THE HABITAT AND FEEDING ECOLOGY OF THE KLIPSPRINGER

Oreotragus oreotragus (Zimmermann,1783)

IN TWO AREAS OF THE CAPE PROVINCE

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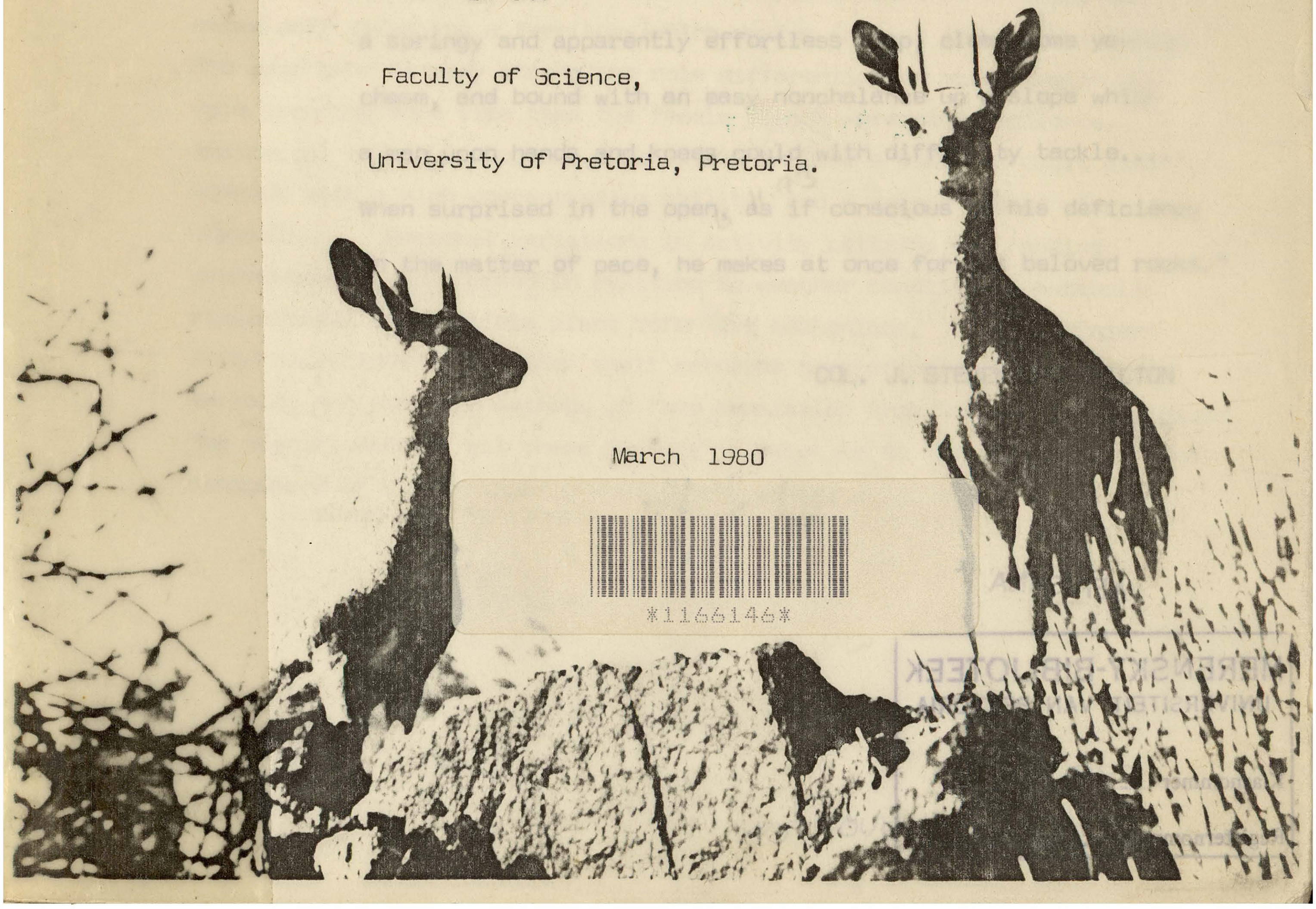

To the couple

who taught me to love and respect the mountains

"Often, as the wayfarer passes beneath some towering crag, he may notice silhouetted against the skyline, hundreds of feet above his head, a compact little form, the ears inquisitively cocked, and the nose extended in his direction. As he lingers to obtain a better view he sees the animal, by a springy and apparently effortless leap, clear some yawning chasm, and bound with an easy nonchalance up a slope which a man upon hands and knees could with difficulty tackle..... When surprised in the open, as if conscious of his deficiency in the matter of pace, he makes at once for his beloved rocks.'

COL. J. STEVENSON-HAMILTON

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by

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ABSTRACT

The study investigates the habitat preferences and ecological adaptations of the klipspringer in the Namaqualand and the southern Cape mountains. Klipspringer social organisation was found to consist of a monogamously mated pair defending a territory which varies in size according to rainfall. The pair bond is very strong and role differentiation occurs, with the male spending more time than the female in anti-predator vigilance. Anatomical and physiological adaptations include a modified digit structure, kidneys with a high concentrating ability, and a unique pelage for insulation. Seasonal variations in activity patterns and feeding preferences are discussed in relation to weather conditions, metabolic requirements and possible plant defensive mechanisms. Klipspringers avoid competition with other small antelope by preferring more rocky terrain, and possible methods of food separation from dassies are suggested. The significance of all these factors in relation to the conservation and management of klipspringer populations is examined.

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CHAPTER 1 : GENERAL

INTRODUCTION

The klipspringer, Oreotragus oreotragus (Zimmermann 1783), has one of the widest geographical ranges of any antelope in Africa, occurring from the mountains of the southern Cape northwards to the highlands of Ethiopia. However, in spite of this range, it has received very little attention from scientists and, until recently, not much was known about even the most basic aspects of its biology. This is largely because of its preference for inaccessible rocky mountain habitats which makes study difficult.

In the Cape the presence of klipspringers has been recognised for some time, with the first record of klipspringers on Table Mountain as long ago as 1679 (Raven-Hart 1966). They have been hunted for many years, especially for their coarse hair which was popular for stuffing saddles (Harris 1840, Inverarity 1899), though their flesh was also popular (Sclater and Thomas 1897, Vaughan-Kirby 1899). This has led to the extermination of the klipspringer in some areas, such as the Cape Peninsula, and a marked decline in numbers over most of its range.

This project was initiated to study the species and its relationship to rocky habitat in the Cape Province, so that its conservation status may be realistically determined and so that various management practices such as translocations, re-introductions and controlled hunting may be organised on a sound scientific basis.

Since both of the recent major studies on klipspringers by Tilson (in press) in South West Africa and by Dunbar and Dunbar (1974 and in press) in Ethiopia concentrated mainly on aspects of the behaviour of the species, the present study was orientated towards the habitat and the ways in which klipspringers have adapted to cope with the rugged conditions of mountainous areas, not only in feeding behaviour and social organisation but also with regard to anatomical and physiological adaptations. This helps us to understand exactly what is suitable habitat for klipspringers, how the buck is affected by the different factors in its environment, how it fulfills its energy requirements from the unique fynbos vegetation of the southwestern Cape, and how wild populations should be managed to maintain a stable state.

LITERATURE

Most of the literature on klipspringers consists of short general accounts of habits and distribution as part of works on large groups of mammals, but the only important field studies specifically on the klipspringer were those of Wilson and Child, Dunbar and Dunbar, and the study of Tilson's (May 1976 - June 1979) that ran concurrently with the present study.

Wilson and Child (1965) analysed 90 carcases of klipspringers shot during tsetse control operations in Zambia, giving mainly weights and measurements, but with some observations on feeding, group size and habitat preference. Dunbar and Dunbar (1974) made a useful preliminary study of klipspringer social organisation and ecology, and have followed this up (in press) with more detailed studies of pair-bonding and behavioural ecology.

Tilson has written a paper on social structure and predator avoidance (in press), and has others on energetics and pair-bonding in preparation. Odendaal (1974) analysed the results of sightings of klipspringers by foresters on patrol in the southern Cape forestry areas and gives some interesting observations on population dynamics.

Qvortrup and Blankenship (1974) analysed the stomach content of a female klipspringer shot in Kenya, and Jacobsen and Catto (1974) give a few observations on behaviour and feeding in the Magaliesberg of the Transvaal. Cuneo (1965), Niethammer (1942) and Priemel (1942) give information on klipspringers in captivity with some references to free-living animals.

STUDY AREAS

Although the klipspringer is completely restricted to rocky habitats, it is a wide-ranging species, and any attempt to evaluate its habitat preferences should thus include as wide a range as possible. However, due to the limited time available for the project, it was decided to concentrate on two main study areas which were selected for the contrast they offered in habitat conditions.

As Tilson's research on klipspringers covers the extremely arid environment of the Kuiseb Canyon in South West Africa, it was decided that the habitat conditions selected should be semi-arid and medium to high rainfall to possible in topography and vegetation. The main study areas at Springbok and Gamka were chosen because they have semi-arid and medium rainfall regimes, and are characterised by very different landscapes with granite and sandstone substrates respectively.

The Springbok study area is situated in the Hester Malan Nature Reserve about 10 km south-east of Springbok (Fig. 1). The main study area covers about 400 ha on the Carolusberg mountain, though the whole reserve is about 5200 ha. The main klipspringer study territory is situated about 2 km north-west of the Carolusberg beacon, around 29° 38' S 19° 59' E.

The Gamka study area is situated in the Gamka Mountain Nature Reserve in the mountains west of Oudtshoorn. The reserve is about 9400 ha in extent, but only a small area of about 200 ha was used for the intensive study. The main klipspringer study territories are located around 33° 44' S 21° 56' E.

Additional work was started in the high rainfall Zacchariashoek Catchment Experiment area of the La Motte State Forest in the mountains between Paarl and Franschhoek in the western Cape, although this area proved unsuitable for detailed study. The tame group of klipspringers that was used for growth studies was kept in the Augrabies Falls National Park west of Upington in the northern Cape.

CLIMATE

Precipitation

The Springbok study area is situated in the semi-arid winter rainfall region of the Namaqualand, while the Gamka study area has a medium rainfall which falls in both winter and summer.

The nearest long-term weather station to the Springbok study area is at Okiep, 10 km to the north-west, where there is a mean annual rainfall of about 160 mm, of which 75% falls from April to September (Fig. 2). There is considerable local variation, both within the reserve and in the surrounding areas, due to the presence of isolated thunderstorms in summer (Rösche 1978, Le Roux in prep.). In addition, the rainfall fluctuates markedly from year to year, as shown by the low figures of 127 mm for 1977 and only 55 mm for 1978 at the office of the Hester Malan Nature Reserve

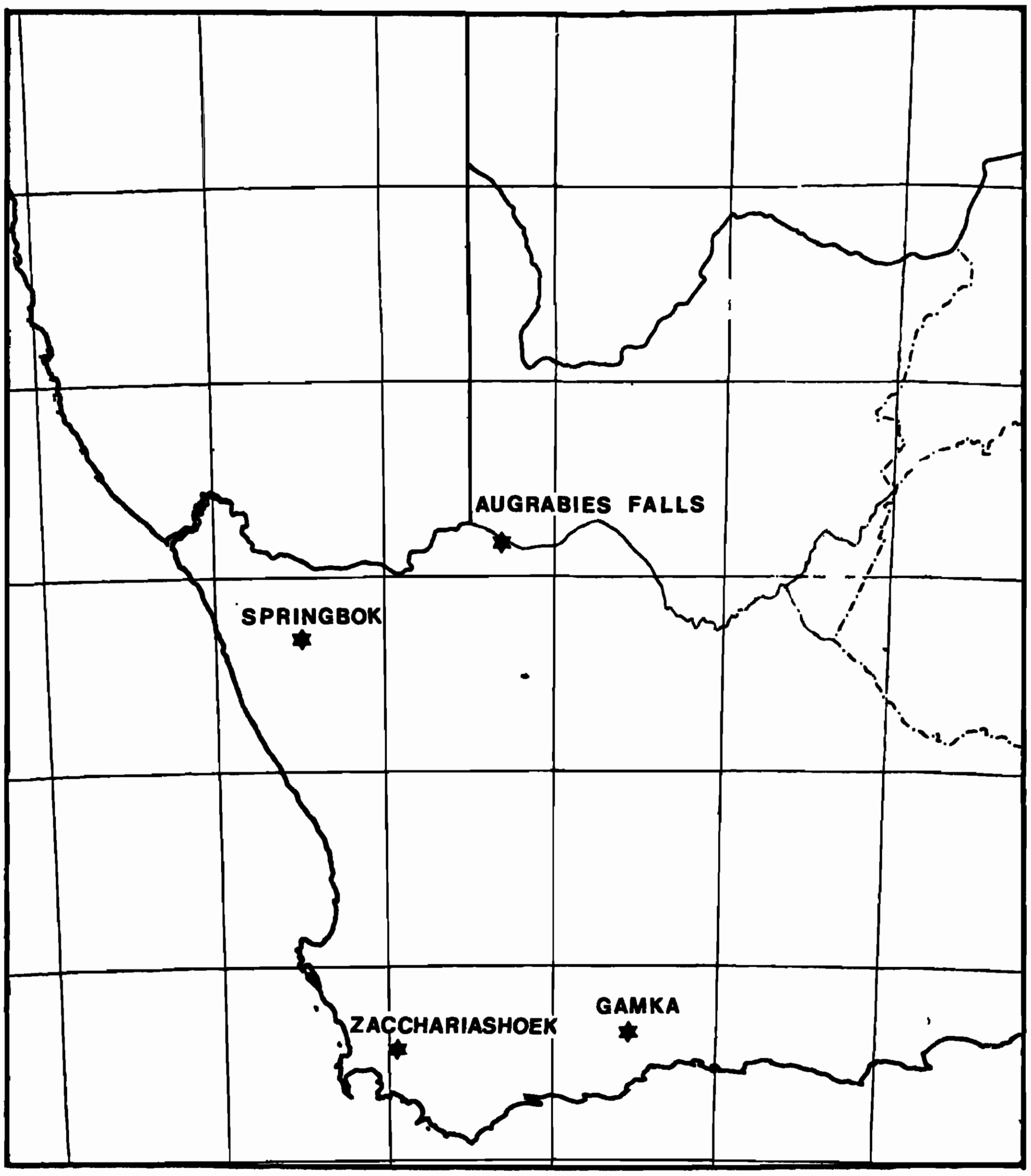


Fig. 1: Localities of klipspringer study areas in the Cape Province of South Africa.

