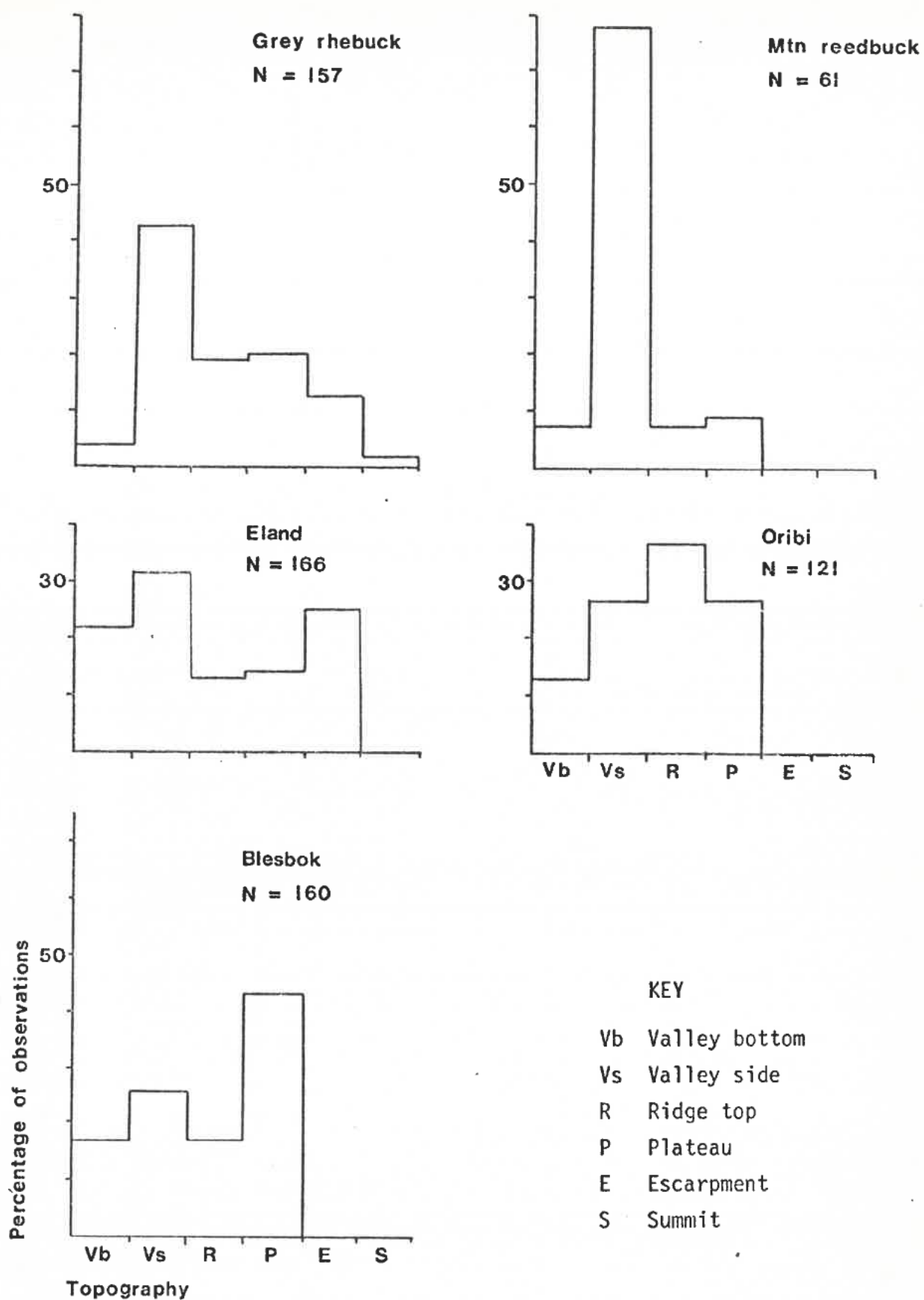


Figure 2.5 Distribution of five GCGR antelopes in relation to topography.

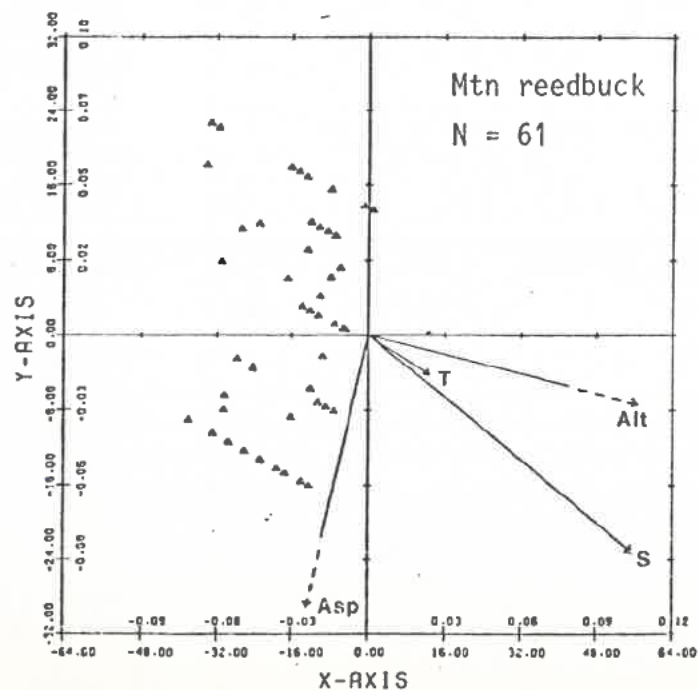
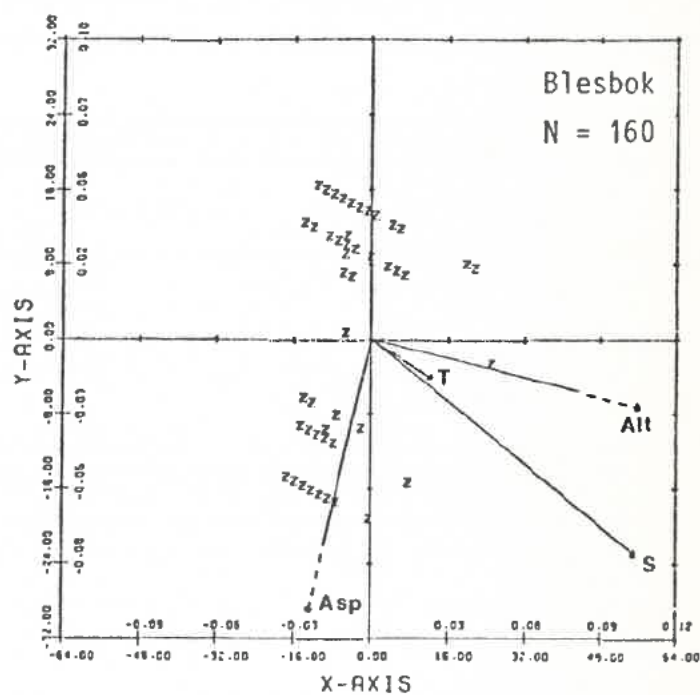
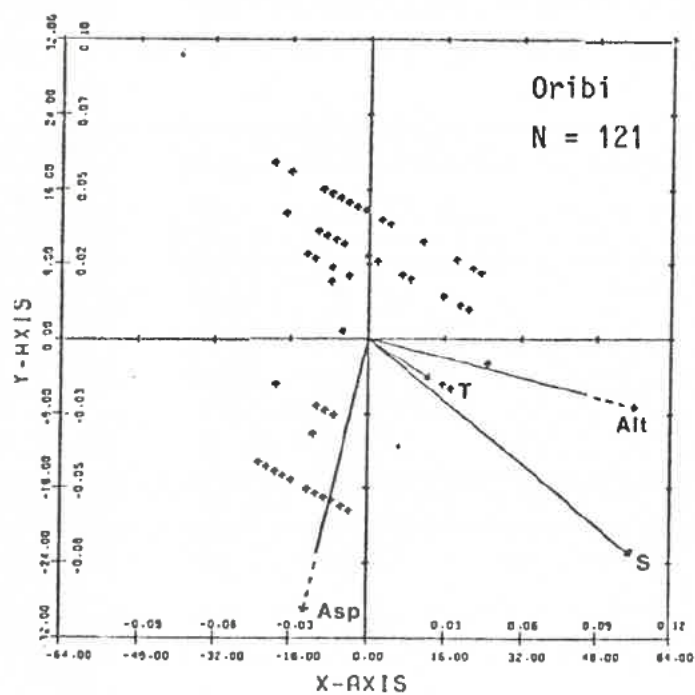
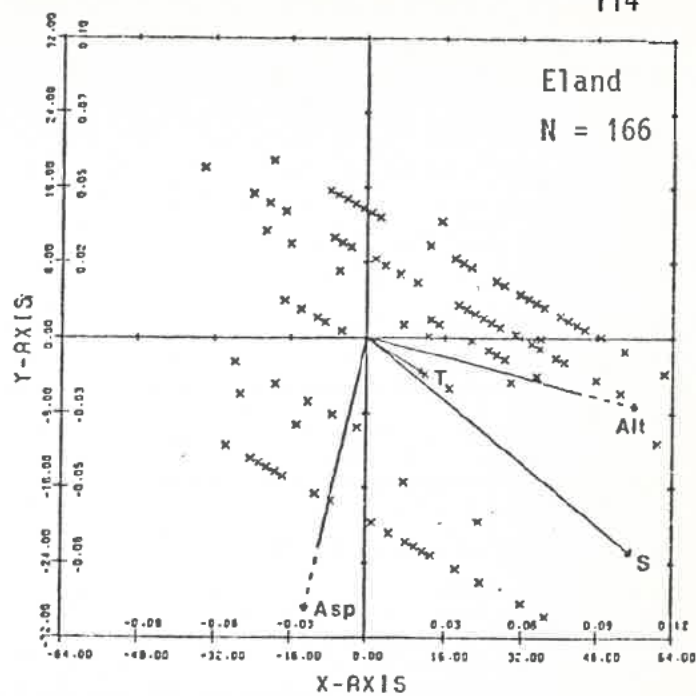
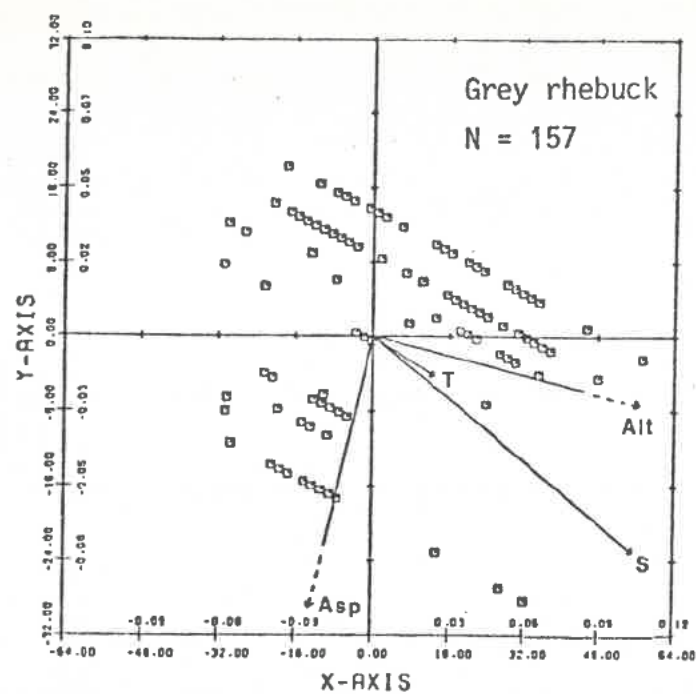


Figure 2.6 Biplot of the distribution of five GCGR antelopes in relation to the variates altitude, topography, degree of slope, and aspect. Variances of the variates are indicated by the arrows, labelled Alt (altitude), T (topography), S (slope), and Asp (aspect).

DISCUSSION

Although varying degrees of overlap exist in the habitat preferences of the most abundant antelopes in respect of vegetation type and physical parameters of the environment, ecological separation occurs in the food and feeding styles of those sharing similar habitat preferences.

Eland live mainly on grasses during spring; take grasses and forbs during summer and autumn; and grasses, forbs, and browse during winter (Scotcher in prep.). Furthermore, the eland feeds unselectively and therefore falls into Jarman's (1974) feeding style class e, which includes species that "feed unselectively on a wide range of grasses, or grasses and browse, in a number of vegetation types".

Grey rhebuck live mainly on forbs, selecting predominantly for leaves and flowers, and taking very little woody material (Esser 1973). In Ohrigstad Dam Nature Reserve (Transvaal), where Esser (1973) made direct observations on the plants eaten by grey rhebuck, he recorded this antelope feeding on at least 50 forb species and only seven grass species. On all occasions that grey rhebuck fed on small shrubs, only leaves were taken. In the Orange Free State Ferreira (in prep.) determined grey rhebuck diet by faecal analysis: during summer 79 % of the diet comprised dicotyledonous plants, and throughout the rest of the year the dicotyledonous component was 90 % to 92 %. The grey rhebuck therefore falls into feeding style "class b" (Jarman 1974) which includes antelopes that feed entirely on grasses or entirely on browse, being very selective for plant parts.

Mountain reedbuck are predominantly grazers (Mason 1977), and in the northern sub-species (Redunca fulvorufula chanleri) Irby (1977a) recorded 99,5 % occurrence of monocotyledonous plants in rumen contents. Major grasses in the diet of R. f. chanleri were Themeda triandra and Hyparrhenia spp., which were taken in greater proportions than they occurred in the vegetation. These observations support the classification by Jarman (1974) of mountain reedbuck as "class b" feeders, i.e. although being entirely grazers, they feed selectively. In GCGR Hyparrhenia spp. occur mainly in Montane Belt Themeda-dominated grassland (Scotcher in prep.), and the Sub-alpine Belt grassland just above the sandstone is also dominated by Themeda triandra (Scotcher and Clarke 1981), which is less prevalent at higher altitudes. The distribution of mountain reedbuck in GCGR coincides with the distribution of these grasses, although there may be other grasses below 1 900 m which are also favoured by the antelope.

Oribi have been recorded feeding mainly on grasses, but also on forbs

(Viljoen 1975). The species displays a high degree of selectivity, not only for particular plants, but also for certain portions of plants (Viljoen 1975).

Blesbok display almost identical habitat preferences to those of oribi (Table 2.1, Figs 2.2 to 2.5), but feed only on grasses (du Plessis 1972), taking a wide variety of species. On recently-burnt veld they are relatively unselective, but on veld unburnt for some time they tend to become selective for certain species (du Plessis 1972). The major difference between blesbok and oribi therefore lies in the feeding style: oribi falling into Jarman's (1974) class b, and blesbok into class d ("feed on grasses, being unselective for species but more selective for plant part or growth stage").

Taking the preferred terrain and the feeding styles of the antelopes into account, eland occupy the broadest niche in GCGR. Terrain-wise grey rhebuck occupy as wide a niche as do eland, but the overall niche is narrowed by the antelope's specialised feeding style. Mountain reedbuck, oribi and blesbok occupy narrow niches in comparison with those of the other two antelopes.

Jarman (1974) listed the habitat of both grey rhebuck and mountain reedbuck as grassland on hills. At Highmoor, on the Little Berg, Oliver et al. (1978) found that there was little distributional overlap of the two species: grey rhebuck preferring a large plateau area, and mountain reedbuck preferring the steep valley sides. Grey rhebuck habitat in Ohrigstad Dam Nature Reserve resembles that in GCGR, being open mountain grassland and protea woodland (Esser 1973). In Bontebok National Park the species occurs in open areas in coastal renosterbos and Leucadodendron communities (Esser 1973).

In studies done elsewhere in South Africa, viz Loskop Dam Nature Reserve (Irby 1973), Kruger National Park (Irby 1976), and Jack Scott Nature Reserve (Mason 1977), mountain reedbuck have shown a preference for well-grassed slopes in open woodland. Mason (1977) found that of the 18 ungulates observed, mountain reedbuck made greatest use of steep slopes. Mason (1977) also commented on the fact that mountain reedbuck did not occur in large expanses of open grassland (plains habitat), but utilised only the fringes near cover. In GCGR more cover is available below the sandstone and in valleys than on plateaux and ridge tops at higher altitudes, hence the preference shown for lower altitudes (Fig 2.2) and valley sides (Fig 2.5), almost to the degree of complete avoidance of open areas.

The oribi is generally recognised as a grassland species (Jarman 1974, Mason 1973, Tait 1969, Viljoen 1975). On the Transvaal highveld Viljoen

(1975) identified the preferred habitat as open grassland and mountain sourveld on plateaux. Ninety-seven per cent of the oribi observations made by Mason (1973) were in grassland, only 3 % in protea woodland, and acacia woodland and denser woody vegetation were completely avoided.

In southern Africa the eland occurs in a wide range of habitats which include savanna, woodland, open grassland plains, and montane grassland (Jarman 1974). Its adaptability is well illustrated in GCGR where eland aggregate in large herds during summer when they concentrate on recently-burnt grassland, while during the dry months they split up into small groups and are found in all habitats, except the summit.

The blesbok has been broadly categorised as a grassland species (Jarman 1974). Past distribution records indicate that it was a plains species (S.F. du Plessis 1969, S.S. du Plessis 1972) distributed over the grassland areas of the southern Transvaal, Orange Free State, and north-eastern Karoo. In the Transvaal, where blesbok have been introduced to a number of different areas, they thrive best in open sour grassland (Kettlitz 1962). The species does not appear to have occurred naturally in GCGR. It has been stated in early reports that blesbok moved into Natal only during winter, on to the plains at the base of the Drakensberg (du Plessis 1969). The introductions to GCGR have been successful, but suitable habitat is limited, therefore local distribution of this gregarious migratory species is confined to plateaux and broad, relatively flat ridge tops.

The other two introduced alcelaphines are also typical plains species (Kok 1975, von Richter 1971). The small population of red hartebeest (ca 30) is not sedentary, and the animals move over a great portion of the reserve and the adjoining Forestry Department land at Highmoor, favouring grassland on more gentle slopes. The black wildebeest in GCGR were very sedentary, and limited their choice of habitat to level or almost level areas. Their concentration on such areas resulted in serious over-grazing and erosion. Almost all of the wildebeest have been removed from GCGR to more suitable areas, and at present only seven remain.

The other four indigenous antelopes (common reedbuck, klipspringer, bushbuck, and grey duiker) are rare in GCGR, obviously because of the lack of suitable habitat.

Although only 21 observations were made on common reedbuck, the species showed a preference for tall grassland (67 % of observations) and favoured valley bottoms (71 % of observations) to other topographical features. Jungius (1971) found that common reedbuck preferred tall grassland and vleis

in the Kruger National Park, and also utilised woodland when the grass was long.

Scotcher (1980) identified klipspringer habitat in another Drakensberg game reserve (Royal Natal National Park) as dwarf scrub growing on steep rocky slopes. In GCGR such areas occur only on the upper slopes of the escarpment, below the main basalt cliffs. It is axiomatic to state that bushbuck are limited by the amount of forest and dense scrub in GCGR. Although grey duiker are generally recognised as ubiquitous, with broad habitat tolerances (Jarman 1974), the species does favour good cover. In GCGR forest and dense scrub are favoured, but the species occurs also in more open scrub and in tall grassland when there is good cover.

INFLUENCE OF FIRE ON DISTRIBUTION AND ABUNDANCE

The immediate effects of fire will be dealt with first; then the results of counts in burnt and unburnt veld along the Airstrip route at 1 900 m and along the Bannerman route at 2 200 to 2 300 m will be given; and finally distribution and abundance of antelopes in relation to time since burning and season of burn, based on random observations, will be detailed.

IMMEDIATE EFFECTS

No antelope are known to have been burnt to death in any controlled burn during the study period, and Schofield (pers. comm.*) recorded no such deaths from 1976 to 1981.

Two eland were trapped by a runaway fire in August 1978 and died as a result of being burnt. One of these animals was pregnant and in poor condition. During September carcasses of four eland, a bushbuck, and a common reedbuck were found, all of which had apparently been burnt in the same fire and died later.

The runaway fire, started on the escarpment by arsonists, and fanned by a strong wind which at times exceeded 100 km/h, spread rapidly over a wide front, eventually burning out most of the southern portion of the reserve. This was in complete contrast to controlled burns which are executed under suitable wind conditions and confined to much smaller areas.

LONG-TERM EFFECTS

Airstrip route

It was not possible to monitor the biennial burns over the intended full two-year period. During June 1978 about 35 % of the grassland along the Airstrip route was accidentally burnt, then during August the rest of the area was burnt in the big runaway fire referred to above. In August 1979 the southern portion was intentionally burnt again so that the regime of biennial spring burning could be continued. Comparative counts (5/month) were then done in the two spring burns (one burnt during 1978 and the other during 1979) for the next 12 months.

Throughout the year more antelope were counted on the spring 1979 burn (grass < 12 mo old) than on the spring 1978 burn (grass 12 to 24 mo old)

* A.M. Schofield, Warden, Giant's Castle Game Reserve.

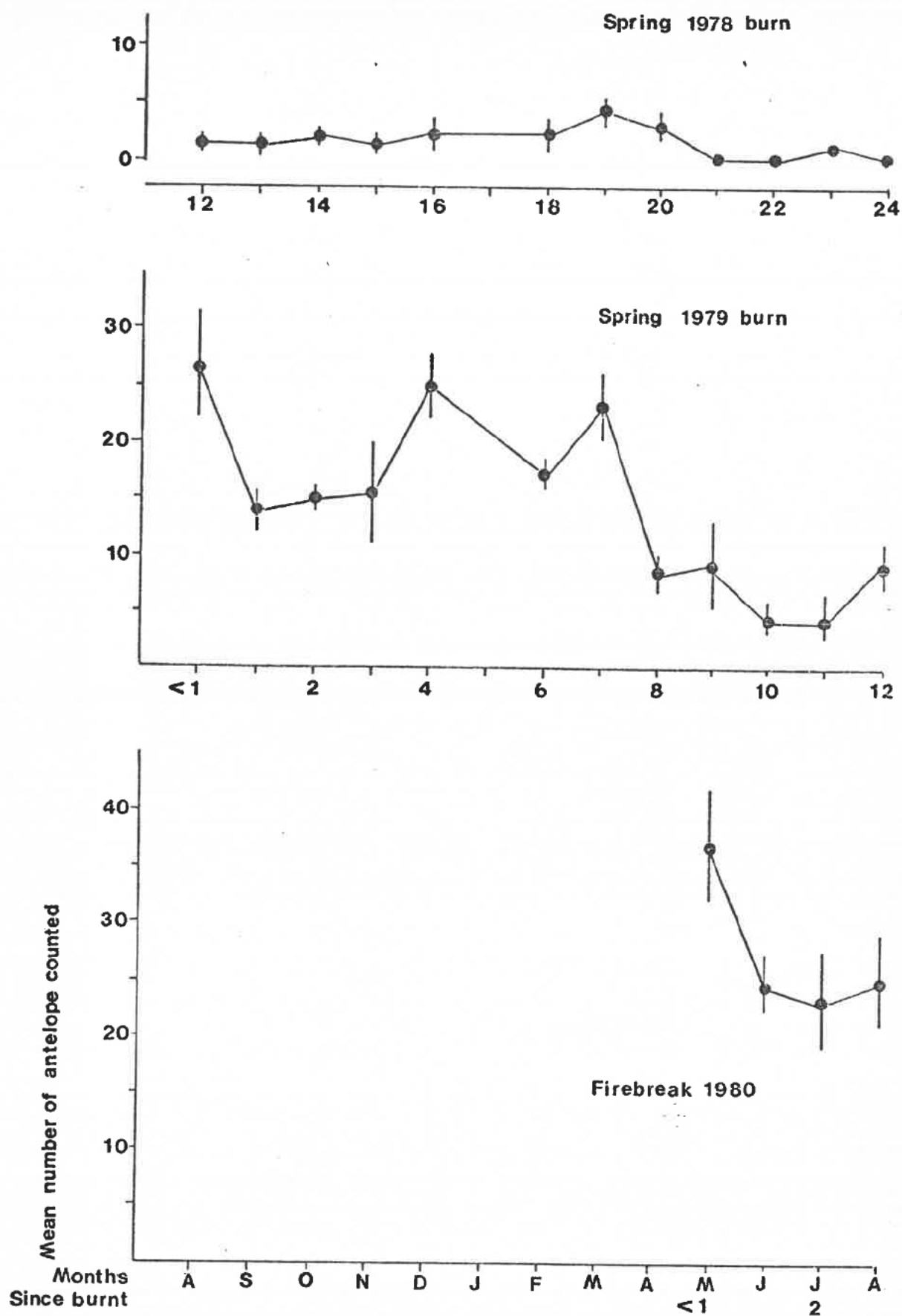


Figure 2.7 Mean number of antelope counted along the Airstrip route on three different burns. Vertical lines indicate twice the SE of the mean.

(Fig 2.7). Paired t-tests of the counts on the two burns were done and revealed that the means differed significantly from August until March ($P < 0,01$), but were not significant from April to August.

A firebreak was burnt between the two spring burns during May 1980. Shortly after it had been burnt the grass began to grow again and from then on until the next spring burning at the end of August, more antelope were counted on the firebreak than on either the 1978 or 1979 burns (Fig 2.7). Two-way analysis of variance of the numbers of antelope counted on the two spring burns and the firebreak revealed that they differed significantly ($P < 0,01$ for all months).

Grey rhebuck, mountain reedbuck, oribi, and blesbok were the four antelopes regularly counted along the Airstrip route. Eland, hartebeest, and common reedbuck were occasionally encountered.

Patterns of veld utilisation by the four regularly-counted antelopes (Table 2.2) followed the overall pattern illustrated in Figure 2.7. There was greater utilisation by all species of the young veld (1 to 8 mo old) than of older grassland available at the same time (12 to 20 mo old); followed by a movement on to the firebreak and at that time virtually no utilisation of the 21 to 24 mo-old grassland, and very little grazing in the 9 to 12 mo-old veld (Table 2.2).

Bannerman route

With the exception of one occasion when a group of mountain reedbuck was recorded on the Bannerman route, all other antelope seen were either grey rhebuck or eland. Numbers of both species were generally higher on more recently burnt veld (Table 2.3). Eland were more numerous in the Bannerman area during autumn and early winter, which is the time of year when they disperse over a wide altitudinal range and a greater variety of habitats.

During 1978 and 1979 antelope were counted on a 1978 spring burn (< 12 mo old) and a 1976 burn (24 to 34 mo old). The mean number of antelope counted on the 1978 burn was 7,9/h and on the 1976 burn 1,3/h. Although the numbers of antelope counted were low on both burns (Fig 2.8), counts on the younger veld were significantly higher ($P < 0,01$) than on the older.

In August 1979 part of the 1978 burn was intentionally burnt. Counts were then done on burns of three different ages (Fig 2.9). The mean number of antelope counted on the < 12 mo-old veld was highest (13,5/h), followed by 5,1/h on 12 to 24 mo-old veld, and 1,6/h on 36 to 48 mo-old veld. Paired t-tests confirmed that antelope numbers were significantly higher on the

TABLE 2.3 Number of grey rhebuck (GR) and eland (E) counted per hour of walking in the Bannerman area, on burnt and unburnt grassland, from October 1978 to June 1980.

Month	Season and year burnt					
	Spring 1976		Spring 1978		Spring 1979	
	GR	E	GR	E	GR	E
Oct 1978	0,3	0	4,0	0		
Nov	0	0	0,8	2,0		
Feb 1979	4,5	2,1	0,9	2,4		
Apr	0	0	2,0	17,8		
May	0	4,3	0	9,2		
Aug	0	0	0	2,5	1,0	9,9
Nov	0,3	0	0,8	0	2,9	5,2
Feb 1980	0,7	0,4	4,3	0	3,1	4,5
Jun	4,5	2,9	2,0	7,0	3,8	28,6

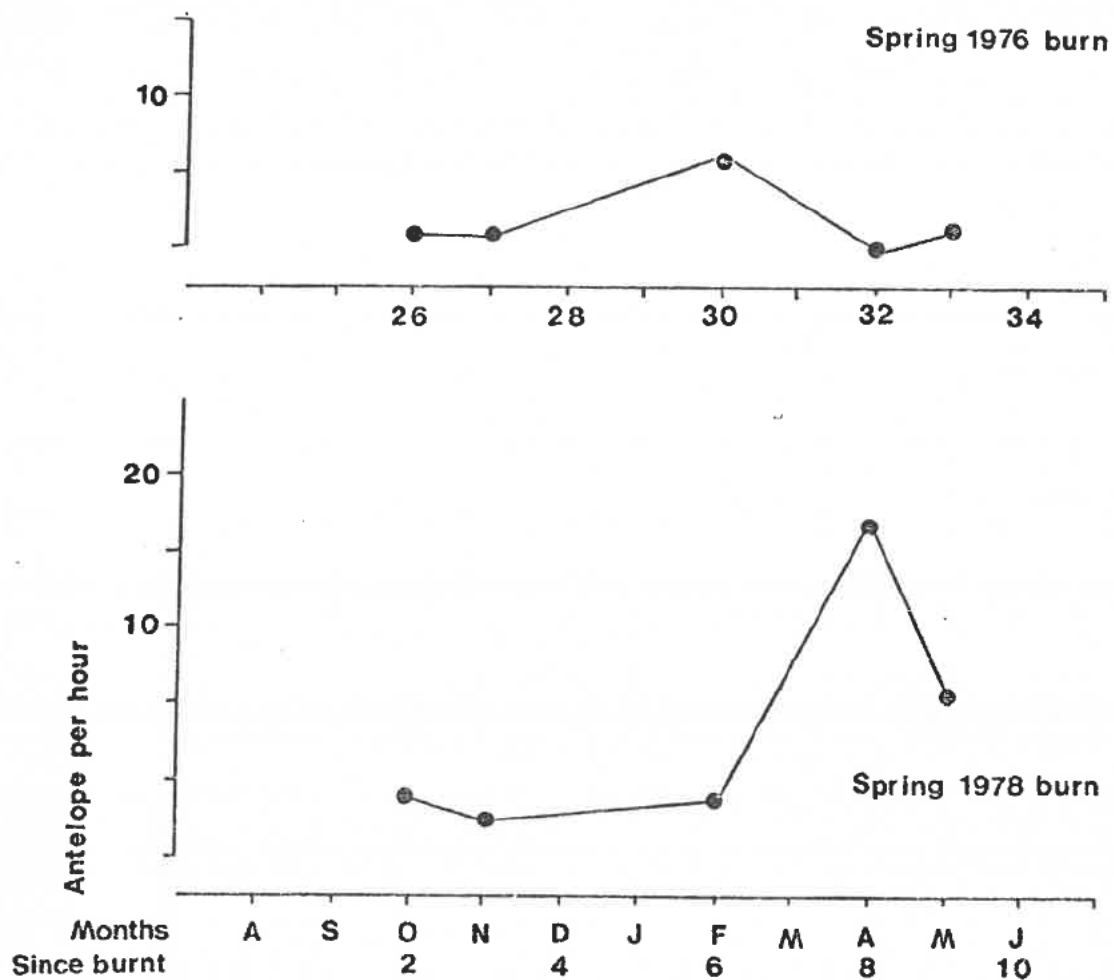


Figure 2.8 Number of antelope counted per hour of walking on two burns in the Bannerman area, during 1978 and 1979.

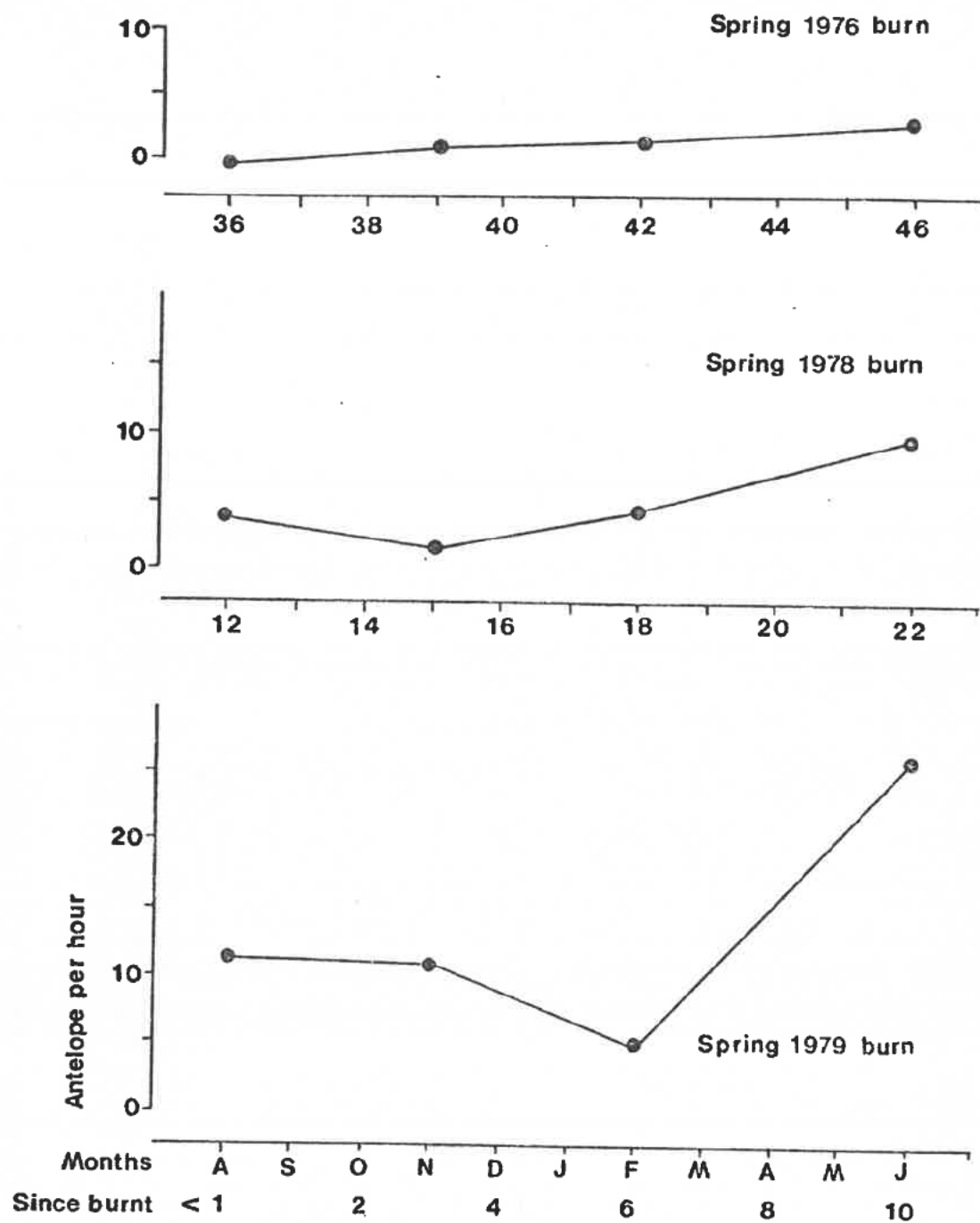


Figure 2.9 Number of antelope counted per hour of walking on three burns in the Bannerman area, during 1979 and 1980.

1979 burn than on the 1978 and 1976 burns ($P < 0,05$ and $0,01$ respectively), but that the differences between the two older burns (1978 and 1976) were not significant. When all three burns were tested against each other, using two-way analysis of variance, only two of the counts differed significantly ($P < 0,05$).

Random observations

Most of the study area (southern GCGR) was burnt in the August 1978 run-away fire, therefore it was not possible to observe the antelopes' responses to biennial burning until the biennial fire regime was restored in 1979.

As biennial burning is practised about half the reserve is burnt annually. Antelope therefore have approximately equal areas of grassland < 1 y old and 1 to 2 y old available during each year. All of the five most abundantly-recorded antelopes preferred < 1 y-old veld to 1 to 2 y-old grassland (Table 2.4). Differences were most marked in the three grazers (mountain reedbuck, oribi, and blesbok) and least in eland, the unselective mixed feeder. Grey rhebuck, mountain reedbuck, oribi, and blesbok all displayed similar responses to burning (Figs 2.10 to 2.13). Shortly after the firebreaks had been burnt (mainly during June 1979), most antelope left the spring 1978 burns and fed on the firebreaks. After the 1979 spring burns had taken place (mainly during late August and early September) most antelope continued to feed on the firebreaks and moved on to the new burns in significant numbers only when they began to turn green. From this stage onwards numbers recorded on the firebreaks were low, but it should be pointed out that firebreaks occupied a much smaller area than did the 1979 spring burns. Until May 1980 greater use was made of the spring 1979 burns than of the 1978 burns, then once the 1980 firebreaks were burnt during May 1980, the cycle of leaving older grass and moving on to fresh burns started again.

Eland did not concentrate on the firebreaks shortly after they were burnt as did the other four antelopes, but continued to feed on the 10 to 11 mo-old spring burns (Fig 2.14). The main movement on to the recently-burnt veld took place during August, when the 1979 spring burns and the firebreaks were utilised. Until the next spring burns took place, the eland used the 1979 burns in preference to the 1 to 2 y-old veld. When the 1980 firebreaks were burnt during May the eland continued to feed on the 10 to 11 mo-old veld (as was the case in 1979), moving on to recently-burnt veld in significant numbers only during August.

TABLE 2.4 Percentage of random observations on five antelopes made in grassland of < 1 y old and in 1 to 2 y-old veld. N = number of observations, not number of antelope.