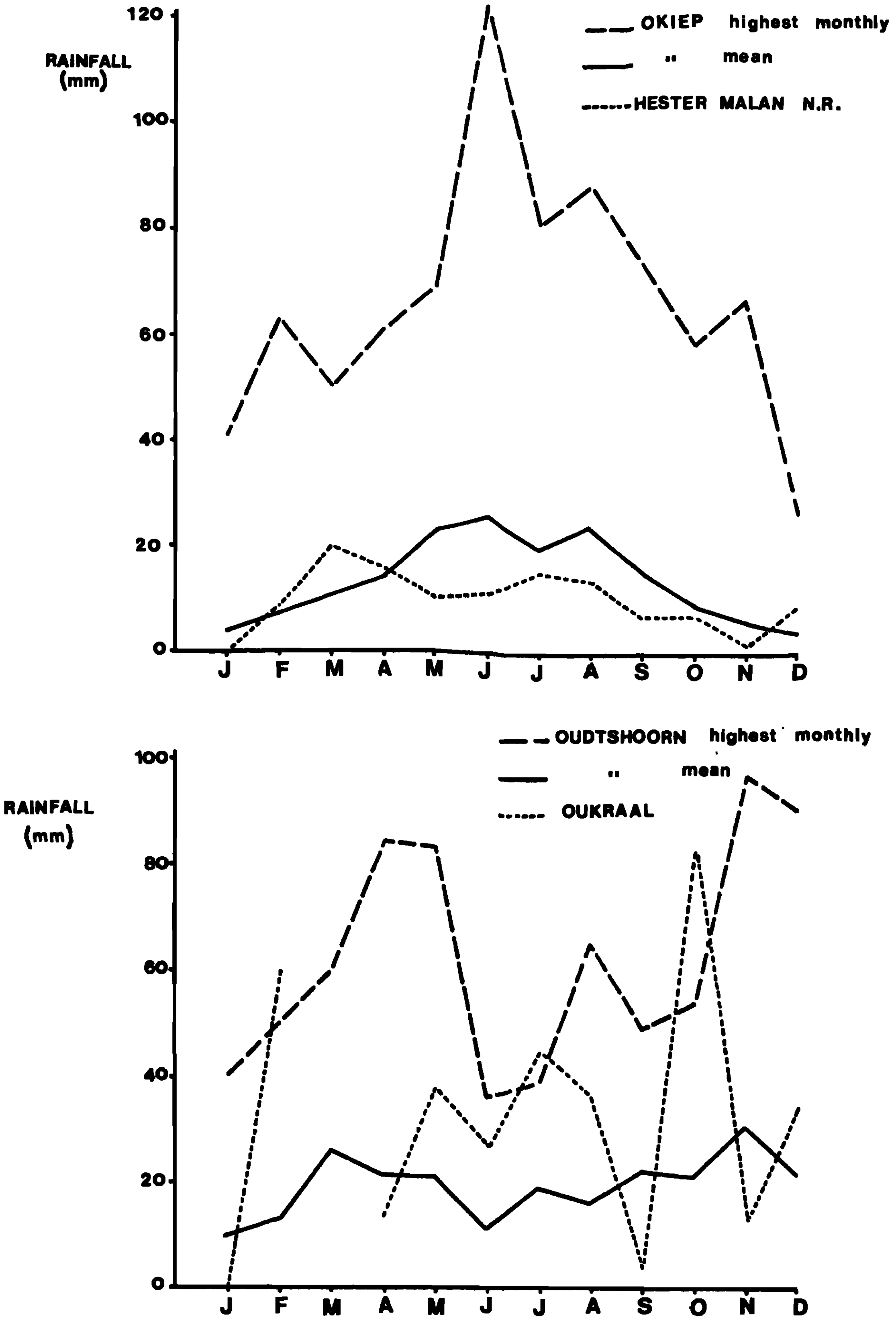


Fig. 2: Seasonal variation in rainfall in the main study areas at Springbok and Gamka.
a) The monthly rainfall at the Hester Malan Nature Reserve for 1977 (monthly reports C.D.N.E.C.) is shown in relation to the mmean and highest monthly rainfall at Okiep for the years 1881 - 1950 (Dept Transport 1954).
b) The monthly rainfall at the "Oukraal" station at Gamka for April 1976 - February 1977 (unpublished records C.D.N.E.C.) is shown in relation to the mean and highest monthly rainfall at Oudtshoorn (Convent Station) for 1926 - 1950 (Dept Transport 1954).

(unpubl. records C.D.N.E.C.), and the very high values for the highest monthly rainfall in 70 years at Okiep. Besides rainfall, dew and mist precipitation from the moisture-laden westerly wind that comes up from the coast forms an important source of moisture for the plants and animals in the area.

For Gamka the nearest long-term weather station is 25 km away at Oudtshoorn, which is likely to receive less rainfall due to its lower altitude, but with a similar seasonal variation. The 1 : 250 000 rainfall map for the area shows an estimated rainfall of over 400 mm, and the total of 352 mm for April 1976 to February 1977 at the Oukraal station at Gamka (Fig. 2) suggests that the annual rainfall in the study area is about 350-450 mm. Figure 2 shows that at Oudtshoorn the rain falls evenly throughout the year, with 47% of the annual total from April to September, but there are slight peaks from March to May and from September to November. However, the seasonal pattern at Gamka may prove to be slightly different due to an increase in orographic rainfall in winter.

Temperature

The seasonal variation in air temperatures in the study areas is shown by the monthly values for 70 years at Okiep and for April 1976 to February 1977 at the Oukraal station at Gamka (Fig. 3). For Gamka the values from the Oudtshoorn station were not used because of its much lower altitude. There is little difference between the graphs for the two study areas, though Gamka appears to be slightly colder with temperatures regularly below 0°C in winter, while the mean lowest monthly temperature at Okiep seldom drops as low as freezing point. In both areas the highest monthly temperatures rise to over 35°C in the summer.

GEOLOGY AND GEOMORPHOLOGY

The landscape of the Gamka Mountain Reserve can broadly be described as rocky mountainous terrain (Fig. 4). The reserve is situated on a large mountain massif surrounded by alluvial plains in the Little Karoo region of the Cape Fold Belt.

The mountain forms one of the numerous smaller anticlines which make up the minor ranges of the southern belt of the Cape System (King 1963).

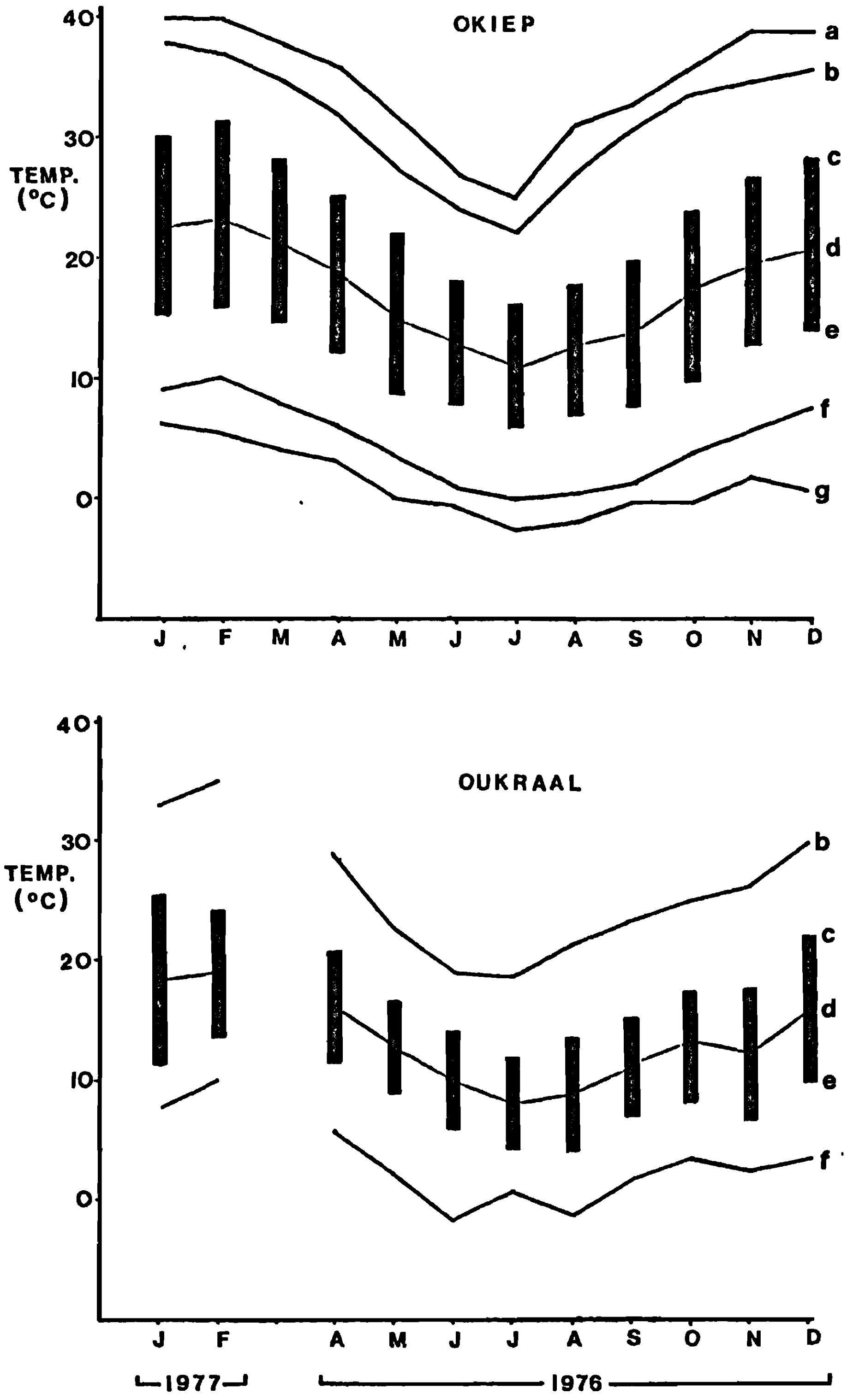


Fig. 3: Seasonal variation in temperature at Okiep for the years 1881 - 1950 (Dept Transport 1954) and at the "Oukraal" station at Gamka for April 1976 - February 1977 (unpubl. records C.D.N.E.C.).

a - Absolute maximum
b - Mean monthly maximum
c - Mean daily maximum
d - Mean daily
e - Mean daily minimum
f - Mean monthly minimum
g - Absolute minimum

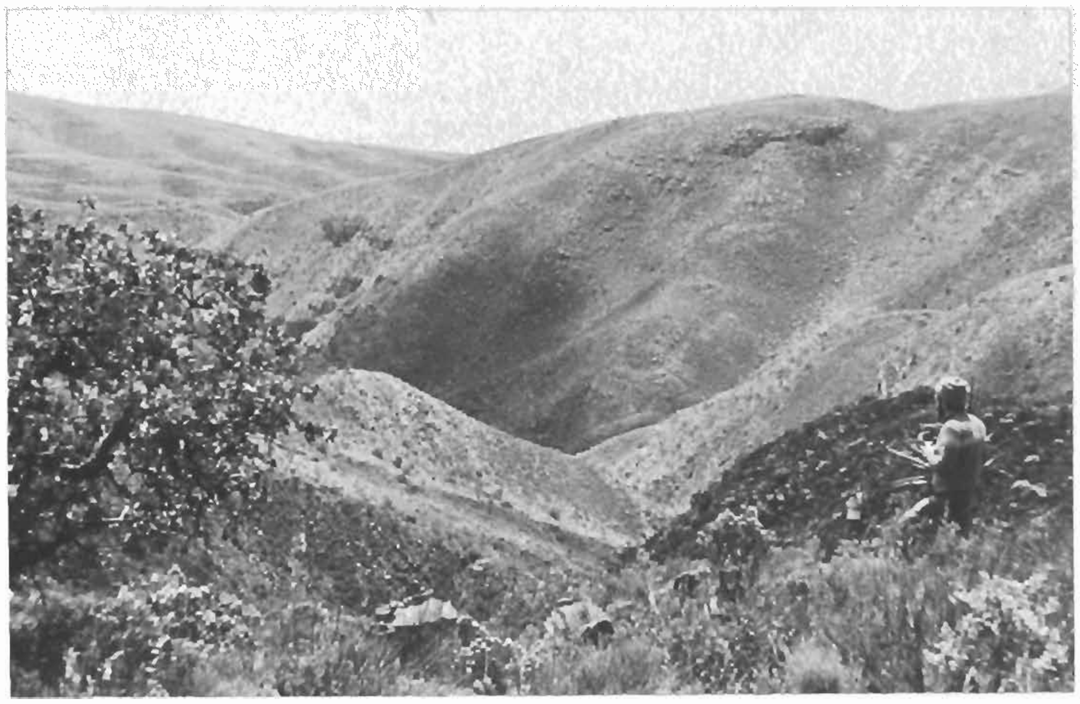


Fig. 4: General view of the terrain at Gamka, showing the level plateau divided by deep valleys.

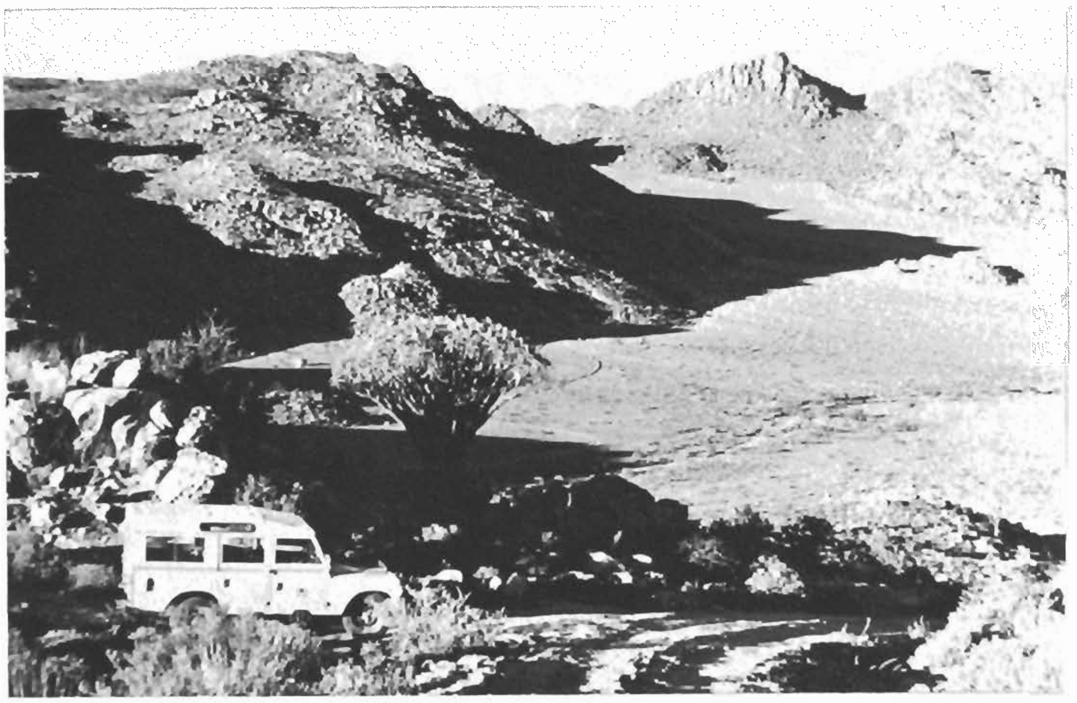


Fig. 5: General view of the terrain at Springbok, showing rocky koppies separated by sandy flats.

It is roughly half-way between the major ranges of the Swartberg to the north and the Langeberg to the south, and the strike is east-west and parallel to these ranges. The mountain consists basically of Table Mountain Sandstone covered by shales of the Bokkeveld series, although these have been eroded away over most of the reserve area.

The mountain is dissected by deeply incised valleys which start off as broad shallow basins but gradually deepen and narrow to form steep-sided gorges. The main klipspringer study area at the top of Tierkloof consists of a fairly level plateau of Table Mountain Sandstone with two drainage systems that have eroded to form deep valleys running east and west from the narrow bridge that separates them (Fig. 8).

The highest point in the reserve is Bakenskop (1106 m) which is just north of the main study area. The bridge between Tierkloof and Klippe se Kloof is at about 1005 m.

The Springbok study area is situated in the Granite-Gneiss region of the Namaqualand Basement Complex (Truswell 1970). The land form shows an intermediate stage in the pediplanation cycle, with large granite koppies rising out of gently-sloping alluvial plains (King 1963). Towards the east the landscape becomes more and more mature as the inselbergs decrease in size and abundance until they are completely covered by the flat sandy plains of the Bushmanland.

The koppies consists of large granite exfoliation domes which rise abruptly from the plains, as is typical of landscapes formed under arid and semi-arid conditions (Fig. 5). There is some variation in the type of weathering the rocks have undergone, with extensive flat slabs with loose thin sheets resulting from the exfoliation of concentric layers in some places, while in others large rounded boulders have separated from the parent rock to give a "parapet" form to the koppies (King 1963).