Antelope	Time since burnt		N
	< 1 y	1 to 2 y	
Grey rhebuck	87,6 %	12,4 %	203
Mountain reedbuck	91,4	8,6	81
Oribi	96,2	3,8	159
Eland	74,8	25,2	230
Blesbok	96,2	3,8	208

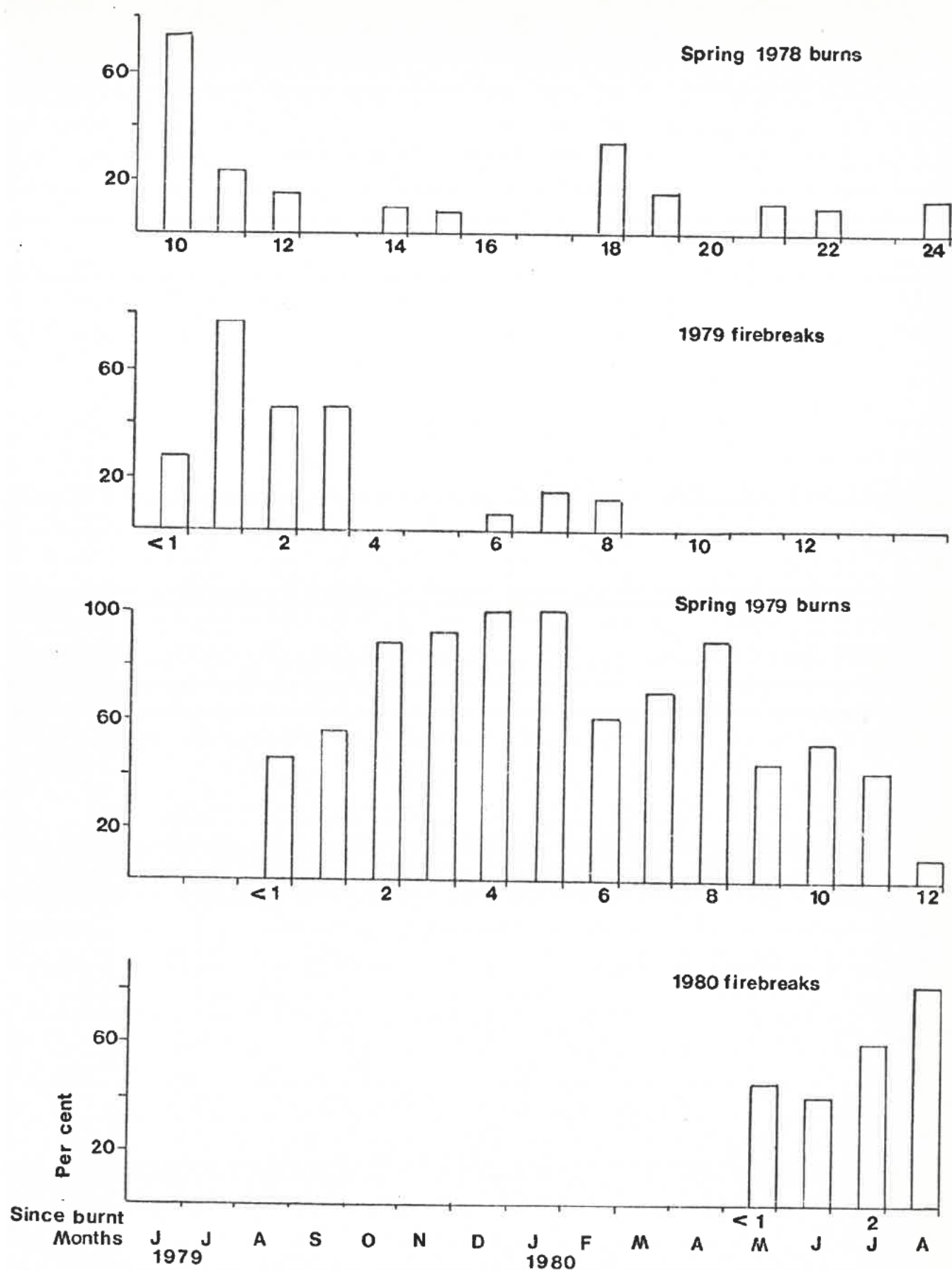


Figure 2.10 Percentage of monthly observations of grey rhebuk on spring burns and firebreaks in GCGR during 1979 and 1980.

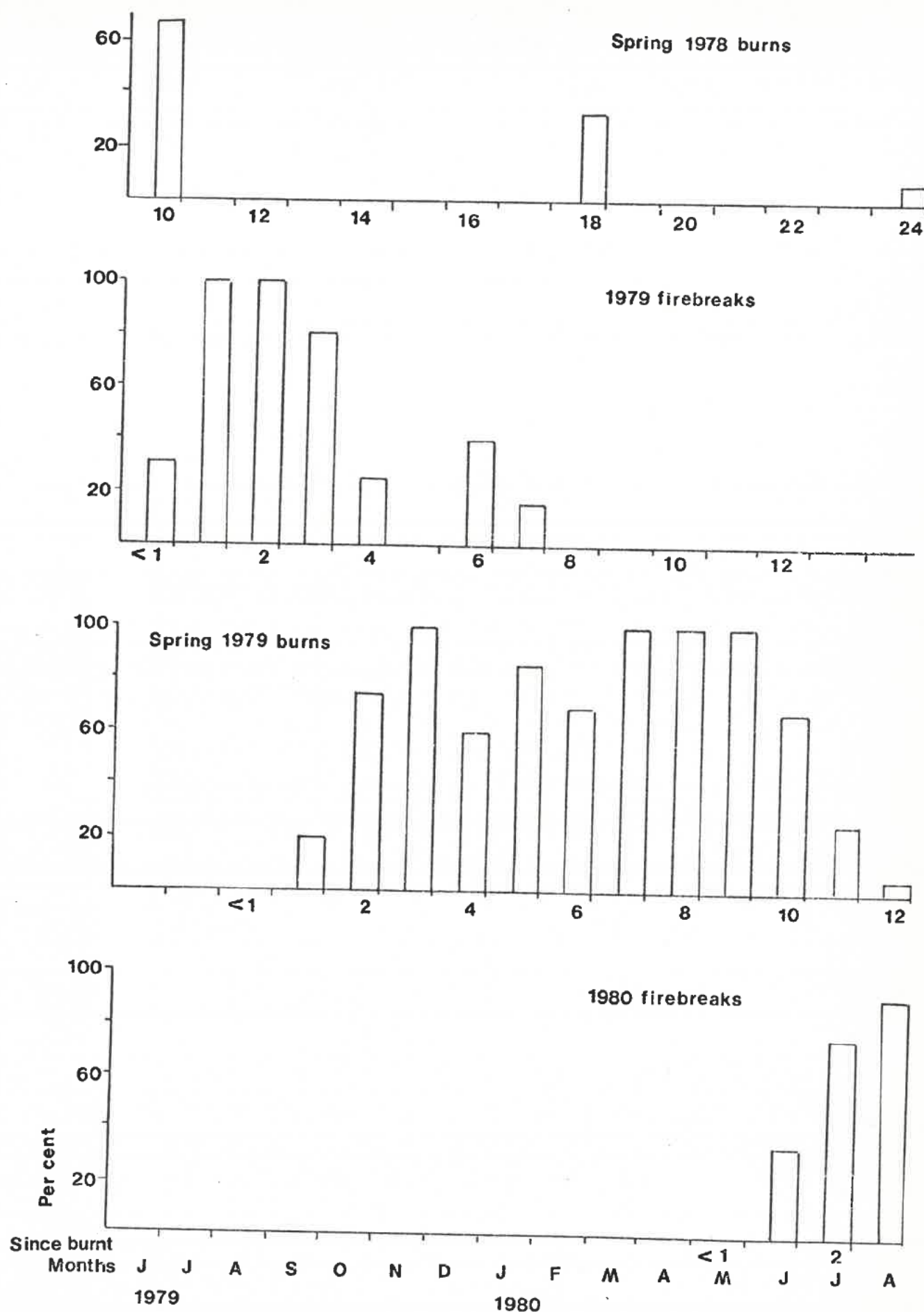


Figure 2.11 Percentage of monthly observations of mountain reedbeak on spring burns and firebreaks in GCGR during 1979 and 1980.

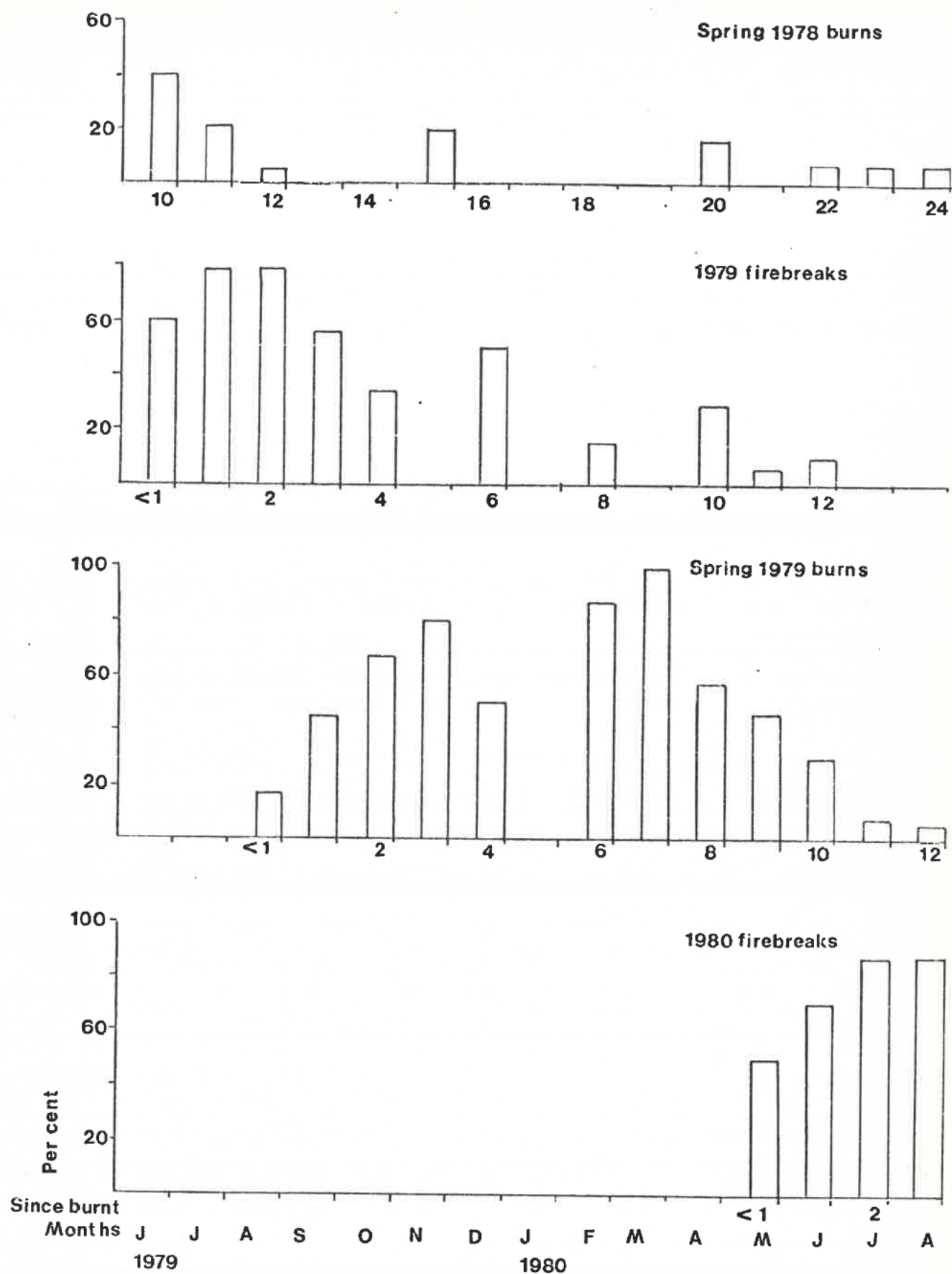


Figure 2.12 Percentage of monthly observations of oribi on spring burns and firebreaks in GCGR during 1979 and 1980.

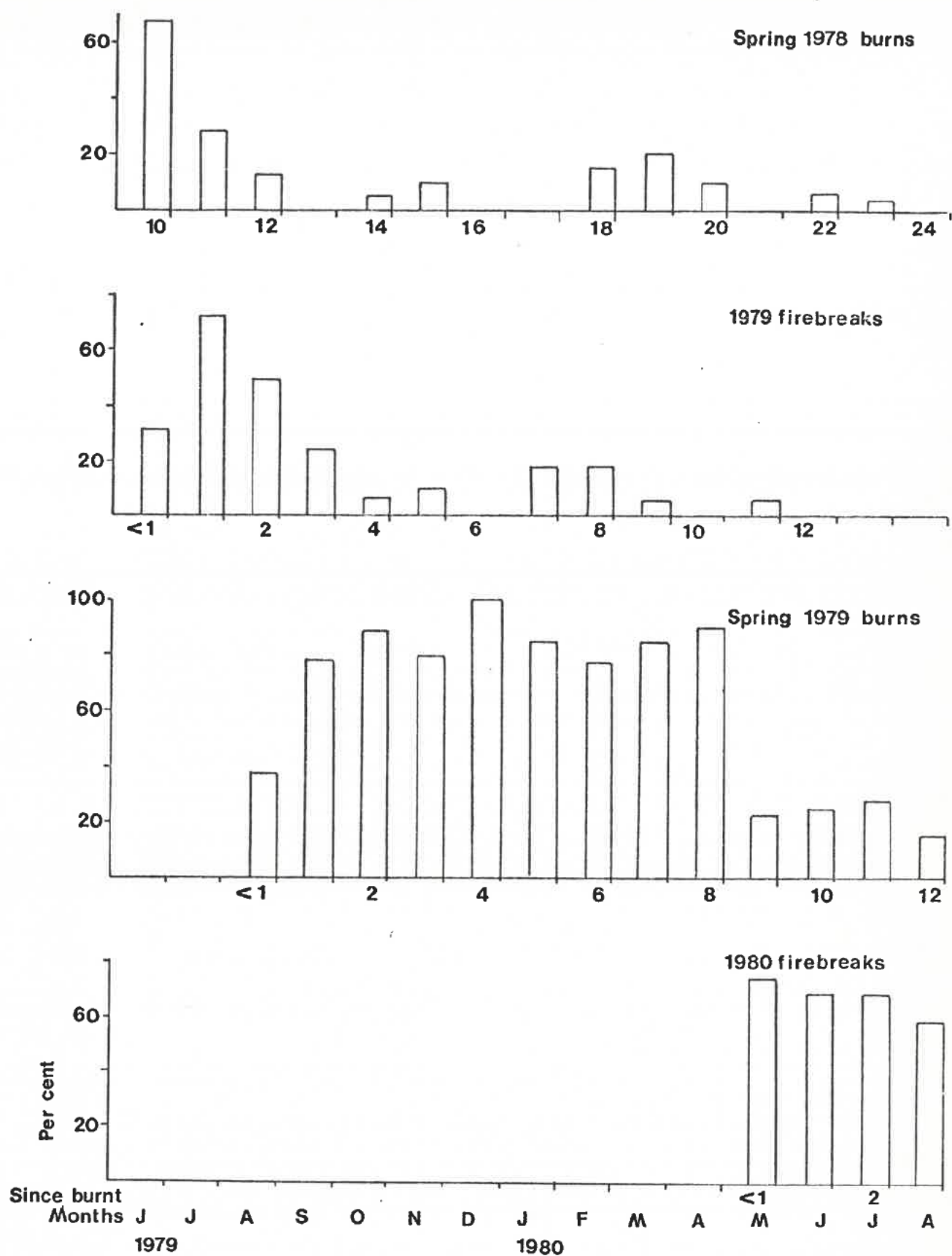


Figure 2.13 Percentage of monthly observations of blesbok on spring burns and firebreaks in GCGR during 1979 and 1980.

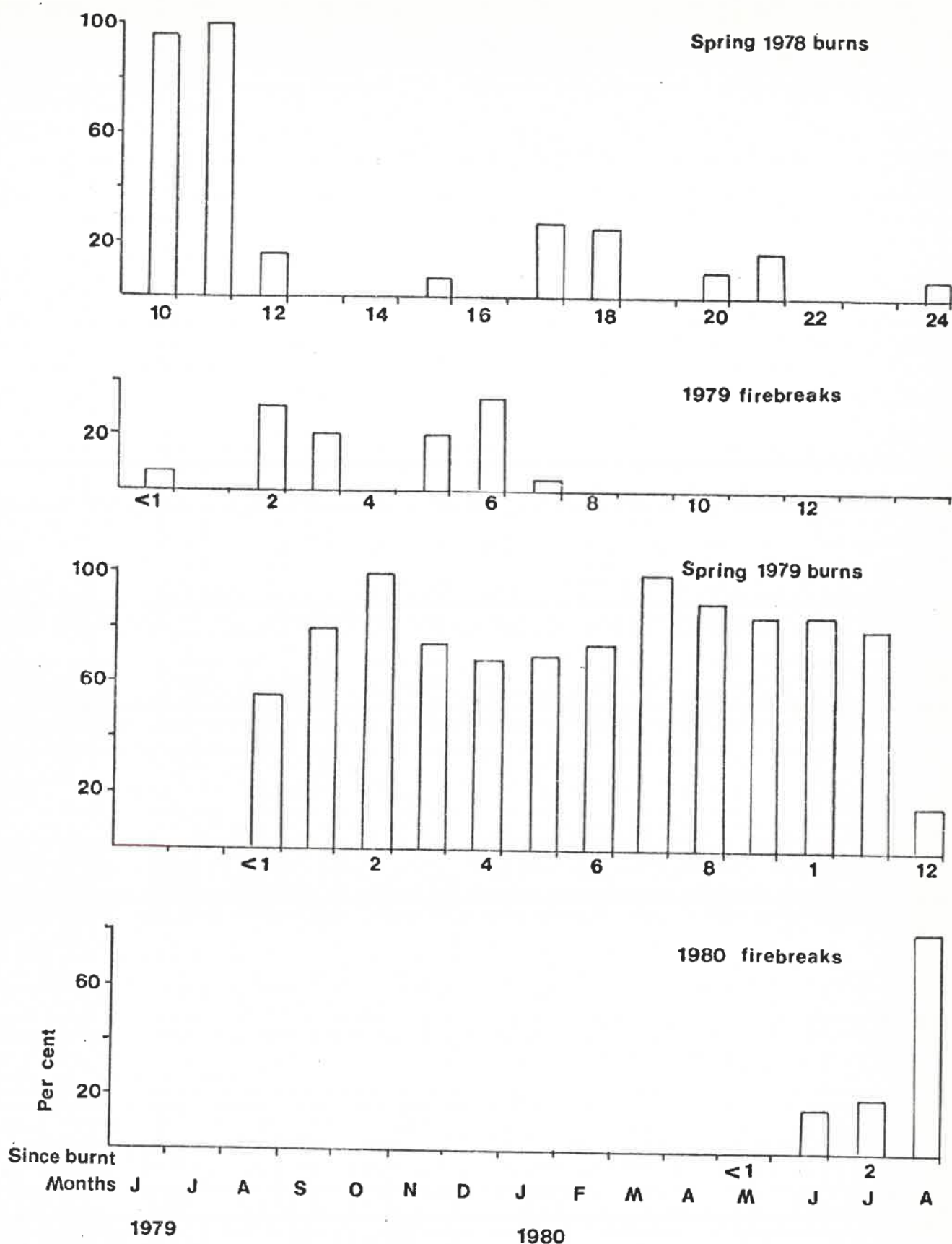


Figure 2.14 Percentage of monthly observations of eland on spring burns and firebreaks in GCGR during 1979 and 1980.

DISCUSSION

A number of authors have reported that African ungulates are attracted to recently-burnt veld (Brooks and Berry 1980, Brynard 1964, Lemon 1968, Mason 1973, Melton 1978, Oliver *et al.* 1978, Pienaar 1968, Smuts 1972). However, few quantitative data are available, particularly for the antelopes dealt with in this study. The most detailed accounts are contained in Brooks and Berry (1980) who gave the responses of 18 lowveld ungulates to veld burning in the Hluhluwe-Umfolozi Game Reserves complex, and Melton (1978) who dealt with responses of eight ungulates (also lowveld species) to fire in portion of Umfolozi Game Reserve. Mason (1973) gave the percentages of observations on 18 ungulates made in burnt and unburnt veld in Jack Scott Nature Reserve, an area which is part bushveld and part highveld; and Oliver *et al.* (1978) gave the percentage of observations made on grey rhebuck, mountain reedbuck, and oribi in burnt and unburnt veld at Highmoor on the Little Berg.

Although burnt veld was much smaller in area than unburnt veld, Mason (1973) recorded more mountain reedbuck, oribi, and blesbok on burns. Eland on the other hand were recorded mainly (63 %) in unburnt veld. At Highmoor the responses to burning of grey rhebuck, mountain reedbuck, and oribi were similar to those recorded in GCGR. Immediately after the veld was burnt at Highmoor there was little response by all three species, but from one month after a burn onwards burnt veld was preferred (Oliver *et al.* 1978).

The grassland antelopes in this study probably preferred recently-burnt veld because of its higher nutritional value. It has been found that the nutritional value (crude protein content) of grass is higher in burnt than unburnt veld during the growing season (Lemon 1968, Mentis 1978, Scotcher *et al.* 1980b). In the analysis of the entire sample (green and dry grass) Lemon (1968) reported crude protein levels in 3 y-old and 11 y-old grass in Malawi as being about half of those in < 1 y-old grass. Mentis (1978), who examined entire herbage samples, found that the crude protein content of burnt (< 1 y old) veld was twice as high as that in 1 to 2 y-old and 2 to 3 y-old veld in the Drakensberg. Scotcher *et al.* (1980b) separately analysed green grass leaf, dry grass, and forbs from GCGR samples. Their findings were that the crude protein content of green grass and forbs in < 1 y-old veld was approximately twice that of 2 to 3 y-old veld (Fig 2.15). Everson (in prep.) investigated the nutritional content of green living material only (grass and forbs) in Drakensberg grassland, and found that the crude protein content of samples from 1 to 2 y-old veld was slightly lower than

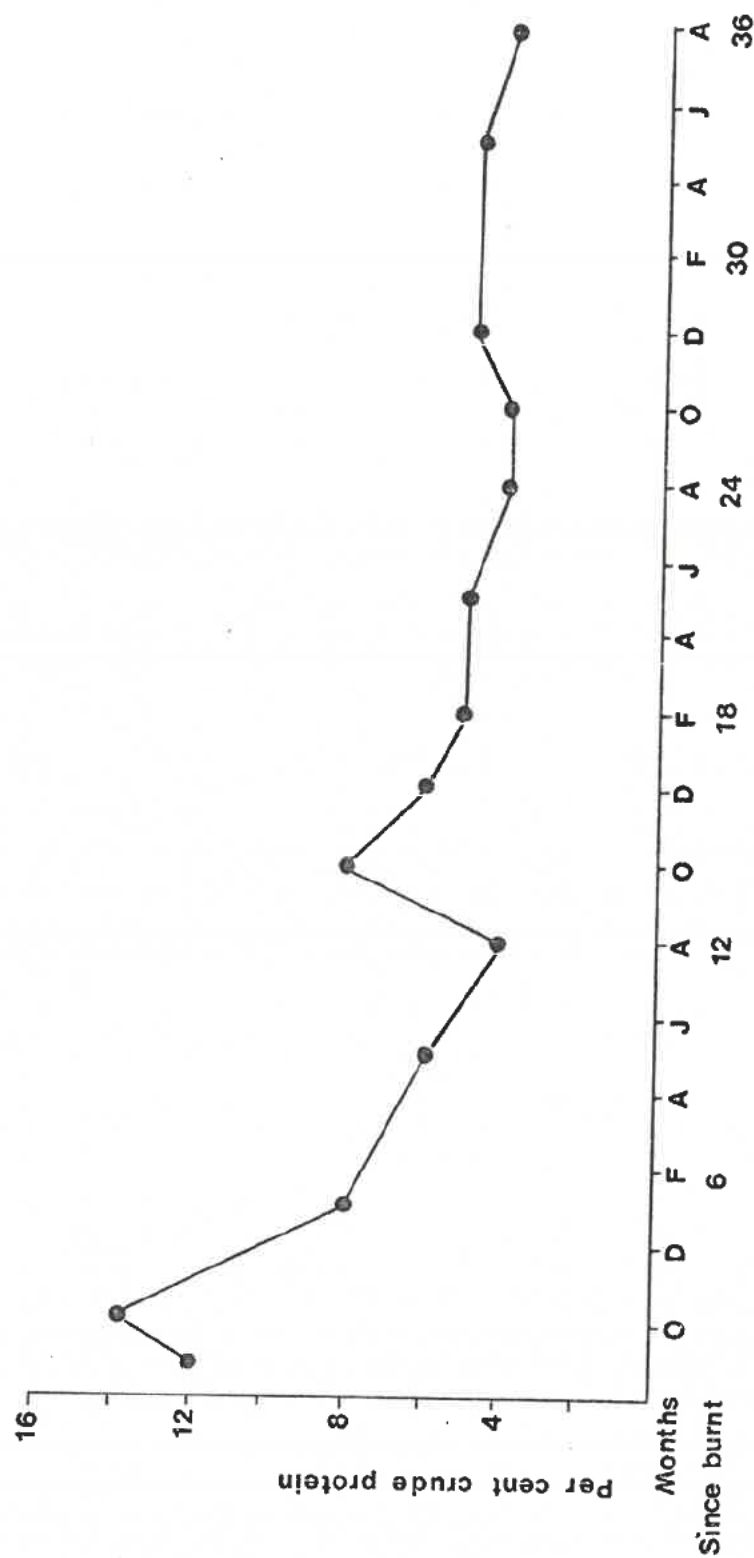


Figure 2.15 Per cent crude protein in green grassleaf and forbs in relation to the time since the veld was last burnt. (Based on data from Scotcher *et al.* (1980b) and Everson (in prep.)).

that in < 1 y-old veld (Fig 2.15).

In addition to favouring recently-burnt veld for its higher nutritional content, the antelopes probably also prefer it to 1 to 2 y-old veld because the living material is more exposed and available, and not combined with dry grass which has a much lower crude protein content (Scotcher *et al.* 1980b).

The preferences of the selective grazers, mountain reedbuck and oribi, for recently-burnt veld were more obvious than those of grey rhebuck, a selective forb eater (Figs 2.10 to 2.12). The blesbok, an unselective grazer, also showed a marked preference for recently-burnt veld. Although a number of blesbok observations were made in grassland burnt during the previous spring, almost all of these involved single males (probably territorial) in their core areas. As can be seen from Table 2.2, the numbers of blesbok counted along the Airstrip route were much lower on the spring 1978 burn than on the other two burns. These animals also were mainly recognisable single territorial males.

Regrowth of green grass on firebreaks burnt during May or June is not as rapid as on spring burns where growth is accelerated by precipitation and increasing temperatures. The smaller antelopes appear to be able to feed on the very short grass shoots, whereas eland are not able to do so, which accounts for their lack of immediate response to the recently-burnt firebreaks (Fig 2.14). The response to the 1979 spring burns was fairly rapid, however, and there was marked utilisation of the May 1980 firebreaks only during August when significant green growth was apparent, but before the 1980 spring burning took place.

One of the explanations given by Jarman (1974) for different feeding strategies is that large antelopes are not capable of being as selective as are smaller ones. Although Underwood (1975) has shown that eland are capable of feeding on parts of certain browse plants by "nibbling and stripping", there are limits to this large antelope's ability to select, and the cropping of very short grass shoots on winter firebreaks obviously falls outside these limits.

Comparative antelope counts were not done in the fire protection plot at 1 500 m, protected since 1957 and burnt once only (in 1969), and in adjacent burnt veld. In the collection of random data, however, the only antelopes recorded in the protected area were eland (occasionally), grey duiker, and common reedbuck in a tall grassland portion. Before the other protection plot (16 y old) at 1 760 m was burnt out in August 1978, only eland were occasionally recorded in it.

It has been shown in this study that three antelopes indigenous to the area, viz grey rhebuck, mountain reedbuck, and oribi, favour recently-burnt grassveld. In scrub, thicket, and forest bushbuck and grey duiker occur, but these vegetation types are not utilised by the three grassland species. Eland differ in that recently-burnt grassland is favoured during summer, while during winter scrub and forest are also utilised. It has been suggested by Mentis and Rowe-Rowe (1979) that Drakensberg antelopes, like francolin and small mammals, have evolved either in a situation of regular burning of exposed areas, or in areas inaccessible to fire and which were never or very infrequently burnt, or only partly burnt. As was the situation with francolin and small mammals, no antelopes favour areas protected from fire for intermediate periods.

In grassland which remains unburnt for a long time, and is not heavily grazed, certain unpalatable grasses increase, e.g. Tristachya leucothrix (= Apochaete hispida), and certain favoured food species (Themeda triandra) decrease (Tainton 1981). In the Drakensberg one of the plants which increase in the absence of fire is bracken (Pteridium aquilinum) which shades out the constituents of Themeda triandra grassland and eventually results in a completely different set of grasses and forbs developing (Killick 1963). Bracken itself, which may dominate for a few years in such a situation, before the eventual invasion of tall herbs, is not eaten by any Drakensberg antelopes.

In view of the responses of the antelopes to veld burning (this study), and the positive advantages regarding nutritional value and availability of new growth (Scotcher *et al.* 1980b), the burning of grassland in the Drakensberg is obviously a management practice which favours the antelopes. Although annual late winter or early spring burning does not reduce basal cover or affect plant species composition (Tainton 1981), biennial burning is recommended. If biennial burning is practised there will be approximately equal areas of burnt and unburnt veld, so if a very dry period were to follow veld burning and little new growth took place, the unburnt food reserves, although lower in nutritional value, would be available. Furthermore the unburnt areas provide cover which is particularly important to grey rhebuck, mountain reedbuck, and oribi, as lying out behaviour is practised by all of these species for at least six weeks after the young are born (Esser 1973, Oliver *et al.* 1978, Viljoen 1975).

Scotcher and Clarke (1981) examined plant species composition and basal cover of grassland burnt biennially during spring, summer, and autumn in

GCGR. They concluded that spring burns were the most suitable for the area, found that retrogression in both basal cover and palatable species took place in summer burns, and expressed doubts about the suitability of autumn burns, suggesting that more research was necessary. Winter burns were not examined by Scotcher and Clark (1981), but it is unlikely that they will adversely affect the veld, as it is burnt during the dormant stage (Tainton 1981).

The most suitable fire regime for GCGR therefore appears to be one of biennial spring burning, with perhaps biennial winter burning of the escarpment to reduce the amount of fuel and help to prevent the rapid spread of arson-induced fires to the rest of the reserve at the end of the dry season.

POPULATION TRENDS AND RELATIVE ABUNDANCE

ROUTE COUNTS

Annual and seasonal trends

Totals for the five routes were combined and yearly (Table 2.5) and monthly (Figs 2.16 to 2.20) means of the five most abundantly-recorded antelopes were calculated.

Analysis of variance indicated that the annual means differed significantly for grey rhebuck, mountain reedbuck, and blesbok ($P < 0,01$) but not for oribi and eland ($P > 0,05$). When differences between years were compared by months, however, variation was not as marked in grey rhebuck and blesbok: significant differences ($P < 0,05$) were observed in June only for grey rhebuck and during December in blesbok, but differences remained significant in mountain reedbuck with $P < 0,05$ in six months (autumn and spring).

All five antelopes showed seasonal fluctuations in mean monthly counts (Figs 2.16 to 2.20) but these did not follow the same pattern for all species, and in some instances differed from year to year within a species.

1. Grey rhebuck

There was no obvious pattern in the numbers of grey rhebuck counted (Fig 2.16). During 1978 and 1980 slight May and August peaks were demonstrated, but this pattern was not apparent in 1979 and 1981. Variation between months within the year was significant only in 1980 ($P < 0,05$).

2. Mountain reedbuck

Peaks in the numbers of mountain reedbuck counted were observed in July or August of each year (Fig 2.17). The overall pattern observed in 1980 was similar to that in 1978, and the 1981 trend appears to follow that of 1979.

Most mountain reedbuck were recorded below the sandstone on routes 2 and 4 (Table 2.6) and the higher numbers counted during autumn and spring in 1978 and 1980 are undoubtedly related to the animal's responses to recently-burnt veld. The higher counts during autumn 1980 followed the burning of part of the veld along route 2 at the beginning of March of that year.

Seasonal variation in counts was significant in 1978 and 1980 ($P < 0,01$) when spring and autumn burning was carried out along routes 2 and 4, but not during the other two years when grassland below the sandstone along

TABLE 2.5 Mean annual count (sum of routes 1 to 5) for five antelope species, 1978 to 1981.

	1978 (N = 30)			1979 (N = 36)			1980 (N = 36)			1981 (N = 36)		
	\bar{x}	SE	CV*	\bar{x}	SE	CV	\bar{x}	SE	CV	\bar{x}	SE	CV
Grey rhebuck	63	2,9	4,6 %	51	2,5	4,9 %	52	2,8	5,3 %	42	1,5	3,6 %
Mountain reedbuck	23	2,3	10,0	20	1,1	5,6	34	2,8	8,2	18	1,4	7,8
Oribi	13	1,2	9,4	15	1,1	7,0	15	1,1	7,2	16	1,0	6,3
Eland	170	15,8	9,3	190	18,0	9,5	209	26,6	12,7	154	17,1	11,1
Blesbok	25	1,9	7,7	31	1,9	6,1	37	2,1	5,5	16	1,2	7,5

* Coefficient of variation = SE as a percentage of the mean (Rayner 1967).

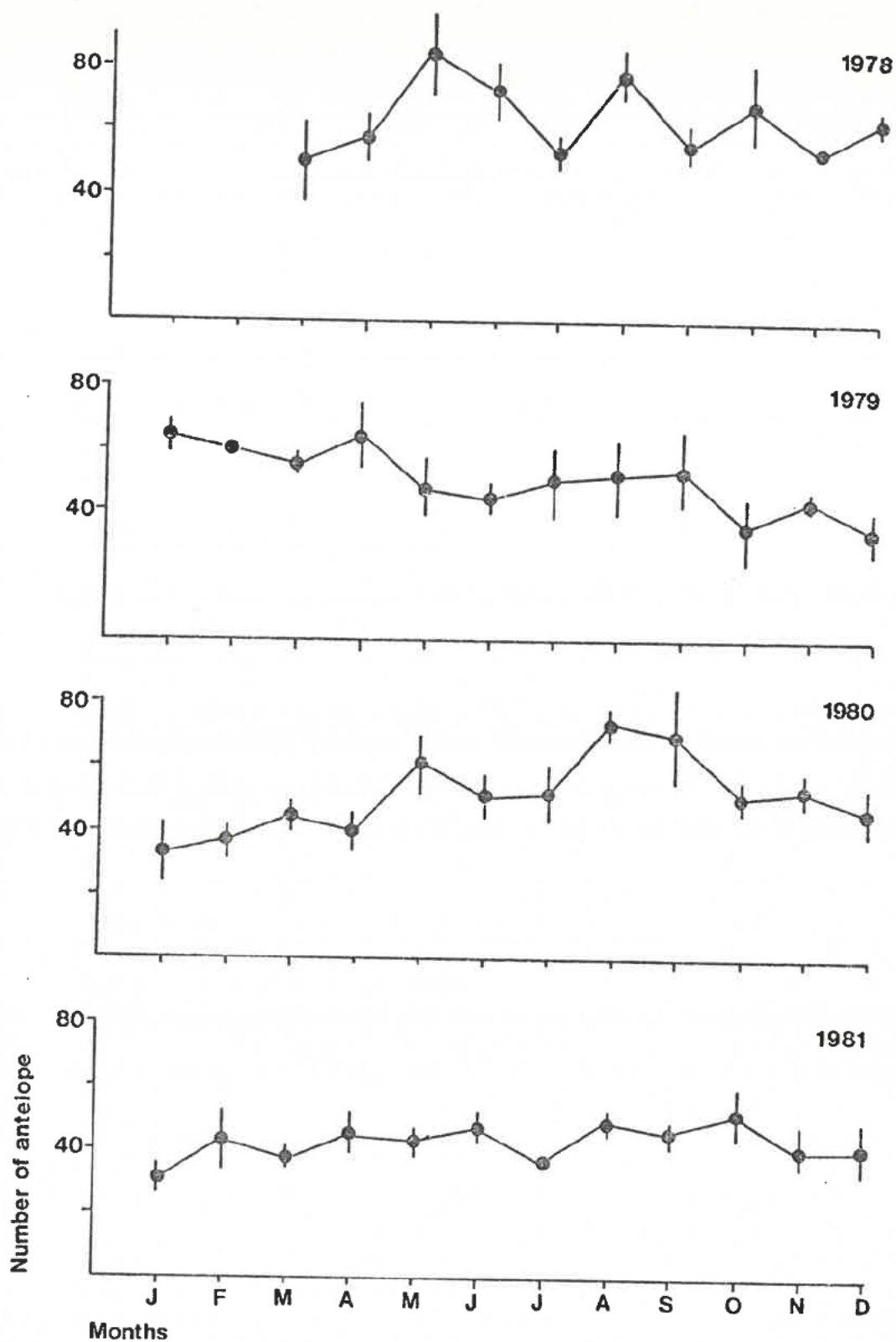


Figure 2.16 Mean number of grey rhebuck (sum of five routes) counted in GCGR, by months. Vertical lines indicate twice the standard error of the mean.