The main klipspringer study group occupied a territory at an altitude of about 1280 m, about two kilometres north-west of Carolusberg which, at 1345 m, is the highest point in the reserve.

VEGETATION

The vegetation of the Gamka Nature Reserve is heterogeneous, since three of Acocks' (1953) veld types are represented there and each one belongs to a different major group. The "Succulent Mountain Scrub or Spekboomveld" (No. 25) is considered to be a "karoo" type and occurs on the dry north-facing slopes at low altitude on the northern side of the reserve. "Mountain Rhenosterbosveld" (No. 43), a "False karoo" veld type, and "False Macchia" (No. 70), a "False Sclerophyllous" bush type, are both represented on the higher parts of the mountain that collect more precipitation.

At Springbok the vegetation is more homogeneous, and only two veld types are represented in the Hester Malan Nature Reserve. On most of the rocky areas the vegetation is of the "Namaqualand Broken Veld" (No. 33) type, while a small amount of "False Succulent Karoo" (No. 39) occurs in the flatter north-western corner of the reserve.

GENERAL METHODS

A two or three week field trip was made to each study area during each season from April 1977 to July 1978. The first priority was to carry out at least three days of continuous activity study on two or three main groups in each study area. During the activity study all social behaviour was noted or described on tape for later transcription. In addition, feeding records were made by describing on tape the location of the shrubs for later checking.

At all times during the fieldwork the size and composition of klipspringer groups sighted was noted. These were plotted on large-scale aerial photographs for analysis of densities and territory size. Individual groups were recognised by noting unusual features such as ear patterns, horn length, colour, and scars. No systematic census of the klipspringer groups was made, but this method proved sufficient to determine the approximate densities and territorial boundaries.

To assess resource partitioning between klipspringers and other small antelope at Gamka, all sightings of steenbok, grysbok and vaalribbok were noted in the same way as klipspringer sightings and their position marked on aerial photographs for analysis of habitat preferences. Since individual groups of these small antelope could not be recognised, a census was carried out in February 1979 to estimate the approximate numbers of small antelope in the study area.

Food separation of klipspringers and dassies was studied by shooting a small sample of dassies during each visit and preserving their stomach content for later analysis of feeding preferences. In the main klipspringer study territory at Springbok spatial separation of the two species was assessed by plotting their dung sites on aerial photographs.

There are certain aspects of the biology of wild animals that can only be studied by examination of fresh carcases of those animals. Thus late in the fieldwork period a small sample of five klipspringers, two from Springbok and three from Gamka, was shot. Their stomach contents were analysed for comparison with the observational feeding records, and their skins, kidneys, liver, blood and urine samples were collected for physiological and anatomical studies. Further material was collected from a young klipspringer caught by black eagles at Springbok and a klipspringer shot because it was causing damage to a vineyard on a farm near Franschhoek.

The habitats occurring at Gamka were described by sampling 79 plots spread throughout the study area and noting the cover of rock, bare ground and vegetation, and the different vegetation height classes. In addition, the phenology of the vegetation was monitored during each visit in eight of the plots on the rocky slopes. At Springbok a smaller number of habitat analysis plots was laid out as there is less variation and the detailed studies of Le Roux (in prep.) and Rösche (1978) could be used. In both study areas the frequency and cover of the most important shrub species were noted for the plots on the rocky slopes. These could be converted to overall cover and related to the frequency in observational feeding records to give an idea of klipspringer feeding preferences.

Data on growth of young klipspringers were gathered from two semi-tame individuals, one at Springbok and the other at Augrabies Falls. At Augrabies the tame family group was watched to compare some aspects of their behaviour with that of the wild populations.

Capture of wild klipspringers was first attempted unsuccessfully on a farm near Ladismith, and later a more successful capture operation was carried out in the Vrolijkheid Nature Reserve near Robertson.

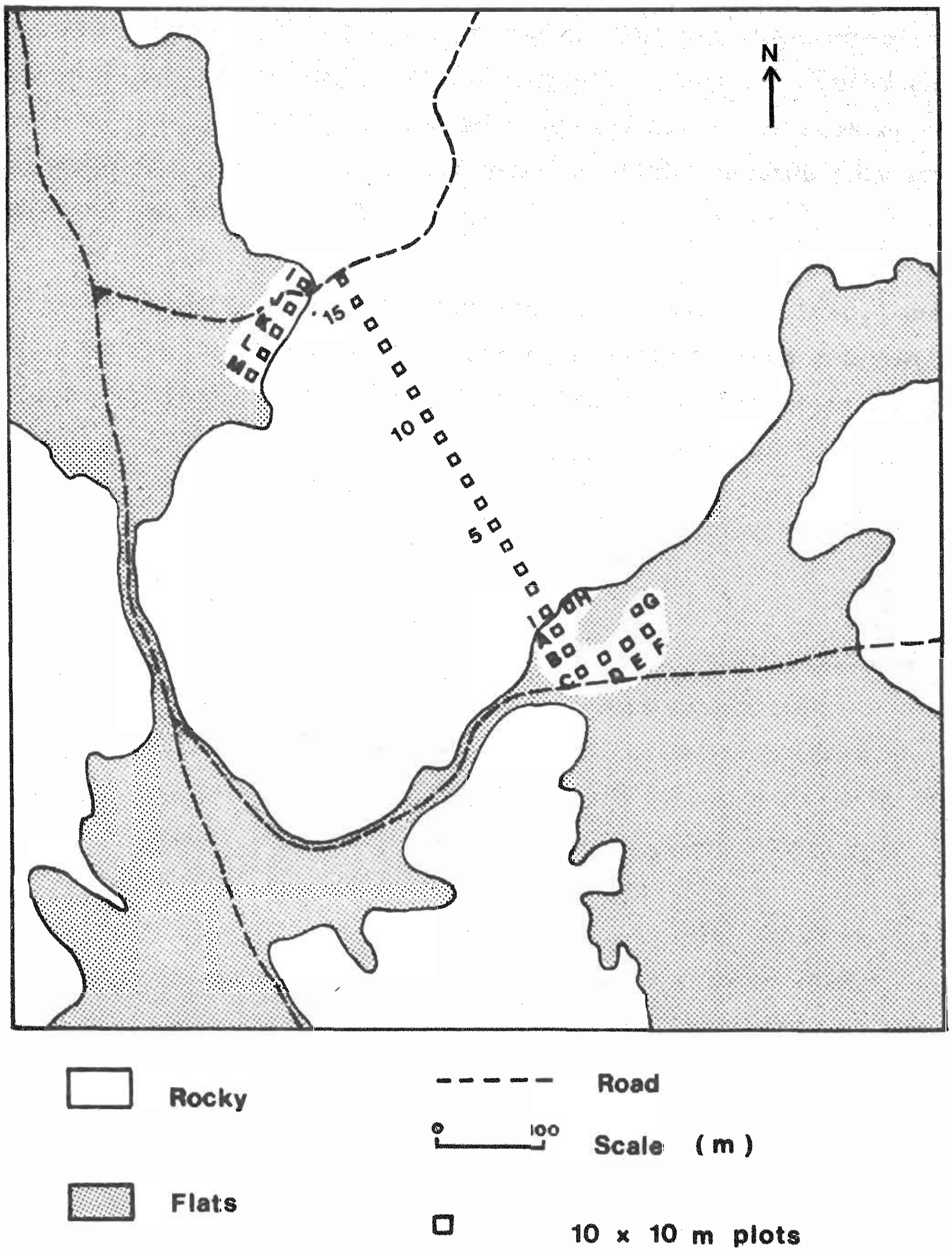


Fig. 6: Location of vegetation plots in the main klipspringer study group's territory at Springbok.

CHAPTER 2 : HABITAT

Quantitative description of the habitat is one of the most time-consuming and laborious problems facing the animal ecologist. Even if a detailed botanical study of the area has already been carried out, this usually has a different emphasis and often misses out aspects of the habitat that are very important to the animals under study.

During the present study the botanical research of Le Roux (in prep.) and Rösche (1978) provided the background at Springbok and at Gamka a broad vegetation survey by Boshoff* (unpubl.) formed the basis from which to work.

METHODS

To describe the habitats 10 X 10m quadrats were laid out throughout the study areas and the relative proportions of rock, bare ground and vegetation were estimated, as well as cover in the different vegetation height classes. At Gamka the proportion of the vegetation made up by the various floristic elements represented in the area was also noted.

Since the koppie terrain at Springbok is relatively uniform (Le Roux, in prep.) only a few plots were laid out in the main klipspringer study territory (Fig. 6). Because most of the boulders are very large it was difficult to place the quadrats subjectively in such a way that they would give a good assessment of the proportions of rock and vegetation. Therefore a more systematic sample of a line transect with a 10 X 10m plot every 25m was taken. This gave 16 plots in the koppie terrain over a 400m transect. A further 13 plots were placed in the sandy flats, with some along the same transect and others in lines nearby, close to the koppies (Fig. 6).

At Gamka the habitats are far more variable than at Springbok. This variability is particularly important because of the effect it has on the distribution of other small antelope species which may compete with klipspringers. For this reason it was important to describe the habitats more accurately, so a total of 79 quadrats was sampled. In order to describe as much of the variation as possible and to eliminate intermediate readings on heterogeneous quadrats, the plots were placed subjectively within areas that were reasonably uniform, over the whole study area (Fig. 7).

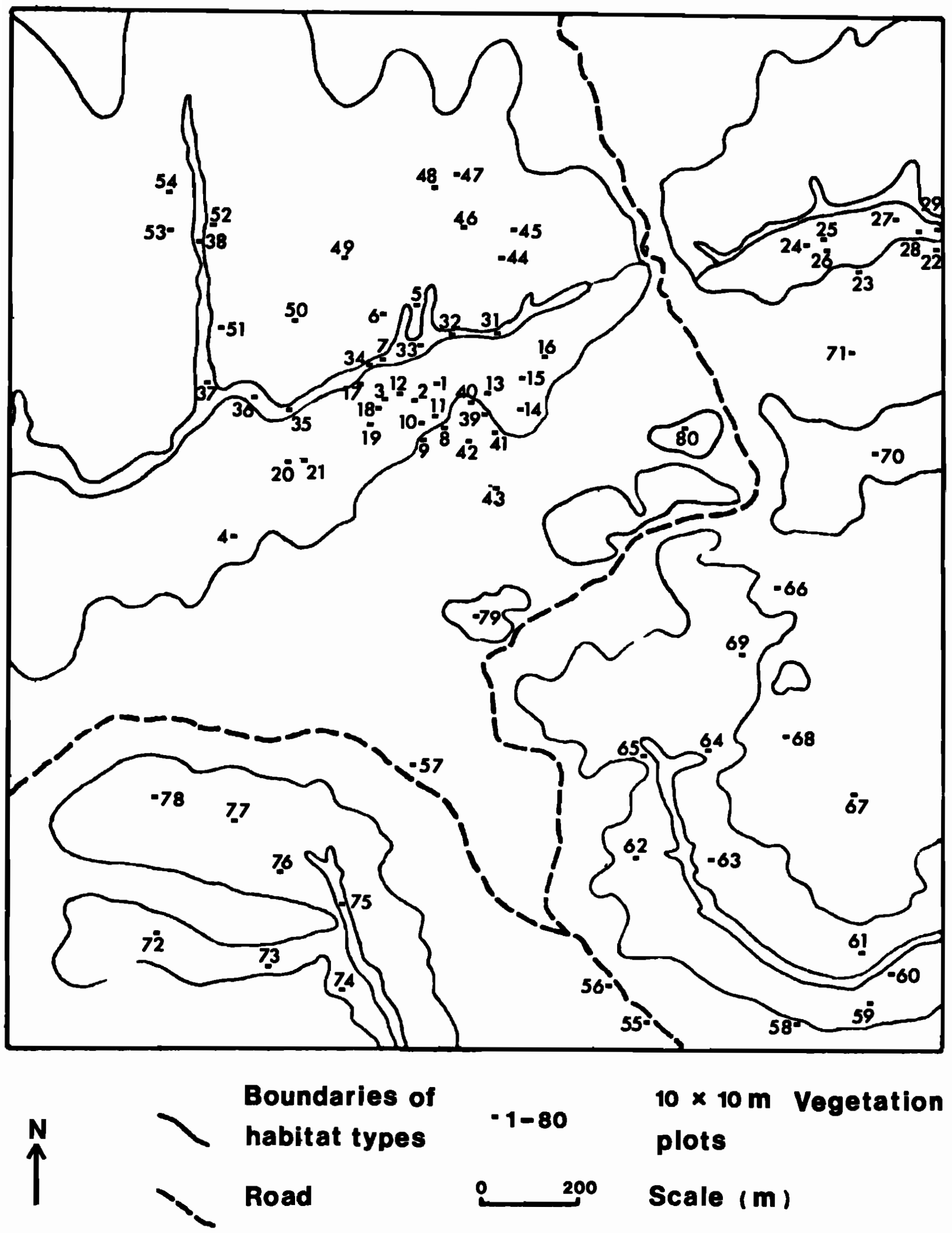


Fig. 7: Location of vegetation plots in the main study area at Gamka.

In each plot the first figures noted were the percentages of the total cover made up by rock, bare ground and vegetation, estimated to the nearest 5%. Then the vegetation was divided up into three classes of less than 0,5m, between 0,5m and 1,0m, and greater than one metre. If there was some overlap of layers a mean value was taken. After this the most important shrubs and herbs were listed and assigned cover values according to the Braun-Blanquet cover scale (Kershaw 1973), but using the percentages of the vegetation cover rather than the total cover. This was necessary to assess the proportion of the vegetation made up by each plant species for the food preference ratings (Chapter 8).

The final step at Gamka was to estimate the percentage frequency of the different floristic elements in the vegetation of the plot and thus give an idea of the phytogeographical affinities of that particular habitat type. The proportions were estimated to the nearest 5% with an additional class of 2% at the lower end of the scale and a plus if plants of that group occurred, but made an insignificant contribution to the vegetation cover.

Eight of the plots in the main klipspringer territories at Gamka were visited during each visit to monitor the phenology of the plants in the area. The presence of green leaves, flowers and fruits was noted for each species on a three-point scale of few, some and many. This was later combined with a similar assessment during the inspection of feeding records to give an idea of the seasonality of the vegetation in the area. For Springbok the results of Rösche's (1978) phenological study were used.

During all field work sightings of klipspringer groups were plotted on large scale aerial photographs for analysis of habitat preferences.

RESULTS AND DISCUSSION

GAMKA

Vegetation

Though two of Acocks' (1953) veld types are represented in the main klipspringer study area at Gamka, there is no clear-cut division between the two and the vegetation can best be described as consisting of several different components, viz. ericoid, proteoid, restioid, renosterbos, graminoid, and succulent. These occur in different proportions according to micro-habitat conditions, especially with respect to moisture. Superimposed on this is the effect, during recent years, of deliberate veld-burning by farmers, and heavy grazing pressure from domestic stock.

The fynbos elements, characterised by the families Ericaceae and Proteaceae, occur mostly on the well-drained but moist rocky slopes, particularly low down on the steeper south-facing slopes, although scattered Protea arborea may be found on the drier north-facing slopes as well.

Restio species and other members of the Restionaceae are also more common on the moister slopes, but show a patchy distribution on the dry slopes. Grasses are widespread in all habitat types but their local distribution and abundance depends largely on the area's recent burning history.

The renosterbos element, represented most typically by Elytropappus rhinocerotis and E. adpressus, occurs in patches in all habitat types apart from the dry rocky slopes, but only becomes really prominent on the plateau, where areas that have not been burned for a decade or more often consist of dense stands of renosterbos scrub.