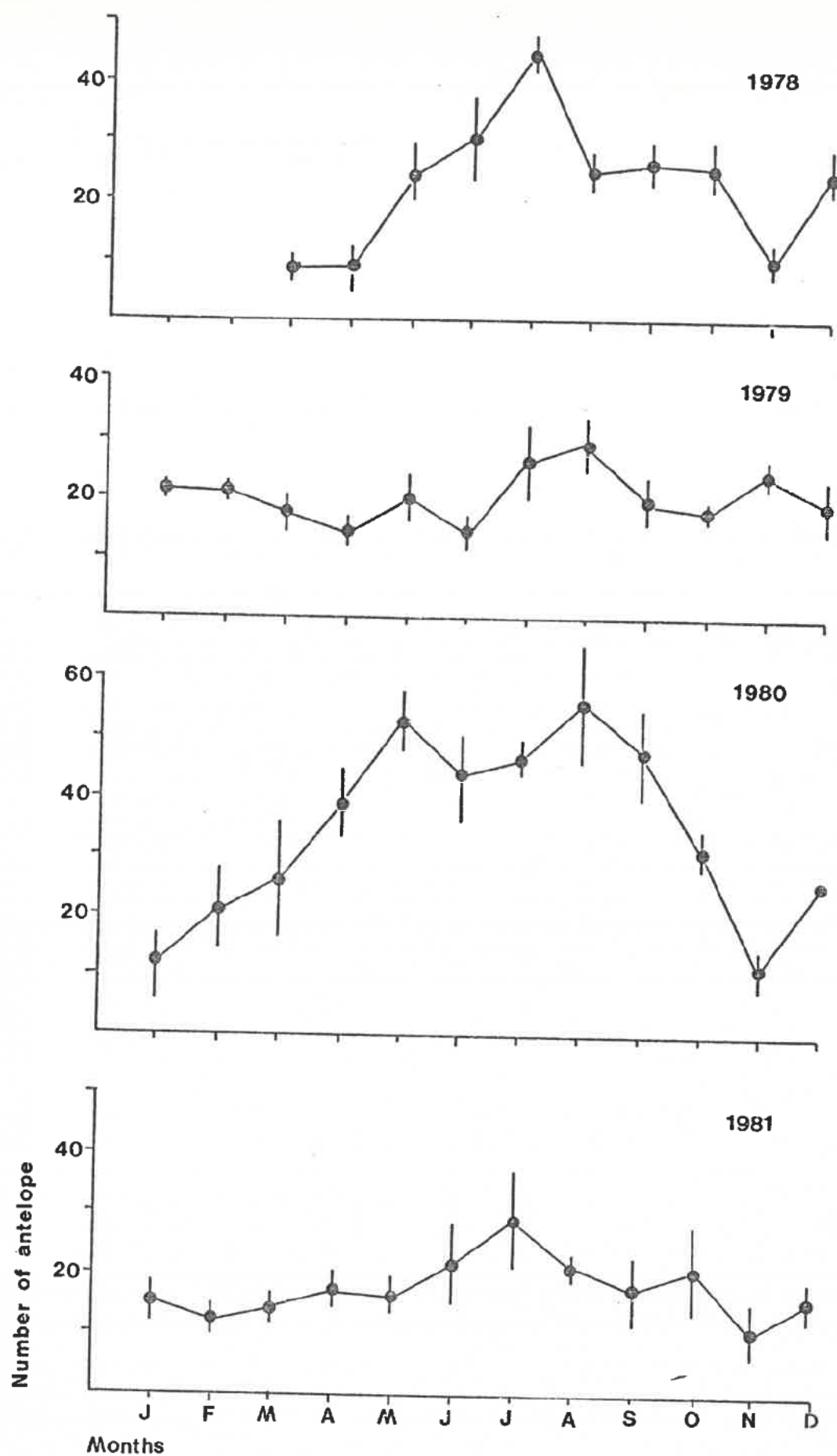


Figure 2.17 Mean number of mountain reedback (sum of five routes) counted in GCGR, by months. Vertical lines indicate twice the standard error.

these two routes was not burnt.

3. Oribi

Seasonal variation in the numbers of oribi counted was significant during each year ($P < 0,05$), with peaks being recorded during July or August (Fig 2.18). During these months oribi were counted mainly on fire-breaks where they were feeding on short green grass.

The seasonal and annual trends followed similar patterns over the four-year period.

4. Eland

Peaks in eland numbers were recorded during late spring and early summer (Fig 2.19) and lowest numbers were counted during July. The monthly increases to summer peaks were significant for each year ($P < 0,01$).

Trends in eland counts can be related to the antelope's social and feeding behaviour: during summer they form large herds and feed mainly on grassland above the sandstone, but during winter they split up into small groups and disperse throughout the reserve.

Along route 3, which traverses plateaux and ridge tops of the Little Berg (i.e. above sandstone but below the escarpment) for its entire length, numbers remained high during the wet season and dropped sharply during the dry season (Fig 2.21). Along route 4, entirely below sandstone and in valley woodland and grassland, numbers were highest during the dry season. On route 1, which runs along the escarpment for half of its length, more eland were counted during the wet season but numbers remained fairly high during the dry season.

Means from routes 2 and 5 are not illustrated in Figure 2.21 as route 2 traversed a variety of habitats and topographical features, and numbers along route 5 were too low to be of value statistically.

5. Blesbok

Seasonal fluctuations (autumn and spring peaks in numbers counted) were significant during 1978 ($P < 0,01$) but not during the other years (Fig 2.20).

Blesbok numbers were high during 1978 to 1980, reaching a peak in 1980, but dropped during 1981. The only two routes along which blesbok were counted were routes 2 and 3. As already discussed, blesbok favour short, recently-burnt grass. During 1978 and 1980 portion of the grassland traversed by route 3 was burnt during early autumn, and during 1980 an autumn burn

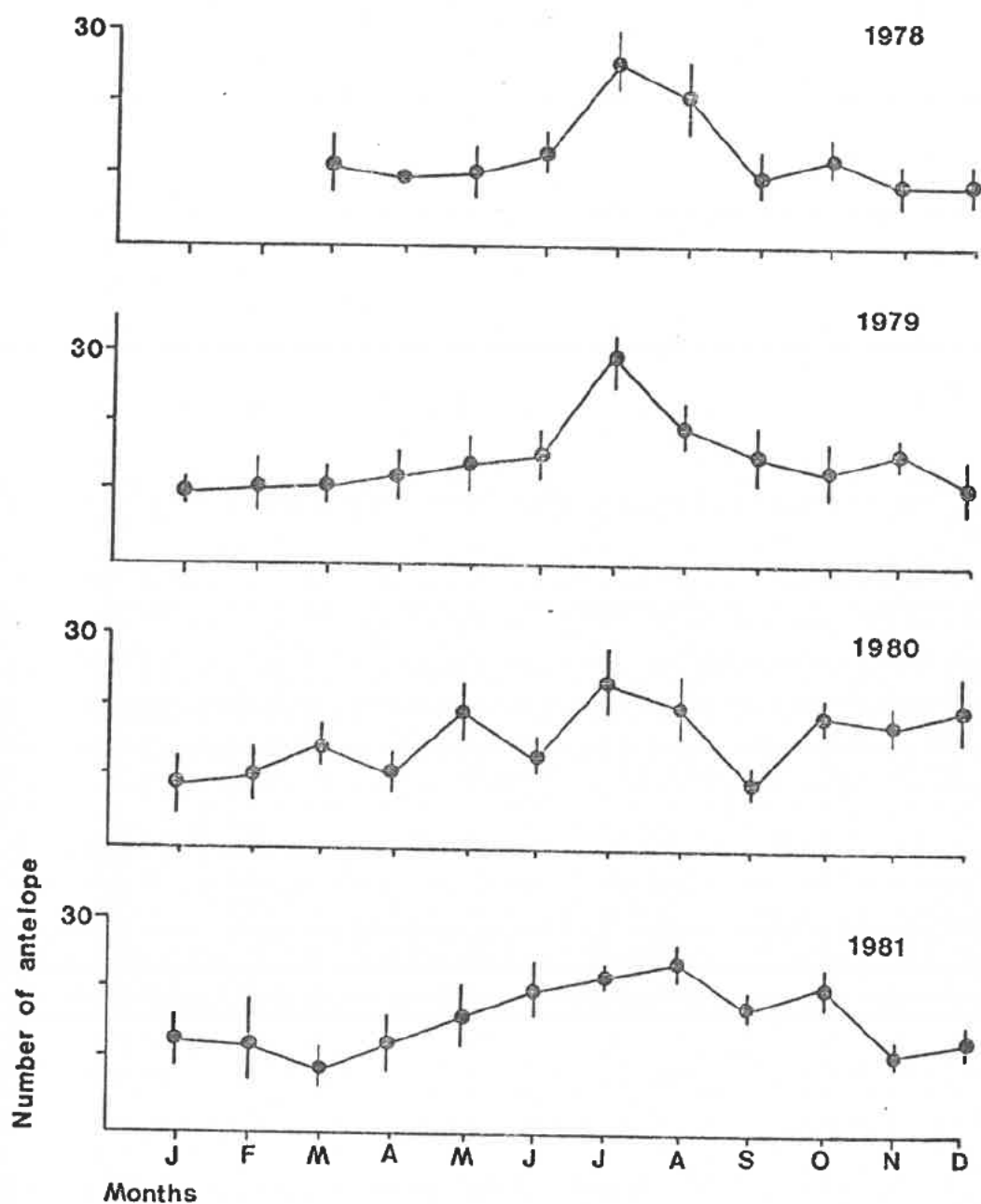


Figure 2.18 Mean number of oribi (sum of five routes) counted in GCGR, by months. Vertical lines indicate twice the standard error.

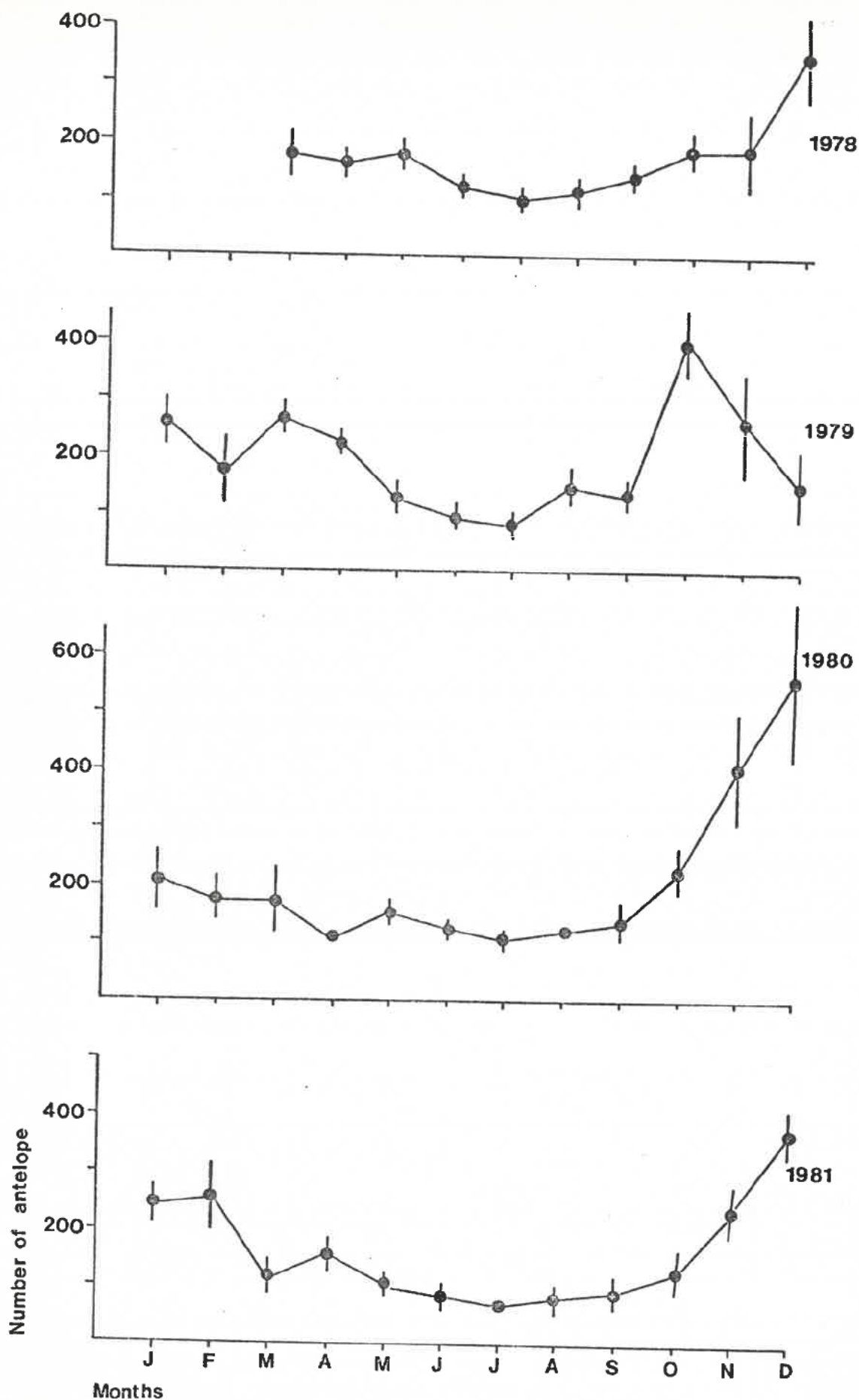


Figure 2.19 Mean number of eland (sum of five routes) counted in GCGR, by months. Vertical lines indicate twice the standard error.

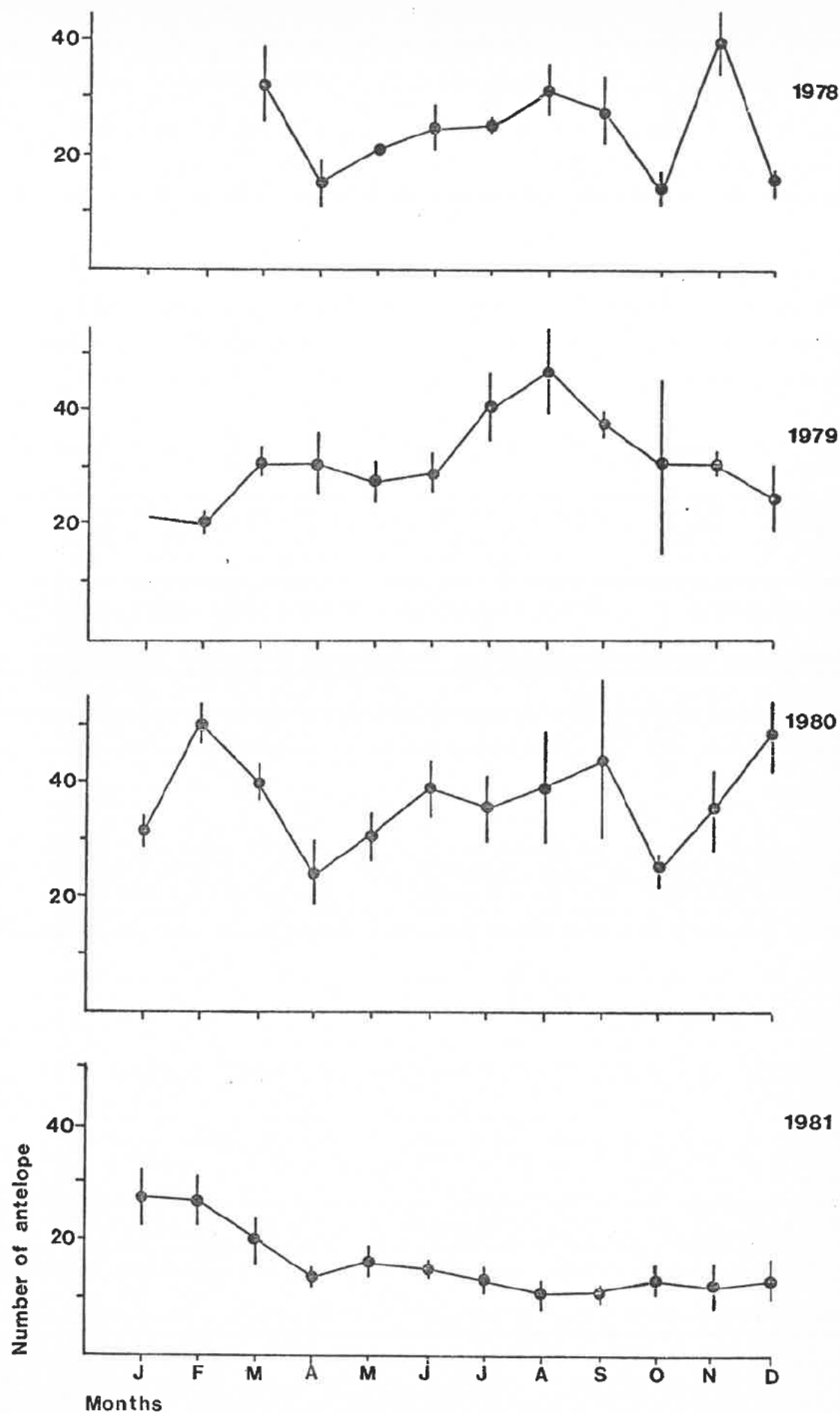


Figure 2.20 Mean number of blesbok (sum of five routes) counted in GCGR, by months. Vertical lines indicate twice the standard error.

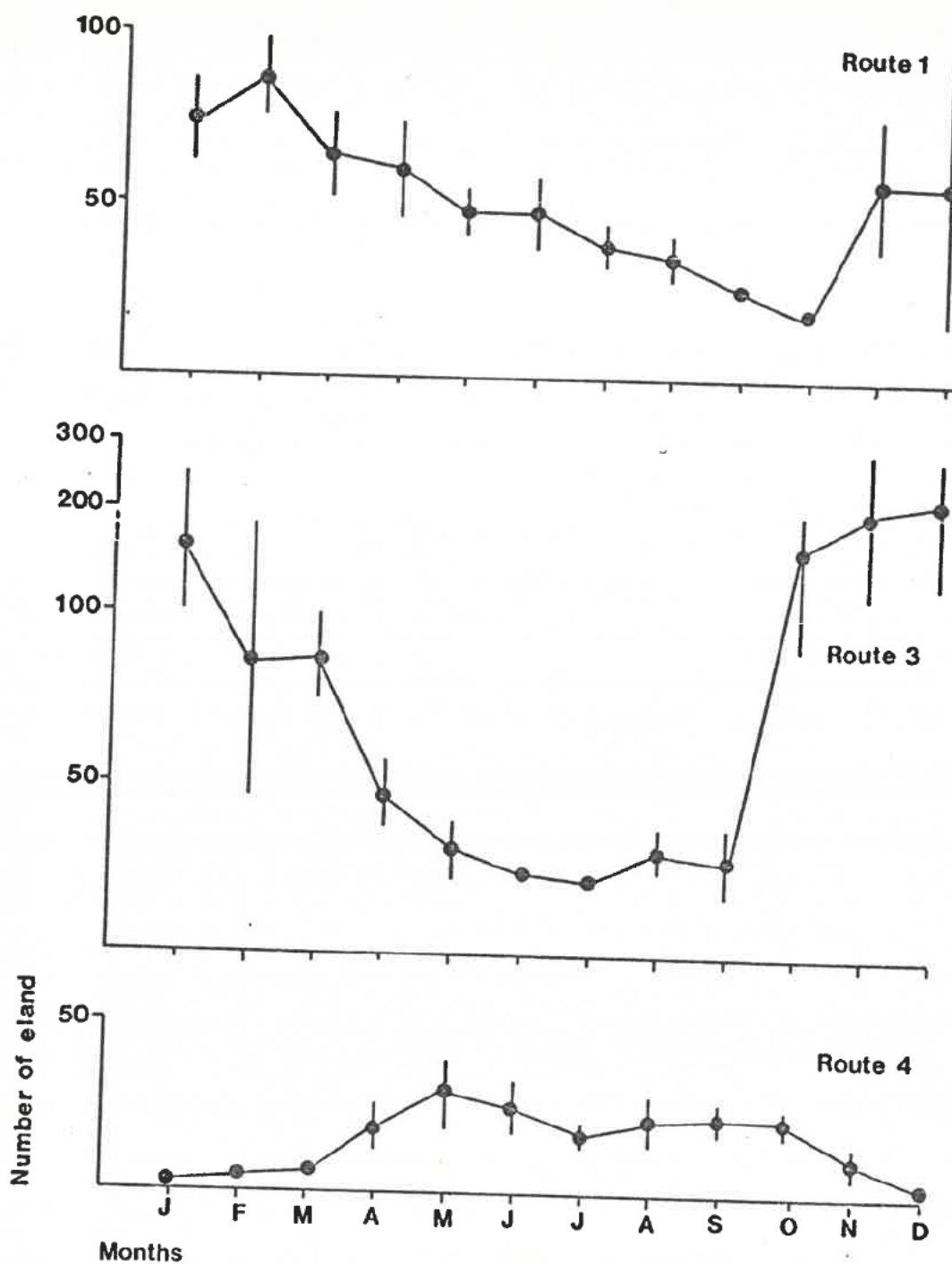


Figure 2.21 Mean number of eland counted along routes 1, 3 and 4, during 1978 to 1981. Vertical lines indicate twice the standard error of the mean.

was effected also along part of route 2. From 1978 to 1980 spring burning was done along routes 2 and 3. During 1981 no autumn burning was done along the two routes. Numbers were particularly low along route 2 (Table 2.6), the blesbok from this area having moved initially to an autumn burn not traversed by route 2, then remaining on firebreaks and finally spring burns along the Airstrip route and north of it where an average of 55 were counted along 12 km of vehicle tracks at the end of 1981 when the mean on route counts was 17.

Relative abundance of antelopes and differences between routes

The mean annual numbers of antelope counted per route are given in Table 2.6. The numbers of the five major species are expressed as percentages of the total in Figure 2.22.

Route 1

Annual relative abundance of the four species counted along route 1 remained fairly constant, with eland the dominant antelope, outnumbering the next species, grey rhebuck, by about 4:1. Numbers of oribi and mountain reedbuck were low.

Route 2

The relative numbers of grey rhebuck and mountain reedbuck were similar during 1978 and 1979, but during 1980 a greater number of mountain reedbuck was recorded. During this year high numbers of mountain reedbuck coincided with the autumn burning of about half of the route and spring burning of the other half. Numbers of blesbok also increased in response to burning.

Route 3

During 1980 the relative abundance of eland increased by about 15 % with consequent decreases in the relative numbers of other antelopes. The higher 1980 eland mean was the result of a number of very large herds being counted during November and December.

Route 4

No oribi or blesbok were ever recorded along route 4, a valley route clearly not favoured by these two antelopes. The habitat is better suited to mountain reedbuck, which generally occurred in greater numbers than did grey rhebuck.

TABLE 2.6 Mean number of antelope counted along routes 1 to 5 from 1978 to 1981.

Antelope	Year	Route				
		1	2	3	4	5
Grey rhebuck	1978	12,1	9,1	21,9	5,0	14,8
	1979	9,0	7,8	16,3	3,5	12,3
	1980	11,6	8,8	13,0	8,8	10,4
	1981	10,3	5,5	12,8	2,1	11,4
Mountain reedbuck	1978	1,5	8,0	1,8	8,8	3,2
	1979	2,9	7,2	1,4	5,8	3,2
	1980	3,3	11,5	3,9	8,9	5,8
	1981	1,9	4,8	4,3	3,5	2,8
Oribi	1978	1,2	3,5	5,4	0	2,4
	1979	1,4	3,0	6,8	0	3,8
	1980	0,8	4,1	7,0	0	3,1
	1981	1,3	2,7	6,8	0	4,8
Eland	1978	55,2	28,0	62,0	13,3	10,6
	1979	53,5	33,2	71,0	14,9	16,7
	1980	49,0	28,0	110,0	23,3	7,3
	1981	32,8	25,3	73,9	5,5	17,3
Blesbok	1978	0	6,9	18,0	0	0
	1979	0	13,0	18,3	0	0
	1980	0	21,5	14,7	0	0
	1981	0	3,8	11,7	0	0

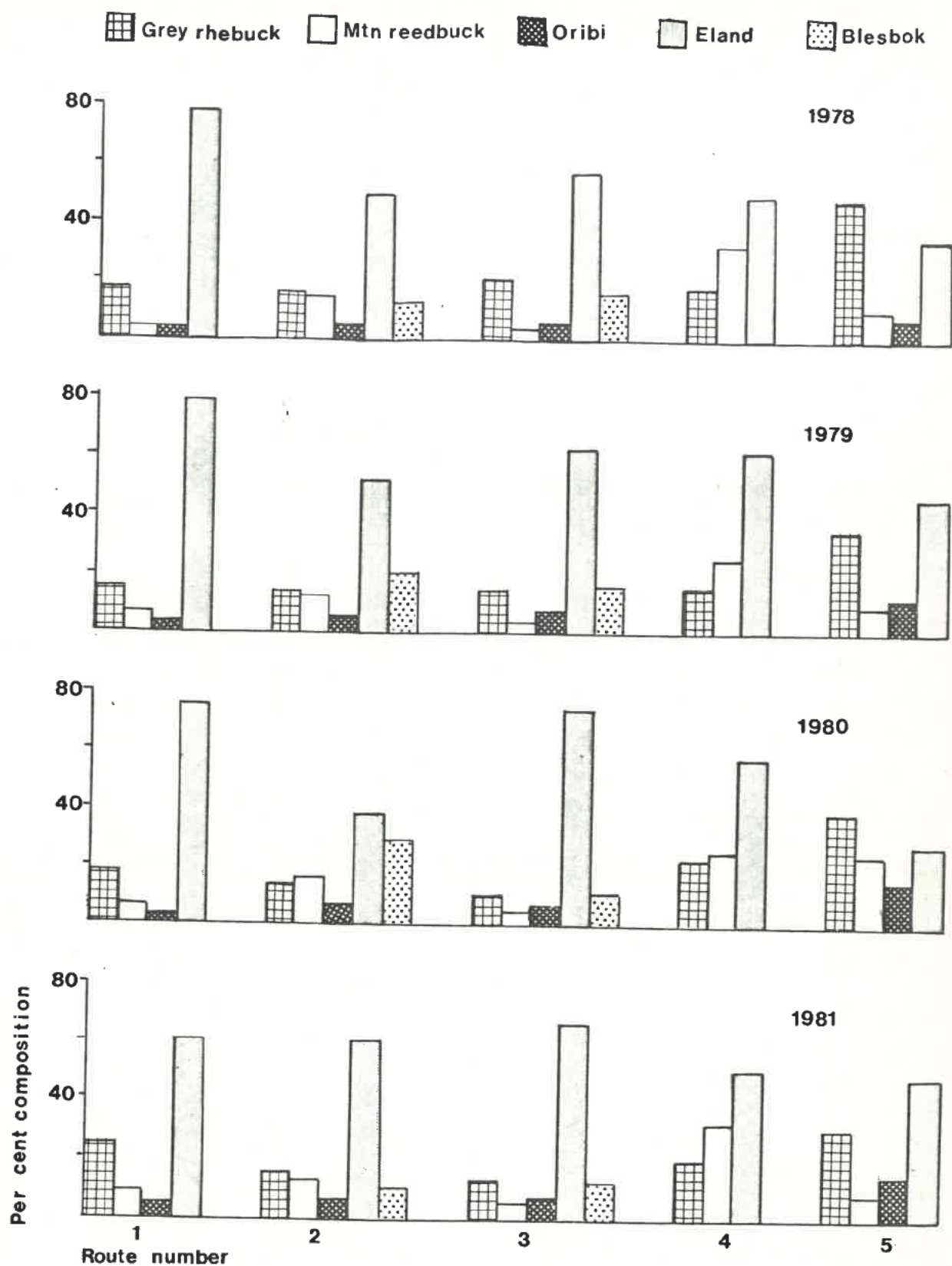


Figure 2.22 Relative abundance of five antelopes counted along routes 1 to 5 from 1978 to 1981.

Route 5

Route 5 was the only route which was not completely dominated by eland. Both the numbers and relative abundance of grey rhebuck were highest during 1978 when the whole area along the route was burnt, and the numbers of mountain reedbuck were highest during 1980 when the veld was burnt below the sandstone.

PAST AND PRESENT COUNTS

Counting procedures

Figures are available for antelope counts done in 1962, 1972 and 1973, and 1976 and 1977. Unfortunately counting methods differ so that direct comparisons are impossible.

During 1962 an attempt was made to count all grey rhebuck, mountain reedbuck, and oribi. This was done during August when the winter-burnt firebreaks were green and fairly well-grown, and these three antelopes were attracted to them. The count was done over five days by driving or walking along all firebreaks. Isolated August counts were also done along the jeep track from Witteberg to Injasuti from 1962 to 1977.

In 1972 and 1973 ground counts of all antelopes were done throughout the reserve. Twenty routes were covered once or twice a month. During 1976 and 1977 antelope were counted along ten fixed routes once a month, and from 1978 onwards the current system of counting along five routes three times a month was introduced.

A number of total ground counts and aerial counts of eland were done between 1962 and 1981, and from March 1978 to February 1979 monthly aerial counts were done.

Comparative counts along the Injasuti jeep track

During August 1980 nine counts of grey rhebuck, mountain reedbuck, and oribi were done along the Witteberg - Injasuti jeep track, which has a firebreak running along its entire length, to compare with past figures for the route. Great variation in numbers of the three antelope species was recorded, viz grey rhebuck (\bar{x} 17; SD 8,4; range 7-27), mountain reedbuck (\bar{x} 15,9; SD 7,9; range 6-27), and oribi (\bar{x} 12,9; SD 6,0; range 5-24).

As statistical comparisons with past game counts are complicated by wide variation in numbers counted and the small number of counts done in some years, it was decided to compare the best August figures from different years for the three antelopes (Table 2.7).

TABLE 2.7 Best August count along the Witteberg - Injasuti track, 1962 to 1980.

Antelope	1962	1965	1966	1967	1969	1975	1976	1977	1980
Grey rhebuck	39	24	31	21	19	10	8	16	27
Mountain reedbuck	19	3	10	18	21	8	14	9	27
Oribi	28	14	47	26	34	8	0	12	24

With the exception of the count of 39 grey rhebuck in 1962, the 1980 best count is not markedly lower than earlier figures, and is in fact third highest. The highest mountain reedbuck count, on the other hand, was recorded in 1980. Only the 1966 and 1969 best counts for oribi were markedly higher than the 1980 figure. Current counts do not, therefore, indicate any declines in these three antelopes since 1962.

Comparative route counts

Actual numbers of antelope counted on past and current route counts cannot be directly compared because of the differences in the numbers of routes and the distances covered. The only possible comparison which can be made is that of the relative abundance of antelopes counted (Table 2.8).

Mountain reedbuck is the only antelope which was markedly more abundant proportionately during 1972 and 1973 than during other years. During these two years, however, greater coverage was given to areas below the sandstone than was done in counts from 1976 onwards.

Population estimates

Scotcher (in prep.) has estimated the eland population in GCGR to be stable at approximately 640, based on past and present aerial and ground counts. The eland is probably the only antelope in GCGR that can be accurately counted from the air: the animal is large, and in summer counting is made easier when large herds are formed. The blesbok population of 120, based on ground counts, is probably also an accurate estimate, as the animals are conspicuous and limited in their distribution within the reserve.

During the study period no ground counts covering the whole reserve were done for grey rhebuck, mountain reedbuck, or oribi. As the eland population was known from aerial counts done during the study period a corrected index ("Index and control", Caughley 1977) was used to calculate the approximate totals of grey rhebuck, mountain reedbuck, and oribi, based on the relationship between their numbers on route counts and the number of eland counted on the same route counts.

One of the most important assumptions of the index is that both the species of known population size and the species being compared should be dispersed in a similar way throughout the study area (Caughley 1977). As eland are widely dispersed during the middle of winter only, population estimates were based on route counts done during July, taking the eland population as 640. Other assumptions which need to be taken into account are

TABLE 2.8 Relative abundance of antelopes counted in GCGR, expressed as percentages, based on the mean of all counts done during each year.

Antelope	*		**		***	
	1972	1973	1976	1977	1978	1980
Grey rhebuck	20,5	21,3	16,3	16,5	20,5	14,2
Mountain reedbuck	15,3	13,5	7,4	5,4	7,5	9,3
Oribi	6,8	7,3	5,7	5,4	4,2	4,1
Eland	40,8	42,9	54,6	52,9	55,2	57,2
Blesbok	9,2	8,5	11,1	14,9	8,1	10,1
Common reedbuck	0,8	1,4	0,6	0,6	2,6	2,2
Bushbuck	0,3	0,3	0,1	0,2	0,1	0,2
Grey duiker	0,2	0,3	0,1	0,2	0,3	0,5
Red hertebeest	1,1	1,0	2,0	2,2	1,3	1,9
Black wildebeest	4,9	3,4	2,0	1,5	-	-

* Twenty observers, one or two counts per month.

** Ten fixed routes, one count per month.

*** Five fixed routes, three counts per month.

that both species are equally conspicuous and that they react similarly to the observer (Caughley 1977). These two assumptions were impossible to satisfy in population estimation calculations, but will be dealt with in the Discussion section of this chapter.

Estimated population sizes based on index and control calculations are given in Table 2.9, and also listed are the actual numbers of the three small antelopes counted during 1962, 1972 and 1973. The significance of the population estimate figures in comparison with past counts will be dealt with in "Discussion".

DENSITY AND STANDING CROP

From the formula proposed by Mentis and Duke (1976) it was calculated that one animal unit (AU) is equal to 8,8 grey rhebuck, 8,1 mountain reedbuck, 17,5 oribi, 1,1 eland, or 4,9 blesbok. Using these figures the standing crop, i.e. the number of ha/AU for each of the five species was calculated (Table 2.10). Both density (ha/antelope) and standing crop are given for the entire reserve in Table 2.10, as it was not possible to determine the exact amount of ideal habitat for each species.

DISCUSSION

Current route counts

Variation occurred in numbers counted both within most months and between most months for each of the five antelopes. Annual and seasonal differences have already been related to the burning regime in the reserve. Mentis (1978) found that other factors influencing route censuses of antelopes were the time of day when counts were done, and wind force. The influence of time of day on the GCGR figures can be ignored, as all counts were done at the same time: starting early morning and being completed by mid-morning or around noon at the latest. On the other hand Mentis (1978) found that more grey rhebuck and oribi (the only antelopes dealt with in his study) were counted along the same route between 06h00 and 09h00 than in the period 09h00 to 12h00, so it is likely that numbers counted in GCGR were lower along the latter part of a route than at the beginning.

Another factor likely to be responsible for variation is the topography of the area. The smaller antelopes occur at low densities and therefore have large home ranges. At the time that a route count is done a single antelope or group may well be obscured from view in the broken terrain.

Mentis (1978) showed that better repeatability was achieved with grey rhebuck and oribi in the Drakensberg when an observer used the "known group"

TABLE 2.9 Estimated population sizes of grey rhebuck, mountain reedbuck, and oribi in GCGR, based on actual total counts in the years marked * and on index and control calculation (Caughley 1977) applied to transects from 1976 onwards.

Antelope	1962*	1972*	1973*	1976	1977	1978	1979	1980	1981	\bar{x}	SE	CV
Grey rhebuck	473	358	383	445	305	339	441	317	416	386	20,2	5,2 %
Mountain reedbuck	258	271	309	230	228	288	234	281	298	266	10,2	3,8 %
Oribi	289	118	155	215	218	166	242	143	234	197	18,5	9,4 %

TABLE 2.10 Estimated density, standing crop, and per cent metabolic biomass of five antelopes in GCGR.

Antelope	Estimated population	Density (ha/antelope)	Total AU	Standing crop (ha/AU)	Metabolic biomass (%)
Grey rhebuck	400	90	45,5	791	6,5
Mountain reedbuck	270	133	33,3	1 081	4,8
Oribi	200	180	11,4	3 157	1,6
Eland	640	56	582,0	62	83,5
Blesbok	120	300	24,5	1 469	3,5
Total	1 630	22	696,7	52	99,9

method of census. This method involves the observer concentrating on a given area (in the case cited 1 500 ha) and "identifying and familiarising himself with individual groups of antelope on the basis of group size and age and sex composition, and of home range properties" (Mentis 1978).

Oliver *et al.* (1978), counting grey rhebuck, mountain reedbuck, and oribi along fixed routes at Highmoor, also recorded variation within months and between months. The proportionate differences between the lowest and highest mean monthly figures were similar to those recorded in GCGR. Times of peak counts, however, did not correspond to the months in which highest numbers were counted in GCGR. In all three species Oliver *et al.* (1978) recorded highest numbers during February or March, which they related to seasonal breeding. Veld burning did not appear to have as marked an effect on route count totals at Highmoor as was observed for example in mountain reedbuck in GCGR, but less veld was burnt at Highmoor than is done annually in GCGR (Oliver *et al.* 1978).

At Royal Natal National Park (RNNP), north of GCGR in the Drakensberg, total monthly ground counts of antelope have been done by management staff since 1973, and during 1978 grey rhebuck and mountain reedbuck were counted along three fixed routes. The variation in numbers of the two antelopes from total counts (Natal Parks Board unpubl. records) and route counts (Southgate 1979) show similar patterns. Mountain reedbuck numbers were highest during autumn (April) and spring (September and October), and grey rhebuck counts were usually highest during autumn with a minor peak in spring.

The fire regime in RNNP is one of biennial autumn burning of all areas below the sandstone cliffs (about 60 % of the reserve), and biennial spring burning above the sandstone. Southgate (1979) attributed the peaks in counts (particularly in mountain reedbuck) to positive responses to recently-burnt veld and the fact that the antelopes were more easily seen on the burns. The pattern in RNNP closely resembles that observed during 1980 in GCGR when both autumn and spring burning of the mountain reedbuck habitat occurred, and there were similar peaks.

Population estimation

Scotcher (in prep.) considers the period late spring to early summer best for obtaining accurate total counts of eland. At this time of year he obtained good correlations between ground and aerial counts. The eland are then rutting and occur in large herds on the green spring-burnt grass on the

Little Berg. Counting from the air becomes more difficult during late summer and autumn when the grasses flower and turn brown; and during winter the eland are too widely dispersed to allow accurate counting.

Accurate aerial counts of grey rhebuck, mountain reedbuck, and oribi cannot be made (they are small, inconspicuous from the air, and widely dispersed), therefore these three species have to be counted from the ground.

Oliver *et al.* (1978) attempted population estimates of the three small antelopes using King's census technique (Leopold 1933), but abandoned the method, concluding that it could not be used in the Drakensberg due to the limitations imposed by the low densities of these antelopes. There are therefore three possible ways of obtaining population estimates in GCGR, viz by total ground counts; by route counts and applying index and control calculations (Caughley 1977), using eland as the known population; or by the known group method (Mentis 1978).

Total counts done during 1972 and 1973 revealed as much variability as did fixed route counts (Table 2.11). The 1972 and 1973 total count figures (Table 2.9) were the best counts for the three antelopes. If the same patterns were repeated in 1972 and 1973, and the highest counts occurred in the same months, it would be possible to select a certain month as the best in which to carry out total counts, but this was not the case.

Estimating populations from route counts can be done only when the index species (eland) is more or less evenly distributed throughout the reserve, viz in July. But the question which then arises is whether the three small antelopes are evenly dispersed at that time. Mountain reedbuck and oribi counts were highest during July in GCGR, possibly due to their being attracted to firebreaks, therefore the population estimates for these two species may be slightly exaggerated. Grey rhebuck counts, on the other hand, were average or below average during July, therefore the estimate for this species may be more accurate than for the other two.

Two other assumptions in the index and control method of population estimation are that the three small antelopes should be as conspicuous as eland and that they should react to the observer in a similar way. This was not the case. Eland, by virtue of their large size and more docile behaviour, are more conspicuous than the other three species, which in turn are not equally conspicuous and react differently to the observer.

Data were collected on the reactions of eland and the other three species and, as they are relevant to counting, will be discussed here. The distance at which an antelope fled (= flight distance) when an observer on

TABLE 2.11 Total counts of three antelopes done during 1972 and 1973 in GCGR.

Antelope	1972 (N = 19)			1973 (N = 21)		
	\bar{x}	SE	CV	\bar{x}	SE	CV
Grey rhebuck	256	14,9	5,8 %	273	16,7	6,1 %
Mountain reedbuck	195	15,3	7,8	173	16,6	9,6
Oribi	86	5,3	6,2	94	7,3	7,8

foot approached was recorded, and so too was the antelope's behaviour.

Grey rhebuck had the greatest mean flight distance, viz 467 m ($N = 42$, SE 38). The flight of a group was always led by an adult female, sometimes in response to a warning bark by the herd male, although sometimes a female issued the warning. Unless it was impossible to do so, grey rhebuck always fled uphill, sometimes pausing at the top of the hill before disappearing over the horizon. The possible effects of this behaviour on counting are that the observer may not hear a warning bark and the group may flee unnoticed (cf. the great flight distance of this antelope). On the other hand, an observer may become aware of a group only after initial flight has taken place, when an adult male pauses at the top of a slope and barks before disappearing over the horizon. If this occurs part of a group may well be missed, having already fled out of sight.

Mountain reedbuck allowed a closer approach (mean flight distance 299 m, $N = 25$, SE 46). They often remained dead still or moved quietly into cover. If standing or lying in cover they often waited until the observer was fairly close before suddenly jumping up and bounding away. As this antelope does not always issue a warning whistle it could seek cover or remain undetected. Flight in mountain reedbuck, as in the case of grey rhebuck, is always led by an adult female. In contrast to grey rhebuck, however, they flee downhill, rapidly disappearing from view without stopping to look back.

The mean flight distance of 197 m ($N = 24$, SE 27) for oribi was lowest amongst the three small antelopes. When encountered in the open oribi flee in a conspicuous manner, running rapidly and occasionally bounding high above the ground. In long grass they usually lie down and remain dead still until the observer is 20 to 40 m away. If undisturbed they may remain undetected.

Eland had a mean flight distance of 258 m ($N = 24$, SE 33). Flight usually followed the contour of a hill, and when in flight, they sometimes initially even ran towards the observer in an attempt to remain on the contour and avoid steep ascents or descents.

From these observations it can be seen that the three small antelopes, besides being small and more cryptic than eland, are less easily detected because of their particular reactions to the observer.

A behavioural feature of each of the three small antelopes which should be considered in conjunction with their reaction to observers is activity pattern. All three species were most active during early morning and late afternoon when they were feeding, and were least active during the middle

of the day when they were either lying or standing. These observations are supported by those of Ferreira (in prep.), Irby (1981), Oliver *et al.* (1978), Southgate (1979), and Viljoen (1975). Oliver *et al.* (1978) found that grey rhebuck spent 36 to 50 % of their time lying, and observations on a single oribi revealed that it spent 73 % of the day lying down. Eland, due to their large size, are easily seen, even when lying down.

If the flight behaviour and activity patterns of these three species are taken into account as factors affecting counting, then the estimated populations (Table 2.9) may be regarded as the minimum for each of the small antelopes.

Mentis (1978) recorded better repeatability in counting grey rhebuck and oribi when employing the known group method than when using a fixed transect. It would not be practicable to apply the known group method to the entire area of a game reserve as large as GCGR, but a number of suitably-sized areas typical of the habitats that occur in the reserve could be selected, densities could be determined, and extrapolations made.

A fourth method of population estimation, as yet not tested in GCGR, is that of using the proportions of antelopes recorded in random observations and calculating the population of each species in relation to that of the known eland population. This could be done if all management staff recorded all antelope seen over a given period. Prerequisites of this method would be that observers give full coverage to the reserve and that all species are evenly dispersed. Once again, because of the social and feeding behaviour of eland, this could be done only during the winter months (June to August).

Past and present counts

If the 1976 to 1981 population estimates are reliable (Table 2.9), there is no evidence of a decline in numbers of the three small antelopes when compared with the 1962 total count, the coefficient of variation being less than the accepted 10 % (Rayner 1967) for all three species. No claim of a decline in numbers of eland has been made - in fact, the claim made concerning eland was that the population was remaining stable, and this was one of the problems investigated by Scotcher (in prep.). Analysis of eland counts done between 1961 and 1981 revealed a CV of 3,3 % (\bar{x} 643; $N = 16$; SE 21,3; range 487 to 817). The coefficient of variation is in actual fact similar to that recorded for grey rhebuck and mountain reedbuck (Table 2.9).

The similarity of population estimates to actual counts of grey rhebuck

and mountain reedbuck lends support to the supposition that the estimates are reliable. The greater variability in oribi totals makes it more difficult to assess the reliability of the estimates for this antelope. The much lower counts in 1972 and 1973, when compared with 1962, indicate a decline in oribi numbers. Autumn and winter burning were the only fire regimes practised in GCGR from 1906 to 1965. There was therefore more short grass for longer periods each year than under the regime of spring burning above the sandstone from 1966 onwards (see Fig 1.11), and as oribi favour short grass, it is possible that numbers declined as a result of the change in burning practice. Staff of the Natal Parks Board Farm Game Section have noted that oribi do best on farms where autumn burning is practised, or large areas of grass are kept short by mowing (Collinson, pers. comm.*).

One of the reasons why (to persons familiar with GCGR in the past) there appeared to be a decline in the populations of small antelopes might lie in the degree of the use of vehicles and in the number of jeep tracks in past and present management. Prior to 1974 there were more jeep tracks in use in GCGR (91,5 km), but due to serious erosion and maintenance problems all but the 31,5 km currently used (Fig 0.1) were closed. Whereas vehicles were regularly used in the reserve in the past, their current use is strictly controlled in the interests of preventing erosion and of fuel conservation. An observer using a vehicle covers a lot more ground than does one on foot, and furthermore, shy and cryptic antelopes do not flee as readily from a vehicle. When I travelled in a vehicle it was found, for example, that the mean flight distance of grey rhebuck was 113 m (N = 16, SE 21) compared with 467 m when I was on foot.

Density and standing crop

At Highmoor densities of grey rhebuck (1/42 to 57 ha), mountain reedbuck (1/89 ha), and oribi (1/57 to 96 ha) were estimated to be about twice as high as those in GCGR (Oliver *et al.* 1978, Mentis 1978). The GCGR densities of one antelope/90, 1/133, and 1/180 ha for the three species respectively, however, were calculated in relation to the whole reserve. The relative proportions of the reserve below sandstone (preferred mountain reedbuck habitat), the Little Berg (preferred grey rhebuck habitat), and escarpment slopes were estimated from a 1:50 000 map. The estimates are: 24 % (8 640 ha) below sandstone, 63 % (22 680 ha) Little Berg, and 13 % (4 680 ha) escarpment. If mountain reedbuck density is based only on the area below

* R.F.H. Collinson, Natal Parks Board, Pietermaritzburg.

sandstone then density is ca 1/32 ha, and similarly if grey rhebuck density is calculated in the Little Berg area, then it is ca 1/57 ha.

The GCGR grey rhebuck density is then similar to the figures given by Oliver et al. (1978) and Mentis (1978) which were calculated in typical grey rhebuck habitat on the Little Berg. Ferreira (in prep.) recorded lower grey rhebuck densities of 1/83 ha to 1/125 ha in the Orange Free State, mainly on farmland.

In areas of suitable mountain reedbuck habitat in Transvaal nature reserves density has been estimated to be between 1/15 ha and 1/33 ha (Irby 1973, 1977b; Mason 1977). In a portion of Royal Natal National Park constituting ideal mountain reedbuck habitat, Southgate (1979) estimated a density of 1/22 ha. Crude density for RNNP, about 60 % of which is below sandstone, is 1/32 ha (Natal Parks Board unpubl. records).

Suitable oribi habitat in GCGR is estimated to be approximately 6 475 ha therefore the ecological density of oribi is ca 1/33 ha. Besides the estimates on oribi density made by Mentis (1978) and Oliver et al. (1978), there are no published figures. Viljoen (pers. comm.)* recorded densities of between 1/20 ha and 1/100 ha in the Transvaal.

Eland, the antelope having the highest density and standing crop in GCGR (Table 2.10), is by far the dominant species, contributing ca 83 % of the total biomass (standing crop) in the reserve. The overall antelope standing crop of 52 ha/AU estimated for GCGR is much higher than that of ca 300 ha/AU recorded on the Highmoor plateau (Mentis 1978) and slightly higher than the 60 ha/AU estimated for portion of RNNP (Southgate 1979). Although densities of the three small antelopes are higher in other parts of the Drakensberg (Mentis 1978, Oliver et al. 1978, Southgate 1979) eland are either absent (RNNP) or occur only seasonally or in low numbers (Highmoor) in these areas. Densities of the three small antelopes should therefore be compared only when the overall standing crop of the area is taken into account.

My overall conclusions regarding antelope populations in the Drakensberg are in agreement with the findings of Mentis (1978) and Oliver et al. (1978), viz that numbers are limited by the poor quality of the veld during winter (see Fig 2.15). The period of lowest nutritional content in herbage coincides with the coldest, driest time of the year (Everson in prep., Mentis 1978, Scotcher et al. 1980b). It is during late winter and early spring (August to October), following this period of low food quality and

* P.C. Viljoen, Nature Conservation Division, P Bag X209, Pretoria.

harsh climatic conditions, that most antelope die (Mentis 1978, Oliver et al. 1978, Scotcher in prep., this study - Table 3.7 and Figure 2.25).

The standing crop of 52 ha/AU in GCGR is much lower than the potential carrying capacity of 1,5 and 5,0 ha/AU proposed for Highland Sourveld and Montane Grassland respectively (Edwards 1981). These, however, are agriculturists' figures, proposed for cattle during the grazing season only, and under a system of rotational grazing. Mentis (1978) falsified the hypothesis that antelope in the Drakensberg can occur at a standing crop size approaching that at which cattle might be stocked in summer. The antelope, particularly during winter, will need to feed selectively to obtain sufficient nutritious, easily digestible, food.

In view of the fact that antelope populations in GCGR are apparently stable and occur at a standing crop of 52 ha/AU, and that in RNNP where a similar situation exists and the standing crop is 60 ha/AU, I conclude that the antelope carrying capacity of the Drakensberg is ca 50 ha/AU.

POPULATION DYNAMICS

POPULATION STRUCTURE

Antelopes in GCGR have high flight distances, making it difficult to approach close enough to collect information, for example on sexes of young animals, or to assign them accurately to age classes. Throughout the study, therefore, attempts were made to sex adults only, and only two age classes were used, viz immature (< 12 mo old) and adult (> 12 mo old). In grey rhebuck males horns emerge at 4,5 mo (Rowe-Rowe 1973a), but are difficult to detect in the field until the animal is at least 7 mo old; young oribi males' horns emerge at 9 mo (Mason 1973) but are not obvious until at least 12 mo; and young male mountain reedbuck horns emerge only at 12 mo (Rowe-Rowe 1973b).

Sex ratio

With the exception of oribi, the adult sex ratio of the other four most abundant antelopes in GCGR significantly favoured females (Table 2.12).

The grey rhebuck male:female ratio of 1:1,47 reflects a slightly lower female component than that in the ratios of 1:1,72 and 1:1,93 recorded in other Drakensberg areas (Oliver *et al.* 1978, Southgate 1979). The preponderance of females in the GCGR mountain reedbuck sample is similar to the situation recorded elsewhere in South Africa. In Transvaal nature reserves, ratios of from 1:1,96 to 1:2,22 have been reported (Irby 1977b, Mason 1977) and data collected in GCGR in 1970 and 1971 (Irby 1977b) reflected a ratio of 1:1,79. Elsewhere in the Drakensberg ratios of 1:1,94 and 1:2,63 have been recorded (Oliver *et al.* 1978, Southgate 1979).

The sex ratio of oribi at Highmoor slightly favoured males (1:0,84), as in GCGR, but again, did not differ significantly from parity (Oliver *et al.* 1978).

The male:female ratio of 1:1,66 in the GCGR blesbok sample is lower than the ratios of 1:2,36 to 1:2,61 recorded by du Plessis (1972) at van Riebeeck Nature Reserve near Pretoria. Prior to the commencement of the Pretoria study, however, the population was harvested for a number of years with more males than females being shot (du Plessis 1972). There are no figures for blesbok sex ratios in "natural" populations with which to compare the GCGR figure because, as has been pointed out by Mentis (1972), available data are all from populations in which selective harvesting has been done.

TABLE 2.12 Adult sex ratio of five antelopes in GCGR and Chi-square evaluation for deviation from parity.

Antelope	Males	Females	Ratio	Chi-square	P
Grey rhebuck	150	220	1:1,47	13,24	< 0,001
Mountain reedbuck	60	115	1:1,92	17,29	< 0,001
Oribi	91	81	1:0,89	0,58	NS
Eland	124	196	1:1,58	16,20	< 0,001
Blesbok	134	222	1:1,66	21,75	< 0,001

NS = $P > 0,05$

The eland sex ratio of 1:1,58 was based on adult animals in small herds. Scotcher (in prep.) did more detailed sex and age classifications of eland in GCGR, and the sex ratio of ca 1:2 from his adult sample is similar to the figure which I recorded. At Loskop Dam Nature Reserve the male:female ratio was similar to that in GCGR, ranging from 1:1,52 to 1:2,27 (Underwood 1975).

Klein (1970) found that sex ratios of North American deer were greatly altered by food quality and quantity, and that differential mortality increased markedly when populations outgrew their food supply, with mortality in males being higher than in females. Klein stated that although heavier male mortality took place during the first year of life, it continued throughout all age classes. If this phenomenon applies also to the GCGR antelopes, then the sex ratios indicate that they occur at the maximum density which the reserve can carry.

The sex ratio at birth of mountain reedbuck, eland, and blesbok is 1:1 (Mentis 1972). Although Mentis (1972) was unable to give figures for grey rhebuck and oribi, he found a 1:1 ratio at birth in almost all other antelopes for which data were available, therefore it is unlikely that the natal sex ratio differs from parity in these species. Data from GCGR and elsewhere reflect adult sex ratios in favour of females in grey rhebuck, mountain reedbuck, blesbok, and eland, whereas in oribi it is 1:1. Mortality amongst males must therefore be higher in the first four species, the reason for which I will attempt to explain by the following hypothesis:-

All four of these antelopes are herd-forming with an average of more than one female per male. Grey rhebuck and blesbok are territorial (Esser 1973, Lynch 1974), and observations on mountain reedbuck indicate that they too are territorial (Mason 1977, Oliver et al. 1978). In grey rhebuck and blesbok yearling males leave the herd or are driven from it at about the time that lambing takes place (Esser 1973, Lynch 1974, Rowe-Rowe 1973c), and adult male mountain reedbuck have been seen chasing yearlings. Yearling females are not driven from the herd and therefore continue to live with adult females and territorial males in preferred habitat, whereas non-territorial males live under social stress in less suitable habitat. Therefore, during times of environmental stress non-territorial males are likely to succumb more easily than females.

Although eland are non-territorial, a dominance system exists among males (Underwood 1975), so younger and smaller males would be under similar stress to that which exists in territorial herding species.

Oribi are territorial (Tinley 1971, Viljoen 1975), but the antelope is

one which exists in pairs rather than in herds. In the herding antelopes selection appears to have taken place for an expendable surplus of males, whereas in oribi selection has taken place for pair formation and equal chances of survival between the sexes. Although Jarman (1974) grouped oribi together with grey rhebuck and mountain reedbuck in social organisation "class B", the data collected in the Drakensberg suggest that they would be better placed in "class A" (antelope which occur singly or in pairs). There is little sexual dimorphism in the small antelopes in class A and both males and females occur singly - single oribi females being more abundant than was the case in grey rhebuck and mountain reedbuck (Table 2.13). The single oribi female is therefore at the same risk as the male, and competes with him on equal terms, at least for food and shelter.

Group size and composition

Mean and typical group sizes were calculated using the method of Jarman (1974). Typical group size is the size of group in which most individuals find themselves (Jarman 1974) and need not be the modal group size.

1. Grey rhebuck

Grey rhebuck were recorded in groups of from one to nine (Fig 2.23) with a mean group size of 2,84 and a typical group size of 3,94. Most herds consisted of an adult male and two or more females and their young (Table 2.13). Two adult males were recorded together once only - both were estimated from their horn length to be about 18 mo old. Monthly variation in group sizes was not significant ($P > 0,05$).

Mean and typical group sizes and group composition are very similar to those recorded by Oliver et al. (1978) and Southgate (1979).

2. Mountain reedbuck

Mean group size was 3,27 and typical group size 5,1, with a range of from one to 14 (Fig 2.23). The social organisation was similar to that observed in grey rhebuck (Table 2.13). No significant variation in mean monthly group sizes was observed ($P > 0,05$).

Group composition was similar to that reported in mountain reedbuck populations elsewhere (Irby 1977b, Mason 1977, Oliver et al. 1978, Southgate 1979). Mean and typical group sizes were larger than those recorded at Highmoor (Oliver et al. 1978) but similar to the figures for RNNP (Southgate 1979).

TABLE 2.13 Group composition of adult grey rhebuck, mountain reedbuck, and oribi in GCGR.

Composition	Per cent occurrence		
	Grey rhebuck	Mountain reedbuck	Oribi
1 male and 1 female	23,3	36,8	58,8
1 male and > 1 female	39,8	35,3	3,9
Single male	26,9	16,2	24,5
> 1 male	0,6	0	1,0
Single female	3,7	5,9	11,7
> 1 female	5,5	5,9	0

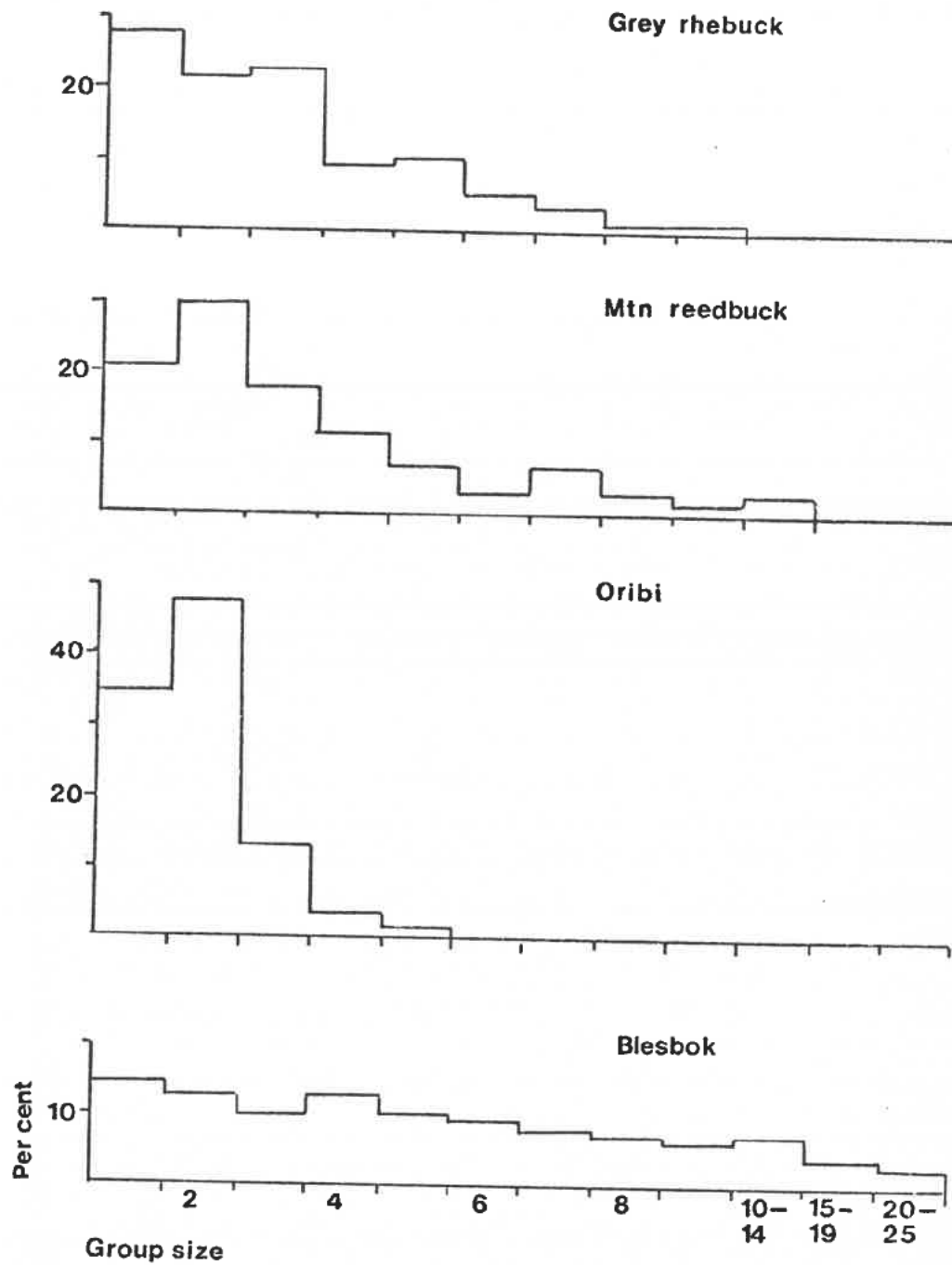


Figure 2.23 Group size frequency in four GCGR antelopes.

3. Oribi

Oribi differed from grey rhebuck and mountain reedbuck mainly in respect of their being organised primarily in pairs rather than small herds (Table 2.13). The mean group size was 1,87 and typical group size 2,24. Monthly variation in mean group size was not significant.

The mean and typical group sizes recorded in GCGR are almost identical to those of 1,89 and 2,22 respectively reported from Highmoor by Oliver *et al.* (1978), and so too is group composition.

4. Eland

Eland were recorded in groups of from one to 212 individuals. Monthly means (Fig 2.24) differed significantly ($P < 0,01$). Because of the marked seasonal variation, overall mean and typical group sizes were not calculated.

The pattern at GCGR follows that recorded by Underwood (1975): Group sizes increase during the calving season (September and October) when large herds of females and calves are formed. At the end of the calving season these nursery herds are joined by males which have come from male groups, the dominant ones among them taking part in the rut. By April the large nursery/male herds have split up and form a complexity of small groups made up of animals of various age classes and sexes, and in various combinations.

5. Blesbok

Social organisation in blesbok follows one pattern in large populations (Lynch 1974) and a slightly simpler one in small populations (Rowe-Rowe 1973c). In GCGR organisation was typical of that in large populations: territorial males start herding females (preventing them from leaving the territory) throughout the rut (February to April). These harem herds then break up, the territorial males remaining solitary and the females and the previous year's young forming female/nursery herds. When 10 to 12 mo old males leave the herd (or are evicted) but females usually remain.

Mean and typical group sizes were 5,6 and 8,83 respectively (range 1 to 25), with no significant monthly variation ($P > 0,05$).

Herd sizes in GCGR are smaller than those reported by du Plessis (1972) in van Riebeeck Nature Reserve (where the study by Lynch (1974) was also done). The mean number of females/herd in GCGR was 4,72 (range 1 to 16), whereas du Plessis recorded a mean of 10,4 (range 3 to 23). In GCGR the largest bachelor herd consisted of seven non-territorial males, whereas Lynch (1974) recorded herds of 75 to 140. The reason for these differences lies primarily in the different blesbok densities in the two reserves. In the 3 000 ha van Riebeeck Nature Reserve there were 892 blesbok (du Plessis 1972), but in GCGR the density was much lower (ca 120 animals), and the

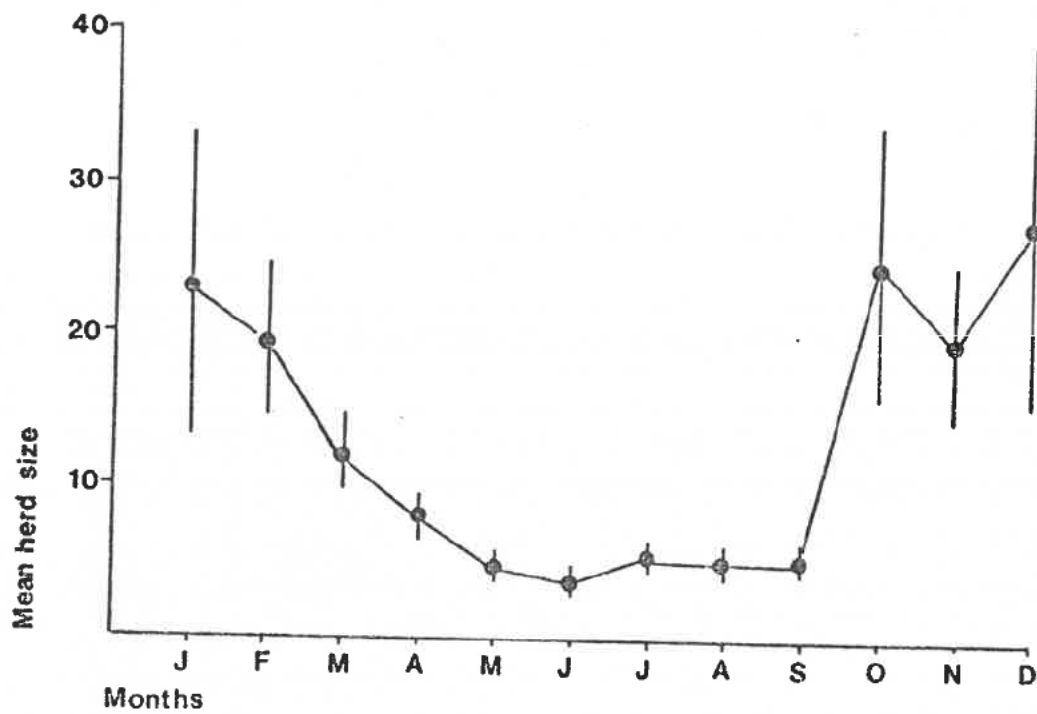


Figure 2.24 Mean monthly herd sizes of eland. Vertical lines indicate twice the SE of the mean.

different groups of blesbok occupying areas of suitable habitat within the 36 000 ha area were widely dispersed and may almost be regarded as sub-populations within the large reserve.

The observations on group size and composition of the GCGR antelopes are in agreement with the classification by Jarman (1974), who suggested that a relationship exists between body size, feeding style, and typical group size. Jarman (1974) placed grey rhebuck, mountain reedbuck, and oribi in "class B" which includes small species which feed in style b (see chapter on "Habitat preferences"). The GCGR data suggest, however, that oribi might well be placed in social organisation "class A" which Jarman (1974) defined as including those antelopes which occur singly or in pairs. Group size and composition of blesbok in GCGR suggests that they should be placed in either class C or D. As blesbok have already been recognised as feeding in "style d", i.e. antelope "which feed on grasses, being rather unselective for species ..." (Jarman 1974), I group them in "class D" despite the fact that the very large aggregations typical of alcelaphines do not occur in GCGR where blesbok densities are low. Small scale migrations (typical of "class D" antelopes) to areas of better grazing were observed in blesbok (see "Influence of fire on distribution and abundance").

Age-class structure

The numbers and proportions of adult (> 12 mo old) and immature antelope (< 12 mo old) are given in Table 2.14.

No unsexed animals are listed under grey rhebuck, mountain reedbuck, and oribi. For each of these antelopes there were some unclassified individuals (24, 8, and 43 respectively) but these have been omitted from the analysis. If a group of any of these small antelopes was seen, and it was too distant to sex the animals, they were listed as unclassified as they could also have been erroneously categorised as adult or immature. Mason (1973), for example, made a number of observations on a known group of oribi and noted that an immature male at the age of nine months was as large as the adult female.

Unsexed adult eland and blesbok are listed in Table 2.14. There is very little chance of making the mistake of classifying a < 12 mo-old individual of these two antelopes as an adult, mainly due to colour and horn length differences, and the fact that both have a very marked breeding season. The high numbers of unsexed individuals in these two species is due

TABLE 2.14 Sex and age group classification of five GCGR antelopes.

	Grey rhebuck	Mountain reedbuck	Oribi	Eland	Blesbok
Adults (> 1 y old)					
Males	150	60	91	124	134
Females	220	115	81	196	222
Unsexed	0	0	0	337	190
Total	370	175	172	657	546
Immature (< 1 y old)					
	103	34	29	136	131
Ratios					
Immature:adult	0,28:1	0,19:1	0,17:1	0,21:1	0,24:1
Immature:female	0,47:1	0,29:1	0,36:1	0,34:1*	0,38:1*

* Adjusted ratio - see text.

to the fact that both sexes bear horns. Unless the observer is close enough, even when using 8 x 30 binoculars as I did, or uses a powerful telescope (which I did not), it is difficult to tell the sexes apart.

Assuming that the sex ratios of eland and blesbok in the unsexed samples were the same as those observed in the sexed sample, the immature:female ratio was based on the adjusted figures of 402 and 341 females respectively, calculated as follows: unsexed adults x proportion of females in the sexed sample + sexed females.

There are few recorded data with which to compare the GCGR immature:adult female ratios for grey rhebuck, mountain reedbuck, and oribi. Irby (1977b) found that the ratio of immature:adult female (also using < 12 mo old:> 12 mo old animals) in mountain reedbuck in two Transvaal nature reserves ranged from 0,08 to 0,57. Some of the information included in the report by Irby (1977b) was collected in GCGR - in 1970 the immature proportion was 0,59 and in 1971 0,25 of adult females. Oliver *et al.* (1978) and Southgate (1979) did not give an overall mean ratio for the populations which they studied. At Highmoor monthly immature proportions ranged from 0 to 0,54 for grey rhebuck; 0,01 to 0,26 for mountain reedbuck; and 0 to 0,40 for oribi (Oliver *et al.* 1978). Monthly proportions at RNNP were lower, ranging from 0,01 to 0,18 for grey rhebuck; and from 0,04 to 0,19 for mountain reedbuck (Southgate 1979).

Although it is difficult to make comparisons with the other data, the GCGR proportions appear to be similar to those at Highmoor but higher than the RNNP figures.

In the eland population at Loskop Dam Nature Reserve Underwood (1975) found that calves of 6 mo old were in the ratio of 0,18 to 0,20 to all eland > 1 y old, and ca 0,32 to 0,42 to all females > 1 y old. These ratios are similar to the GCGR figures (Table 2.14).

Du Plessis (1972) did age and sex classifications of the blesbok population in van Riebeeck Nature Reserve in two consecutive years. The proportion of < 12 mo-old to > 12 mo-old individuals was 0,05 and 0,21; and the ratio of < 12 mo-olds to > 12 mo-old females was 0,08 and 0,32 in the first and second years respectively. The second set of figures is similar to the overall figures for GCGR (Table 2.14). Du Plessis (1972) attributed the lower proportions during the first year to undue heavy losses amongst lambs which did not occur during the second year.

The similarity in the proportions of immature animals in the populations of the five most abundant antelopes in GCGR, to those recorded in other areas, indicate that mortality amongst young animals in GCGR is not abnormally

high. In GCGR the immature:adult female ratios of grey rhebuck, mountain reedbuck, oribi, and blesbok do not differ markedly from the immature:adult female ratio in eland (Table 2.14). It has already been suggested that nutrition and the harsh climate of the area are the major population limiting factors in GCGR antelopes (chapter on "Population trends" and section on "Mortality" in this chapter), therefore if jackal predation was also a major limiting factor, and large numbers of young grey rhebuck, mountain reedbuck, oribi, and blesbok were killed by jackals, then one would expect the proportion of immatures:adult females in these four antelopes to be much lower than that in eland. (No claim has ever been made that jackals kill eland calves.)

REPRODUCTION

The study of reproduction was limited to recording reproductive behaviour and sightings of very young antelope. Where possible very young antelope were classified as infant or juvenile, following the classification guide by Ansell (1966) according to which an infant is defined as a young animal with withers below the adult female's elbow, and a juvenile as one whose height at the withers reaches halfway between the female's elbow and the top of her shoulder. As already pointed out, antelope observations are generally made from great distances in the Drakensberg, so that detailed categorisation of the young of the three small species was not always possible, and therefore for the purposes of recording the data on lambing season, animals were often subjectively classed only as very young (i.e. either infant or juvenile).

The monthly ratios of very young antelope to adult females are given in Table 2.15. The overall pattern which these data indicate is that mountain reedbuck breed throughout the year but with a summer peak, and that parturition in the other four species is seasonal, occurring mainly in late spring or early summer.

Although the proportions are highest during January and February in grey rhebuck, mountain reedbuck, and oribi this does not necessarily mean that most young are born during these months. All three of these species practise lying-out behaviour (Esser 1973, Oliver *et al.* 1978, Viljoen 1975), therefore the young are not seen until some weeks after they are born. Esser (1973) stated that young grey rhebuck lie-out until the age of about six weeks, therefore the peak in sightings during January and February actually reflects a peak in births during November and December. Mountain reedbuck and oribi have been recorded as lying-out for up to four weeks

TABLE 2.15 Very young antelope (i.e. both infant and juvenile animals) expressed as a proportion of the adult females.

Month	Grey rhebuck	Mountain reedbuck	Oribi	Eland	Blesbok
Jan	0,21	0,19	0,16	0,47	0,25
Feb	0,20	0,25	0,11	-	0,39
Mar	0,12	0,09	0,21	-	0,28
Apr	-	-	-	-	-
May	-	0,02	-	-	-
Jun	-	0,02	-	-	-
Jul	-	-	-	-	-
Aug	-	-	-	-	-
Sep	0,02	0,09	-	0,33	-
Oct	0,02	-	-	0,38	0,05
Nov	0,03	0,02	0,03	0,40	0,22
Dec	0,06	0,03	0,16	0,56	0,24

(Oliver et al. 1978) and Viljoen (1975) found that young oribi were regularly seen only once they were three months old, so for these species the peak in births is probably also at the end of the year.

Grey rhebuck were seen copulating during March and May and one mountain reedbuck copulation was recorded in October. Oliver et al. (1978) recorded mounting by grey rhebuck between March and June, and in oribi during April and May. Taking the gestation periods (Mentis 1972) of these two species into account, grey rhebuck births would have occurred during November to February, and oribi in November and December.

Eland and blesbok showed distinct seasonal breeding. In eland parturition starts some two months earlier than in blesbok, and extends from late August to November, with a peak in September and October. Most blesbok are born during November and the first half of December, with only a few others being born before and after these months.

The very young:adult female proportions of eland and blesbok were higher throughout the breeding season than those observed in the three small antelopes. This does not, however, necessarily reflect lower breeding rates in the small antelopes. As already mentioned, not all the recently-born young of these species were counted as some might have been lying-out, and difficulty was experienced in categorising the young as "juvenile" due to the great distances from the observer. Young eland and blesbok, on the other hand, were much easier to identify because of their distinctly lighter colour.

The overall immature (< 1 y old):adult female proportions (Table 2.14) of the three small antelopes are higher than the very young:adult female proportions (Table 2.15). This further illustrates the fact that the very young of these species are not seen during the first few months after birth. Estimates of minimum breeding success should therefore be based on the immature:adult female ratios.

The reproductive seasons observed in the five GCGR antelopes do not differ from those previously recorded in other South African studies. Seasonal breeding of grey rhebuck is supported by the observations of Oliver et al. (1978) and Southgate (1979). In mountain reedbuck breeding has also been recorded throughout the year, with a peak in the wet season (Mason 1977, Oliver et al. 1978, Southgate 1979). In both the Drakensberg (Oliver et al. 1978) and the Transvaal (Viljoen 1975) oribi have been recorded as breeding seasonally, with a parturition peak in November and December.

In southern Africa eland have been reported as breeding seasonally,

with most births during late winter and spring (Mentis 1972). Stainthorpe (1972) stated that most calves in the Drakensberg are born during September and October, which is supported by Scotcher (in prep.).

Rowe-Rowe and Bigalke (1972), in considering 230 recorded births from four game sanctuaries in Natal, reported marked seasonal breeding in blesbok, with 65,7 % of the births during November and 25,2 % during December. Elsewhere in South Africa peaks have been recorded during November or December (Mason 1973, Mentis 1972), and Skinner and Huntley (1971) found that adult male blesbok have a marked sexual cycle, reaching a peak during the autumn rut.

The monthly ratios of very young mountain reedbuck:adult females recorded in GCGR were similar to those observed at Highmoor (Oliver *et al.* 1978). During one season at Highmoor the very young:adult female proportions in grey rhebuck and oribi were similar to those in GCGR, but during the second season of the study they were higher (Oliver *et al.* 1978). At RNNP, however, Southgate (1979) recorded lower monthly proportions than those observed in GCGR for grey rhebuck and mountain reedbuck. The differences in antelope reproductive rates in these areas might be real, but on the other hand the differences might lie in the subjectivity of the observer's categorisation.

Calving percentage estimates can be made only if the age at first parturition of the species is known and if details of the various age-classes of the females in the population are determined.

Age at first parturition is not known for grey rhebuck and oribi. Rowe-Rowe (1973b) recorded a first parturition at 29 mo in a known-age mountain reedbuck, and in the closely related *Redunca fulvorufula chanleri* Irby (1977b) reported pregnancies in yearling females. It would appear, therefore, that mountain reedbuck females are capable of reproducing during their second year. Knowing the age at first parturition in the three small antelopes would not be of major assistance in assessing calving rate in a field study, however, due to the difficulty of assigning > 1 y-old females to age classes, unless destructive sampling is done.

Blesbok females usually calve for the first time at 3 y (du Plessis 1972) but sometimes first parturition is at the age of 2 y (Rowe-Rowe and Bigalke 1972). The age classification of the GCGR population is not detailed enough to calculate breeding success in relation to > 2 y-old or > 3 y-old females. From Tables 2.14 and 2.15 it can be seen that it is at least 0,38 for all females > 1 y old. There are few population studies with

which to compare the GCGR breeding success. Du Plessis (1972) recorded proportions of 1 mo-old blesbok:females > 2 y old on farms and nature reserves in the Transvaal. These ranged from 0,04 to 0,78 (\bar{x} ca 0,46), depending on year recorded and the management of the herd. Although du Plessis (1972) estimated a pregnancy rate of 84 % in females > 3 y old in van Riebeeck Nature Reserve, the proportion of immature blesbok to these females after one year was 0,33. Mason (1973) found that the calf crop amounted to ca 38 % of the population at the end of the calving season (January), but did not give the sex ratio of the adults, so the ratio of calves to adult females cannot be calculated.

In eland in the wild age at first parturition is 3 y (Mentis 1972). Scotcher (in prep.) has collected data on eland population structure in GCGR on a monthly basis. At the end of the calving season calves constitute ca 0,38 of the population, gradually decreasing to ca 0,19 by the next calving season. Breeding success (calves:> 3 y-old females) has been estimated to be 0,93, but by the end of the calving season the figure has already dropped to 0,72, finally falling to 0,36 by the next calving season. These figures are comparable with the proportions of 0,49 to 0,59 6 mo-old calves:> 3 y-old females reported from Loskop Dam Nature Reserve (Underwood 1975).