Because of this mosaic of interwoven floristic elements, it was decided to classify the habitats according to physiographic features rather than floristic affinities. Thus four main habitat types were differentiated (Fig. 8).

Dry rocky slopes

The steep (± 40°) north-facing rocky slopes (Fig. 9) consist largely of outcrops of bedrock, and these make up about one fifth of the total area of this habitat type (Fig. 10). The rest of the area is composed of a scree of loose rocks and small boulders which have retained pockets of soil and thus provide a substrate for the vegetation.

Because the rain-bearing winds come from the southwest and, to a lesser extent, the southeast, these northern slopes tend to receive less moisture from rain and mist precipitation than the plateau and southern slopes, due to a "rain-shadow" effect. In addition the steep run-off, very shallow soils, and the drying effect of the sun, emphasised by the northern aspect, are all factors that work against retention of water and therefore its availability to plants. This means that the area supports a sparser

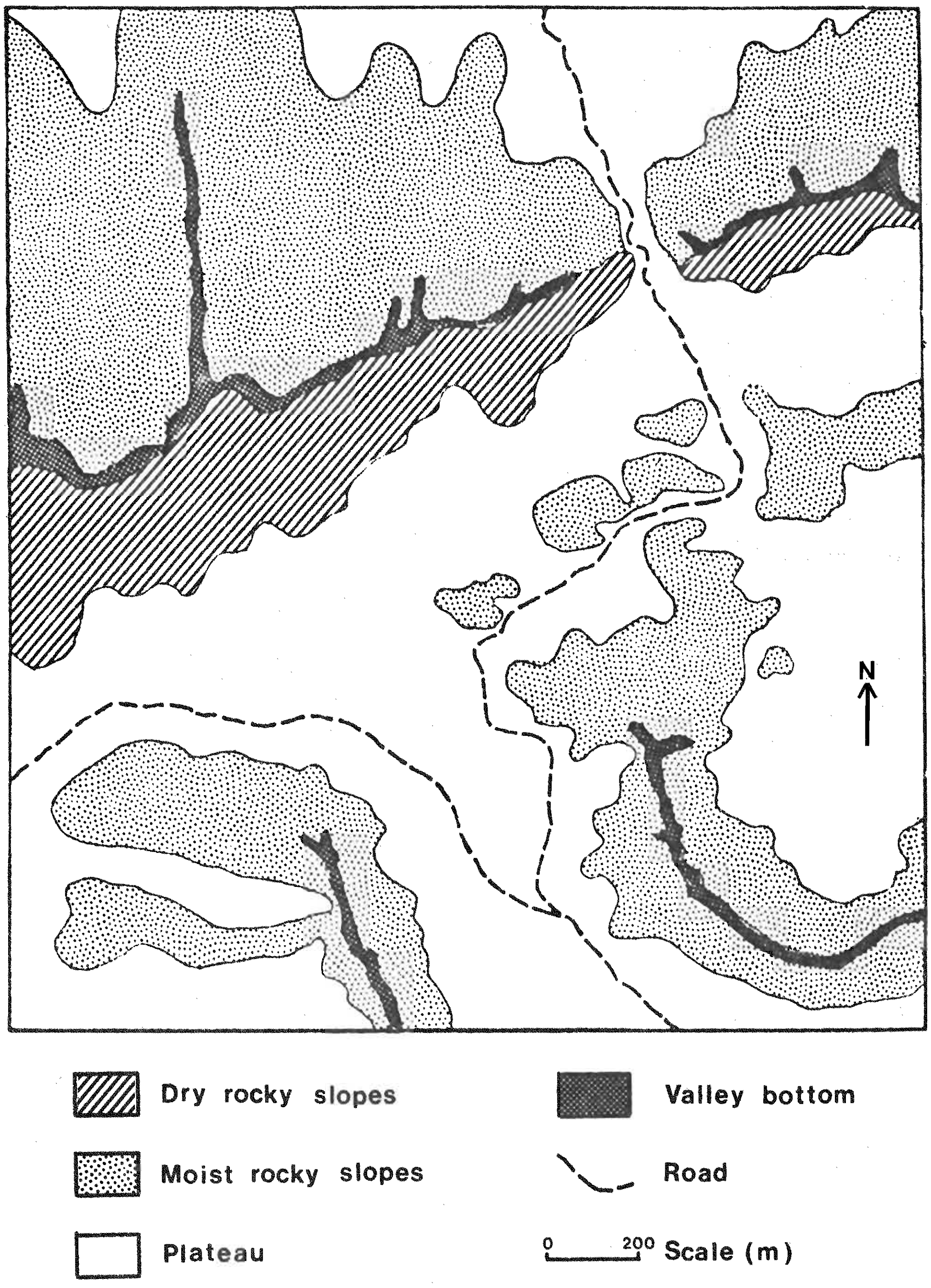


Fig. 8: Distribution of habitat types in the main study area at Gamka.

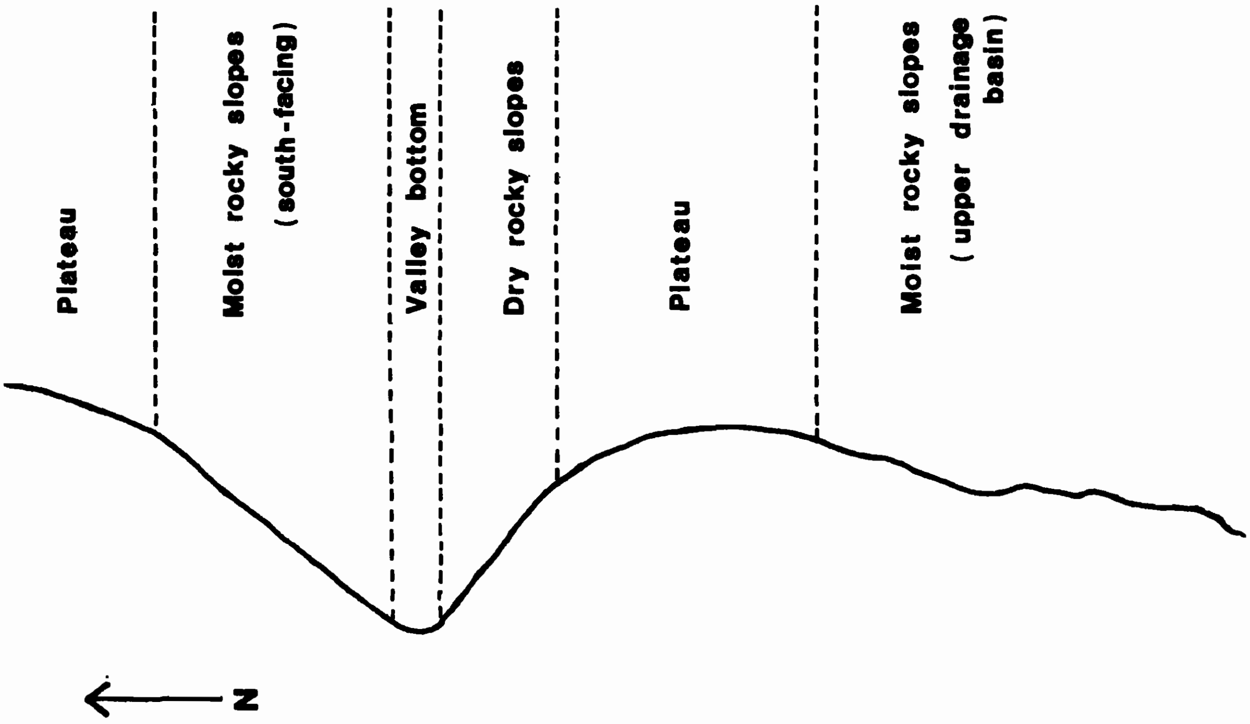


Fig. 9: Schematic topographical profile of a line travelling north-south through the main study area at Gamka, showing distribution of habitat types.

Fig. 10: "Dry Rocky Slope" habitat at Gamka. Note steeper regions of outcrop rock and flat scree slopes. "Moist Rocky Slope" and "Valley Bottom" habitats in left foreground have denser and higher vegetation.

Fig. 11: Outcrop in "Dry Rocky Slope" habitat at Gamka, showing high cover of large boulders and shrubs, and some grass.

vegetation than the other habitat types.

In regions of outcrop the rocks are physiognomically dominant, occupying over 48% of the total surface area while the vegetation makes up only 42% of the cover (Appendix C, Fig. 11). However on the flat scree slopes the situation is reversed with the vegetation forming an average of 53% of the total cover (Fig. 12), increasing to over 60% in the drainange depressions. Rocks still make up a large proportion (35%) of the total area. There is little bare ground (13%) on the scree slopes, and even less (10%) on the outcrops.

The vegetation is generally of low profile with nearly all plants less than one metre in height. However, on the outcrops, where the plants collect extra run-off from the large boulders, larger shrubs such as *Colpoon compressum*, *Maytenus oleoides* and *Rhus lucida* are more common.

Grasses form a low proportion (8%) of the vegetation on the outcrops, but are more abundant on the scree slopes at a mean of 18%, but up to as much as 55% in some places. This may be partly due to the fact that fire spreads more easily on the scree slopes than on the outcrops. Restios form a very small proportion of the total vegetation cover and show a patchy distribution, though they may become important over small areas (up to 30% of the vegetation cover).

The dominant shrubs on the scree slopes are *Eriocephalus africanus*, *Aspalathus hirta* and *Hermannia sp.* with many small *Agathosma sp.*. *Pentzia elegans* is scattered, but may become dominant in patches. Larger *Maytenus*, *Colpoon* and *Rhus* also occur on the scree, especially where there is more moisture in drainage depression, but are not as common as on the outcrops. Smaller shrubs common on the outcrops include *Felicia filifolia* and *Berkheya angustifolia*. On large outcrops with resident dassie colonies the high nitrogen content of their dung piles provides a suitable substrate for *Solanum tomentosum* and *Diospyros dichlorophylla* which then become dominant locally, but are restricted to these micro-habitat conditions. Young *Solanum* plants may often be found growing in klipspringer middens.

Moist rocky slopes

Although this habitat type covers an area with a wide range of topography, its vegetation cover is reasonably homogeneous and cannot easily be

Fig. 12: Scree slope in the "Dry Rocky Slope" habitat at Gamka. Rock cover is lower, grasses predominate and restios are common.

Fig. 13: General view of "Moist Rocky Slope" habitat of the south-facing slopes at Gamka. Vegetation cover is high and large shrubs are common.

classified. It includes the fairly steep (30-35°) south-facing slopes of the major valleys such as Tierkloof (Fig. 13), as well as the rather broken terrain of the upper drainage basins where outcrops of rock alternate with well-vegetated drainage lines (Fig. 14). In some places it merges gradually with the plateau habitat type and includes areas of exposed outcrop on this plateau.

The basic factor common to all the sections of this habitat type is that they receive more precipitation in the form of mist and rain than do the dry slopes, due to the favourable exposure. The increased moisture allows a relatively dense vegetation cover to develop which, combined with the more gentle slope, helps the retention of soil, to the point where the rocks are largely covered by soil and overgrown by plants. In areas with a lot of outcrop, especially where the slope is more to the east or west and thus more sunny, the conditions may become drier and approach those of the dry rocky slope habitat. However, these are not considered separately due to the small areas that they cover.

Rocks make up an average of 26% of the cover for the whole habitat type, varying from around 15% on the southern slopes and upper drainage to 38% on the outcrops. The vegetation cover is correspondingly low on the outcrops, though at 53% this is not nearly as low as that on the outcrops of the dry slopes (42%). This cover increases rapidly to an average of 68% on the southern slopes (Fig. 15) and to over 76% in the depressions of the upper drainage basin. Bare ground makes up a small proportion of the cover (mean 12%) but several plots on the south slopes showed 20% or higher.

The characteristic plants of this habitat type are the proteas and ericas. Large shrubs and trees of <u>Protea arborea</u> are the conspicuous physiognomic dominants while smaller shrubs of <u>Leucadendron salignum</u> are also common, especially on slopes with a more southwesterly aspect, which are probably moister. Ericas are widespread and make up an average of 16% of the vegetation cover with the highest values on the southern slopes and in the upper drainage basin, but with a very low importance on the outcrops (3%).

On the south-facing slopes of Tierkloof other important large shrubs include <u>Rhus lucida</u>, <u>Aspalathus hirta</u>, renosterbos (<u>Elytropappus adpressus</u> and <u>E. rhinocerotis</u>) and tall thin shrubs of <u>Metalasia muricata</u>, <u>Aspalathus sceptum-aureum</u>, <u>Thesium nigromontanum</u> and <u>Montinia caryophyllacea</u>. At a

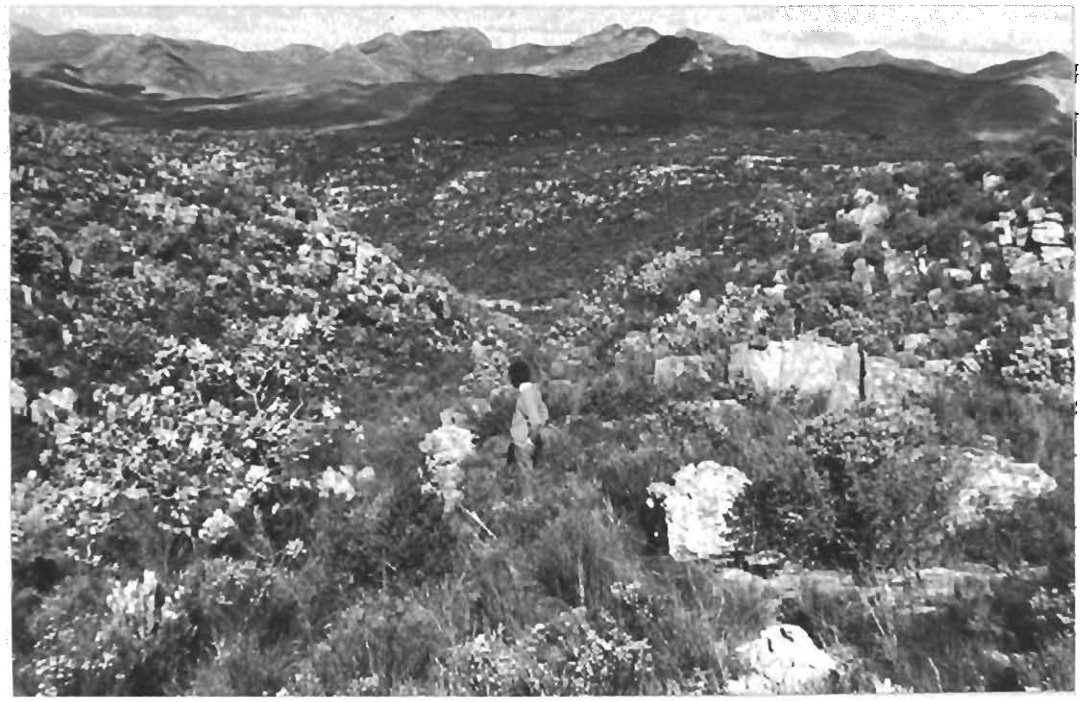


Fig. 14: "Moist Rocky Slope" habitat in the upper drainage basin of Keurkloof at Gamka. Protea arborea and other large shrubs are conspicuous on the outcrops.

Fig. 15: Dense vegetation cover in the "Moist Rocky Slope" habitat at Gamka. Large shrubs include Aspalathus hirta, Leucadendron salignum and Elytropappus adpressus.

lower level (less than one metre) *Metalasia gnaphaloides*, *Stoebe microphylla*, *Elytropappus gnaphaloides* and *Cliffortia pulchella* are common.