MORTALITY

Between January 1978 and December 1980 275 antelope deaths were recorded in GCGR. In most instances (73 % to 88 % depending on species) the cause of death could not be determined (Table 2.16), although observers often added the comment that the animal appeared to have been in poor condition. Confirmed predation by jackals was low in the three small antelopes (Table 2.16).

Most antelope in GCGR die at the end of winter or in early spring (Fig 2.25). Of the 275 recorded mortalities 55 % occurred during the months of August to October. The months of June to August are the coldest and driest in the year, and furthermore this is also the period of poorest herbage quality (Scotcher et al. 1980b). Many of the deaths in the three-month period August to October were recorded after sudden cold spells, usually accompanied by rain or snow.

Mentis (1978) and Oliver et al. (1978) also concluded that herbage quality and severe climatic conditions were the major factors responsible for limiting grey rhebuck, mountain reedbuck, and oribi populations and that the effects of jackal predation were negligible. The data presented in Table 2.16 and Figure 2.25 support this conclusion and so too do the results

TABLE 2.16 Cause of death in GCGR antelopes recorded from January 1978 to December 1980, expressed as a percentage of the total deaths for each species.

Cause	Grey rhebuck N = 27	Mountain reedbuck N = 40	Oribi N = 15	Eland N = 131	Other antelopes* N = 62
Unknown	81	88	73	73	88
Jackal	4	3	7	0	0
Caracal	7	5	0	0	2
Black eagle	0	0	0	0	2
Broken leg	0	0	0	4	3
Fell over cliff	0	2	0	5	2
Burnt	0	0	0	5	3
Lightning	0	0	13	1	0
Poachers	7	2	7	12	0

* Common reedbuck, bushbuck, grey duiker, blesbok, hartebeest, black wildebeest

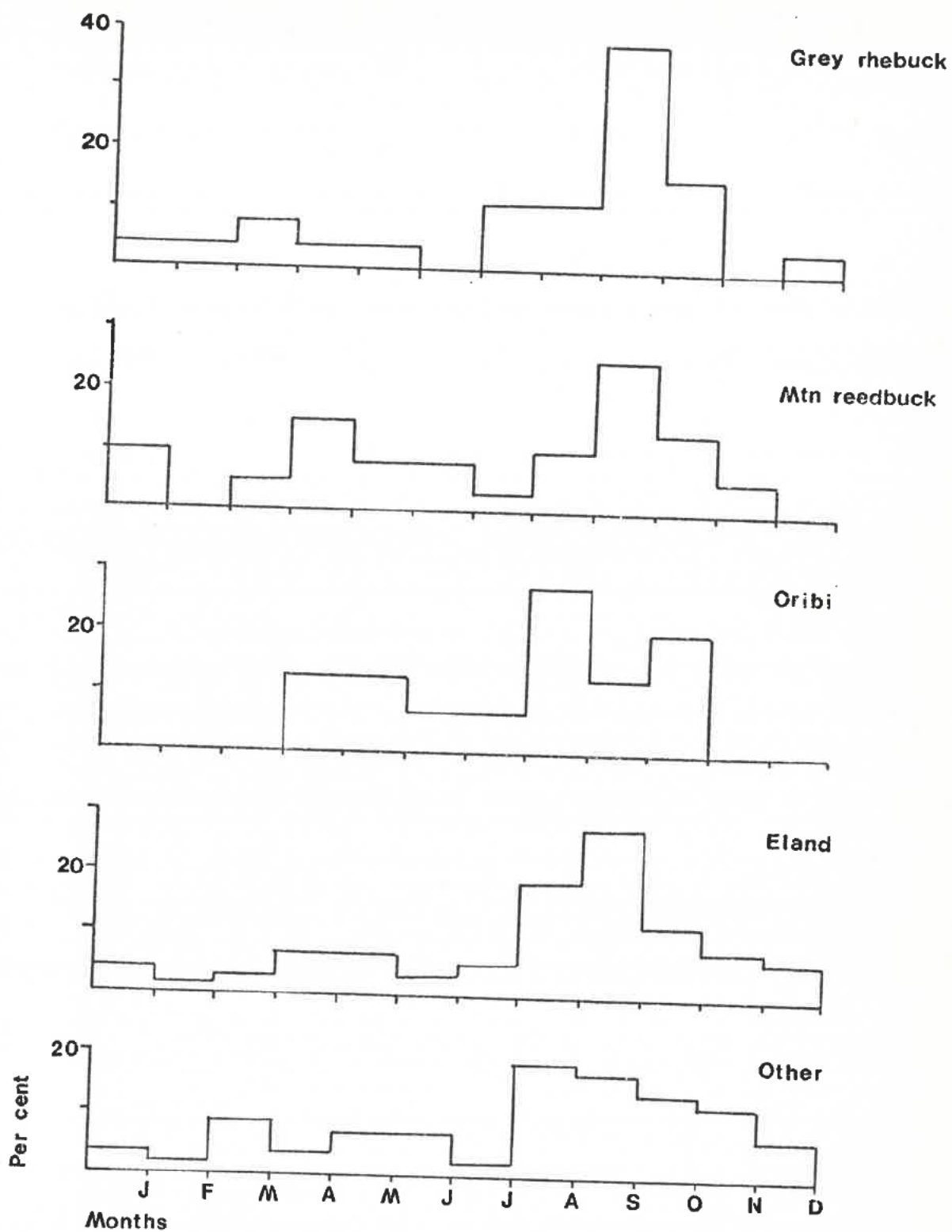


Figure 2.25 Monthly variation in the mortality of antelopes in GCGR, 1978 to 1980.

TABLE 2.17 Sex and age structure of deaths in four GCGR antelopes, 1978 to 1980.

Antelope	Adult			Immature*		
	Males	Females	Unsexed	Males	Females	Unsexed
Grey rhebuck	7	8	8	2	0	2
Mountain reedbuck	18	12	2	1	1	6
Oribi	9	3	2	1	0	0
Eland	23	24	22	15	9	38

* Animals < 1 y old in grey rhebuck, mountain reedbuck and oribi; but including yearlings in eland.

of the analyses of jackal faeces which indicate that these antelopes are not major items in the predator's diet (Table 3.4).

It has been assumed that GCGR antelope populations are stable (chapter on "Population trends") and recruitment has been estimated at ca 20 % (Table 2.14). Annual mortality must therefore be approximately equal to annual recruitment. Mortality records, however, do not equal theoretical mortality, being as low as 11 % of the expected for grey rhebuck and as high as 34 % for eland. These discrepancies can be attributed to the fact that it is impossible for the management staff who record the deaths to cover the entire reserve, and that the remains of antelopes, particularly those of the small species and very young animals, are consumed or removed before being found.

The numbers of recorded deaths for the different antelopes clearly do not reflect their proportions in GCGR. The proportions of grey rhebuck: mountain reedbuck:oribi in recorded deaths was 0,68:1:0,38; whereas proportions of the estimated population totals are 1:0,68:0,50. Both grey rhebuck and oribi are species which favour open habitats on the Little Berg, whereas mountain reedbuck occur mainly in the valleys. The chances of a carcase being completely consumed by vultures and the bones being taken by lammergeyers (Gypäetus barbatus) are far greater in an open situation than in steep valleys, which are not favoured by these birds (Brown, pers.comm.*).

The proportions of adult and immature mortality records amongst small antelopes are probably biased in favour of adults (Table 2.17), as the carcasses of the young of these species can be completely consumed or removed by scavengers. (There are two records of black eagle (Aquila verreauxi) picking up and flying off with the carcasses of infant grey rhebuck and mountain reedbuck.)

It is not possible to draw any reliable conclusions regarding the sex ratios of antelopes from the mortality records, other than to state that none of the ratios differed significantly from parity ($P > 0,05$). There is a high proportion of unsexed animals in the eland sample: often only bones or skulls were found and as both sexes have horns, the sex could not be determined.

* C.J. Brown, Dept of Zoology, University of Natal, Pietermaritzburg.

CONCLUSIONS

The Giant's Castle antelope study did not provide significantly new information on the population dynamics of grey rhebuck, mountain reedbuck, and oribi additional to that from a study done at Highmoor, also in the Drakensberg (Oliver et al. 1978), but does corroborate the findings of these authors. The more detailed analyses of the habitat preferences of these three antelopes in GCGR extends the basic information provided by Oliver et al. (1978), and in addition a better understanding of the co-existence of Drakensberg antelopes is provided by the inclusion of information collected on eland and blesbok, which were not studied by Oliver et al. (1978). Positive responses to recently-burnt veld by grey rhebuck, mountain reedbuck, and oribi were reported by Oliver et al. (1978) at Highmoor. Information collected in the Giant's Castle study supplements these findings, provides information on two additional species, and provides comparative data from burnt and unburnt veld during all months, which was not done at Highmoor.

The suggestions that winter malnutrition plays an important part in limiting antelope populations (Mentis 1978, Oliver et al. 1978) are confirmed by the findings of this study, the investigation of eland-vegetation interactions in GCGR (Scotcher 1982), and seasonal changes in herbage quality (Scotcher et al. 1980b).

The greatest value of the Gaint's Castle antelope study lies in the identification of the specific habitat preferences of all common species, the estimation of their population densities, the quantification of suitable habitat available to each, and the interpretation of the use of fire in providing herbage of suitable quality and growth stage. The findings on these aspects provide an understanding of reasons for the relative abundance of the antelopes, and coupled with consideration of marked seasonal variation in food quality, which is linked to climatic extremes, an understanding of the major population-limiting factors.

Sufficient data were collected on the five most common species (eland, grey rhebuck, mountain reedbuck, oribi, blesbok) to undertake detailed analyses of their distribution, habitat preferences, and responses to veld burning; to investigate population demography; and to consider possible population limiting factors.

Analysis of the habitat preferences of the remaining six antelopes (common reedbuck, grey duiker, bushbuck, klipspringer, and the introduced red hartebeest and black wildebeest) was not attempted beyond stating the

type of terrain and vegetation in which they occurred, as too few data were collected on them.

In GCGR eland display the widest usage of vegetation types and terrain, and are the least selective feeders, living on grass and browse. Although grey rhebuck, like eland, were associated with a wide range of physical characteristics of the environment, they do not use the full range of vegetation types and are selective feeders, taking only forbs. Mountain reedbuck, oribi, and blesbok displayed narrower usage of the terrain than did eland and grey rhebuck. Distribution in vegetation types was slightly broader in mountain reedbuck, which were recorded in grassland and open woodland, than was the case in oribi and blesbok, which were associated only with grassland, and furthermore each of these three antelopes practises a different degree of selective feeding, showing preferences for certain grass species, particular growth stages, or only certain portions of the plant (p 115). Population estimates indicate that eland, with the widest habitat tolerance in the reserve, are most abundant, followed by grey rhebuck, mountain reedbuck, oribi, and blesbok, occurring in the proportions of 39,2 %; 24,5 %; 16,5 %; 12,3 %; and 7,4 % respectively.

The numerical dominance of eland is further emphasised if relative size and energy consumption are taken into account, and the standing crop (metabolic biomass) of the antelopes is expressed in animal units (Mentis and Duke 1976). Percentages in the overall standing crop are then 83,5 % eland, 6,5 % grey rhebuck, 4,8 % mountain reedbuck, 3,5 % blesbok, and 1,6 % oribi.

The numbers and proportions of the five most abundant antelopes in Giant's Castle Game Reserve are closely correlated with and probably determined by the amount of suitable habitat and the degree of specialisation of the individual species. This is to be expected in a system where food, and in particular food quality, is the main factor limiting population size.

The eland population of GCGR has been estimated by total counts conducted from the air and on the ground (Scotcher 1982). Censusing grey rhebuck, mountain reedbuck, and oribi posed a number of problems as they are small and cryptic, widely dispersed, and respond to the observer by remaining hidden or taking flight at great distance.

The population estimates for grey rhebuck and mountain reedbuck, based on an index and control formula, with eland as the control, were similar to those obtained from total counts in earlier years (1962 - 1973). The coefficient of variation for estimated populations of these two antelopes fell

within acceptable limits lending support to the supposition that the estimates were reliable. Variation in estimates of the oribi population was greater. Comparison with the 1962 count indicated that numbers have possibly declined, but have since stabilised at a new level. It seems likely that grey rhebuck and mountain reedbuck populations have not declined since 1962. The apparent decline in the oribi population may have occurred as a result of a change from a policy of predominantly autumn burning prior to 1966 to one of spring burning. Oribi favour short herbage. On an autumn burn herbage growth is slower and there is therefore short vegetation for a longer period during the year than is the case on a spring burn (see page 54 and Fig 1.11).

An important limiting factor in using the index and control formula for population estimation in GCGR is that eland, the control species, are evenly distributed throughout the reserve only during mid-winter, therefore it is at this time of year that estimates must be made. Winter or early spring peaks were recorded in the number of mountain reedbuck and oribi counted along transects, but this was not the case with grey rhebuck. It is therefore concluded that the estimates of mountain reedbuck and oribi might be slightly exaggerated while those of grey rhebuck are likely to be more reliable. Nevertheless, a long term monitoring programme employing the same fixed counting routes will serve the purpose of indicating population trends, and show whether these assumptions hold.

The density of eland, which concentrate on the recently-burnt grasslands of the Little Berg during summer and disperse throughout the reserve during winter, is calculated as 1/56 ha for the entire reserve. Estimates were made of suitable grey rhebuck, mountain reedbuck and oribi habitat. The approximate ecological densities of these three species are 1 grey rhebuck/57 ha, 1 mountain reedbuck/32 ha, and 1 oribi/33 ha in suitable habitat. Although much smaller in size than eland, grey rhebuck occur at similar density. The most likely explanation is that whereas eland are mixed feeders taking a wide variety of grasses and browse plants, grey rhebuck feed selectively on forbs only.

The total antelope standing crop of 1 AU/52 ha for GCGR appears to be low when compared with potential carrying capacities for domestic livestock in similar areas. Important considerations in the game reserve situation, however, are that agriculturalists' figures are proposed for cattle during the grazing season only, and under a system of rotational grazing. Furthermore, whereas cattle are bulk feeders, the antelope dealt with in this study all display varying degrees of selectivity in their feeding. The antelope,

particularly during winter, will need to feed selectively to obtain sufficient, nutritious, easily digestible food. As the overall standing crop at GCGR was found to be similar to that in Royal Natal National Park (1 AU/60 ha), another Drakensberg game reserve in which there are no eland and in which the other antelopes occur in different proportions from those in GCGR, it is concluded that the antelope carrying capacity in the Drakensberg is ca 1 AU/50 ha.

All five of the antelopes studied showed positive responses to the effects of fire, preferring burnt to unburnt veld. Reasons for preferring burnt veld are presumably because of its higher nutritional value and because the green living material is more exposed and available, and not combined with dry grass which is high in fibre and low in crude protein content.

The preferences of the selective grazers, mountain reedbuck and oribi, for recently-burnt veld were more obvious than those of grey rhebuck, a selective forb eater. It is probably not as difficult to locate a green forb in unburnt veld as is the task of locating the green portions of grasses amongst dry material. The blesbok, an unselective grazer as far as grass species are concerned, but selective for stage of growth, also showed a marked preference for recent burns. Whereas the other four antelopes responded immediately to new growth on burns, the responses of eland took place later. The reason appears to lie in the ability of the smaller antelopes to feed on shorter grass shoots.

In GCGR observations on grey rhebuck, mountain reedbuck, blesbok, and eland produced results in agreement with Jarman's (1974) social organisation of antelopes in relation to their ecology in which he categorised antelopes in classes based on body size, food, feeding style, and social organisation. The only exception is the oribi, which in GCGR fits better in class A than in class B as categorised by Jarman (1974). Reasons for considering the species better placed in class A are: the oribi is a small antelope (10 - 16 kg) in which females may be larger than males (Viljoen 1975), whereas class B antelopes are larger (25 - 55 kg) and females are smaller than the males; The species feeds mainly on grasses and also takes forbs, but being highly selective for plant species and parts (Viljoen 1975), whereas class B antelopes are either selective grazers or selective browsers; and oribi occur predominantly in pairs with a population sex ratio of 1 : 1, whereas class B antelopes occur in groups of one adult male and several adult females, and the population sex ratio is in favour of females.

Jarman's (1974) main reason for placing oribi in class B appears to be

based on group size - his records indicate an average of approximately two adult females per male. In southern Africa, however, the species occurs in pairs (Tinley 1971, Viljoen 1975, this study), and the larger groups reported by Jarman (1974) from further north in Africa may be the result of different (possibly more suitable) habitat. Jarman (1974) noted, for example, that in very favourable habitat klipspringer, which he placed in class A, formed groups resembling those in class B.

Of the five antelopes studied the oribi was the only species in which the sex ratio was 1 : 1, and in the other four antelopes there was a significant preponderance of females. Consideration of the social organisation of the antelopes offers a likely explanation.

The oribi is a small antelope which feeds very selectively and therefore needs to be widely dispersed. For a highly selective feeder to be able to obtain sufficient food the species needs to exist singly or in pairs (Jarman 1974). In such non-herd-forming antelopes greatest productivity is achieved by a 1 : 1 sex ratio. In eland, grey rhebuck, mountain reedbuck and blesbok herds are formed in which one male serves a number of females. Non-territorial or subordinate males live under social stress and in less suitable habitat, therefore being more likely to succumb than females under unfavourable conditions. The preponderance of females therefore ensures maximum productivity in these species.

Mountain reedbuck was the only species in which calving was recorded throughout the year, although there appeared to be a summer peak. In both grey rhebuck and oribi calving extended over spring and summer, whereas in eland and blesbok it was limited to a short period during spring. In the very selective feeders (mountain reedbuck, grey rhebuck, and oribi) an extended breeding season probably spreads the increased nutritional demands of the pregnant or lactating females on the vegetation over a longer period. In eland and blesbok, which feed less selectively, the breeding season is much shorter, because in these two species food availability is not as limiting a factor as in the selective feeders. The calving peak in blesbok is, furthermore, typical of plains species and is believed to have evolved as a means of forming a glut of calves and therefore reducing the effect of predation on the population as a whole. Lying-out behaviour is not practised, as is done by the young of grey rhebuck, mountain reedbuck, and oribi; but the young are capable of running almost as fast as the adults within a few days of being born, therefore reducing the vulnerable period.

The adult : immature (< 1 y-old animals) ratios were similar in all five antelopes. In eland calf mortality during the first year has been es-

established as 66 % (Scotcher 1982), and as the adult : immature ratios in the other four antelopes were similar to the ratio in eland, it is presumed that calf mortality is similar to that in eland. Jackals were alleged to prey heavily on the young of the small antelope species but not on young eland. The similar adult : immature ratios of all species, however, do not lend support to the allegation of heavy jackal predation. If there are major differences in the longevity of eland and the other antelopes this argument may be considered invalid. Unfortunately little is known of their life-spans in the wild, and the only comparative information, which does not indicate great differences, is derived from animals in zoos (Mentis 1972).

Of the 275 antelope deaths recorded during this study 55 % occurred during the months of August to October. From May to September mean daily minimum temperatures at grass level remain below breezing point, and following the sharp drop in temperature and first frosts during May, nutritional content of the herbage remains low throughout the winter. The critically low quality of the food over a period of four or five months, and the harsh climatic conditions prevailing at this time, appear to be major reasons for the high number of deaths at the end of winter and early spring.

Finally, antelope populations in GCGR appear to be stable. Numbers of the species considered in this study are limited by the amount of suitable habitat and food quality, which is linked with the severe winter climate. Predation by the black-backed jackal, the most common mammalian predator, is not considered to be a major limiting factor. Evidence further supporting this statement will be given in Part 3.

At the same time that my antelope study was being conducted at GCGR, Scotcher (1982) undertook a detailed investigation of the eland population in the game reserve. Aspects investigated by Scotcher (1982) were eland-vegetation interactions, age and sex structure of the population, seasonal physiological condition, conception rate, recruitment, and mortality. Some of the findings of his study were that the conception rate amongst adult females was high, but that the mortality rate, particularly amongst calves and yearlings, was also high, mainly during late winter and early spring. At this time of year, which coincided with the period of poorest food quality and the most adverse weather conditions, physiological condition was also lowest. Scotcher (1982) concluded, similarly, that the eland population was stable and that the most important population-limiting factor was food quality and availability at the most critical time of the year.

PART 3 : BLACK-BACKED JACKAL

METHODS

COLLECTION OF POPULATION DATA

All jackals seen in GCGR during the study period were recorded. Data on sexes, mass, and approximate ages of animals were obtained from 350 jackals which were killed in the Drakensberg by Natal Parks Board foxhounds between 1962 and 1971, and from material collected during this study (jackals which were trapped, shot, run over by vehicles, or killed by coyote getters).

Approximate ages of young jackals were determined from tooth eruption sequences (Lombaard 1971) and body mass (Butynski 1975, Lombaard 1971).

MOVEMENTS, HOME RANGE, AND DENSITY

Jackals were captured in padded steel-jawed foot traps (Rowe-Rowe and Green 1981), immobilised with ketamine hydrochloride or ketamine in combination with acetylpromazine (Rowe-Rowe and Green 1980), and fitted with collars to which a radio transmitter and battery pack were attached. Details concerning capture and immobilisation are given in Appendices 5 and 6.

Ultra high frequency (UHF) telemetry equipment operating on 403.1 MHz was used. The receiver and tracking antennae were obtained commercially (Microlink, Frankston, Victoria, Australia) and transmitters were made privately. Technical details of the UHF system have been given by Newgrain and Horwitz (1979).

UHF equipment was selected for the GCGR study in preference to other commercially available systems which operate on lower frequencies, because of the small tracking antenna (360 x 400 mm) and the reputedly good ranges achieved (Lawson *et al.* 1976). For use in the mountainous study area in which there are few roads, portability of equipment was a prime consideration.

Initially line of sight range of the equipment was 3 to 4 km, but this was increased to at least 12 km by connecting a wide-band television mast-head amplifier between antenna and receiver. A slightly larger (390 x 650 mm) antenna with six directors was also used, but did not prove to be more accurate than the smaller model which had two directors.

Collared jackals were radio-tracked from various high points in the reserve, which were reached by vehicle or on foot. Each relocation was

obtained by triangulation, based on at least two bearings. When a jackal could not be tracked from the ground a light aircraft was used to fly over the game reserve and surrounding areas. If a signal was picked up the jackal's position was pin-pointed by dropping in altitude and flying in ever-decreasing circles. The small size of the tracking antenna made it possible to hold it in the cabin of the aeroplane.

Home range sizes were calculated using the "minimum home range" method (Mohr 1947). Estimations of jackal density were based on number of animals trapped, home range size, and social organisation.

DIET

The contents of eight jackal stomachs collected in GCGR during the study period were examined. Faeces were collected throughout the game reserve during all months. Altogether 477 samples were examined. Each scat was soaked in water until soft, then macerated and sieved under running water. Small mammals were identified mainly from jaws and other mammals from hair colour. In instances of doubt antelope hair was examined microscopically, using the methods of slide preparation outlined by Brunner and Coman (1974), and identified from scale pattern and cross-section. Detailed examination was not attempted on remains of other taxa, which were generally not identified beyond the level of class or order.

Occurrence of items was recorded and data were evaluated in terms of relative per cent occurrence. Relative percentages were calculated by totaling all occurrences and expressing actual occurrence of each item as a percentage of the total occurrences. Relative per cent occurrence was selected as it has been shown that in the analysis of large numbers of scats this method gives results which closely approximate the proportions of different items actually consumed (Erlinge 1968, Rowe-Rowe 1977b, Scott 1941).

DISTRIBUTION

Black-backed jackals have been recorded throughout GCGR in all vegetation types and over the full altitudinal range of the reserve.

Sight record data do not indicate differential utilisation of recently-burnt and unburnt areas. Information collected on some of the radio-tracked jackals has shown that if an animal's home range includes recently-burnt and older veld, it might continue to return to the burnt area during periods of inactivity if its normal lying-up place happens to be there, but most periods of activity are spent in the unburnt area. Differences in habitat utilisation became less marked within 5 to 6 mo after burning and are probably related to availability of small mammals, which form the bulk of the jackal's diet (see chapter on "Diet"). Details of jackal movements will be given in the chapter on "Home range".

POPULATION DYNAMICS

SEX RATIO

In the trapped sample the sex ratio was 7 males:8 females. Of the 15 incidentally collected jackals, four were unsexed and the remainder consisted of 5 males:6 females.

The sex ratios of these small samples do not differ significantly from parity, but in the sample killed by hounds, in which 331 animals were sexed, males outnumbered females by 191:140 and the 1,36:1 sex ratio differs significantly from parity (Chi-square 7,86; $P < 0,01$). Between 1964 and 1971 jackals killed were classified as adult or immature, i.e. < 1 y old (see "Population structure"). The adult ratio of 1,43:1 (96 males:67 females) differed significantly from parity ($P < 0,05$), but in immature jackals the sample of 26 males:29 females did not.

Jackals were killed by hounds on Drakensberg farms, in GCGR, and in other Natal Parks Board and Forestry Department game sanctuaries. The sex ratio of the GCGR sample (69 males:58 females) and that from other reserves (52 males:44 females) did not differ significantly from parity, but in the sample from farms (70 males:38 females) the preponderance of males is significant ($P < 0,01$).

Bigalke and Rowe-Rowe (1969) suggested, after finding a significant preponderance of males in hound-killed jackals from the Drakensberg, that females were more difficult to capture than were males, particularly during the period when they were caring for young. Statistical analyses of monthly samples do not indicate significant differences, however. Bigalke and Rowe-Rowe (1969) did not separately consider the sex ratios of jackals killed in reserves and those killed on farms. The preponderance of males killed on farms possibly results from the method of hunting and the behaviour of the jackal: hunts on farms usually started at a sheep lamb killed by a jackal, where the hounds were set on to the jackal's scent. An alternative explanation for the preponderance of males killed may therefore be that jackal males tend to kill more sheep than do females.

On farmland in Transvaal the sex ratio of jackals killed by coyote getters was 1,20:1 (151 males:126 females) which does not differ significantly from parity (Bothma 1971a), further suggesting that hunting with hounds on farms results in a biased sample.

GROUP SIZE

During the study period 872 sightings of jackals were recorded. Mean group size was 1,25. Most sightings (677; 78 %) were of single animals, 170 (19 %) were of two, 23 (3 %) were of three, and two groups of four were seen.

Mean group sizes were smallest during July to October (1,12 to 1,18) and greatest from November to February (1,26 to 1,40). Analysis of variance of the data indicated that the decline in mean group size during the second half of the year was significant ($P < 0,05$; df 6 and 497; F 2,65), but means during the first half did not differ significantly ($P > 0,05$).

Seasonal variation was also observed in the number of single animals, twos, and groups of three or more (Fig 3.1). The monthly differences were statistically significant for groups of two only (Chi-square 35,89; $P < 0,001$; 11 df) but nevertheless followed a pattern which was related to reproduction and social behaviour. Mated adult jackals often hunt in pairs (Ferguson 1980, Lamprecht 1978). Most young jackals in the Drakensberg are born during July (Rowe-Rowe 1978a, this study) and as one of the parents (particularly the female during the suckling stage) would be caring for the young, fewer adult pairs and more single animals can be expected to be seen from July onwards. Furthermore, when an adult female jackal has a litter, immature animals from the previous litter may remain as helpers (Moehlman 1979) or become independent lone sub-adults (this study), therefore increasing the number of single animals. Even those jackals that remain as helpers would be solitary, as sub-adults and unmated subordinate adults do not hunt in pairs (Ferguson 1980, Lamprecht 1978).

Young jackals begin to forage with the adult female, or both parents, at the age of 14 weeks (Moehlman 1980), therefore most groups of three or more can be expected from November onwards.

Seasonal differences in jackal group sizes have not previously been related to social organisation and reproduction.

Ferguson (1980) reported mean summer and winter group sizes of 1,2 and 1,3 respectively in black-backed jackals in Kalahari Gemsbok National Park, with no significant differences between seasons. In a study on coyotes (*Canis latrans*), which have a similar social organisation to that of black-backed jackals, Bekoff and Wells (1980) recorded mean group sizes of 1,3 during summer and 1,8 during winter. These authors attributed the variation to differences in available food - during summer the coyotes lived chiefly on rodents, but mainly carrion was taken during winter, and the clumped food resources appeared to result in larger groups. This was not observed in

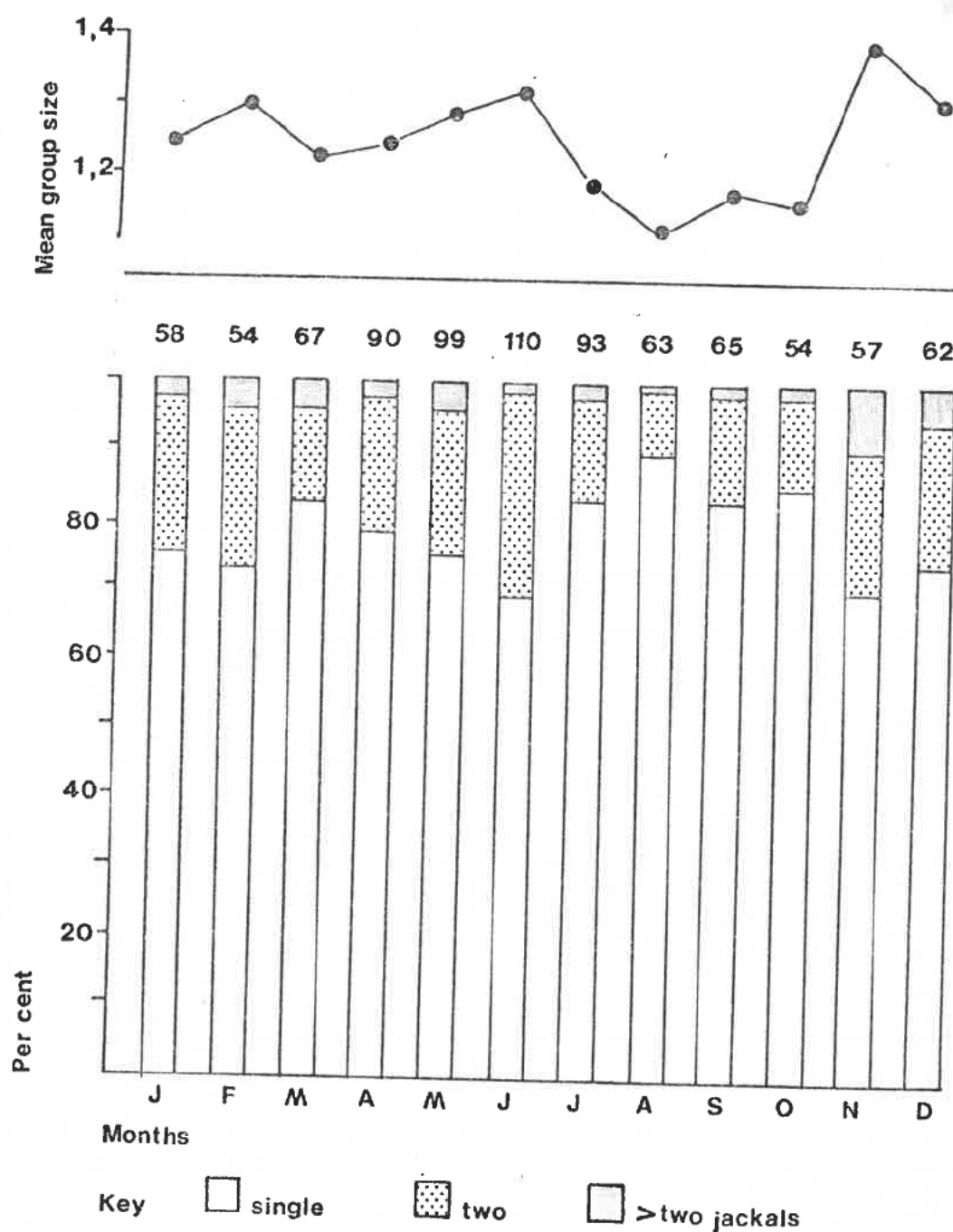


Figure 3.1 Mean monthly group size of jackals (upper graph), and percentage of groups of one, two and more than two (histogram). Monthly sample sizes are given above the histogram.

GCGR, where carrion does not lie long enough to attract large numbers of jackals over a long period of time (see "Diet").

POPULATION STRUCTURE

All jackals captured were classified as immature (< 1 y old), sub-adult (1 to 2 y old) or adult (> 2 y old). Age class categorisation was based on the amount of wear on the incisors (Lombaard 1971). Of the 15 jackals trapped two were classified as immature, four as sub-adult, and nine as adult. Two of the five adult females were parous.

The ages of the 15 incidentally killed jackals could be more accurately determined from the skulls, following Lombaard (1971). The numbers of jackals in each age class were: < 1 y (1), 1 to 2 y (3), 2 to 3 y (4), 3 to 4 y (4), 4 to 5 y (2), and > 7 y (1).

In the overall sample of 30 jackals broad age class categorisation was therefore three immature (10 %), seven sub-adult (23 %), and 20 adult (67 %).

Between 1964 and 1971 jackals killed by hounds were classified by hunters in the field as < 6 mo old if they did not have a full complement of teeth, 6 to 12 mo old if they had a full complement of teeth but there was no wear on the upper incisors, and as adults (i.e. > 1 y old) if the teeth were worn. Most < 6 mo-old animals were killed between October and December and most 6 to 12 mo-old jackals between January and March (Fig 3.2). Very few jackals were killed in the dry months of May to August as hounds had difficulty in following jackal scent in dry conditions (Bigalke and Rowe-Rowe 1969), so inadequate samples are available for this period, but at the same time a sampling bias in favour of adults was avoided: young are born from June to September (see "Reproduction"), and they remain in the vicinity of the den until about 14 weeks old.

In the 1964 - 1971 hound-killed sample there were 162 jackals > 1 y old, 58 < 1 y old, and 46 were unclassified. Eighty-one of the classified animals (67 > 1 y old and 14 < 1 y old) were killed on farms and the remaining 139 in GCGR and other Drakensberg reserves. The reserves sample was made up of 95 > 1 y old jackals (53 males:42 females) and 44 < 1 y old.

The 42 > 1 y-old females would have included a number of non-breeding animals. Although jackals are physiologically capable of breeding by the end of their second year (Smith, pers.comm.*), Ferguson (1980) stated that they probably do not breed before the end of their third year. There are insufficient data on Drakensberg jackal populations to enable an accurate

* L. Smith, National Zoological Gardens, Pretoria.



Figure 3.2 Percentage of jackals killed by hounds, classified as < 6 mo old, 6 to 12 mo old, and > 1 y old.

estimate to be made of the percentage > 3 y-old jackals, but if it is assumed that approximately 33 % to 50 % fall into this age class, then the proportion of breeding females : < 1 y-old animals would be 1 : 3 or 1 : 2. The number of young animals in the sample may, however, be exaggerated, as it is possible that young and inexperienced jackals were more easily caught by hound.

Lensing (1972) compiled life tables from two samples of 164 and 136 jackals killed in Transvaal, and estimated that approximately 31 % of the population was > 3 y old. Of the 23 jackals trapped by Ferguson (1980) in the Transvaal a similar number (39 %) were > 3 y old and 17 % were < 1 y old.

REPRODUCTION

Ages of 10 young jackals which did not yet have a full complement of teeth (i.e. < 6 mo old) were determined from tooth eruption (Lombaard 1971) and body mass (Butynski 1975, Lombaard 1971). There was a high correlation ($r = 0,96$; $P < 0,001$) between ages determined by the two criteria, therefore it was decided to also estimate the ages of all other < 6 mo-old jackals for which body mass figures but no skulls were available, and to calculate approximate month of birth. The histogram indicating approximate months of birth (Fig 3.3) is therefore compiled from data obtained from the skulls of 10 animals, the mass of 57 jackals killed by hounds, and the mass of an additional three animals.

The data indicate a distinct breeding season with 81 % of the births between June and August.

Five pregnant females were collected between July and October. Three contained five fetuses each and the other two contained four and eight respectively. Two litters of six were dug out of dens during September. Mean litter size calculated from these figures is 5,6. Pup survival in Drakensberg reserves is estimated at approximately two/litter, based on the adult : young ratio and composition of groups sighted.

Parturition in jackals elsewhere, although not reported for the same months as in the Drakensberg, also takes place during the dry season or at the end of it (Fairall 1968, Smithers 1971, Stuart 1981, Wyman 1967). It is at this time of year that most carrion is available in the Drakensberg (Mentis 1978, this study). Litter sizes in the Drakensberg are slightly larger than those recorded in the Cape Province ($\bar{x} = 4$, Stuart 1981) and similar to those recorded in Serengeti (Moehlman 1979, Wyman 1967). Estimated pup survival is also similar to that in Serengeti where Moehlman (1979) recorded a mean of 2,8 survivors/litter, but lower than the three or four

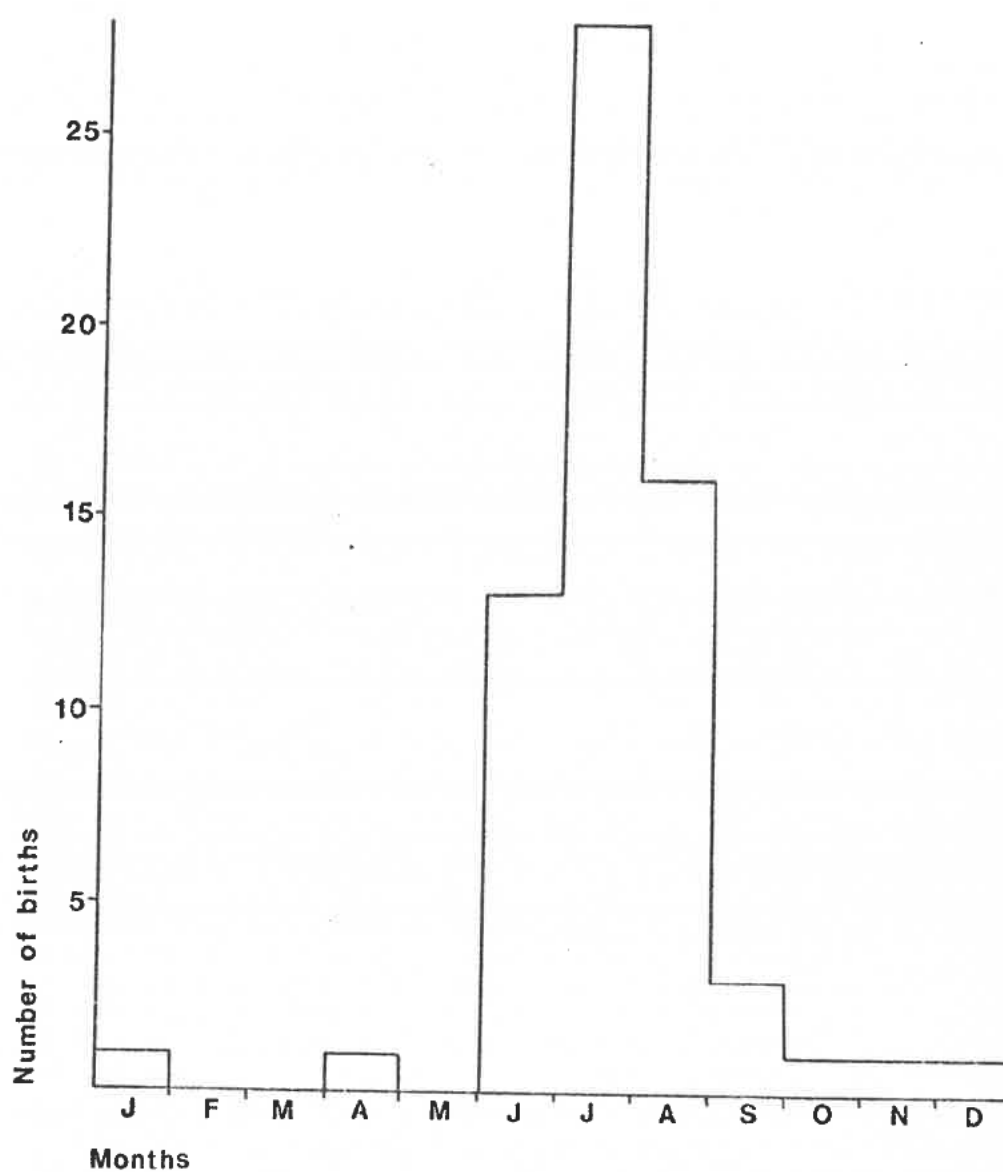


Figure 3.3 Approximate month of birth of 70 young black-backed jackals collected in the Drakensberg (incorporating data from Rowe-Rowe 1978a).

survivors/litter estimated by Wyman (1967). In a highveld area of the Transvaal Ferguson (pers. comm.)* estimated a similar survival rate to that recorded in the Drakensberg.

Moehlman (1979) found that most deaths in jackal litters took place before the pups were 14 weeks old, and that chances of pup survival increased if yearlings remained with the adults to help in providing food. Survival beyond the 14 week-old stage is therefore clearly related to nutrition during the early stages of the pups' life.

* J.W.H. Ferguson, S.A. Lombaard Nature Reserve, Bloemhof.

MEASUREMENTS

The addition of recently-collected information to existing data (Rowe-Rowe 1978a) did not change the mean mass of > 1 y-old male and female jackals. Mean male mass is 8,4 kg ($n = 140$; range 6,4 - 11,4; SE 0,08) and mean female mass is 7,7 kg ($n = 92$; range 5,9 - 10,0; SE 0,08). Males are significantly larger than females ($P < 0,001$; $t 6,13$; $df 230$).

Most males have body mass between 7,5 and 9,5 kg and most females fall between 7,0 and 8,5 kg (Fig 3.4).

A much smaller sample of other body measurements was available (Table 3.1), but in these too, males were clearly larger than females in all parameters.

Sexual size dimorphism has been reported from jackal populations in the Transvaal and Botswana (Bothma 1971a, Rautenbach 1978a, Smithers 1971). The mean mass of Transvaal jackals is very similar to that of the Drakensberg sample, but the Botswana animals are about 800 g lighter.

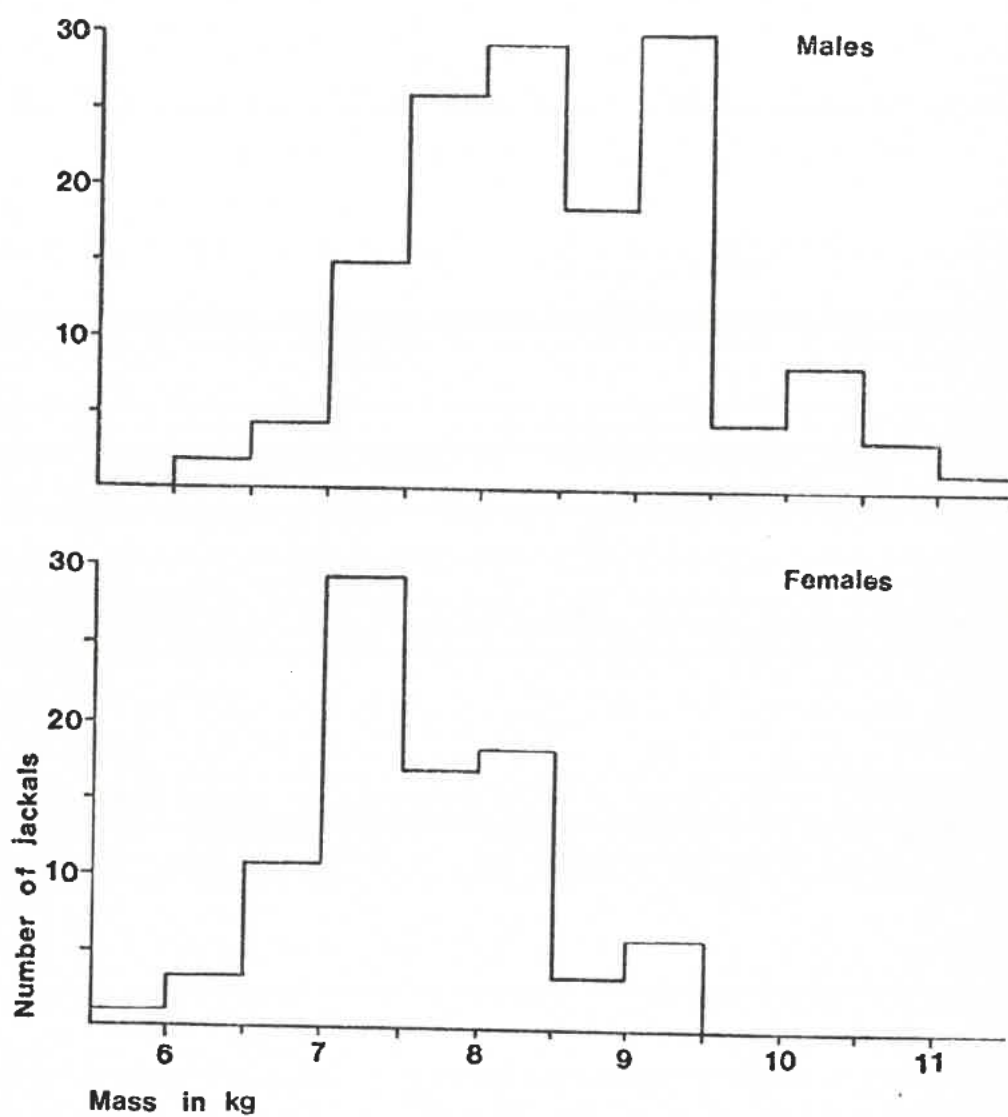


Figure 3.4 Frequency distribution of black-backed jackal mass, in 0,5 kg divisions.

TABLE 3.1 Measurements of > 1 y-old black-backed jackals collected in the Drakensberg.

	\bar{x}	SE	Range	N
Males				
Head and body	751 mm	18,2	711 - 812 mm	5
Tail	319	5,1	305 - 330	5
Hind foot	163	-	152 - 170	4
Ear	109	-	102 - 114	4
Mass	8,8 kg	0,15	8,3 - 9,1 kg	5
Females				
Head and body	693 mm	9,2	673 - 720 mm	6
Tail	302	8,4	267 - 318	6
Hind foot	156	2,2	152 - 165	6
Ear	106	3,1	96 - 114	6
Mass	7,5 kg	0,36	6,6 - 9,1 kg	6

HOME RANGE, MOVEMENTS, AND DENSITY

HOME RANGES

Twelve of the 15 jackals trapped were fitted with collars and radio transmitters (Table 3.2). Two animals died from overdoses of anaesthetic (Rowe-Rowe and Green 1980) and one was marked with a coloured collar but not fitted with a transmitter. Sufficient data were collected on the movements of nine of the radio marked jackals to plot home ranges (Fig 3.5).

The patterns and significance of the home ranges illustrated in Figure 3.5 are meaningless unless the age classes, sexes, and social organisation of the jackals are considered. It became obvious after studying the movements of the different animals that three basic groups (A, B, and C) were being dealt with, and that these groups occupied three discrete areas. Two additional jackals captured appeared to belong to other groups. The home ranges and movements of the jackals in each group will be dealt with separately.

Group A

When captured at the end of September ad female A was thin-haired around her enlarged nipples, but was not lactating. Ad male A, captured 15 days later, may have been her mate, as he was once relocated at the same time that she was at her most regularly-used lying-up place, and they had partially overlapping home ranges.

Two young animals were estimated to be 1 y old, and were classified as sub-adults (see "Population structure"), as they would have been starting their second year, assuming that they were born during the previous July or August. Sub-ad female A was tracked for three weeks, then she succeeded in discarding her collar which had been improperly riveted at the join. Five of the six relocations of this animal were within the adults' home range (Fig 3.6).

Sub-ad male A was relocated two days after his capture, but never again, despite exhaustive aerial searches in the game reserve and surrounding areas. Transmitter or early battery failure was suspected. Thirteen months later sub-ad male A's collar was picked up on a well-used jeep track within the group's home range, 2 km from his point of capture (Fig 3.6).

No immature animals were caught, but as trapping was done in this area from 25 September to 15 October, it is unlikely that jackals from that year's breeding would have been in the trappable population.

TABLE 3.2 Details of black-backed jackals captured and radio-tracked in GCGR.

Group	Jackal	Home range km ²	Weeks tracked	Total relocations	Remarks
A	Ad male A	20,5	5	8	
	Ad female A	17,8	28	53	
	Sub-ad male A	-	-	3	Battery failure
	Sub-ad female A	4,0	3	6	Discarded collar
B	Ad male B	21,5	12	54	
	Ad female B	16,5	4	28	
	Imm male B -	9,0	11	22	
	Sub-ad male B	33,0	8	27	
	Imm female B	8,5	14	6	Weak transmitter signal
C	Ad male C	-	-	-	Died
	Ad female C1	-	-	-	Died
	Ad female C2	25,0	5	11	Disturbed - see text
	Sub-ad female C	18,5	51	40	Final home range
	Sub-ad male C	32,8	43	48	
		-	-	-	Marked - no transmit- ter
D	Ad female D	-	1	2	
E	Ad male E	6,0 + ?	5	5	Very broken terrain - difficult to track

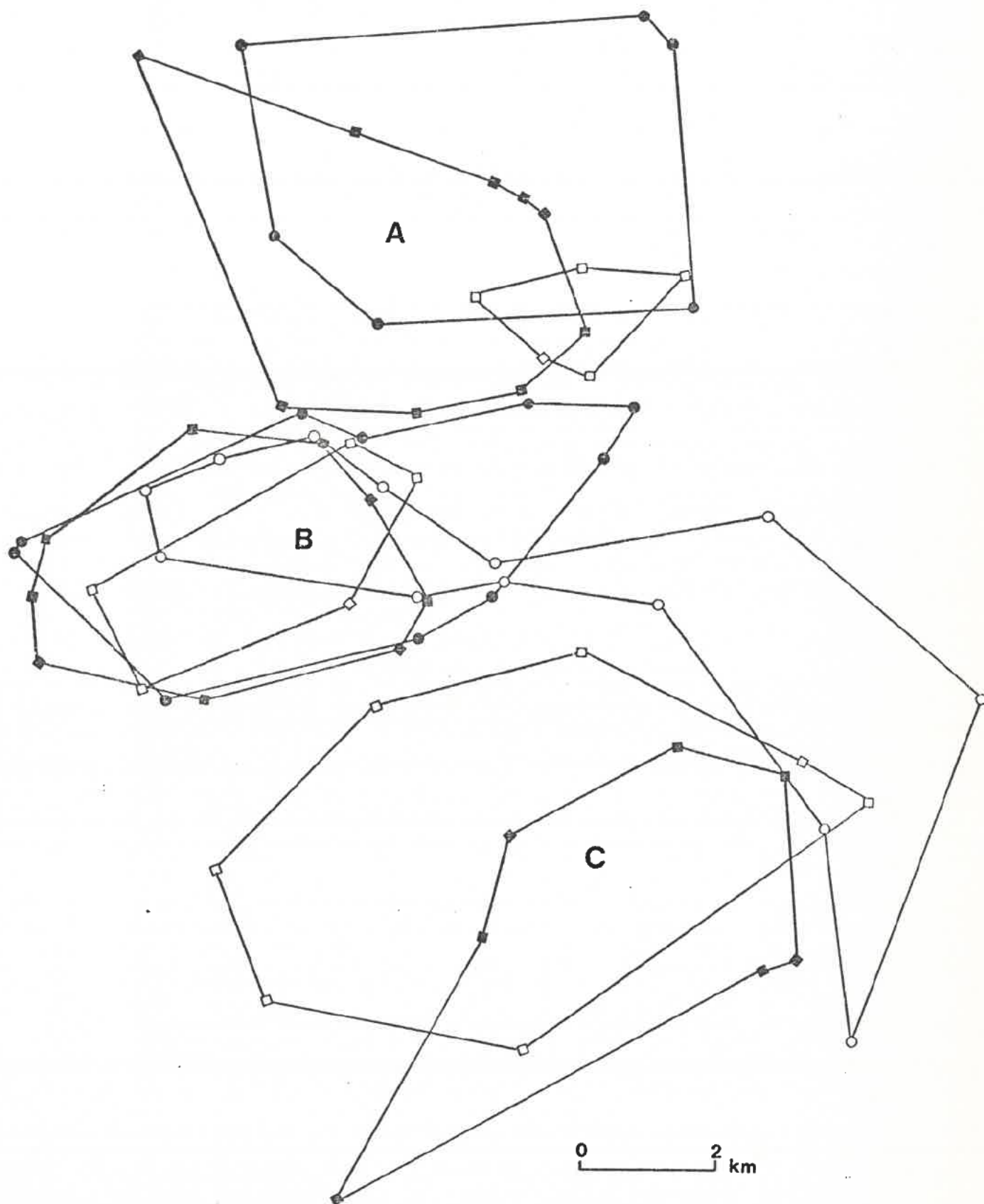


Figure 3.5 Home ranges of three groups of black-backed jackals in GCGR.

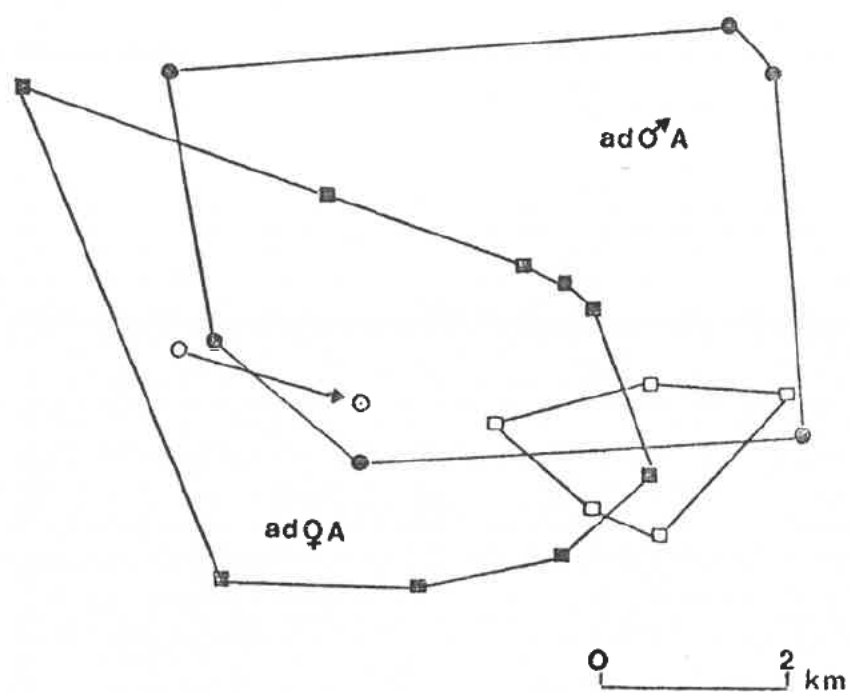


Figure 3.6 The home ranges of ad female A \blacksquare — \blacksquare , ad male A \bullet — \bullet , sub-ad female A \square — \square and the capture site and point at which sub-ad male A's collar was found \circ — \circ .

At least two unmarked jackals, one of which appeared to be an adult, were seen in ad female A's home range.

Group B

Two adults were presumed to have been a mated pair. Each had three lying-up places, two of which were shared. There was almost complete home range overlap, that of ad female B lying within the male's and smaller by 5 km².

Two immature jackals, estimated to be 8 mo old when caught, had home ranges of 8.5 and 9 km² within the adults' range (Fig 3.7). They too were relocated at one of the lying-up places shared by the adults.

The transmitter fitted to imm female B was not well-tuned to the receiver. Signal strength was therefore weak and could be picked up only when 2 to 3 km away, but the six relocations were recorded over a period of 14 weeks.

Initially imm male B had a home range of 9 km². During June, when he would have been approaching the age of 1 y, he left group B's area (Fig 3.8), moved to the east and south-east for a month, then returned to his old home range. At this stage the transmitter stopped working. The extended home range was 33 km².

No sub-adults were captured in group B's range, but at least one other unmarked jackal was known to be in the area.

Group C

The boundaries of area C were based on the movements of ad female C2 and sub-ad female C. On the same day that the non-parous ad female C2 was caught, non-parous ad female C1 was also trapped, and two days later ad male C was captured. Both ad female C1 and ad male C were accidentally killed by overdoses of ketamine. These animals are assumed to have belonged to group C, but may have been adults from the north (Fig 3.9). Sub-ad male C, captured within the area, may also have belonged to group C. It is less certain whether ad female D, captured at the edge of area C, belonged to group C or another group.

When ad female C2 was caught she was injected with radio-active sodium and radio-active water. The intention was to recapture or relocate and shoot the animal after two to six weeks, then extract blood to determine food and water turnover (Green 1978). During the initial five weeks when ad female C2 was disturbed by these hunting activities she moved as far as 9 km north of her capture point (Fig 3.10) and her home range covered an area of 25 km².

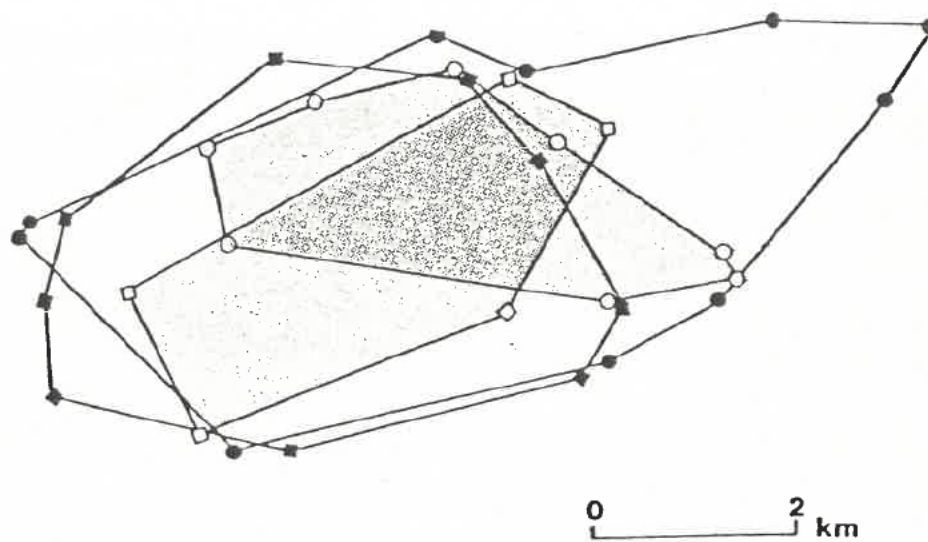


Figure 3.7 Home ranges of the jackals in group B: ad male B ●—●, ad female B ■—■, imm male B ○—○, and imm female B □—□. The immature jackals' home ranges, falling within the adults', are shaded.

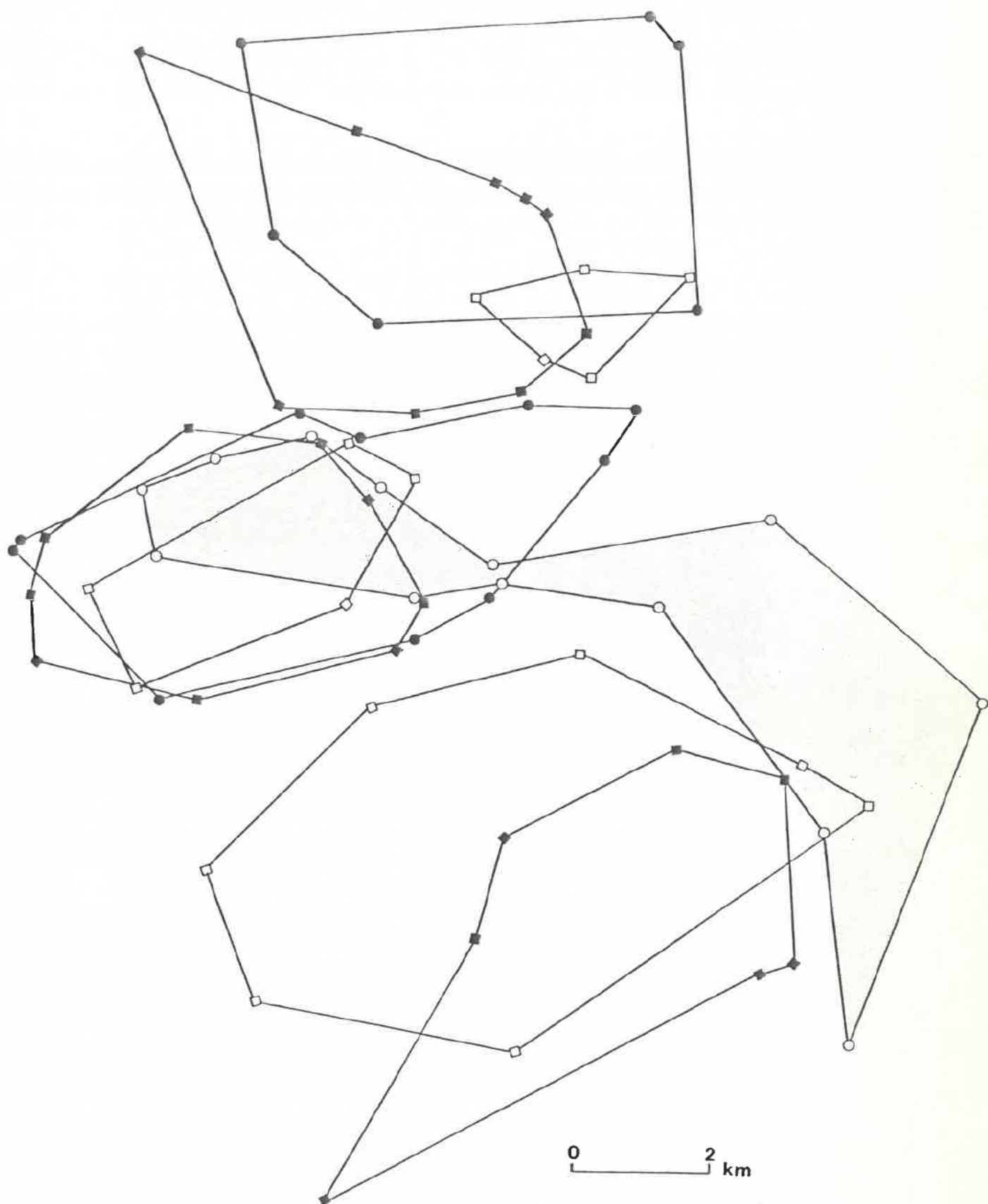


Figure 3.8 The home range (shaded) of sub-ad male B.

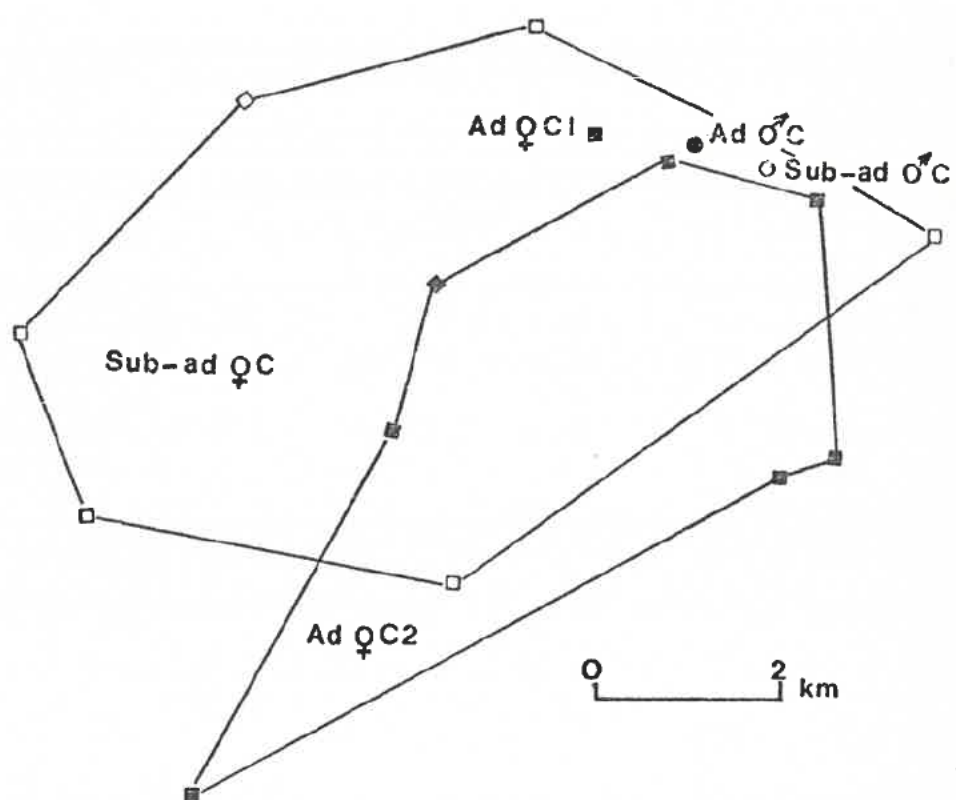


Figure 3.9 The home ranges of ad female C2, sub-ad female C, and the capture sites of three other jackals in area C.

When no more attempts were made to shoot her, she returned to the area in which trapped and occupied a home range of 18,5 km² until the transmitter stopped functioning 51 weeks later.

Sub-ad female C was trapped five months after ad female C2 returned to area C. For the next 26 weeks, during which the transmitter of ad female C2 also continued to function, sub-ad female C's home range overlapped that of the adult female (Fig 3.9) and extended to the west of it, having an area of 32,8 km².

Sub-ad male C, marked with a coloured collar and not fitted with a transmitter, was never seen again.

At least one other unmarked jackal, which appeared to be adult, was known to be in the area.

Jackal D

Ad female D was trapped at the edge of area C, and relocated once in area C two days later, then north of the area a week later. Thereafter no more signals were picked up. It was suspected that the wires connecting the transmitter and battery pack had broken, as the transmitter was one previously used on a lion and a new battery pack had had to be fitted.

Jackal E

Ad male E was trapped near the edge of ad male A's home range, then immediately moved to an area 9 km north-west of the capture point (Fig 3.11). The terrain was very broken and locating the animal on foot proved impossible. During the five weeks that the transmitter functioned the jackal was relocated four times from the air. All of these relocations were in the early morning, therefore the animal was probably close to its lying-up sites. Twelve months later the collar was found near the game reserve boundary, having come apart at the leather/polycarbonate transmitter case joint.

HOME RANGE SIZES

The mean home range size of all jackals, excluding adult male E, and considering the home ranges of imm male B and sub-ad male B separately, was 18,4 km² (N = 10, SE 3,04). Mean adult home range size (excluding ad male E) was 19,0 km². The home ranges of the two adult males (\bar{x} 21,0 km²) were slightly larger than those of the three adult females (\bar{x} 17,6 km²). The home ranges of the two immature jackals (8,5 and 9,0 km²) were significantly smaller than those of the adults ($P < 0,001$; t 8,02; df 5).

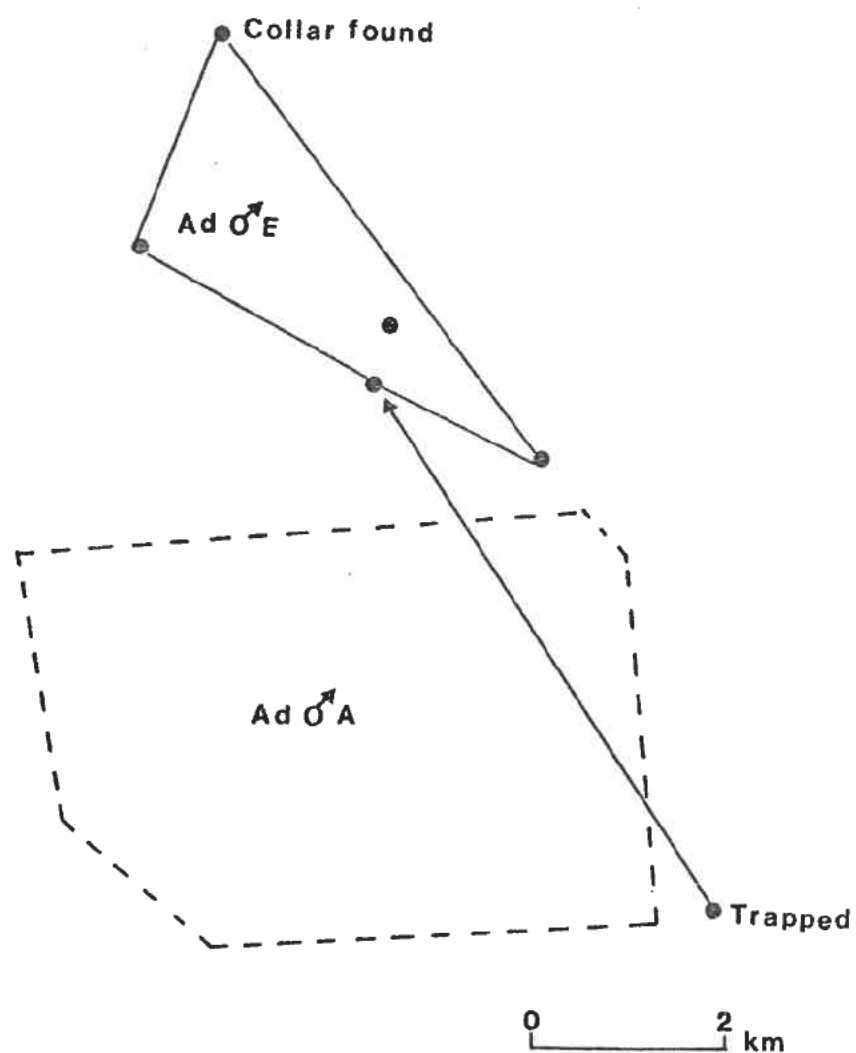


Figure 3.11 The capture point and relocations of ad male E in relation to the home range of ad male A.

The small home range size of sub-ad female A might be as a result of the short period over which the jackal was tracked and/or the small number of relocations recorded. On the other hand, sub-ad female A might have remained with the mated ad female A as a helper (Moehlman 1979). The mean home range size of 32,9 km² for the other two sub-adults was significantly larger than that of adults ($P < 0,001$; t 12,48; df 5).

SOCIAL ORGANISATION

As the home range of ad male A and that of ad female A did not overlap completely, it is possible that they were not a mated pair, and that ad male A was unmated and subordinate to ad female A. (There is at least one record of a 3 y-old male occupying the same home range as a mated pair and being subordinate to them (Ferguson 1980).) One of the other unmarked jackals seen in ad female A's home range may then have been her mate.

There was no overlap in the home ranges of ad female A and those of the mated pair in group B.

The information collected in GCGR suggests that mated male and female jackals have overlapping home ranges which do not overlap those of other mated pairs and that they are therefore territorial. The immature progeny of the mated pair remain within the adults' home range, and unmated sub-adults and adults have home ranges which may overlap those of one or more mated pairs.

DENSITY

If pup survival is two or three/litter, then, during the period that it was monitored, area A was occupied by a possible eight or nine jackals (including at least two unmarked animals). Area B was occupied by four marked jackals. A single unmarked animal was seen on a number of occasions at different localities within the area, therefore there may have been more than one unmarked adult or sub-adult. At least seven (and possibly eight) jackals were accounted for in area C.

The home range of a mated pair therefore supports the young of the year and some unmated sub-adults and adults. Available data indicate that approximately seven or eight jackals occupy such an area. If a mated pair's home range is approximately 20 km², then jackal density is ca 1/2,9 km² to 1/2,5 km².

This density estimate is crude, but until more detailed information is available on population structure, a more refined figure cannot be arrived at.

DISCUSSION

The black-backed jackal has previously been described as a monogamous species (Ferguson 1980, Moehlman 1980, Wyman 1967) in which the male and female mate for life (Moehlman 1980). Mated pairs are territorial (Moehlman 1979, 1980; Wyman 1967) with both males and females defending the territory: mated males defending the area against other mated males, and mated females defending it against mated females (Moehlman 1980). Both male and female parents protect and feed the young (Moehlman 1979). One or more yearling jackals (irrespective of sex) sometimes remain with the parents and help to raise the next litter (Moehlman 1980). While helpers are usually yearlings, in one instance Moehlman (1979) recorded a jackal remaining with its parents up to the age of 2 y, and Ferguson (1980) recorded a 3 y-old helper.

Jackals which do not stay on with the parents as helpers may remain within the original home range or begin to wander further afield. These animals are usually solitary. Whereas mated jackals often hunt in pairs, sub-adults and subordinate adults do not (Ferguson 1980, Lamprecht 1978).

In group B the immature male obviously did not stay on as a helper but became a lone sub-adult at the age of 1 y when the next litter of pups was born. Sub-ad female C was probably also a lone animal, moving over a large area.

Social organisation amongst black-backed jackals is similar to that recorded in golden jackals (Canis aureus) (Moehlman 1980), coyote (C. latrans) (Bekoff and Wells 1980), and wolf (C. lupus) (Mech 1970). All of these canids are monogamous and territorial, and have home ranges which are occupied by the adult pair and more than one generation of young, some of which help to raise subsequent litters. Kleiman (1977) suggested that this type of monogamy and social organisation has evolved in canids which have selected for a greater reproductive burden (large litters) than a solitary female can handle. Moehlman (1979) concluded that helpers improve pup survival and found a positive correlation between the number of helpers and number of surviving pups. "Parental manipulation of progeny" (Mech 1970) therefore improves the reproductive output of the parents.

Solitary non-breeding jackals probably act as a reserve breeding population. The time at which they bear young will depend on the availability of food and territory. Apparently very few black-backed jackals live longer than 6 or 7 y (Lensing 1972). If jackals enter the breeding population at approximately 3 y of age (Ferguson 1980, this study), then by the time that a pair is 6 y old their first progeny will be of breeding age. Moehlman

(1980) cites one instance of a mated pair of jackals eventually disappearing and one of their female progeny then mating with a lone male and holding portion of the original territory.

In black-backed jackal social behaviour studies in Tanzania (the only studies undertaken outside of South Africa) home range sizes were not determined. Moehlman (1980) stated that mated black-backed jackal pairs in Serengeti occupied a "feeding territory" of ca 2,6 km². Wyman (1967), referring to jackals in the same area, gave territory size as ca 8 km². The only density estimate made was that of 1 jackal/2 km² (Waser 1980), also in Serengeti.

The only other study in which home range sizes were determined was that undertaken by Ferguson (1980), who reported that in Kalahari Gemsbok National Park mean adult home range size was 4,1 km² and in Transvaal 27,7 km². Ferguson (1980) is also the only other author who has recorded age-related differences in black-backed jackal home range sizes. In both Kalahari Gemsbok National Park and the Transvaal adults occupied smaller home ranges than did sub-adults.

Differences in home range size in at least three other canids have been related to the age of the animal or its social position. Bekoff and Wells (1980) reported home range sizes in solitary non-territorial coyotes which were about 50 % greater than those of territorial animals. Shaw (1975) found that sub-adult red wolves (Canis rufus) had the largest home ranges and undertook long excursions, and van Ballenberghe et al. (1975) recorded the largest home range in a non-breeding lone wolf which did not belong to a territorial pack.

Although the overall mean home range figure for the Transvaal is similar to that for GCGR, Ferguson (1980) recorded differences within the province. Mean adult and sub-adult home ranges in a nature reserve (Suikerbosrand) were 20,4 and 29,2 km² respectively, but on farmland in the western Transvaal the respective areas were 62,7 km² and 407,5 km².

Ferguson (1980) attributed the differences in jackal home range sizes in the Transvaal and Kalahari Gemsbok National Park to differences in food availability, but did not comment on differences between nature reserve and farmland jackals within the Transvaal. Ferguson (1980) was dealing with jackal populations in three markedly different veld types, and areas of differing habitat utilisation, viz Kalahari Gemsbok Park, Suikerbosrand Nature Reserve, and farmland in the western Transvaal. The habitat in Suikerbosrand Nature Reserve, however, resembles that of GCGR in respect of veld type, and jackal home ranges are similar.

Van Ballenberghe *et al.* (1975) commented on the fact that wolf densities were similar in eastern boreal forest habitats (five studies) but were almost 10 times lower in western and north-western Canada. Variations in carnivore home range sizes have been related to prey density (Erlinge 1978, referring to stoats (*Mustela erminea*)), and Bertram (1973) concluded that lion (*Panthera leo*) density was influenced by food and social behaviour.

It is important to consider the relationship between home range (or territory) size and density. Home range size may not be affected in the short term by changes in the availability of food (cf. Bertram 1973), but pup survival certainly will be. Fluctuations in prey availability may therefore cause short-term changes in density. Mech (1972), for example, reported a decline in wolf pack sizes (= lower density) during a period in which there was a decrease in major prey species. Marked differences in food availability (e.g. in two completely different habitats) would result in a jackal requiring a larger or smaller home range to satisfy its requirements, and consequently density would be affected in the long term.