In the upper drainage basin the depressions are filled with dense stands of waist-high *Leucadendron*, *Elytropappus gnaphaloides*, *Aspalathus spp.* and *Metalasia spp.*, with *Phylica purpurea* and *Amphithalea ericifolia* dominant in patches, and scattered *Helichrysum spp.* and *Eroeda imbricata*. This tall dense vegetation changes gradually towards the outcrops with a decrease in height and cover, making way for an increase in rock cover. The species mentioned above tend to be replaced by *Maytenus oleoides*, *Rhus tomentosa*, *Cliffortia ramosissima* and *Agathosma sp.*, with *Felicia filifolia* on the very dry parts. *Protea arborea* still retains its importance. Although restios contribute only 15% of the total vegetation cover, they are always present and there were few values of less than 10% in the plots sampled.

Grasses also occurred in all plots, though in varying amounts according to past burning regimes. Generally they are not as important in this habitat type as on the plateau or dry rocky slopes, but the higher values for the outcrops show that grasses are more typical of the drier areas with a lower-structured vegetation.

Plateau

The plateau is the area on top of the ridge between the different drainage lines that has not been heavily eroded and is relatively flat and level. Boulders are not conspicuous and are generally completely covered by soil, though small outcrops do occur. Where these outcrops are extensive and carry a proteoid-ericoid vegetation they are considered to be of the previous habitat type.

Large areas of the plateau carry a surface layer of small pebbles, but rocks are only important on the plateau edge near to the rocky slopes, although here they are still mostly covered by vegetation. The rock cover of the open areas is less than 3% but rises to an average of over 20% at the plateau edge, while bare ground covers 23%.

The vegetation on the plateau varies from a low grassland (Fig. 16) to a dense scrub, depending on the burning history. In grassland areas that have been recently burned the vegetation is usually less than one metre in height with a very high proportion of grasses (up to 60% of the total vegetation cover). The most important grasses are *Merxmuellera stricta* and *Themeda triandra*

Fig. 16: "Plateau" habitat at Gamka, showing grassland in the foreground and higher renosterbos shrubland in the background.

Fig. 17: Edge of the "Plateau" habitat at Gamka, near the dry rocky slopes. The ground is more rocky and the vegetation cover lower than in the above photograh.

with other genera such as *Cymbopogon*, *Digitaria* and *Pentaschistis* sparsely distributed but common over small areas. The abundance of the largely unpalatable *Merxmuellera* is unnatural, but can be attributed to excessive burning and grazing pressures during the last few decades.

Scattered shrubs in the grassland include the low-growing *Elytropappus gnaphaloides* and *Eroeda imbricata*, with occasional taller shrubs of *E. adpressus* and *Aspalathus pedunculata*.

In areas that have not been recently burned the proportion of shrubs becomes higher with an increase in species such as *Metalasia langebergensis*, *Eriocephalus africanus*, *Anthospermum spp.* and *Pentzia dentata*. The overall height and density increases to the point where some areas have dense stands of waist-high renosterbos with a total cover of over 80%.

On the plateau edge near the dry rocky slopes the vegetation is also dense, but rocks constitute a higher proportion of the cover, and the total vegetation cover drops to 60% or lower, depending on the amount of soil and the drainage (Fig. 17). The most typical plants of this part of the plateau are *Phylica purpurea* and *Chrysanthemoides monilifera*, which form fairly dense stands in some places. Although they are relatively level these areas can be considered as transitional to the dry rocky slope habitat, since they show an increase in species such as *Maytenus oleoides*, *Aspalathus hirta*, *Muraltia ericaefolia* and *Berkheya angustifolia*, as well as the occasional *Protea arborea*.

Restios are widespread on the plateau but are less common in the areas of well-developed renosterbosveld. However the other fynbos elements, the proteas and ericas, are poorly represented, and their presence usually indicates an ecotone with another habitat type.

Valley bottom

The increased run-off at the bottom of drainage lines in the valleys encourages the development of a denser vegetation than that of the surrounding slopes (Fig. 18). While the vegetation of drainage lines in the upper drainage basin does not differ markedly from the moist slopes nearby, the valley bottom in the deep kloofs such as Tierkloof is clearly of a different habitat type. The substrate varies from piled loose boulders holding pockets of soil between them to a pebbled alluvium of more than a metre that has accumulated in some depressions.

Fig. 18: "Valley Bottom" habitat at Gamka, showing alternating thick bush and rocky areas.

Rocks and boulders constitute about 20% of the cover with bare ground at around 13%, but the most noticeable change is the high value for vegetation cover (over 65%) and the large percentage (18% of the total cover) of plants of more than one metre in height. The most important large shrubs are *Rhus lucida*, *Maytenus oleoides*, *Dodonea viscosa* and *Aspalathus hirta*, with slightly smaller plants of *Chrysanthemoides monilifera* and *Elytropappus adpressus* important in places. At a lower level *Agathosma sp.*, *Pelargonium glutinosum*, *Rhus tomentosa*, *Eriocephalus africanus*, *Polygola fruticosa* and *Cliffortia ramosissima* are also important. Low dense bushes of *Chironia baccifera* are not very common, but are unique to this habitat type. As with the moist rocky slopes, tall spindly shrubs of *Montinia caryophyllacea* and *Thesium nigromontanum* are characteristic, though they do not make up much of the cover.

In the upper drainage basin the same plant species occur in the drainage lines, but the edges are not as clearly defined and the vegetation merges more gradually into the ericoid and proteoid vegetation of the moist slopes.

SPRINGBOK

The main klipspringer study area at Springbok is situated in the rocky part of the reserve and consists of almost continuous granite koppie terrain (Fig. 19) with small stretches of alluvial flats in between. Because of the broken nature of the terrain, the habitat can only be divided into these two main types. Division on a smaller scale would be very difficult due to the large size of the rock boulders and slabs, which gives rise to a great range of micro-habitats. These form an intricate mosaic and are affected by such factors as proximity to large boulders for water run-off and shading insolation, slope, and depth of soil.

While there is a tendency for northern slopes to have a more xeric succulent vegetation due to the dehydrating effect of the sun, this effect can be more than compensated for by run-off from large granite slabs which causes a marked improvement in the water regime of the plants round about. A detailed vegetation survey by Le Roux (in prep.) yielded only one vegetation type, a dwarf-shrub community, for the whole koppie area.

The belt of quadrats over the main klipspringer study group's territory gave a mean rock cover of 34% (Appendix D), but the range of 5 - 75% shows how much the cover varies according to where the plot fell in relation to the large boulders and rock slabs. Bare ground covers a large percentage (27%) of the rocky terrain, leaving only 39% as the average vegetation cover.

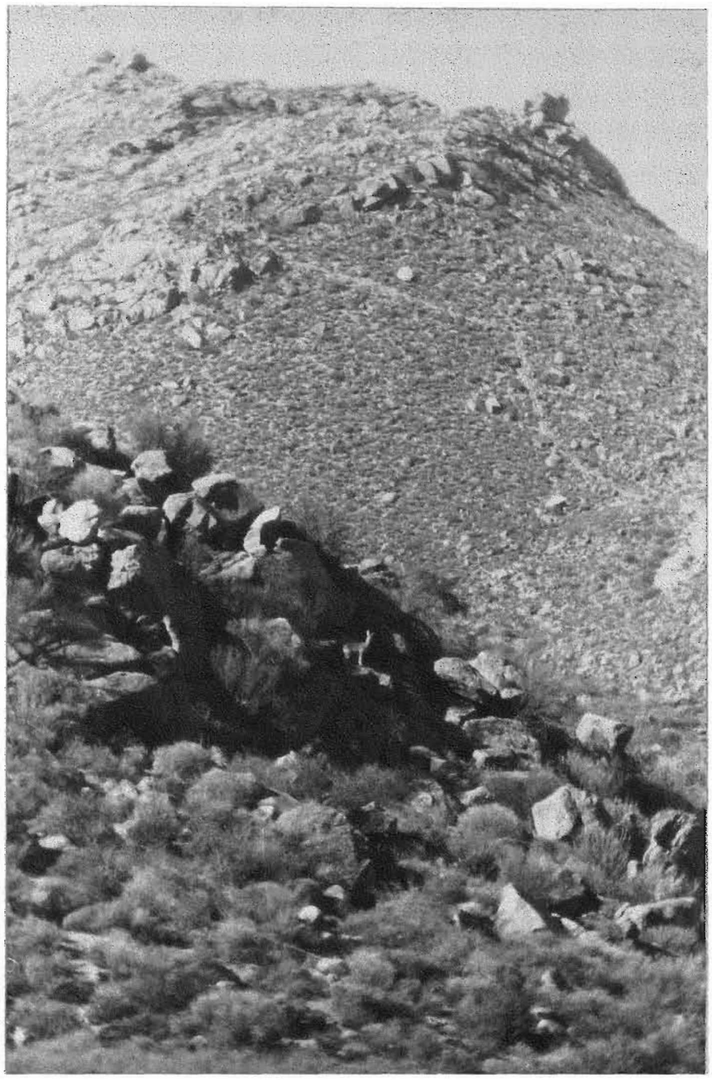
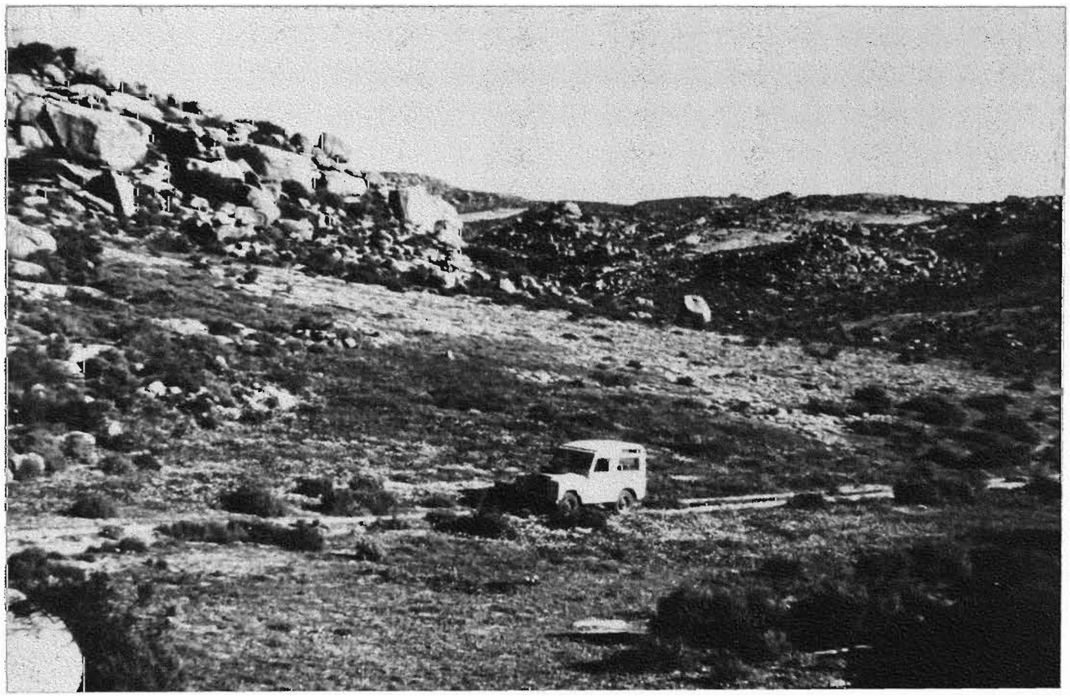


Fig. 19: A klipspringer in "Rocky Koppie" habitat at Springbok, showing the dense shrub cover.

Fig. 20: Sandy "Flats" habitat surrounded by koppies at Springbok.



This is considerably lower than at Gamka and probably reflects the lower rainfall in the area.

The vegetation consists of a dwarf-shrub community with nearly all of the plants less than one metre in height, though Appendix D shows that some plots had higher bushes. These occur next to large boulders where the increased water run-off and deeper soil provide better conditions for large shrubs. The most common large shrubs are mostly *Rhus undulata* and *Indigofera spinescens*, with some *Diospyros ramulosa* and *Antizoma miersiana*. Several species of *Zygophyllum* also form large bushes, and this plant is important in most areas. Other important species on the koppies are *Eriocephalus africanus*, *E. ericoides*, *Pteronia* spp., *Galenia fruticosa*, and *Pentzia incana*. Smaller, but abundant, plants are *Osteospermum* spp., *Arctotis revoluta*, and *Hermannia disermifolia*.

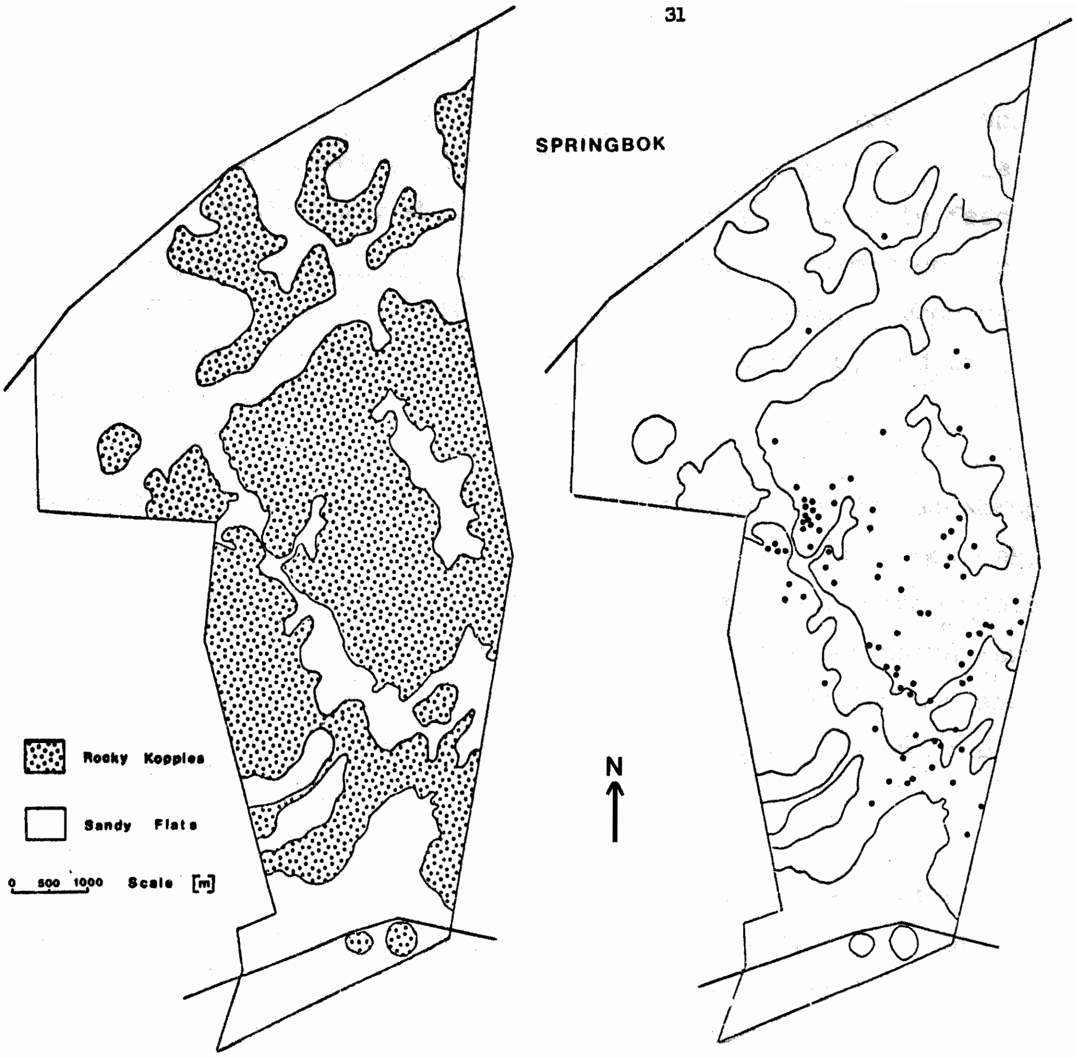
In drier areas, such as north-facing slopes with shallow soil, succulents of the genera *Ruschia*, *Leipoldtia* and others become important to the point where they completely dominate the vegetation. *Euphorbia mauritanica* and *E. decussata* are two other very succulent species that are widespread and common.