Although some of the jackals captured in GCGR were trapped close to boundaries of the reserve, and had home ranges which virtually bordered on certain reserve boundaries, there was little or no movement on to farmland. Exceptions are: sub-ad male B was recorded a short distance outside the reserve on a cattle ranch, ad male E's collar was found on subsistence agricultural land just outside the boundary, and one unidentified collared jackal was killed by shepherds in neighbouring Lesotho.

Small mammal sampling was done on a cattle farm adjoining GCGR. The farm, like other adjoining farms and subsistence agricultural areas, is burnt annually and fairly heavily grazed. In 11 mo-old grass small mammal trapping success was 2/100 trap nights, whereas in grassland at the same stage of growth within GCGR, trap success was 10 to 13/100 trap nights, and was as high as 20/100 trap nights in certain habitats.

As small mammals are important in the jackal's diet, there is little natural food to attract them on to farmland outside the reserve, and furthermore, as little or no small stock is farmed in adjacent areas (except across the 3 000 m-high escarpment in Lesotho) there is not the attraction of young domestic stock as a source of food. Jackals which move into adjoining farming areas are likely to be unmated adults or sub-adults.

DIET

STOMACH CONTENTS

In the eight stomach contents examined during the study period (Table 3.3) only one item previously unrecorded in Drakensberg jackal stomachs (Rowe-Rowe 1976, 1978a), was present, viz antelope dung. Sample size is too small to evaluate the data by calculating relative per cent occurrence, but the overall pattern is similar to what Rowe-Rowe (1976, 1978a) found in the stomachs of jackals from Drakensberg nature reserves, viz predominantly mammal remains, including carrion.

SCAT CONTENTS

Small mammals make up more than half of the jackal's diet in GCGR (Table 3.4). Both in number of occurrences and in number of individuals identified O. irroratus was present in greater numbers than was R. pumilio. In 212 O. irroratus occurrences 247 individuals were identified, and in 132 occurrences of R. pumilio, 153 individuals were accounted for. Small mammal sampling by trapping suggested that R. pumilio were more abundant, outnumbering O. irroratus by 8:1 in the trapped sample. There are a number of reasons which may account for disproportionate representation of these two species in both the trapped sample and jackal scats.

An aspect already discussed is that O. irroratus is not easily trapped. A second possibility is that the jackal's activity pattern overlaps that of O. irroratus to a greater degree than that of R. pumilio, and O. irroratus is therefore more exposed to jackal predation (see chapter on "Activity pattern"). Furthermore, jackals may actually select for and specifically hunt O. irroratus. A final possibility is that O. irroratus remains might be easier to detect in scats than those of smaller animals. Weaver and Hoffmann (1979), in experiments done with coyote (Canis latrans), showed that 100 % detectability is achieved only with rodents which have a mass > 100 g. Only about 34 % of rodents which had a mean mass of 25 g were detected in the scats. If this applies also to the jackal, then the proportion of R. pumilio:O. irroratus consumed might be as high as 459:247.

Shrews, although common in trapped samples, were poorly represented in the scats. Possible reasons are that they are difficult to hunt, not selected for, or under-represented in scats due to their small size and difficult detectability. Each of the 80 occurrences of unidentified small mammals might have included one or more shrews or small rodents which were

TABLE 3.3 Occurrence of items in eight black-backed jackal stomachs from Giant's Castle Game Reserve.

Food category	Actual occurrence	Details (number of occurrences)
Carrion	4	Calf 1 <u>Redunca arundinum</u> 1 <u>Felis catus</u> 1 unidentified (no hair) 1
Small mammal	4	<u>R. pumilio</u> 2 <u>O. irroratus</u> 1 <u>M. minutoides</u> 1
Medium mammal	1	<u>Pronolagus crassicaudatus</u> 1
Antelope	2	Young <u>Redunca fulvorufula</u> 1 Young <u>Tragelaphus scriptus</u> 1
Reptile	1	Lizard 1
Insect	4	Coleoptera 2 Orthoptera 1 Isoptera 1
Plant food	2	Fruit 2
Dung	1	Antelope dung 1
Grass	8	

TABLE 3.4 Actual and relative per cent occurrence of items in 477 black-backed jackal scats from Giant's Castle Game Reserve.

Food category	Occurrence		Details (number of occurrences)
	Actual	Rel %	
Small mammal	349	55	<u>O. irroratus</u> 212 <u>R. pumilio</u> 132 shrews 22 <u>Amblysomus hottentotus</u> 18 <u>Cryptomys</u> sp. 11 <u>Dendromus</u> sp. 2 <u>M. minutoides</u> 1 unidentified 80
Medium mammal	57	9	<u>Procavia capensis</u> 19 <u>Lepus saxatilis</u> 14 <u>Pronolagus crassicaudatus</u> 7 unidentified hare 2 <u>Thryonomys swinderianus</u> 1 jackal 3 <u>Ichneumia albicauda</u> 1 <u>Ictonyx striatus</u> 1 unidentified 6
Antelope	70	11	<u>Taurotragus oryx</u> 26 <u>Pelea capreolus</u> 26 <u>Redunca fulvorufula</u> 11 <u>Ourebia ourebi</u> 3 <u>Tragelaphus scriptus</u> 3 <u>Damaliscus dorcas</u> 1
Domestic mammal	24	4	Horse 11 sheep 8 goat 5
Unidentified mammal	13	2	Mainly pieces of bone

Continued overleaf

Food category	Occurrence		Details (number of occurrences)
	Actual	Rel %	
Bird	59	9	<u>Francolinus</u> sp. 3 unidentified small bird 55 eggshell 1
Reptile	13	2	Lizard 8 unidentified 5
Insect	26	4	Orthoptera 13 Coleoptera 4 Coleoptera larvae 5 unidentified 4
Crab	7	1	<u>Potamonautes</u> sp.
Plant food	7	1	Fruits and seeds
Dung	7	1	Antelope dung
Unidentified object	4	trace	
Grass	244	-	Non-food (see text)
Dicot. leaves	11	-	Non-food (see text)

not identified as no jaws or teeth were found.

Dassies (Procavia capensis), hares, and other carnivores were categorised as medium mammals. Some of the dassies and hares appeared to have been eaten as carrion, as Diptera larvae were present in the scats in which the remains occurred. The jackal remains consisted of portion of a jackal's foot in one scat, and quantities of jackal hair in two. No bones were present in these two samples so the hair could have been the animal's own, resulting from excessive licking.

All the eland (Taurotragus oryx) must have been eaten as carrion, although fly larvae were not found in all scats containing eland remains. The presence of fly larvae would depend on how long after death the jackal found the carcass, the time of year that the antelope died, and the portions eaten by the jackal. (Fly larvae which were found together with mammal remains were not recorded separately as insects.) Some of the other antelopes - grey rhebuck (Pelea capreolus), mountain reedbuck (Redunca fulvorufula), and bushbuck (Tragelaphus scriptus) were also eaten as carrion as fly larvae occurred with the remains.

Although many scats were collected along the boundaries of the reserve, domestic mammals contributed only 4 %. Sheep and goats would have been eaten in adjacent Lesotho or on farmland. Horse remains may have originated from outside the reserve, but could also have been from Natal Parks Board horses which died in GCGR.

Some of the unidentified mammal remains were hair, but most were pieces of bone of large mammals. These probably originated from lammergeyer (Gypaëtus barbatus) feeding stations where pieces of bone and meat are put out for the birds. On a number of occasions jackals were recorded feeding at these sites.

All the bird remains indicated that small species had been taken, judging by the sizes of feathers, beaks, and feet found.

The unidentified reptile remains were pieces of belly skin which could have been from snakes or lizards. No attempt was made to identify lizard remains to species level, but they appeared to be from skinks (Mabuya spp.) or crag lizards (Pseudocordylus spp.) which are the most abundant lizards in the reserve, and one was identified as Agama sp.

Grass (both green and dry) which occurred in 244 scats, was usually represented by a few blades only. In a few rare instances 20 to 50 % of the remains in a scat were grass. As no digestion of grass takes place it is not regarded as food. Much of the grass is probably ingested incidentally when a jackal bites at a small animal, but some may be intentionally

eaten - cf. the habit of doing so in dogs (Canis familiaris), cats (Felis catus), and large-spotted genet (Rowe-Rowe 1971).

Dicotyledonous leaves, similarly, showed no signs of digestion, are presumed to have been incidentally ingested, and are therefore regarded as non-food.

Seasonal variation

Seasonal comparisons of the jackal's diet were made (Table 3.5). Chi-square evaluations were done to test whether the seasonal percentages differed significantly from the overall percentage in each food category. Significant deviation from the expected was observed only in the categories of antelope (Chi-square 9,19; $P < 0,05$; df 3) and insects (Chi-square 9,75; $P < 0,05$; df 3).

The amount of antelope remains in the diet was highest during spring. A monthly breakdown of the antelope component shows that most antelope remains were found in late winter and early spring scats (Table 3.6). Grey rhebuck remains were recorded throughout winter and early spring, whereas eland occurred mainly during early spring, with a peak in September. The data in Table 3.6 can be compared with the recorded antelope deaths in the reserve during the months that jackal scats were collected (Table 3.7).

Fifty-five per cent of all antelope deaths during this study period were recorded between August and October (Fig 2.25), a phenomenon previously reported by Mentis (1978) who recorded most grey rhebuck and oribi deaths from August to October, following the coldest, driest month of the year (July) when herbage quality is poorest, and Scotcher (in prep.) who found that over a number of years the peak in eland deaths occurs in September or October.

The smaller summer peak of antelope remains in scats could be the result of infant deaths, or predation by jackals on infants of the smaller antelope species. One December and one January scat contained definite evidence of infant grey rhebuck, in the form of hoof remains. The number of infant small antelope in the diet is, however, not alarmingly high.

Although seasonal differences in the amounts of small mammal were not significant, the highest percentage was recorded during autumn. The reason for this could be that small mammal numbers reach a peak at the end of the breeding season, but might also be that with less carrion available, jackals concentrate more on hunting small mammals.

TABLE 3.5 Actual and relative per cent occurrence of items in black-backed jackal scats from GCGR, by seasons.

Food category	Spring		Summer		Autumn		Winter	
	100 scats		107 scats		83 scats		187 scats	
	Act.	Rel. %	Act.	Rel. %	Act.	Rel. %	Act.	Rel. %
Small mammal	63	52	77	52	68	59	141	56
Medium mammal	12	10	8	5	12	10	25	10
Antelope	20	17	17	11	3	3	30	12
Domestic mammal	6	5	4	3	6	5	8	3
Unidentified mammal	1	1	3	2	1	1	8	3
Bird	14	12	17	11	10	9	18	7
Reptile	2	2	1	1	5	4	5	2
Insect	1	1	14	9	6	5	5	2
Crab	0	0	4	3	1	1	2	1
Plant food	0	0	3	2	1	1	3	1
Dung	1	1	0	0	1	1	5	2
Unidentified object	1	1	1	1	1	1	1	trace
Grass	47	-	57	-	46	-	94	-

TABLE 3.6 Percentage of jackal scats containing antelope remains, by months in GCGR.

Antelope	Months											
	J	F	M	A	M	J	J	A	S	O	N	D
Eland	11	3	-	-	-	3	-	8	20	10	-	5
Grey rhebuck	7	5	-	-	3	6	8	8	4	6	-	5
Mtn reedbuck	4	5	-	3	-	-	3	3	4	-	-	-
Oribi	-	-	-	-	-	3	-	-	-	3	-	3
Bushbuck	-	-	-	-	-	-	1	1	-	3	-	-
Blesbok	-	3	-	-	-	-	-	-	-	-	-	-
Total percentage	22	15	0	3	3	12	12	20	29	23	0	13
N scats	27	40	13	31	39	33	76	88	45	31	24	40

TABLE 3.7 Numbers of antelope carcasses found in GCGR during the period that jackal scats were collected, by months.

Antelope	Months											
	J	F	M	A	M	J	J	A	S	O	N	D
Eland	5	-	-	4	-	1	2	14	25	16	7	5
Grey rhebuck	1	1	1	1	-	-	2	1	11	-	-	-
Mtn reedbuck	4	-	-	3	2	-	1	3	6	5	2	-
Com reedbuck	-	-	-	-	-	1	-	3	2	3	1	-
Oribi	-	-	-	-	-	-	1	4	1	2	-	1
Bushbuck	-	-	-	-	-	-	-	5	3	-	1	-
Blesbok	2	-	1	1	-	-	-	1	-	1	-	-
Hartebeest	-	1	-	-	1	-	-	-	1	-	-	-
Blk wildebeest	-	-	-	-	-	-	-	2	-	-	-	1
Grey duiker	-	-	-	-	-	-	1	-	1	-	-	-

RECORDED KILLS BY JACKALS

Since 1972 management and research staff working in GCGR have recorded all predator kills found and all sightings of jackal or other predators feeding on antelope carcasses. Information was recorded on forms on which the observer was required to describe the signs diagnostic of the predator's killing pattern.

A jackal kills and feeds on prey of the size of small antelope in a stereotyped manner (Rowe-Rowe 1975): it bites at the throat of its prey, across the trachea, killing it by suffocation; then starts feeding by opening the flank in the abdominal region between ribs and pelvis. If these signs were recorded the antelope was considered to have been killed by a jackal.

During the study period (1978 to 1980) one confirmed jackal kill was reported (a heavily pregnant mountain reedbuck), which I was unable to examine. On one occasion tourists reported seeing a jackal chasing a juvenile grey rhebuck into long grass, then heard the antelope screaming. On the following day I was unable to find the carcass, but found blood, grey rhebuck hair, and rumen contents at the site. There were six sight records of jackals feeding on antelope, but cause of death could not be established. Four other kills which I examined were considered to be caracal (Felis caracal) victims. All were adult females: two grey rhebuck, a mountain reedbuck, and a bushbuck. Three were in perfect health, but one grey rhebuck was old and very thin.

A caracal's killing and feeding pattern differs from that of a jackal in that it kills by biting at the back of the neck and/or the throat; the carcass bears claw marks on the shoulders or back of the neck, and the caracal starts feeding from the groin and the insides of the thighs.

Prior to the start of the GCGR study (1972 to 1977) two confirmed jackal kills were recorded: a juvenile mountain reedbuck and a juvenile grey rhebuck. In one other instance the normal killing bite and initial feeding signs could not be recorded as too much of the prey (a juvenile grey rhebuck) had been eaten - the observer reported that the remains were still very fresh and that an adult jackal and two young were flushed a short distance away. Twelve sight records of jackal feeding on antelope (cause of death not determined) were reported.

DISCUSSION

Adequacy of sample size

The total sample was examined by expressing the relative percentages of food items by 50-scat intervals (Table 3.8). Chi-square tests show no significant differences between the final percentages of any food category in the total sample of 477 scats and those in the smaller samples. Eight food categories were recorded after 50 scats had been examined, 11 categories at 100 scats, and all 12 categories by 150 scats. After 150 scats had been examined, no additional food categories were recorded. Application of the formula for determining adequate sample size in feeding habits studies (Bothma *et al.* 1976) to the GCGR data gives a proposed minimum of 94 scats for the analyses to be representative (95 % confidence limits) of the jackal's diet in GCGR. The sample size of 477 scats therefore appears to be more than adequate for assessing the jackal's diet in the Drakensberg.

As scat analysis is a time-consuming process, it is suggested that in future studies aiming at establishing the main items and their proportions in the jackal's diet, a sample of approximately 100 scats, collected throughout the year, would be adequate.

Evaluation of data

Both Bothma (1971b) and Grafton (1965) found marked differences in the relative importance of food items in jackal stomachs when data were evaluated by percentage volume and percentage occurrence respectively, e.g. insect was ranked sixth in importance by volume and first by occurrence. Items with a large bulk (carrion, antelope, sheep) were recorded in large volumes and their importance therefore tends to be exaggerated by per cent volume, whereas small items with less bulk were present in more stomachs, and may have been exaggerated in per cent occurrence evaluations. Rowe-Rowe (1976) recorded similar rank orders of food items in volume and occurrence evaluations, but sample sizes were much smaller than those of Grafton (1965) and Bothma (1971) - one fifth and one tenth of their sample sizes respectively.

Whereas the examination of stomach contents actually reveals the amounts of each type of food eaten, scat analysis indicates what items have been eaten, provided that undigested integuments, teeth, bones, or seeds are present. Scott (1941) experimented with data evaluation using number of individuals in scats, relative per cent occurrence, dry mass, and volume of individuals. Relative per cent occurrence provided the most reliable indication of the proportions of food consumed. Lockie (1959) tested three

methods of estimating proportions of prey consumed by foxes: relative per cent frequency, the percentage of each item in each scat, and weighing the remains of each item. It was found that all of these methods tended to slightly exaggerate the percentage of small prey and under-estimate medium and large prey.

If Lockie's mean exaggeration and under-estimation percentages are applied to the food items in the GCGR data the relative importance of items in the jackal's diet remains unchanged.

As a result of trials with wolves (Canis lupus) Floyd et al. (1978) derived an equation which, when applied to scat analysis data, gave a better estimate of the relative mass of large (75 kg) and small (1 kg) prey consumed. The equation could not be applied to the GCGR data with the same degree of accuracy: whereas wolves consume a large carcass almost entirely, the smaller, more solitary jackals usually eat only a small portion of a carcass before it is consumed by vultures. This probably also explains why, despite the large amount of carrion which is available at certain times in GCGR, the amounts of antelope remains in the scats are not as high as would be expected.

Feeding strategy of the jackal

Major items in the jackal's diet in different areas, and in some instances at different times in one area, are listed in Table 3.9.

In the Serengeti, which is rich in small game, Wyman (1967) and Lamprecht (1978) recorded similar findings. (Lamprecht's category "small game" included Thomson's gazelle (Gazella thomsoni) and hares.) In the same area Moehlman (1980) rated rodents and fruit as the main items. In Ngorongoro, a big-game area, jackals scavenged mainly the remains of wildebeest (Connochaetes taurinus) and zebra (Equus burchelli) killed by lions (Wyman 1967).

On sheep farms in South Africa (Bothma 1971b, Rowe-Rowe 1976, 1978a) carrion, sheep, and small mammals were most important. In jackal stomachs from Drakensberg nature reserves (Rowe-Rowe 1976, 1978a) carrion occurred more frequently than did small mammals, but in the larger sample of scats (Rowe-Rowe, 1978a), small mammals were most important and the relative importance of major food items was similar to that recorded in GCGR.

In the arid regions of southern Africa insects feature most prominently in the jackal's diet (Smithers 1971, Stuart 1976). Stuart, in comparing three habitats in the Namib desert, found that on the shores of a lagoon where there were many large birds, insects gave way to birds ("probably carrion") as the major food.

TABLE 3.9 Major items in the black-backed jackal's diet in different areas.

Area	Author	Source of material	Evaluation	Main foods
Serengeti	Lamprecht (1978) Moehlman (1980) Wyman (1967)	Scats Observation Scats	Occurrence - ?	Small game, insects, fruit Rodents, fruit Thomson's gazelle, insects, small mammals
Ngorongoro	Wyman (1967)	Scats	?	Carriion
Transvaal (mainly)	Bothma (1971)	Stomachs	Volume Occurrence	Carriion, domestic stock, rodents Insects, rodents, carriion
Drakensberg:				
Game reserves	Rowe-Rowe (1976 + 1978a)	Stomachs	Occurrence	Carriion, small mammals, antelope
Farms				Carriion, sheep, small mammals
Forestry reserves	Rowe-Rowe (1978a)	Scats	Occurrence	Small mammals, birds, antelope
Botswana	Smithers (1971)	Stomachs	Occurrence	Insects, small mammals, carriion
Namib:				
Lagoon	Stuart (1976)	Scats	Occurrence	Birds (probably carriion), insects, fruit
Dry river bed				Insects, plant food, small mammals
Granite out-crop				Insects, plant food, rodents

The overall impression gained from these studies is that the jackal is omnivorous and an opportunistic feeder, living on whatever is most abundant and most easily obtained.

Very few seasonal comparisons of the jackal's diet have been made. In Serengeti both Lamprecht (1978) and Wyman (1967) recorded increased intake of mammal food during the dry season, which then decreased in the wet season when insect and fruit increased. In two of Stuart's (1976) study areas seasonal differences were noted: in the dry river bed the situation was similar to that in Serengeti, with an increase in mammal and a decrease in plant food during the dry season, and the reverse during the wet season. In the lagoon area only the insect component fluctuated.

No detailed reports existed prior to this study concerning jackals and their diet in relation to the availability of prey. Moehlman (1979) referred briefly to rodent densities which she related to territory and pup survival, and Wyman (1967) discussed the jackal's diet in relation to densities of small and large game, but did not consider other prey items.

Griffiths (1980) categorised predators as searchers, pursuers, or subduers. Searchers deal with small, easily-caught and easily-handled prey. The only energy expenditure being the finding of the prey. Pursuers feed on common and/or conspicuous, relatively defenceless but agile, fairly large prey. Subduers deal with large, difficult to overcome prey, relying on their own large body size, strength, and defensive ability.

The black-backed jackal is a versatile predator, being both a searcher living on small prey such as small mammals and insects (Moehlman 1979, Smithers 1971, Stuart 1976, this study) and a pursuer, killing fairly large prey such as hares or the young of small antelopes (Lamprecht 1978, Wyman 1967, this study). Furthermore, the jackal is also a scavenger (Bothma 1971b, Grafton 1965, Wyman 1967, this study) or supplements its diet with plant food (Moehlman 1980). The foraging strategy adopted obviously depends on food availability.

The analyses of jackal stomachs and faeces collected in GCGR indicate that in this area, the predator is predominantly a searcher, and a pursuer and scavenger only opportunistically. In this study it was concluded that GCGR is fairly rich in small mammals (Part 4) but densities of small antelope species are low (Part 2 : "Population trends and relative abundance"). Small mammals were most important in the jackal's diet in GCGR, therefore this predator utilises the most abundant conveniently-sized prey. The significance of the relative abundance of specific small mammals in the jackal's

diet in relation to their relative abundance in GCGR has already been discussed in this chapter, and will also be discussed in relation to the activity patterns of both the jackal and the two most commonly-recorded prey species (R. pumilio and O. irroratus) in the next chapter.

ACTIVITY PATTERN

Radio-tracked jackals generally became active about an hour before sunset and activity ceased approximately one hour after sunrise. No activity was recorded between 09h00 and 14h59. Insufficient data were collected to determine whether jackals remained active throughout the night, or whether there was any decrease in activity after the early evening peak.

Activity data were examined for the period 25 September to 24 March (= "summer") and 25 March to 24 September (= "winter"). During both winter and summer 100 % activity (i.e. all jackals radio-tracked were active) was recorded between 17h00 and 17h59. Winter activity commenced earlier than was the case during summer (Fig 3.12). Differences were significant for the periods 15h00 to 15h59 (Chi-square = 25; $P < 0,001$) and 16h00 to 16h59 (Chi-square 4,90; $P < 0,05$). Cessation of activity took place later during winter than in summer. Differences were significant for the period 06h00 to 06h59 only (Chi-square 4,92; $P < 0,05$).

Variation in onset and cessation of activity during winter and summer almost coincides with the differences in sunset and sunrise times. The difference in time of sunset between mid-winter and mid-summer is 1h 40 min, and the sunrise difference is 2 h 05 min (Fig 3.12). Sunset and sunrise have previously been related to onset and cessation of activity in carnivores and other small mammals (Kavanau and Ramos 1972, Kavanau 1969).

Seasonal changes in daylight affect not only the activity pattern of the jackal, but also that of its prey. Otomys irroratus, the most abundantly recorded small mammal in jackal faeces collected in GCGR, has been described as crepuscular (Davis 1973), but Perrin (1981b) found that the species has regular activity peaks throughout daylight and darkness, therefore coinciding with jackal activity. Rhabdomys pumilio is diurnal, with very little activity recorded before sundown or after sunset (Brooks 1974, Christian 1977b). Activity peaks occur approximately an hour after sunrise and about two hours before sunset. Its activity pattern does not overlap the jackal's to the extent of that of O. irroratus (Fig 3.13), which may be one of the reasons why more O. irroratus than R. pumilio remains were found in jackal faeces, despite the fact that R. pumilio was the commonest small mammal in trapped samples.

Davis (1973) recorded similar seasonal differences in the onset and cessation of activity in O. irroratus to those observed in jackal, and

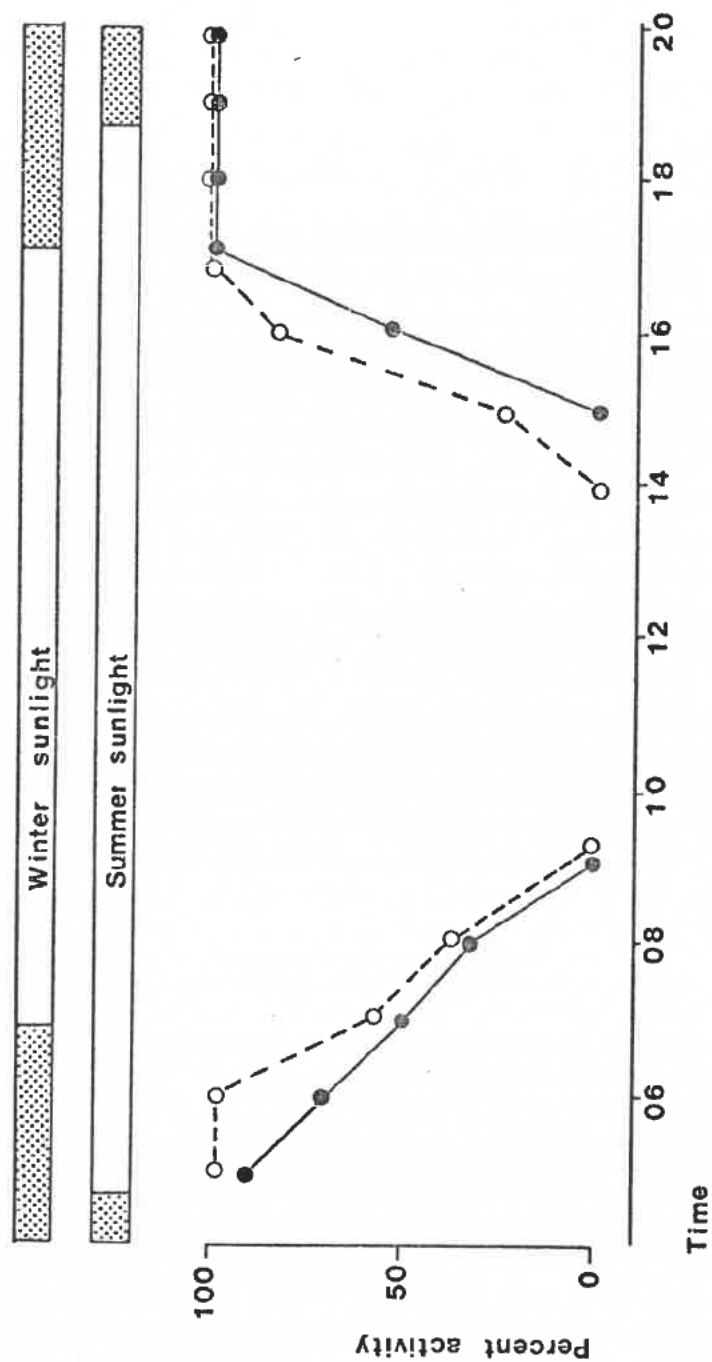


Figure 3.12 Cessation and onset of black-backed jackal activity during winter (○) and summer (●). Activity is expressed as the percentage occasions on which a radio-tracked jackal was active.

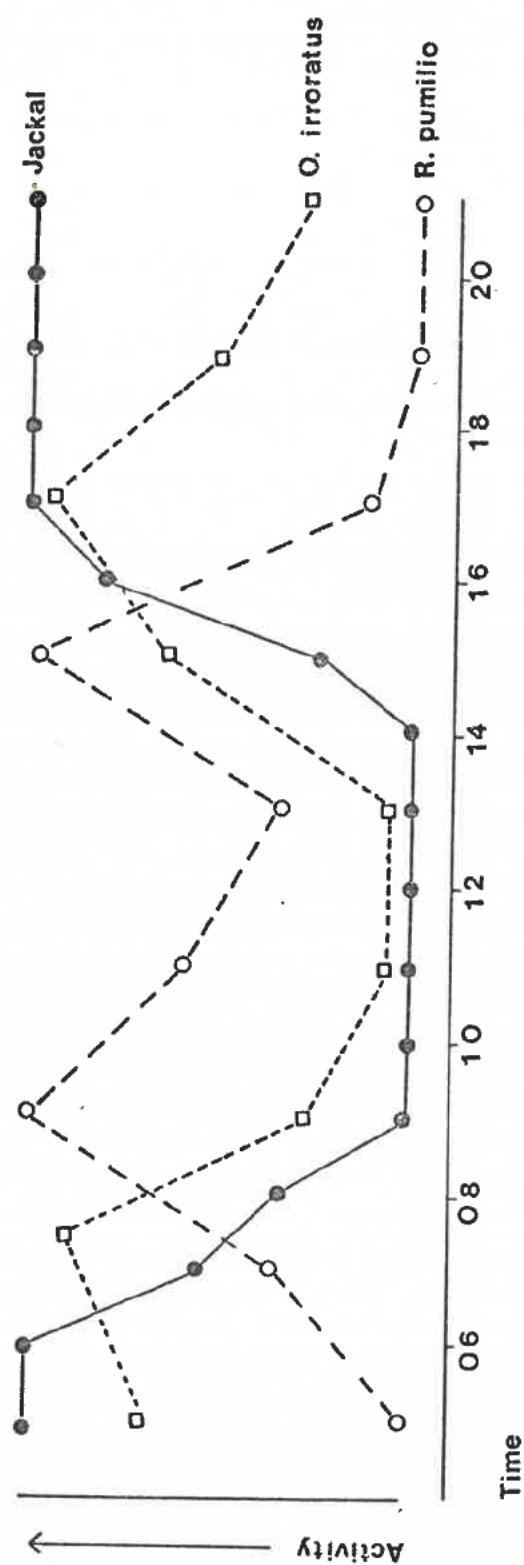


Figure 3.13 Black-backed jackal activity ● in relation to the activity of *Otomys irroratus* □ and *Rhabdomys pumilio* ○ . *O. irroratus* data from Davis (1973) and *R. pumilio* data from Brooks (1974).

Brooks (1974) and Perrin (1981b) found that in R. pumilio summer activity peaks occurred both earlier and later in the day than was observed during winter.

Jackals spent their inactive periods at regularly-used lying-up places. Resting radio-collared jackals were flushed on twelve occasions. One jackal was lying in a patch of scrub, but all others were in the sun in open grass-land situations. All of the open lying-up places, however, were near some form of cover, such as scrub, rocks, or very long grass.

On clear sunny days radio-collared jackals could be located during the hours of inactivity, and it is suspected that they were resting in the open. On cold overcast, rainy, or misty days very few relocations were made during the inactive period, as the jackals had probably taken shelter in holes or under rocks, therefore blocking the radio signals.

Rautenbach (1978a), Rowe-Rowe (1978a), and Smithers (1971) described the black-backed jackal as strictly nocturnal in settled areas, and partly diurnal in game reserves.

Rowe-Rowe (1978a) stated that black-backed jackals in Drakensberg game reserves were both diurnal and nocturnal, and recorded sightings during all daylight hours. Telemetric data collected during this study, however, have shown that diurnal activity is limited to late afternoon and early morning. Rowe-Rowe (1978a) incorrectly interpreted diurnal activity: the numerous daylight sightings were obviously of animals which had been lying-up during the day, and were moving away from the disturbance caused by the observer at the time they were located.

Ferguson (1980), who also used radio telemetry to track jackals and monitor activity, recorded activity peaks at 18h00 to 19h00 and 05h00 to 08h00 in the Transvaal, with decreased activity between 24h00 and 05h00, and almost no activity during daylight. The later times of onset and cessation of activity in Transvaal jackals, when compared with the GCGR animals, probably relate to the later sunset and sunrise times in the more westerly study area.

Ferguson (1980) recorded jackals in Kalahari Gemsbok National Park and in the Transvaal lying-up under bushes in preference to open situations, but did not find them using holes. In South West Africa (Namibia) Shortridge (1934) also recorded jackals sheltering under shady bushes, or using crevices in rocky areas. In the cold to temperate climate of the Drakensberg jackals obviously select more open sites, preferring to remain in the sun, whereas in the warmer habitats in which Ferguson (1980) and Shortridge (1934) made their observations, the animals prefer to rest in shade.

CONCLUSIONS

Although the black-backed jackal has been the subject of a number of studies in South Africa, research has been fragmented, either dealing with one aspect only of the animal's ecology or dealing very generally with the jackal over a large area.

The studies on jackal diet by Bothma (1971b), Grafton (1965), and Stuart (1981) are based on information collected country-wide or province-wide; Lombaard (1971) described age-determination techniques; Bothma (1971a) and Bigalke and Rowe-Rowe (1969) presented information obtained from control operations; Rowe-Rowe (1975) investigated predation on sheep; and Ferguson (1980) concentrated on jackal movements and social organisation on farmland and in game reserves. The study by Stuart (1976) is the only one in which jackal diet is satisfactorily compared in different habitats and in which seasonal comparisons are also made. A comparison of the jackal's diet on farms and in game reserves by Rowe-Rowe (1976) was based on small sample sizes from both areas, therefore only limited comparisons were possible.

The Giant's Castle jackal study differs from the above-mentioned studies in that information on a number of aspects of black-backed jackal ecology was collected from one area. The most comprehensive aspect of the study was that on jackal diet in which sufficient data were collected over a sufficiently long period to make seasonal comparisons possible; and as small mammal and antelope populations were being studied at the same time, diet in relation to food abundance could be considered. The telemetry study contributes to our knowledge of social organisation and provides information which is useful in attempting to estimate density, but is incomplete due to the small sample sizes in each of the age-groups, and the data collected need to be interpreted in relation to the findings of other workers. The information on breeding and population structure and dynamics is an addition to the meagre knowledge which currently exists on these aspects of jackal ecology.

The sex ratios of jackals collected in GCGR, other game and nature reserves, and on farms in the Drakensberg have been considered separately. In GCGR and in the other game sanctuaries the male : female ratio of 1,2 : 1 did not differ significantly from parity, but in the sample of jackals killed on farms the 1,8 : 1 ratio in favour of males was significant, indicating a preponderance of males. Black-backed jackal males are significantly larger than females and therefore probably kill larger prey animals than do

the females. All of the jackals collected on farms were killed by foxhounds which had tracked the jackals down by following the jackal's scent, starting from a recently killed lamb. This will naturally bias the sample in favour of animals killing larger prey, therefore reflecting a biased sample in favour of males on farmland. It is, therefore, suggested that the sex ratio of jackals throughout the Drakensberg, including farmland, is in actual fact 1 : 1.

Moehlman (1980) noted that an adult male jackal hunts and kills for his mate who remains with her pups in the den for the first few weeks after they are born. Samples will accordingly again be biased in favour of males. This could, however, not be shown with the data from farms, although adult males outnumbered adult females in the monthly samples, differences were not statistically significant in any single month. Further research into this aspect and the collection of larger samples might provide an answer to the apparently different sex ratios on farms and in game reserves.

In the sample of 30 jackals trapped and killed in GCGR during this study 10 % were immature (less than 1 y-old), 23 % were sub-adults (1 to 2 y-old), and 67 % were adults (more than 2 y-old). Prior to this study 26 % of 220 jackals collected were classified as immature and the remainder as more than 1 y-old. If the figure of 10 % immature jackals in the sample collected during this study is reliable, then this is indicative of a declining population when compared with the figure of 26 % immature jackals collected from 1964 to 1971. The total sample size of 30 collected during this study, however, is probably too small on which to base any conclusions. Furthermore, 70 % of the jackal trapping effort was during months when there would have been no immature jackals in the trappable population.

As there was a high correlation ($r\ 0,96$; $P < 0,001$) between tooth eruption and body mass in indicating the age of ten < 6 mo-old jackals collected in the Drakensberg (based on techniques described by Lombaard 1971) it is suggested that mass may be used as a rapid field method of age determination in young jackals not having a full complement of permanent teeth (i.e. < 6 mo-old). In adult jackals the amount of wear on the incisors may be used for assigning them to categories 1 y apart (Lombaard 1971).

Age determination and back-dating to birth date in 70 young jackals collected in the Drakensberg indicates that parturition takes place in winter from June to August, with a peak in July. As carrion is most abundant during winter and early spring it is possible that the breeding season in the Drakensberg has been geared to coincide with a period of abundant food supply.

In the Transvaal, Rautenbach (1978a) reported a clinal southwards increase in the size of jackals. As the black-backed jackals in the Drakensberg are larger than those recorded in Botswana, support is lent to Rautenbach's (1978a) hypothesis. Besides this, their large body size in the high altitude and colder climate of the Drakensberg is consistent with Bergmann's "rule".

In the Drakensberg, as has been found elsewhere in southern Africa, black-backed jackal males are larger than females. As black-backed jackals are monogamous and mate for life, the degree of competition amongst males for females is not likely to be as great as in polygamous species, in which large males are most successful in inter-male contests. Alternatively large males might be most successful at obtaining and holding territories. It has already been suggested that jackal males and females do not feed on exactly the same size of prey, therefore males are larger; but the converse might also apply, viz that larger jackal males have evolved to succeed socially, and the larger jackals are consequently capable of killing larger prey.

In the study of jackal movements only one mated pair was recognised with certainty. In this pair the male's territory was 23 % larger than the female's. This suggests that the male, being larger, needs to do more foraging, and, in addition, he would need a larger territory than does the female as he provides her with food during the early life of the pups. Unfortunately there is very little comparative information either in support of or contrary to this postulation. Ferguson (1980) succeeded also in radio-tracking only one mated pair. His findings were that male and female territories were of the same size, so further research on this aspect is obviously needed.

Although only 12 jackals were fitted with radio transmitters in GCGR, the data collected during this study supplement existing knowledge on jackal social organisation and movements, and also provide some comparative information. If the information collected in GCGR is considered together with the findings of recent workers (Ferguson 1980, Moehlman 1980) the following picture of jackal social organisation emerges: the black-backed jackal is a monogamous species in which the male and female mate for life. The mated male and female have overlapping home ranges which do not overlap the home ranges of other mated pairs, and the pair is therefore territorial, the male defending the territory against other mated males and the female defending it against other mated females. Both male and female parents protect and feed the young. Immature progeny have home ranges which fall within the mated adults' territory until they are a year old, at which stage a young

jackal may remain with the mated pair as a helper, or may become a solitary sub-adult and have a home range which extends over a number of mated pairs' territories.

There are therefore four components in black-backed jackal social groups: the territorial mated pair responsible for reproduction; the progeny of the year; helpers which improve pup survival; and solitary non-breeding non-territorial animals (some of which may have previously served as helpers). Solitary adults form the reserve breeding population and the age at which they bear young will depend on the availability of food and territories.

A jackal density estimate of from 1/2,9 km² to 1/2,5 km² is made for GCGR, based on home range size of a mated pair and the number of other jackals sharing the area. The density estimate is crude as it in turn is dependent on other estimates, such as pup survival and the number of unmarked jackals in the area. On the basis of all of these estimates it is suggested that GCGR with an area of 36 000 ha supports a jackal population of between 124 and 144 individuals, of which ca 36 (25 %) are mated adults which raise ca 36 (25 %) young per annum, and that there are ca 72 (50 %) unmated sub-adults and adults.

As there are few figures with which to compare this density estimate (see page 212), it is difficult to state whether jackals occur in GCGR at a high or low population density. My opinion is that the population is viable but stable, with recruitment being approximately equal to mortality (see page 211).

The findings on the jackal's diet show that they are not having a serious effect on antelope numbers (see below), and that they live mainly on small mammals. The predator-prey situation in GCGR is apparently stable: the prey species are limited by the amount and quality of the food, and the jackals are limited by the amount of prey - the prey populations are not limited by the predators. If this latter situation obtained the predators would decrease or deplete their food resources and consequently decrease or deplete their own population numbers.

In determining the diet of the jackal in GCGR the analysis of the contents of 477 scats, collected throughout the game reserve and during all months, is considered to have adequately covered seasonal variation and a large enough proportion of the GCGR jackal population.

As has been found elsewhere in Africa, a wide variety of items was recorded in the jackal's diet. The major food category in GCGR was small mammals which contributed 55 % (relative per cent occurrence) to the diet.

Other important food categories were antelope 11 %, medium-sized mammals (= size of hare) 9 %, and birds 9 %. The remaining 16 % was made up of domestic mammals, reptiles, insects, crabs, plant food, and antelope dung.

The two small mammal species which occurred most frequently in the jackal's diet were Otomys irroratus and Rhabdomys pumilio. Although the small mammal trapping study yielded more R. pumilio than O. irroratus in trapped samples (8 : 1), individual O. irroratus counted in jackal scats outnumbered R. pumilio by 1,6 : 1. Reasons postulated for the disproportionate representation of these two small mammal species in the trapped sample and in jackal scats are: that O. irroratus are not easily trapped, so that trap results do not reflect actual numbers; that the remains of the larger O. irroratus are easier to detect in scat analysis than are those of the smaller R. pumilio; that the jackal's activity pattern overlaps that of O. irroratus to a greater degree than that of R. pumilio, so that it captures a disproportionate number of O. irroratus; and that jackals actually seek and kill O. irroratus as a preferred food item. The amount of energy expended on hunting the small R. pumilio (35 g) is likely to be as much as that expended on hunting the relatively large O. irroratus (100 g), but the reward provided by eating the larger rodent is greater, hence it could well be a sought-after food, and therefore caught in greater numbers.

The amount of antelope in the jackal's diet varied seasonally and the highest percentages coincided with the months August to October during which most antelope die, having lived on a low nutritional plane throughout the winter. Not only does the nutritional content of the green component of herbage decrease rapidly and remain low throughout winter, but so too does the proportion of green material itself. In mid-winter the amount of suitable food available to grazing antelopes is ca 3 % of the mid-summer figure, if both amount of green herbage and nutritional content are taken into account. It is therefore likely that at this time of year most of the antelope remains in the jackal faeces emanated from animals which died of malnutrition, and were not as a result of jackal predation.

Although there was a minor summer peak in the amount of antelope in the jackal's diet and some evidence of young antelope having been eaten, it is concluded that most antelope are eaten as carrion, having died of causes other than jackal predation.

In GCGR the black-backed jackal is predominantly a searcher, hunting for and feeding mainly on small mammals and some other small animals; it fills the role of scavenger opportunistically, probably taking carrion whenever encountered; and occupies the role of a pursuer, by running down and killing small antelope or medium-sized mammals to a lesser extent.

PART 4 : MANAGEMENT RECOMMENDATIONS

If trap success is taken as an indicator of abundance, GCGR supports fairly high numbers of small mammals. The overall figure of 9,4 % is higher than trap successes reported from other South African mountain areas (Bond et al. 1979, Nel et al. 1980, Rautenbach et al. 1980) as well as those recorded in Kruger National Park (Kern 1977) and Itala Nature Reserve (Rautenbach et al. 1981); and similar to the trap successes recorded in the Kalahari (Nel and Rautenbach 1975) and in studies done in Uganda (Cheeseman and Delany 1979, Delany 1964).

Small mammal populations in GCGR appear to be stable, but stabilisation of numbers and equilibrium of species richness are reached at different stages, depending on fire history and complexity of the habitat. In grassland, the first two years after an area has been burnt may be regarded as a dynamic stage, with a number of changes in species richness and composition taking place due to colonisation and extinction. It is during this period too that an initial peak in number of individuals is reached. In grassland unburnt for long periods (ca 10 y) the small mammal numbers are stable and equilibrium of species richness is reached. During periods intermediate between regular burning and total protection of grassland, equilibrium of species richness is reached but numbers of individuals are low.

In more complex habitats such as boulder-beds, scrub, and grouped-tree woodland which are occasionally or partly burnt, a dynamic state prevails with the habitats being occupied by both grassland and forest species. In forest, however, equilibrium has been reached, but with a set of species different from those in grassland.

The Drakensberg situation is therefore one in which two vegetation climaxes exist, viz fire-maintained climax grassland; and climax forest, maintained by climate and the exclusion of fire. Small mammal faunas appear to have evolved along two similar lines. R. pumilio and other grassland species inhabit grassland and open scrub and woodland habitats, but do not occur in forests, where small mammal populations are dominated by G. murinus. This hypothesis is supported by the distribution and habitat preferences of the antelopes in GCGR. Grey rhebuck, mountain reedbuck, and oribi are strictly grassland inhabitants, whereas bushbuck and grey duiker occur in forest and scrub. Eland are an exception in that they occur in recently-burnt grassland during summer, but disperse widely during winter, extending

habitat utilisation to include scrub and forest. M. varius is the exception amongst small mammals, occurring in all vegetation types.

The five most abundant antelopes (grey rhebuck, mountain reedbuck, oribi, eland, and blesbok) all showed a preference for recently-burnt veld, and very little utilisation of habitats unburnt for > 1 y. These preferences were attributed to easier accessibility of herbage and the higher nutritional content of burnt veld.

In selecting a fire regime for GCGR the beneficial and adverse effects to both small mammals and antelopes should be taken into account. For small mammals the two most obvious options are either a regime of a mosaic of biennial burning of alternate compartments, or one of no burning at all. For the antelopes initial assessment suggests that the grassland species would benefit from annual burning of grassland throughout the entire reserve, provided that the controlled fires are staggered to extend over a few months.

Protecting the entire reserve from fire is impracticable in terms of preventing accidental fires or those started by arsonists. When a long-protected area burns, the excessive fuel loads which have accumulated result in very hot fires which can be detrimental to the vegetation, and as basal cover decreases in the absence of fire, more bare ground would be exposed after such a fire and water run-off and soil erosion would be accelerated. Although small mammal numbers are satisfactory in fire-protected grassland, species richness is low. Furthermore, the dense canopy cover inhibits effective hunting by avian predators, therefore they would not benefit from the food supply (small mammals) in such a fire regime; and finally, long-term protected grassland is not favoured by the antelopes in GCGR.

A regime of annual burning is not likely to be as beneficial to small mammals as is one of biennial burning of alternate compartments. In a programme of biennial burning a mosaic of burnt and unburnt islands is created, with the unburnt areas forming reservoirs for the recolonisation of burnt areas. Such a mosaic provides physically the most suitable hunting ground for predators, in terms of accessibility of prey (small mammals), numbers of prey individuals and variety of prey species. Although annual burning would benefit antelopes in terms of large amounts of nutritious and accessible food being available, this situation would prevail only during the growing season, and the limiting factor would be poor herbage quality during winter. In addition, in a system of biennial burning the unburnt areas provide good cover for the antelopes during periods of inactivity, and are particularly valuable for cover during the calving season when the young of grey rhebuck, mountain reedbuck, and oribi in particular lie-out.

It is concluded, therefore, that biennial burning of grassland is more beneficial to small mammals than is annual burning or total protection; that total protection would not benefit antelopes, and that although annual burning would have short-term advantages for the antelopes, biennial burning caters for both suitable food and cover.

Long-term protection of certain grassland areas in GCGR was initiated originally to study vegetation changes in the absence of regular burning, and in an attempt to encourage the growth of woody vegetation. It is recommended that the protection of these areas be continued, as besides the important botanical interest, they provide reservoirs of small mammals.

At present biennial burning is done during three seasons: late winter on the escarpment, autumn in some areas below the sandstone, and early spring throughout the rest of the reserve.

It is recommended that the biennial spring burning and the recently-initiated policy of biennial winter burning of the escarpment be continued. As herbage production on the escarpment is not as great as at lower altitudes the escarpment was originally burnt every three years. It was found, however, that the fuel build-up over three years was too great and that arson fires (which are started mainly on the escarpment) spread very rapidly under these conditions. By having alternate biennially-burnt blocks on the escarpment fuel is reduced and so too is the danger of an unscheduled fire spreading to other areas. It is preferable to burn the escarpment during winter (June or July), after snow has fallen if possible, rather than during early spring, as it is during spring that winds are strongest and arson fires cause most damage. The current number of two burning compartments on the escarpment should, however, be increased to four.

Scotcher and Clarke (1981) expressed doubts concerning the advantages of autumn-burning of grassland as opposed to spring-burning below the sandstone in GCGR. It is recommended that the effect of autumn and spring burns below the sandstone be assessed, paying particular attention to plant species composition and basal cover. Small mammals do not benefit from autumn-burning of grassland due to the longer period of poor cover before rapid grass growth starts six months after the fire (Fig 1.11). Antelope may, however, benefit from any new growth which takes place before the onset of the winter. There is some evidence to indicate that under the system of autumn burning throughout the reserve, which prevailed from 1906 - 1965, oribi numbers were higher. Under the current system the areas burnt are not favoured by oribi. Autumn-burning of areas above the sandstone (favoured

oribi habitat) is not recommended as the colder climatic conditions and earlier frosts at the higher altitude would further inhibit plant growth.

The analysis of the large sample of black-backed jackal faeces collected in GCGR indicates that antelope are a minor item in the predator's diet, and that some of the antelope might have been taken as carrion, as an increase in this component coincided with the period when antelope are in poor physical condition and most deaths are recorded. Jackals were never seen actually killing any antelopes (neither during this study period nor prior to it). That jackals do kill some young antelope is not disputed, but the number of recorded confirmed kills is low. It may be argued that not all remains of young antelope killed by jackals are found, as they may be consumed or removed by scavengers. On the other hand, the low incidence of antelope remains in jackal faeces does not lend support to this argument.

There is no evidence to support the claim that jackal numbers have increased, or that they are increasing. As the jackal is nocturnal low numbers were seen in the course of fixed route game counts, and high variability was recorded (Table 4.1). The mean number of jackals seen per count (if any importance can be attached to these figures) actually reveals a significant decrease ($P < 0,01$; df 3 and 125; F 4,39).

The information collected in this study suggests that jackal density is dependent on food supply and the predator's social organisation. The food supply probably governs the territory size of mated pairs and pup survival must obviously be related to the amount of food which the parents and helpers can obtain for them. Any attempt at reducing jackal numbers in an area as large as GCGR might cause a short-term population reduction. This, however, would probably result in more food for the remaining jackals and a consequent increase in pup survival.

Past and present antelope counts indicate that populations in GCGR are stable. A possible exception is oribi, numbers of which appear to have declined after a change from a policy of autumn burning to spring burning in 1965. Over the past ten years, however, numbers appear to have stabilised at a new level.

Coexistence of the indigenous antelopes in GCGR is dependent on niche separation, based on their specific preferences for vegetation type, physical characteristics of the habitat (altitude, topography, slope, and aspect), food type, and finally on their different feeding styles.

Stability of numbers is possibly determined in the first place by the habitat preferences of the animals and the availability of suitable habitat. The second limiting factor is the quality of the herbage, which although

TABLE 4.1 Mean number of black-backed jackals counted along fixed routes (sum of routes 1 to 5) from 1978 to 1981.

Year	N counts	\bar{x}	SE	CV
1978	30	1,70	0,28	16 %
1979	36	2,14	0,28	13
1980	36	1,19	0,18	15
1981	36	1,04	0,20	19

high during the growing season, crashes to very low levels at the coldest, driest time of the year. No evidence was found to suggest that numbers of small antelopes are limited by jackal predation.

Blesbok, red hartebeest, and black wildebeest, which were introduced into the reserve are not considered indigenous to GCGR as there is no evidence to indicate that they occurred there prior to its proclamation. The introductions of black wildebeest and hartebeest were unsuccessful. It is recommended that the remaining few black wildebeest be destroyed or captured. On the other hand, as the small population of hartebeest has not been the cause of any habitat destruction, they should be left. The blesbok population has become well established and the animals do not as yet appear to have been responsible for any habitat destruction. Suitable blesbok habitat in GCGR is limited, therefore it is recommended that the population be monitored to collect information on population structure and breeding rates. This should be done twice annually: in about August or September (before calving) and at the end of the calving season (in about January). If any signs of population stress or habitat destruction become evident consideration should be given to removing surplus animals.

The method of counting antelope along five fixed routes three times per month, which was employed in this study, has shown that great variability occurs. This was attributed to low densities and the large home ranges of sedentary species, great flight distances, complexity of the terrain, and the influence of veld burning on antelope movements. The method did prove satisfactory, however, for estimating numbers of antelopes in relation to the known population of eland, using an index and control formula (Caughley 1977).

The known-group method of counting, proposed by Mentis (1978) has certain advantages, but disadvantages are that more time, effort, and skill are required. Fixed route counts on the other hand can be efficiently executed by untrained staff.

Southgate (1979), in considering the effects of weather on counting in the Drakensberg, concluded that the period April to July was most suitable. As the index and control formula can be applied to count data only when eland are widely distributed throughout GCGR, it is recommended that route counts throughout the rest of the year be discontinued, but that 10 counts along the same fixed routes used in this study be done during July. If this is impracticable the counts may be spread over the period mid-June to mid-August. Annual total aerial counts of eland are planned (Scotcher in prep.), therefore numbers of a known population will be available.

It is finally concluded that the Drakensberg is an area in which the regular high rainfall during the warm season, and the opposite extremes in temperature and rainfall during the winter, result in extremes in herbage production and its nutritional content. Primary consumers increase during the season of plenty, but are limited by adverse conditions during the critical period. The black-backed jackal is the most successful carnivore in the area as it is an opportunistic feeder which benefits from increased numbers of suitably-sized prey and is able to supplement live prey with carrion during the lean period.

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APPENDIX 1. Species diversity of habitats and relative abundance of small mammals (number/100 trap nights) collected in the Cathedral Peak area. Habitats arranged in order of ascending altitude. AB = annual burn, BB = biennial burn, P = fire protected (with last fire in y), Occ B = occasional burn. Based on data from Rowe-Rowe (1977a).

		Mammal species											
Habitat		<u>M. varius</u>	<u>R. pumilio</u>	<u>O. irroratus</u>	<u>P. natalensis</u>	<u>M. minutooides</u>	<u>C. flavescens</u>	<u>D. mesomelas</u>	<u>I. dolichurus</u>	<u>G. murinus</u>	<u>O. sloggetti</u>	Total	Diversity
Montane Belt													
Tall grassland	P 10 y	-	3	1	3	-	1	-	-	-	-	8	1,21
Boulder-bed scrub	P 10 y	-	30	-	-	0,4	5	-	-	-	-	36	0,48
<u>Themeda</u> grassland	AB	0,3	4	-	1	1	0,3	-	-	-	-	7	0,74
<u>Themeda</u> grassland	BB	1	8	-	-	0,4	0,4	-	-	-	-	10	0,64
<u>Themeda</u> grassland	P 5 y	-	0,8	-	-	-	0,4	-	-	-	-	1	0,64
Scrub	BB	0,4	6	0,8	0,8	0,4	-	0,8	-	-	-	9	1,22
Forest margin	Occ B	3	0,8	-	-	-	-	0,8	0,4	2	-	7	1,37
Forest	P	3	-	-	0,4	-	-	-	0,4	3	-	6	1,08
Sub-alpine Belt													
<u>Protea</u> woodland	P 5 y	2	-	-	-	-	-	-	-	-	-	2	0,00
Tall grassland	BB	3	5	2	-	-	0,8	-	-	-	-	11	1,09
<u>Themeda</u> grassland	AB	-	4	2	-	-	0,4	1	-	-	-	8	1,11
<u>Themeda</u> grassland	BB	3	7	3	-	0,4	0,4	0,4	-	-	-	14	1,30
<u>Themeda</u> grassland	P 11 y	8	4	3	-	-	-	-	-	-	-	15	0,99
<u>Leucosidea</u> scrub	P 11 y	7	7	3	-	-	-	-	-	-	-	16	1,02
<u>Philippia</u> scrub	P 11 y	8	2	0,4	-	-	-	-	-	-	-	10	0,66
Temp grassland	AB	2	-	-	-	-	-	-	-	-	-	2	0,00
Temp grassland	BB	10	-	0,8	-	0,4	0,4	-	-	-	-	11	0,57
Alpine Belt													
<u>Erica-Helichrysum</u>	Occ B	*	-	-	-	-	-	-	-	-	*		

* Present

APPENDIX 3. Occurrence and per cent occurrence of arthropods identified in the stomachs of M. varius and R. pumilio collected in GCGR during April and August. (Identifications provided by Dr R. Miller, Dept of Entomology, University of Natal.)

Arthropod taxon	<u>M. varius</u>		<u>R. pumilio</u>	
	N = 29		N = 42	
	Occ.	% occ.	Occ.	% occ.
Crustacea	2	7	1	2
Myriapoda	3	10	-	-
Arachnida	6	21	6	14
Insecta				
Diptera - adults	2	7	-	-
- larvae	3	10	-	-
Coleoptera - adults	17	58	12	29
- larvae	9	31	1	2
Hymenoptera	10	34	6	14
Lepidoptera - larvae	1	3	4	10
Dictyoptera	1	3	-	-
Orthoptera	11	38	4	10
Hemiptera	6	21	5	12
Psocoptera	1	3	-	-

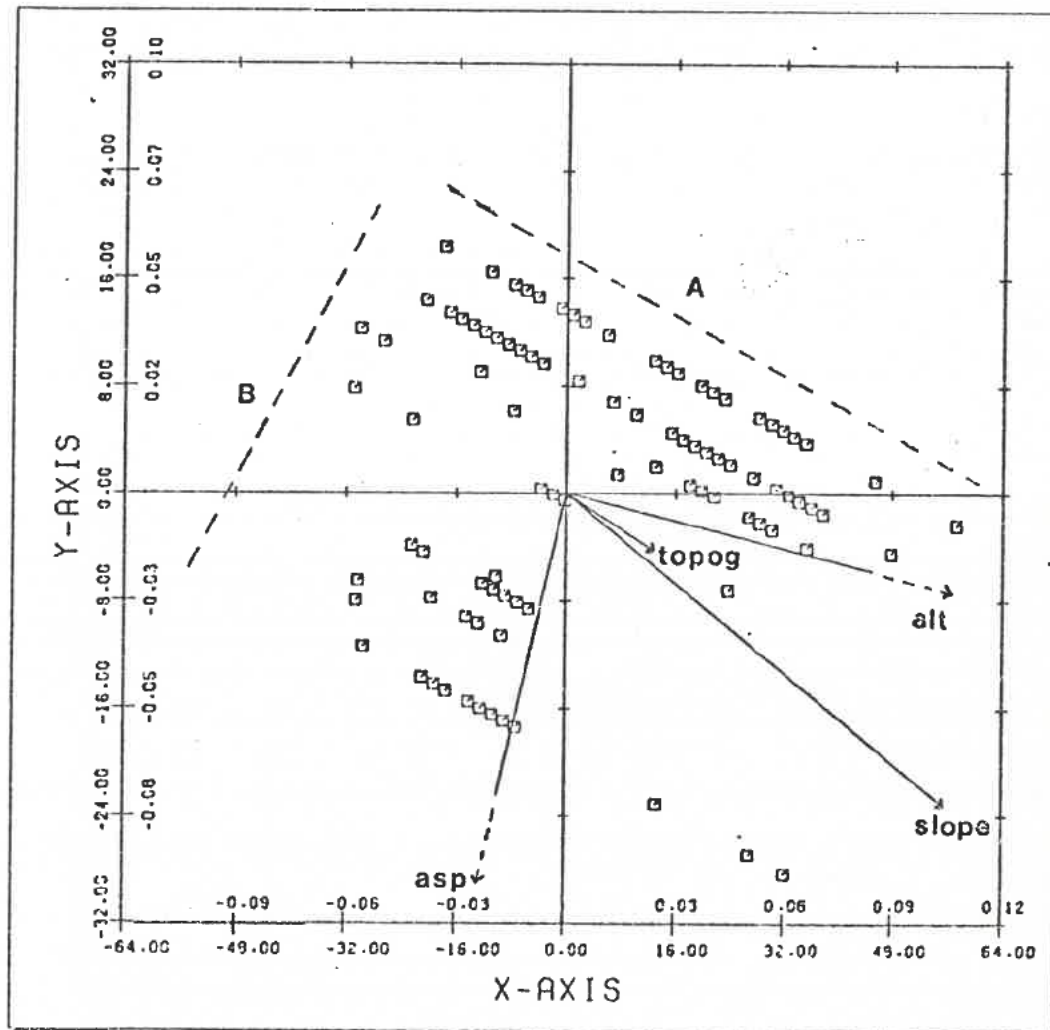


Figure 1. Biplot of the distribution of an antelope in relation to four variates.

1. The length of the variate vector (indicated by an arrow) approximates the variance of the particular variate.
2. The cosine of the angle between the variate vectors (arrows) approximates the correlation between those variates. The larger the angle, the smaller the correlation.
3. In the example (Fig 1) there are therefore high correlations between altitude, topography, and slope; but low correlations between aspect and the other variates.
4. The distribution of the species illustrated in Fig 1 shows a wide dispersion in relation to altitude, topography, and slope (dotted line A). The plot of aspect (dotted line B) on the other hand shows most observa-

tions grouped around the lower values ($= 0^\circ$ to 90° i.e. N to E slopes) and very few in the middle values ($=$ SE, S, and SW slopes).

5. Objects having the same value are located on the same line at right angles to the variate vector (see examples of slope in Fig 2). The range of values increases from left to right for altitude, slope, and topography; and from top to bottom for aspect. Two or more objects of a particular variate would be plotted at different distances from the variate vector if influenced by other variates (Fig 2).

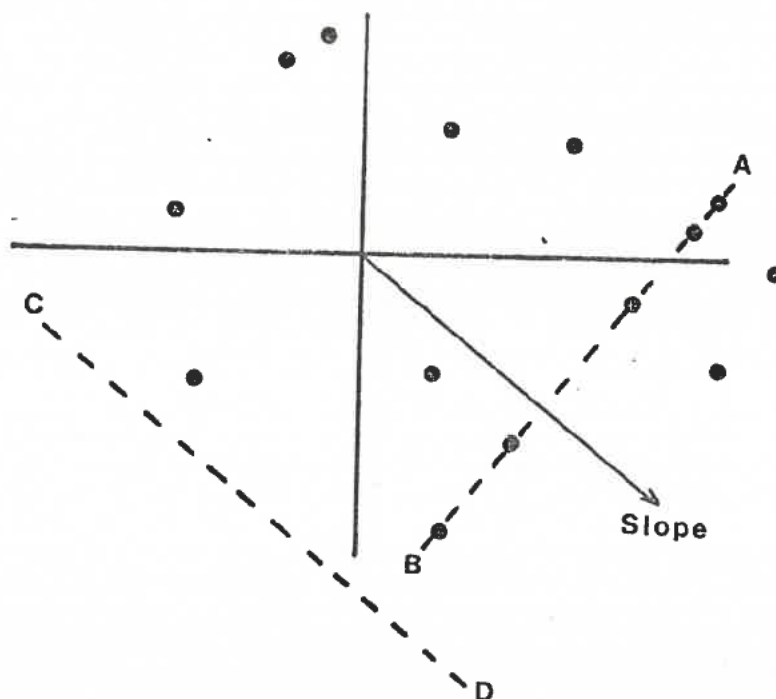


Figure 2. All objects plotted along the line AB, at right angles to the slope vector, will have the same slope value. Their different positions are determined by the influence of other variates. The range of values for slope is indicated by CD, increasing from C to D.

Short communication

Steel-jawed traps for live capture of black-backed jackals

D.T. Rowe-Rowe and B. Green

D.T. Rowe-Rowe*

Natal Parks Board, P.O. Box 662,
Pietermaritzburg, 3200 Republic of South Africa

B. Green

CSIRO Wildlife Research Division, P.O. Box 84,
Lyneham, ACT 2602, Australia

*To whom correspondence should be addressed

Received 26 July 1980; accepted 10 December 1980

Steel-jawed traps have been successfully used for the live capture of some canids, e.g. wolf *Canis lupus* (Kolenosky & Johnston 1967), coyote *C. latrans* (Hawthorne 1971), and dingo *C. familiaris dingo* (Green 1976). Bothma (1971a) captured black-backed jackals *C. mesomelas* using snares, steel-jawed traps, greyhounds, and by digging out dens. Steel-jawed traps proved least successful and capture effort was enormous (Bothma, pers. comm.).

We successfully used steel jump traps to capture black-backed jackals in Giant's Castle Game Reserve (29°15'S 29°30'E), a mountainous, predominantly grassland area. As no published information was available on catching this reputedly wary animal in jump traps, we describe our technique and present our results.

No. 3 Oneida Jump traps (Woodstream Corp., Lititz, PA 17543, U.S.A.) were used. Traps were padded with two layers of cotton mutton cloth, which was first cut into strips about 40 mm wide, then tightly bound around the jaws. Traps were attached to a 300-mm galvanised iron peg by a 500-mm length of chain into which a 200-mm coil spring had been inserted (Figure 1). The spring was capable of withstanding 20 to 25-kg pull before the elastic limit was reached.

Methods of siting and setting traps were based on those used for the capture of dingoes (Green 1976) and those recommended for coyote (Henderson 1970) and foxes *Vulpes* spp. (Fairol 1979), with certain modifications.

Traps were set about 1 km apart beside vehicle tracks and footpaths, not more than 1 or 2 m from the likely path of a jackal. A trowel was used to dig a shallow hole and trench to accommodate trap and chain, all soil removed being placed on a sheet of plastic. After placing the set trap in the hole and anchoring it, a 150 × 150-mm cotton cloth was placed over the trigger plate (to prevent soil from getting under it), and the trap, chain and protruding portion of the peg were buried. A final covering of fine soil was sprinkled over the area and a stick was used to smooth the whole site to remove signs of disturbance. If any soil was left on the plastic sheet, it was discarded in the grass some distance away.

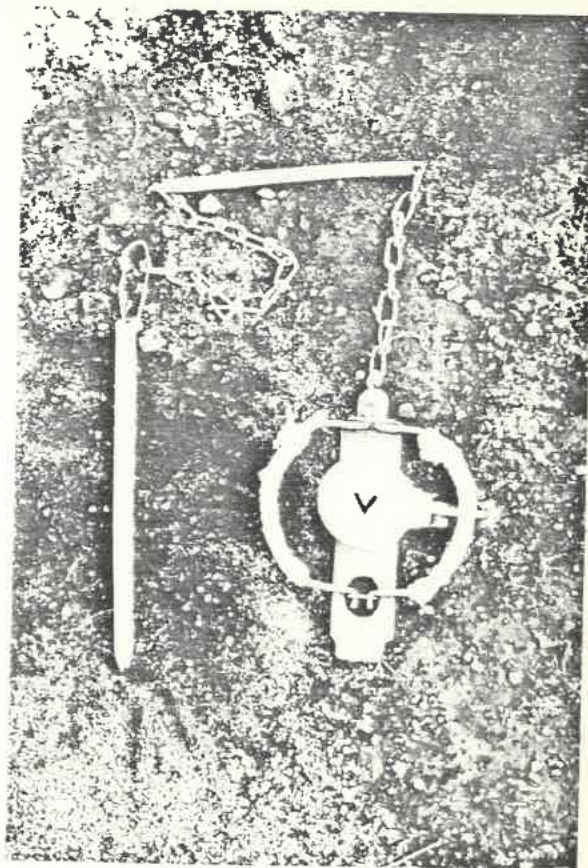


Fig. 1 Oneida jump trap with padded jaws, anchor peg and a spring in the anchor chain.

As far as possible traps were set where natural objects (such as grass tufts) could form the wings (Figure 2), but if these were not present, large stones were placed on either side and at the back of the set (Figure 3) so that the jackal would have to approach the bait by stepping on the trigger plate. A few small stones were placed at the entrance of the set, narrowing access and thereby reducing the chance of the jackal's foot missing the plate (Figures 2 and 3).

A small stick was dipped into the bait and placed about 400 mm from the trigger pan. The bait used was either a mixture of putrified mince meat and canned sardine, or jackal faeces which had been collected in the field and soaked in water. The meat/sardine bait had the disadvantage of attracting a number of non-target animals, whereas the jackal faeces appeared to be more specific in attraction. However, during warm wet periods faecal baits were torn apart and moved by dung beetles (Scarabidae), thereby requiring frequent re-baiting of traps.

Traps were checked as soon as possible after dawn each day. Captured animals were pinned down using two forked sticks: one person pinning the trap and the jackal's leg and the other person the back of its neck, and an immobilising injection was given into the rump (Rowe-Rowe & Green 1980). If an animal had injured itself in the trap it was given an injection of long-acting penicillin and the injury was sutured.

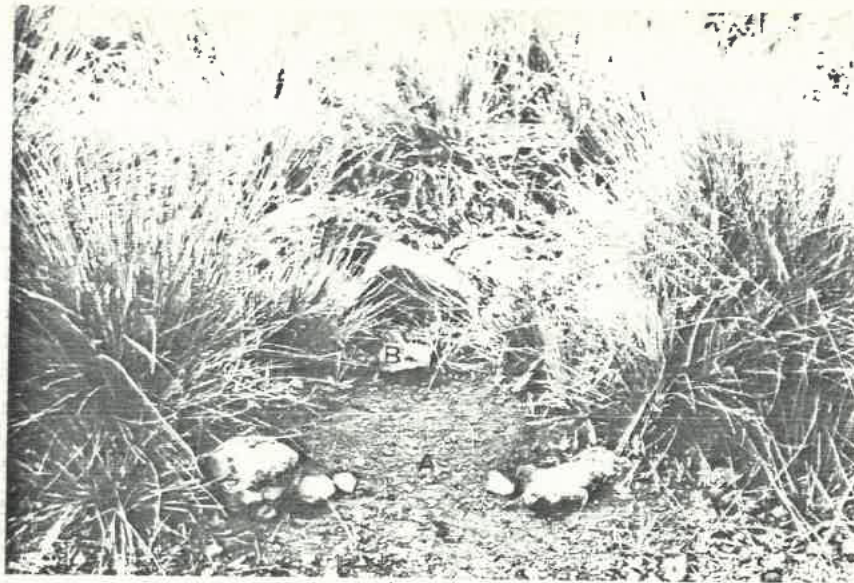


Fig. 2 Natural set, using grass tufts as wings. The trigger plate (A) is just beyond the small stones at the set entrance. The bait stick (B) is placed on a stone at the rear, about 400 mm from the plate.



Fig. 3 Constructed set, with large stones and logs used to form wings and close off the rear.

Fifteen jackals were captured in 462 trap nights, i.e. 31 trap nights/capture. Three animals were completely uninjured, nine suffered minor skin cuts, tendons were exposed in two cases, and one jackal's foot pad was cut. The male:female ratio was seven:eight, 11 jackals were classified as adult, and four as immature (< 1 year old).

Seventeen non-target animals were captured: six birds, nine carnivores, a porcupine, and an antelope. In addition four animals were captured but escaped: a porcupine, a water mongoose, and two which were not identified.

Traps which were set where there was no fresh sign of jackals were unsuccessful (no captures were made in 206 trap nights), whereas traps set where there was fresh sign resulted in 15 captures in 256 nights (17 trap nights/capture). Five jackals were caught on the first night of trapping, seven on the second, one on the third and two

on the fourth. No captures were made after the fourth night, although traps were left in the ground for up to eight nights in some areas.

There are no published comparative figures on the capture of jackals using steel-jawed traps, however, Lensing & Roux (1975) reported an effort of 220 trap nights/jackal using snares.

We do not recommend setting a trap at a particular site for more than five nights. If no captures are made within this period, traps should be moved to where there is fresh jackal sign. When using coyote getters for jackal control (Bothma 1971b) a success pattern similar to ours was observed: most jackals were killed during the first few nights after setting a getter, thereafter its efficiency decreased rapidly and remained low.

Attaching a trap to a drag (either a log or a double hook) is a method which reputedly results in little damage

to the captured animal's foot (Henderson 1970, Cornely 1979). This was not practicable in Giant's Castle as most of the area is treeless and the dense grass cover would make following the trapped jackal virtually impossible.

We believe that injuries are minimised by padded jaws and the use of a spring in the anchor chain. The trap's jaws should, however, not be too thickly padded, as the jackal can then chew the cloth away around its foot, and the padding at the edges holds the jaws far enough apart for it to escape. Failor (1979) recommended using a very short chain for fox capture, but he was concerned with the capture of animals for their pelts, and the short chain was advocated as the fox then had least chance of escaping. Hawthorne (1971), on the other hand, found that padded jaws and a 600-mm chain resulted in least damage to coyote's feet.

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Short communication

Ketamine and acetylpromazine for black-backed jackal immobilization

D.T. Rowe-Rowe and B. Green

D.T. Rowe-Rowe*

Natal Parks Board, Postbox 662, Pietermaritzburg 3200
South Africa

B. Green

CSIRO Wildlife Division, Postbox 84, Lyncham, ACT 2602
Australia

*To whom all correspondence should be addressed

Received 14 March 1980; accepted 29 April 1980

As part of a study of black-backed jackal (*Canis mesomelas*) in the Natal Drakensberg, animals were live-trapped and immobilized. In some instances it was necessary to immobilize the jackal for about 30 min while a radio collar was fitted, or for 4 h to allow the fitting of a collar, separate injections of radio active sodium and radio active water, and the collection of a calibration blood sample in an attempt to estimate food and water turnover (Green 1978).

Mean body masses of adult male and female jackals in the Drakensberg are 8,4 and 7,7 kg respectively (Rowe-Rowe 1978). An initial intramuscular dose of 100 to 150 mg (12–19 mg/kg) ketamine hydrochloride was therefore chosen, which is within the recommended dose rate for canids (Beck 1976, Harthoorn 1976). As the manufacturers of ketamine (Ketalar, Parke-Davis) and Beck (1976) comment on the safety of administering repeated doses of the drug, it was initially decided to adopt this method of maintaining anaesthesia for as long as 4 h.

In this communication we report on the use of ketamine alone and in combination with acetylpromazine for induction and maintenance of anaesthesia in jackals. The pharmacological aspects of ketamine have been dealt with by Harthoorn (1976).

Results

Four jackals (mean mass 8,3 kg; range 7,5–9,0 kg) were immobilized with a single 100 mg intramuscular injection of ketamine (mean dose 12 mg/kg; range 11–13 mg/kg). All of the animals recovered fully. Anaesthesia was induced in 4 to 5 min (mean 4,8 min). Recovery started after about 45 min with the animal raising its head and moving its limbs. Once this stage had been reached, however, the animal would struggle when handled, and reacted to other external stimuli. At about 90 min the animals staggered a few steps, but only gained full locomotor co-ordination at about 150 min.

Maintenance of anaesthesia was attempted in three jackals (7,3; 7,8; & 8,3 kg) by administering initial doses of 21, 13, and 18 mg/kg ketamine respectively, then additional half or full doses over a 4 h period. Induction time was 4 min in each of these animals. Total dosages over 4 h amounted to 400 mg ketamine per animal (i.e. 55, 51 & 48 mg/kg). One jackal (mass 7,3 kg) took more than 10 h to recover. The other two died. After 11 h both of these animals could raise their heads, but recovery did not progress beyond this stage.

For the immobilization of five jackals (mean mass 7,4 kg; range 6,2–8,5 kg) a combination of 100 mg ketamine and 2 mg acetylpromazine (tranquilliser) was used. Mean ketamine dose was 17 mg/kg (range 13–21 mg/kg) and mean acetylpromazine administered was 0,27 mg/kg (range 0,23–0,32 mg/kg). Mean induction time was 4 min (range 3–5 min). All of these animals recovered. After the injection of radio isotopes and the fitting of collars each animal's legs were tied, it was placed in a hessian bag, and left in the shade. In three cases, when removed from the bag after 4 h to take blood samples, the jackal woke up, but remained calm while handled. On release two jackals ran away, but in the third, an immature animal of 6,2 kg, this response was delayed. The other two jackals, which were fitted with collars and not injected with isotopes, ran away when released after 3 h.

Another two jackals (7,3 & 6,2 kg) which were fitted with radio collars only, were immobilized with 50 mg ketamine (7 & 8 mg/kg) and 1 mg acetylpromazine (0,14 & 0,16 mg/kg). Induction times were 4 and 3,5 min. After 21 min the animals raised their heads, attempted to stand and bite when handled at 31 min, and got up and ran a few steps (when approached) at 55 min. Both jackals recovered fully.

Conclusions

The induction of anaesthesia in jackals immobilized with ketamine was rapid, with little difference when doses of between 7 and 21 mg/kg were administered. If jackals are to be immobilized for a brief period we recommend a dose of approximately 8 mg/kg ketamine, preferably in combination with about 0,15 mg/kg acetylpromazine. For longer periods of immobilization we suggest about 15 mg/kg ketamine in combination with about 0,25 mg/kg acetylpromazine.

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