The flats have mostly been cultivated at some time or other, which has resulted in a rather impoverished soil and a pioneer dwarf shrub community (Fig. 20). There are far fewer rocks, so that bare ground occupies most of the cover (68%). Thus the vegetation makes up only 32% of the cover, though this increases considerably in the spring when the well-known Namaqualand ephemerals form an almost continuous carpet. The most important shrub is *Galenia africana*, which is a rather unpalatable pioneer and illustrates the effect of impoverishment due to cultivation and overgrazing. Other important shrubs are *Ruschia* spp. and *Drosanthemum albens*, and *Mesembryanthemum karroense* ("soutslaai") forms large patches of low-level cover.

Habitat preferences of the klipspringer

Figure 21 shows the distribution of klipspringer sightings at Springbok and Gamka.

At Springbok the klipspringers were almost exclusively found on rocky terrain. In some cases they crossed short stretches of the flats to move from one part of the territory to another, but apart from this they were



SPRINGBOK

GAMKA

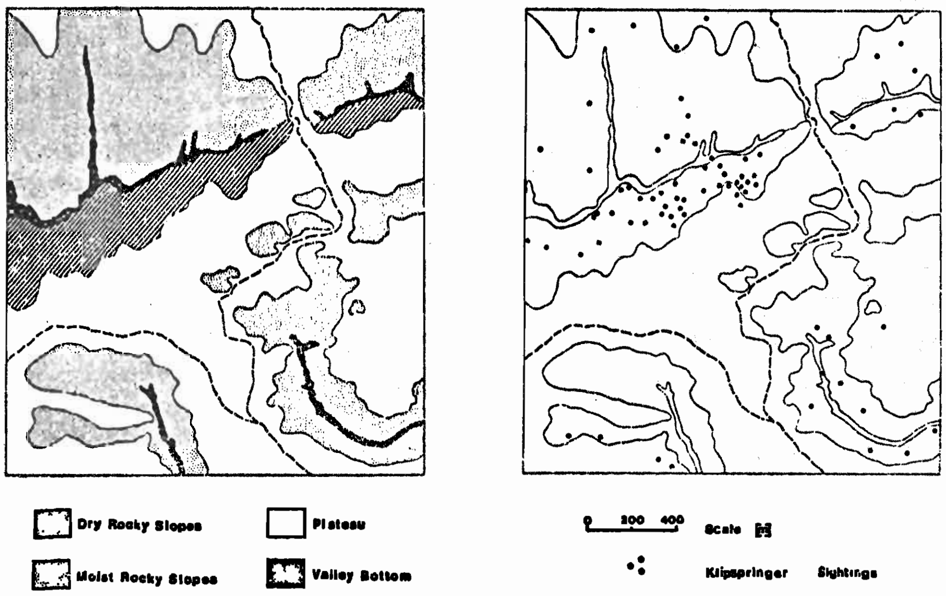


Fig. 21: Klipspringer sightings in the different habitat types of the Hester Malan Nature

seldom seen away from the rocks. On only two occasions were klipspringers seen in a relaxed state some distance from the nearest rocks. Once the main study group moved slowly about 30 m out on to the flats to feed on the succulent Mesembryanthemum karroense growing there. On another occasion a lone adult male was found at least 100 m out on the flats. When he was surprised by the vehicle he ran straight back to the rocks, and then relaxed soon after getting there.

At Gamka the change from one habitat type to the other is not as abrupt, so the habitat preferences of klipspringers were not as clear. However, the klipspringers showed a marked preference for the dry rocky slope habitat. Though there was a small amount of bias in that the klipspringers were most actively looked for in this habitat, the occurrence of 52% of the sightings (see Table 32) in this habitat type, which occupies only 9% of the study area, indicates their preference clearly.

Most of the other sightings (33%) were from the moist rocky slope habitat. More than half of these were from the steep south-facing slopes of Tierkloof and Klippe se Kloof where the klipspringers seemed to spend a fair amount of time, even though the vegetation is higher and visibility not as good as the dry slopes. Klipspringers were seen on several occasions in the moist slope habitat of the upper drainage basins, though they were nearly always on rocky outcrops within this habitat type. Although there were several records of klipspringers in the plateau habitat type, all except one of these were within about 20m of steep rocky areas, to which the buck fled at the slightest sign of danger.

Outside the main study area at Gamka several groups of klipspringers were seen, and they seemed to show the same habitat preferences. A significant factor is that they were seldom seen on the steep gorge sides of the lower part of Tierkloof. Although there were signs of their occurrence and a few actual sightings, their scarcity during several careful searches in the area suggests that the steep gorge sides are not ideal habitat for klipspringers.

From sightings in the main study areas, together with broad impressions gained in other areas of the Cape Province and some records in the literature, a basic pattern of klipspringer habitat preferences has emerged.

The ideal habitat for klipspringers seems to be open rocky terrain with a low-structured vegetation cover which allows good all-round visibility.

While very steep gorge sides and cliffs are used for predator evasion, this type of terrain does not attract a high density of klipspringers. Dunbar and Dunbar (1974) also found that klipspringers were not as common on the steep cliff faces as on the more gently sloping rocky hill slopes, though in Tilson's (in press) study area the steep sides of the Kuiseb River Canyon was the only rocky habitat available and his study animals spent most of the time there.

In the literature there are several records of klipspringers occurring some distance away from the rocky habitat. Stevenson-Hamilton (1917) wrote that they have been found lying up during the daytime in thick bush far from any rocks and Wilson and Child (1965) indicate that they were seen out in the open dambo up to a quarter of a mile from the nearest koppie. However, it seems that most of the records are because they are feeding in the open due to a scarcity of food in the koppies, or else that they are moving from one rocky area to the next. Wilson and Child (1965) recorded that klipspringers in Zambia often feed in the woodland at the base of koppies if their food is restricted during the dry season, but the boulders nearer the top of the koppies are their preferred habitat if food is available there. These authors also say that they cross freely between koppies of the same group. Niethammer (1942) showed evidence that they crossed at least 10 km from the nearest mountains in the plains of South West Africa, and Stuart (1975) recorded that they are frequently encountered on scattered rocky hills around the edge of the Namib Desert, suggesting that they often move around between them.

The importance of rocky substrate for klipspringers is illustrated by the fact that they are found not only in mountainous terrain, but also in other rocky areas, since several workers have reported their occurrence along boulder-strewn river beds in flat plains far from mountain slopes (Vaughan-Kirby 1899, Shortridge 1934, Wilson and Child 1965). In some mountainous areas, such as the Drakensberg of the Eastern Cape, few klipspringers have been reported (Millar and Lloyd 1976), although this may be because all but the steepest slopes support a grassland vegetation, and there is not much rocky scree with low shrubland.

Figure 22 illustrates the densities of klipspringers in the magisterial districts of the Cape Province calculated from Millar and Lloyd's (1976) questionnaire survey of mammals in the Cape. Although the absolute densities calculated are probably very inaccurate, the method was consistent

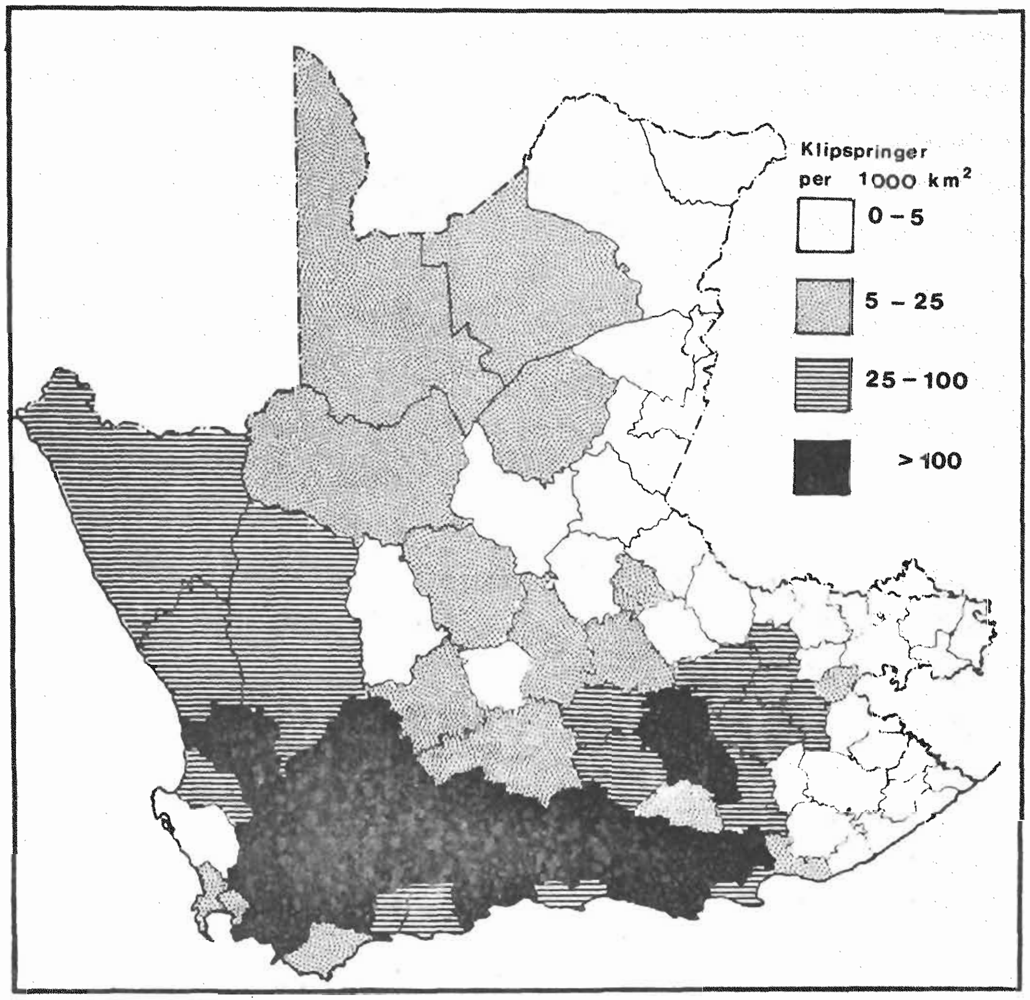


Fig. 22: Distribution of klipspringers and approximate densities in the magisterial districts of the Cape Province (calculated from Millar and Lloyd 1976).

for each district, so the results should give a reasonable idea of the relative densities in the Cape.

The map shows that, apart from the rugged mountains of the Cape Fold Belt which seem to be the most important areas for klipspringers in the Cape Province, these antelope may be found in any area where there is sufficient rocky terrain, and this terrain is near enough to other mountainous areas to have allowed dispersal to take place. Thus klipspringers are common in the rocky terrain along the Orange River in the Northern Cape, and occur some distance out into the Bushmanland if habitat is available, but are absent from the very isolated inselbergs far from mountain ranges, such as in the Brandvlei district. In the sheep-farming areas of the central karoo, klipspringers once occurred in reasonable numbers, according to farmers there, but have now been mostly wiped out because of the accessibility of the koppie terrain which allows them to be hunted easily.

The klipspringer's high degree of specialisation to its rocky habitat has enabled it to compete very favourably with other antelope in this habitat, over a wide range. Thus this species is widely distributed throughout Africa in habitats as different as the Kuiseb canyon of South West Africa and the Simien Mountains of Ethiopia. However, as in the Cape, the basic factor common to all localities where klipspringer are well-established is a rocky substrate, with a certain amount of dictyledonous shrub vegetation to fulfill its feeding requirements.

CHAPTER 3 : POPULATIONS AND BREEDING

METHODS

Analysis of sightings

At all times during the study the size and, where possible, the composition of klipspringer groups was noted. These were plotted on large scale aerial photographs for analysis of habitat preferences and identification of territories and territorial boundaries. Individuals and groups were distinguished by noting characters such as horn length, ear pattern, body colour and scars. Using these characters, combined with the location of the sightings, individual groups could be fairly positively identified if they were seen clearly.

At Springbok the klipspringers were accustomed to vehicles approaching to within 100 to 200m, so it was possible to identify a large proportion of the groups encountered. Thus a reasonable picture of the groups occurring on Carolusberg mountain could be gathered by regularly covering the roads encircling it. No attempt was made to carry on searching the area intensively until each particular group was found, and thereby achieve certainty on territorial limits. However, the large size of the territories and the spacing of the roads allowed a large proportion of the study area to be monitored. In addition, the uniformity of the rocky terrain and the relatively abrupt transition to the "Flats" habitat simplified estimation of the boundaries in areas where the territories did not abut on other klipspringer territories. Boundaries were assumed to remain constant throughout the study period since the method was not refined enough to monitor small changes.

At Gamka the situation was rather more complex. With the wide range of habitats and the gradual transition from one to the other it was not easy to estimate territorial boundaries in areas away from the dry rocky slope habitat. Since the klipspringers seemed to prefer the dry north-facing slopes, but also occasionally moved to the moist south-facing slopes and out on to the plateau edge, territorial boundaries could only be accurately located where there was conflict between groups, or sightings of neighbouring groups occurred close together. In addition, the situation was complicated by the extreme wariness of the study animals. The flight distance was often several hundred metres and they could easily be so frightened by the observer that they would cross right over another group's territory in flight, For the analysis of group size and composition all definite resightings for each visit were left out, as well as any doubtful records that could have represented resightings. Thus the mean group size for all klipspringer groups seen during each visit to the study areas could be calculated with little bias towards the group size shown by the most frequently seen study groups.

Small antelope populations are nearly always underestimated by normal census methods which are very labour intensive, especially in rocky terrain. Therefore a more indirect method was used to give a rough estimate of the numbers of klipspringers on the reserves. The populations were estimated by extrapolating the figures obtained in the main study areas. The estimates were made by stratifying the habitats, measuring the area of each type, and then calculating the total number of territories the area could hold, according to the densities in the intensive study areas. At Springbok the flats and rocky terrain were differentiated on 1:50 000 aerial photographs as the two types were clearly discernable. However, at Gamka the large amount of variation on a small scale made it impossible to separate habitat types on the aerial photographs. Therefore the 1:50 000 contour map was used to divide the area simply on slope, so that plateau, medium slope and steep gorge side were differentiated.

At Springbok the outlying rocky areas, away from the main Carolusberg massif, were considered to be less suitable habitat for klipspringers (Chapter 2), so the expected densities were calculated at half that of the ideal habitat. At Gamka the steep north-facing slopes could be demarcated by referring to the aerial photographs, and the territory size in this area was taken as the density found in the main study area. Although the frequency of sightings on the other medium slopes and steep gorge sides seemed to be very variable, an overall figure of half of this optimum density was used for the calculations.

Growth

The growth of young klipspringers was monitored by measuring two semi-tame buck at Springbok and the Augrabies Falls National Park. The Springbok study animal was a young ram that had been found supposedly abandoned in the veld. Although his exact date of birth was not known, he was still very young, so the date was estimated as during the first few days in June and it is unlikely that this was more than two weeks out. He was hand-reared and grew very tame and was easy to measure, though he became more difficult to weigh as he grew older.

At Augrabies Falls the National Parks Board have for some years kept a family of klipspringers in a small enclosure near the restaurant. The original pair have produced four male offspring but the birth dates of only the last two were recorded.

The most important measurements taken were shoulder height, horn length and body mass (if possible). The shoulder height is a rather inaccurate measurement which varies according to how the buck is standing, so care was taken to measure it when the animal was in the same standing position. In spite of the inaccuracy this proved to be the most useful dimension for assessing the age of wild klipspringer juveniles in the field.

Horn length was measured from its emergence from the skull to the tip. If it was possible to measure both horns accurately and there was a difference between the two, a mean length was recorded. However, in the young rams studied this discrepancy was never more than a couple of millimetres.

Due to logistical problems it was not possible to measure these animals at regular intervals, though the local field personnel helped with some measurements. The figures for body mass and shoulder height just before birth were measured from a very nearly full term foetus taken from a ewe shot in the Franschhoek area.

Lambing season

In antelope that hide their offspring for the first two or three months of their lives it is difficult to monitor the lambing time accurately, especially when the youngsters reach adult size quickly. Thus, during the present study, only a rough assessment of the lambing season could be made by visually estimating the age of young klipspringers seen and converting this to an approximate birth date.

With experience from the semi-tame klipspringers the age of wild juveniles younger than about eight months could be estimated with confidence to within a month. When known juveniles were sighted on different visits the extrapolated birth dates from all sightings showed good agreement. To assess the lambing season the results from all areas and all visits were pooled and care was taken to avoid counting the same individual twice.

Up to about five months, shoulder height was used as the most reliable estimate of age. After that a general impression of body size gave a reasonable indication of age up to about eight months, although the appearance of horns in males at about five months made ageing easier for this sex. Horn length was usable for rams up to about fourteen months, but ewes older than eight months were not assessed because of the error inherent in this type of estimate.

Although they could not be aged accurately, young ewes could usually be distinguished from their mothers until at least 18 months if the group was seen clearly enough. Even though all body measurements are almost completely adult at this age, the general impression clearly identified a younger individual. This visual assessment was confirmed with Tilson* (pers. comm.).

RESULTS AND DISCUSSION

Density and territory size

The average group sizes of all klipspringer groups seen during the study are shown in Table 1. The overall mean of 2,5 (S.D.±1,0) individuals per group is similar to Tilson's (in press) figure of 2,6 (S.D.±0,5), although it is significantly higher than the mean of 2,0 (S.D.±0,6) calculated from Dunbar and Dunbar's (1974) results ($t = 3,59$; $p < 0,001$). However, the reason for this discrepancy is not clear. The distribution of klipspringer sightings and the approximate territorial boundaries on Carolusberg mountain at Springbok are shown in Figure 23. Since the groups were usually seen quite clearly and could be properly identified, the pattern of territories should be reasonably representative, even if the precise boundaries were not known. This gives a range in territory size from about 32 to 64 ha, with a mean of 49 ha for eight territories.

At Gamka territories were far more difficult to delineate (Fig. 24). Although the boundaries in the dry rocky slope habitat were quite clear, the outer boundaries were very vague. Since on several occasions particular groups could not be found anywhere in the territories marked on Fig. 24, the areas of 6ha, 8ha and 15ha are only guidelines, but it is likely that the mean territory size is less than 15 ha.

The figures for the two study areas show that the densities of klipspringers is linked to rainfall (Table 2). At Springbok, with only 160mm of rain

Table 1: Mean group size of all klipspringer groups sighted during the study.

	Number of sightings	Mean	Group size				
			1	2	3	4	5
SPRINGBOK							
May 1977	5	2,8	-	1	4	-	-
Aug-Sept 1977	10	1,8	4	4	2	-	-
Nov 1977	7	2,4	-	4	3	-	-
Feb 1978	17	2,6	4	1	10	2	-
July 1978	13	2,9	2	-	10	-	1
Total	52	2,50	10	10	29	2	1
GAMKA							
April 1977	13	2,5	3	3	5	1	1
July 1977	9	2,4	1	4	3	1	-
Oct 1977	4	3,0	-	2	-	2	-
Jan 1978	4	3,0	-	1	2	1	-
July 1978	12	2,4	2	4	5	1	-
Total	42	2,57	6	14	15	6	1
Overall	94	2,53					

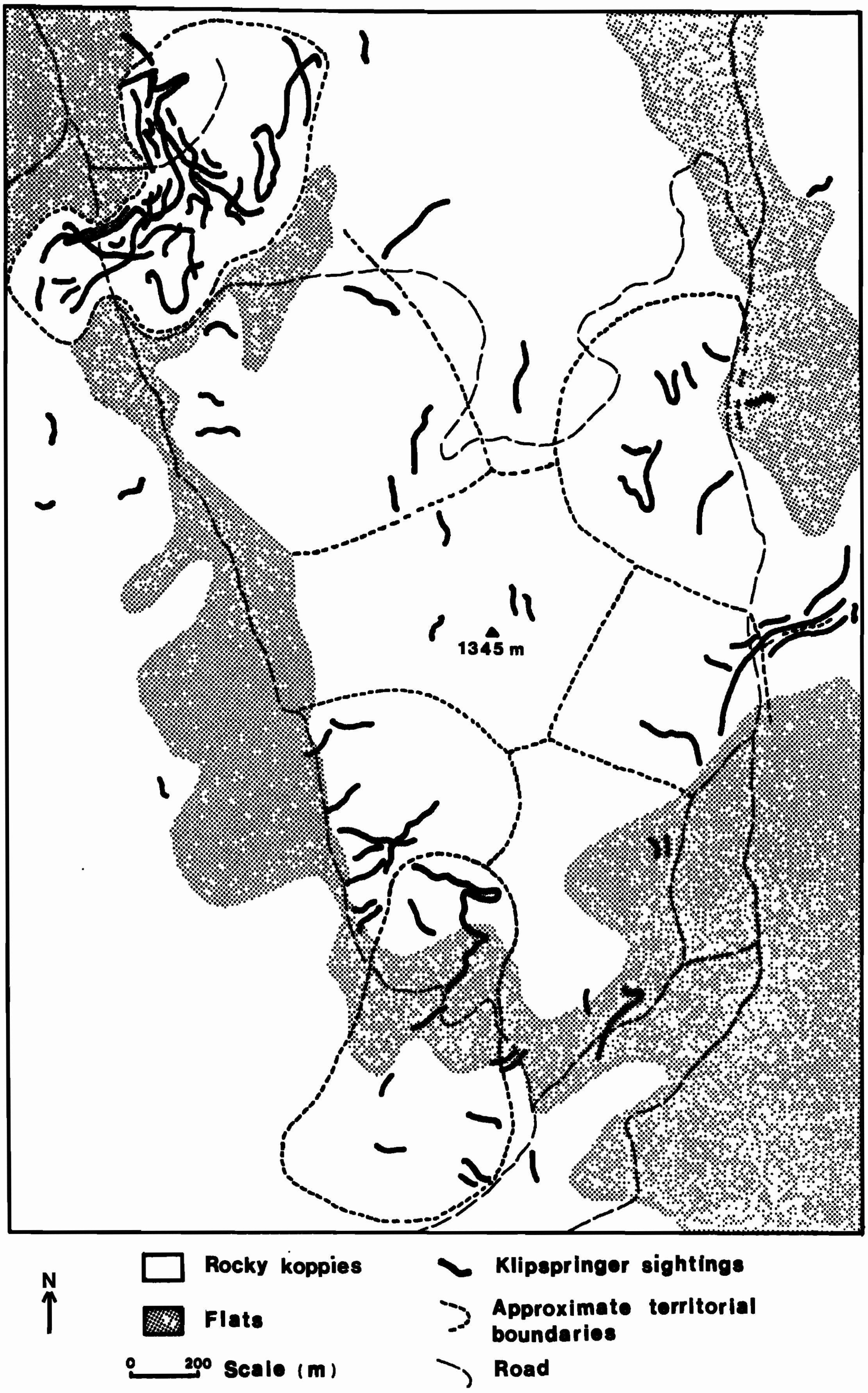


Fig. 23: The distribution of sightings and estimated territorial boundaries of klipspringer groups on Carolusberg mountain at Springbok.

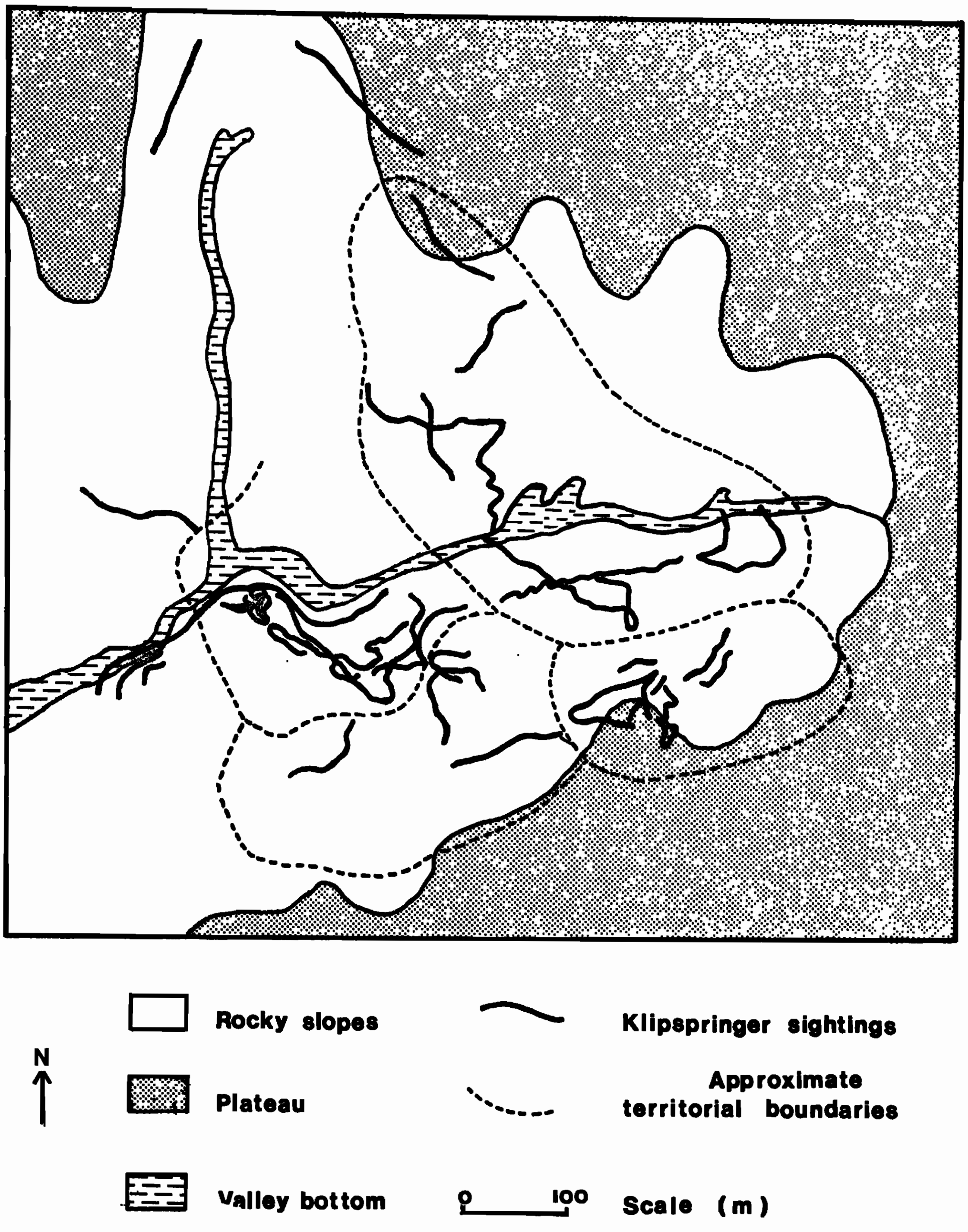


Fig. 24: The distribution of sightings and estimated territorial boundaries of klipspringer groups at the top of Tierkloof, Gamka study area.

per year, the territory size is much larger than at Gamka with 400 mm. Dunbar and Dunbar's (1974) figure also fits this pattern neatly, with even smaller territories in a high rainfall area.

Table 2: Klipspringer territory sizes in relation to rainfall in different areas where they have been studied.

	Territory	Rainfall
Present study Springbok	49 ha	160 mm
" " Gamka	15 ha	400 mm
Dunbar and Dunbar (1974)	8 ha	1300 mm

Although the territory sizes mentioned above are for areas with ideal terrain for klipspringers, the densities arising from these figures were useful to give an indication of the number of individuals occurring in each reserve.

The number of klipspringers in the Hester Malan Nature Reserve was calculated at 101 individuals using these values (Table 3). Regular monthly counts by the reserve staff yielded very variable totals of between 16 and 43 individuals (unpubl. monthly reports. C.D.N.E.C.), but these can be considered as underestimates due to the inaccuracy of the low intensity survey method used. Application of the method of "bounded counts" (Overton 1971) to these data yielded a total of 50 individuals, but with very broad confidence limits (Table 3). Therefore the total population of the reserve is likely to be somewhere between the two, probably at about 70 to 80 klipspringers.

At Gamka the errors involved are likely to be far greater, since factors such as the increased area due to the slope and the extreme variability of the vegetation could not be taken into account. In addition, large areas of the reserve have hardly ever been visited by the reserve staff. Therefore the figure of 407 klipspringers (Table 4) is very approximate, but it seems likely that there are at least 300 individuals in the reserve.

Lambing seasons

Figure 27 shows the monthly distribution of klipspringer births estimated by ageing young animals sighted in the different study areas. A total of 20 juveniles was seen and aged at Springbok, but the other areas yielded only a few records. The results show that in the Cape Province klipspringers

Table 3: Estimates of the total population of klipspringers in the Hester Malan Nature Reserve near Springbok using a) the total area of suitable rocky habitat (Fig. 25) and the mean territory size (Table 2) and b) the method of "bounded counts" (Overton 1971) on the monthly game counts by reserve staff (Unpubl. reports C.D.N.E.C.).

a) Area of rocky habitat

Total area of rocky habitat = 2244 ha
Carolusberg study area = 1727 ha
Outlying koppies = 517 ha

Mean territory size in study area = 49 ha
Mean group size = 2,5 individuals

$$\therefore \text{ Estimated total population} = \frac{1727}{49} \cdot 2{,}5 + \frac{517}{98} \cdot 2{,}5$$

$$= \underline{101 \text{ individuals}}$$

b) Bounded counts

Monthly counts: 1977 - 32, 26, 33, 36, 28, 22, 28, 18, 19, 27, 22, 16

1978 - 32, 22, 27, 28, 21, 25, 23, 19, 34, 28, 43.

$$\text{Estimated total } N = 2n_k - n_{k-1} = 2 \cdot 43 - 36$$

$$= \underline{50 \text{ individuals}}$$

$$\text{Upper Confidence Limit } N_u = n_k + \frac{1-\alpha}{\alpha}(n_k - n_{k-1})$$

$$= 43 + \frac{0{,}95}{0{,}05}(43 - 36)$$

$$= \underline{176 \text{ individuals}}$$

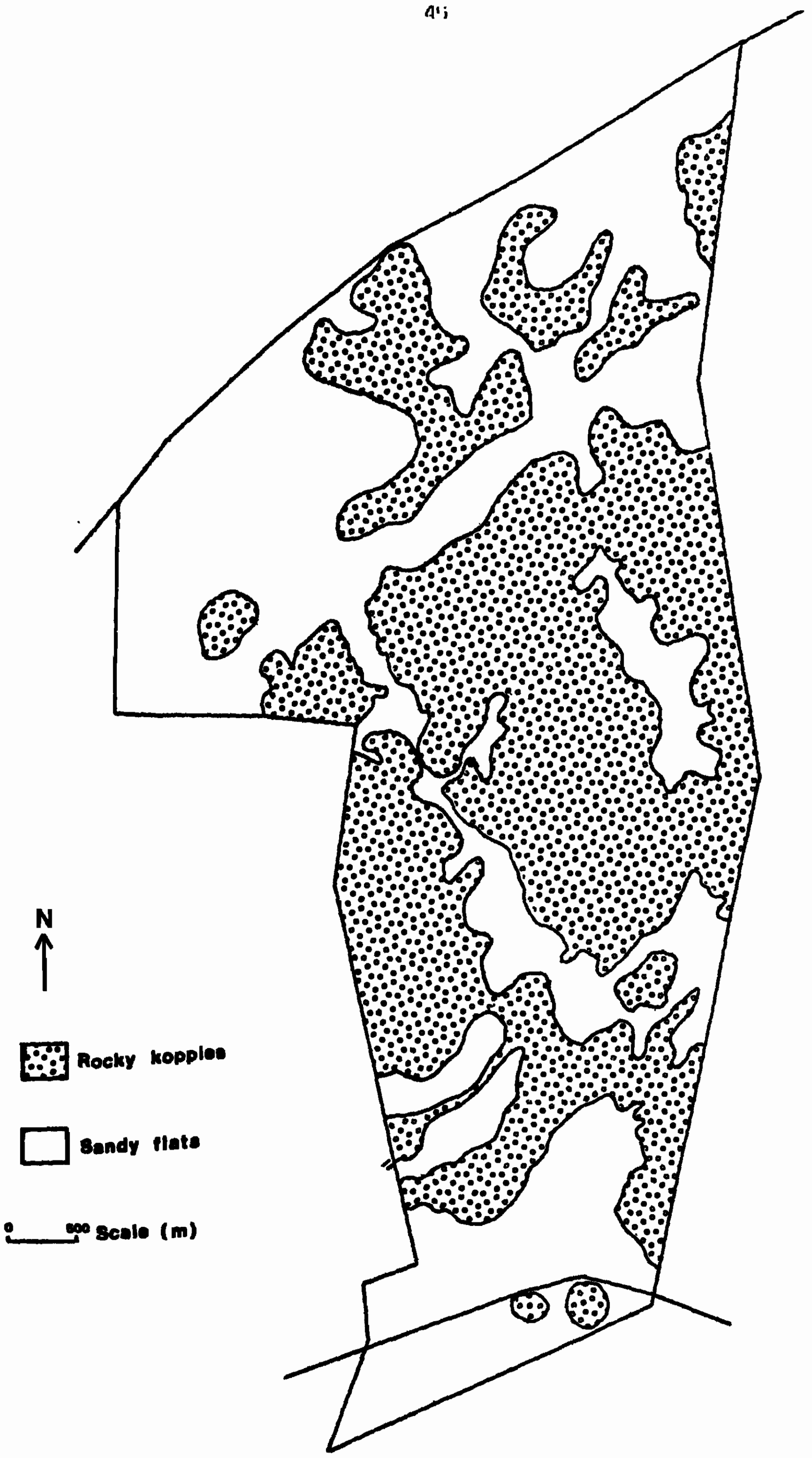


Fig. 25: The distribution and area of rocky habitat in the Hester Malan Nature Reserve near Springbok.

Table 4: Estimate of the total population of klipspringers in the Gamka Mountain Nature Reserve, using the areas of the dry north-facing slopes, medium slopes and steep gorge side habitats (Fig. 26), and the mean territory size for the main study area.

Total area of dry north-facing slopes = 269 ha
" " " other medium slopes = 3765 ha
" " " steep gorge sides = 576 ha

Mean group size = 2,5

If the mean territory size in the dry north-facing slope habitat is 15 ha, and in the other medium slope and gorge side habitat is 30 ha,

$$\text{Total population} = 2{,}5\left[\frac{269}{15} + \frac{3765 + 576}{30}\right]$$

$$= \underline{\underline{407 \text{ individuals}}}$$

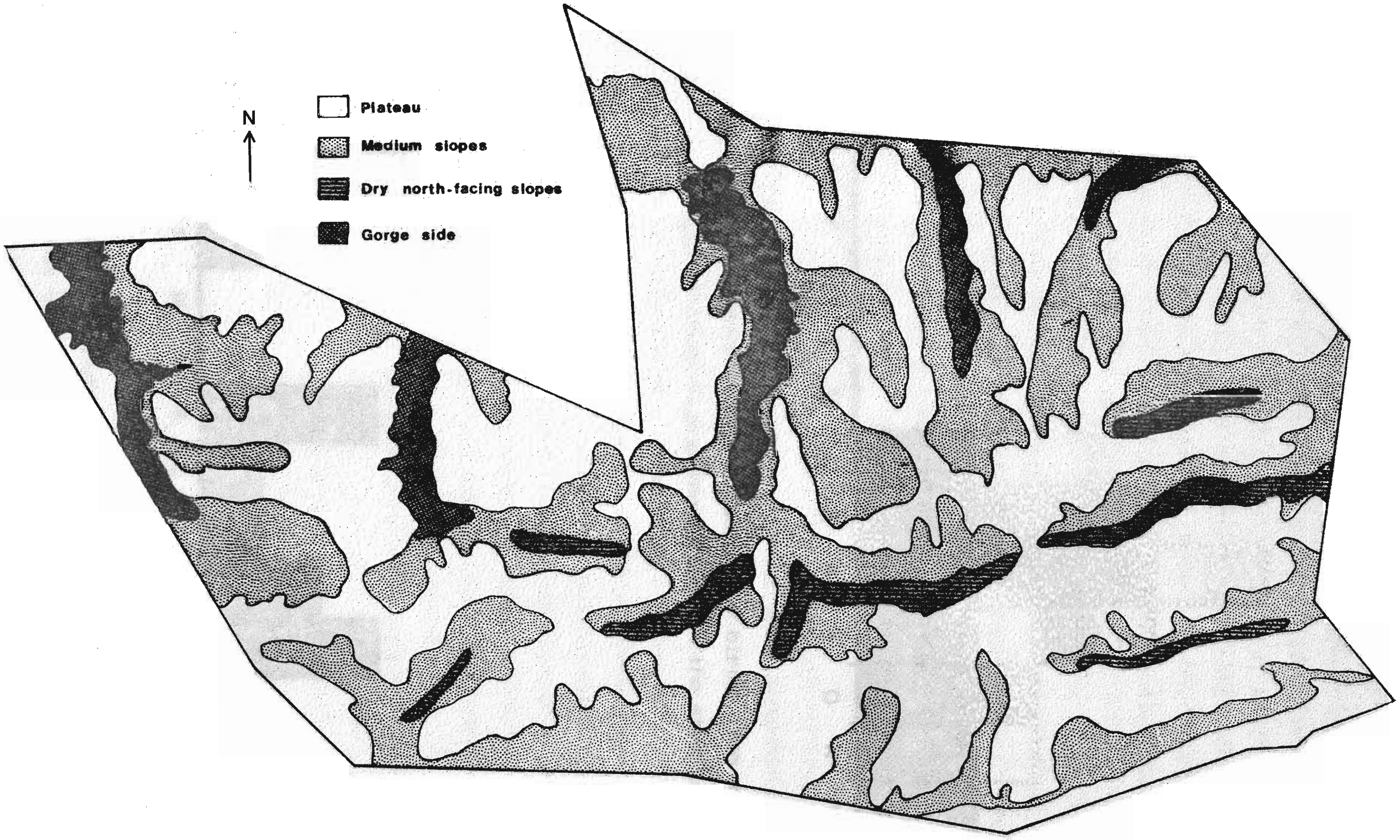


Fig. 26: The distribution and area of medium slope, dry north-facing slope and gorge-side habitat in the Gamka Mountain Nature Reserve.

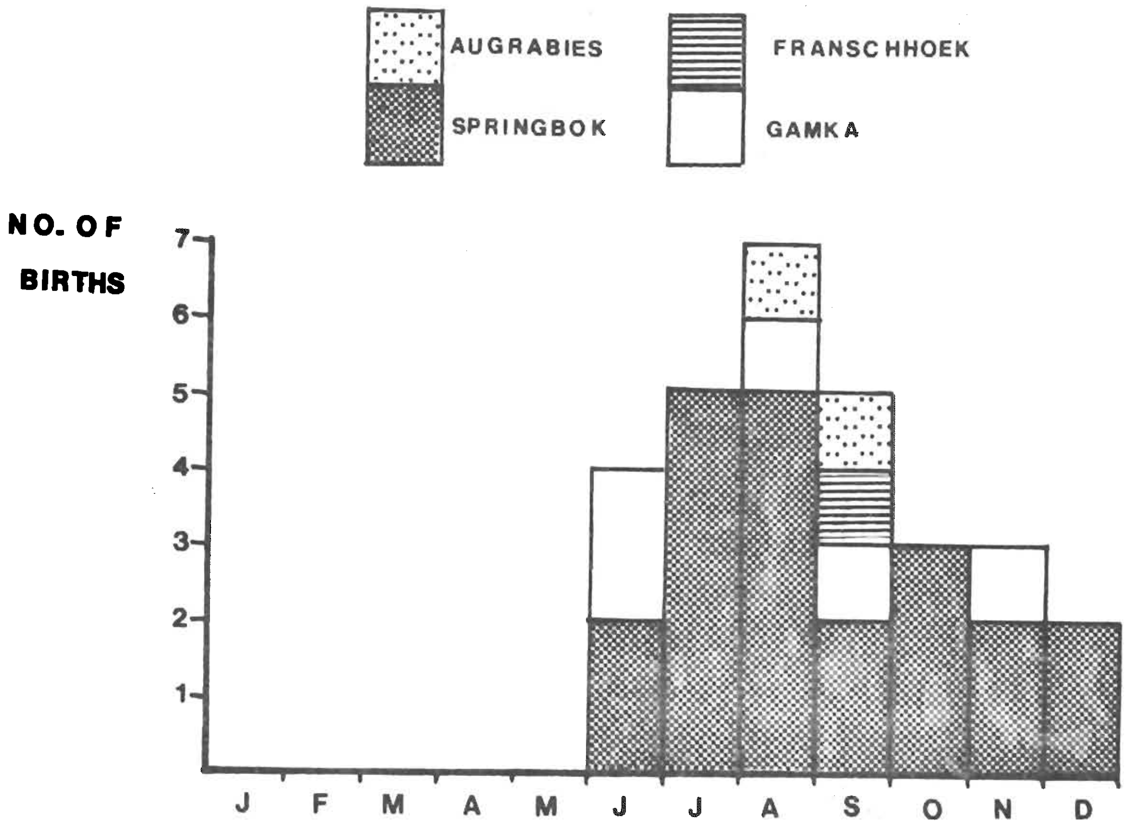


Fig. 27: Monthly distribution of klipspringer births from estimates of ages of young klipspringers seen in the study areas.

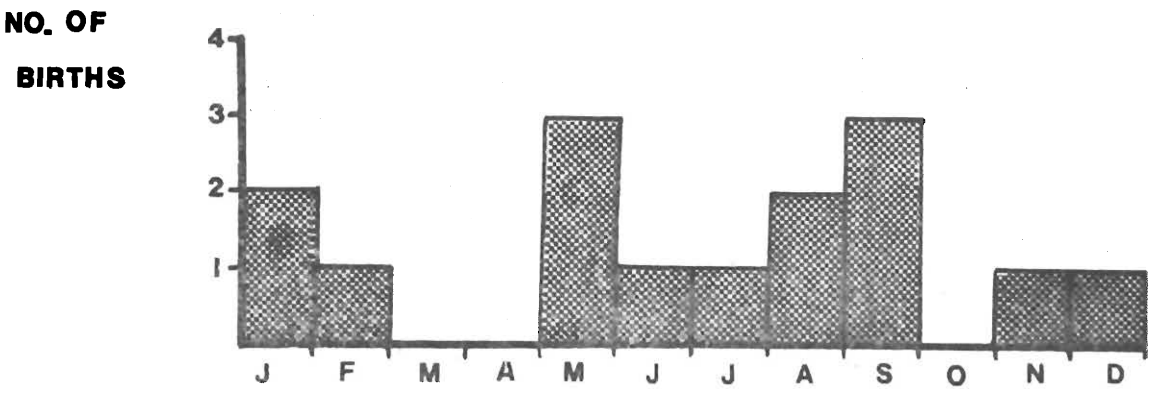


Fig. 28: Monthly distribution of extrapolated births of klipspringer foetuses collected by Wilson and Child (1965) in Zambia. Birth dates were calculated according to Huggett and Widdas (1951), using 160 days as the gestation period and a birth weight of 1250 g.

have an extended lambing season lasting from June to December with a peak in births from July to September.

In other areas there seems to be much variation in breeding seasons. Shortridge (1934) stated that the lambing season in South West Africa is extended with the young born from September to January, which agrees well with the present study. On the other hand, Tilson (pers. comm.) could detect no particular lambing season in the Kuiseb canyon. In Ethiopia Dunbar and Dunbar (1974) suggest a mating season in August-September, which means a lambing season in January-February.

Wilson and Child (1965) interpreted their analysis of shot klipspringers in Zambia to show that there is no lambing peak for this species. However, application of the method of Hugget and Widdas (1951) to their foetal weights, using 160 days as the gestation period and 1250 g as the birth weight, suggests that ten of the fifteen offspring would have been born from May to September (Fig. 28).

There are several factors involved in the evolution of synchronisation and seasonality of lambing in ungulates, and the klipspringer appears to gain advantage from some of these. The first is that a well-developed synchrony of lambing would be a disadvantage in predator avoidance to an antelope that occurs in low densities and hides its young for the first few months. Antelope that occur in very large herds, such as the wildebeest and Thomson's gazelle in East Africa, derive benefit from the "swamping" effect of synchronised breeding (Kruuk 1972). However, all small antelope occur in such low biomasses that synchronised lambing would not produce enough food to swamp the predators, so that a fixed short season might, in effect, tell the predators to look very carefully for hidden juveniles at that time."

Nevertheless, the strain on water and energy metabolism of both the lamb and its mother select for individuals that breed at a particular time of the year. The main factors are the drain on the energy resources of the mother during accelerated foetal development in the last few months of pregnancy, the loss of energy and moisture during lactation, and thermoregulatory stress on the neonate.

At Springbok and Gamka a large proportion of the annual precipitation falls during the winter months (Chapter 1). This means that the vegetation grows mainly in winter, and most of the shrubs produce flowers and fruits in spring.

Thus a spring lambing peak enables the female to assimilate the energy needed for foetal growth and lactation when nutritious food is most abundant, even though the cold temperatures in winter require extra energy for thermoregulation during early pregnancy (Chapter 4). In addition, the greatest moisture drain, during early lactation, occurs when the vegetation is still succulent after the winter rains. In arid areas, such as Springbok, this factor must be particularly important. Although offspring born in June and July may suffer from the cold temperatures, their habit of remaining hidden during the first few months allows them to make use of the more stable micro-climate of their hiding places. When they start to accompany their parents after two to three months, the temperatures have increased enough to present few problems, but they are able to grow to nearly adult size before they have to cope with the heat and water stress of mid-summer.

Thus, in the Cape winter rainfall region, a spring lambing season ensures the best use of the seasonality of the food supply and avoids extremes of temperatures at the critical times in the development of the offspring. However, the lambing peaks reported in the other areas are less easy to explain.

In Ethiopia the seasons are not affected much by day length because the country lies just north of the equator, but the January-February lambing peak suggests that the season is different because of latitude. In their study area Dunbar and Dunbar (1974) record that the wet season lasts from July to September, and during this period freezing temperatures and hailstorms are frequent. This may be the reason why no lambs are born then, but the delay of lambing until well into the dry season cannot be explained easily.

The ill-defined winter lambing season in Zambia found by Wilson and Child (1965) is also difficult to understand, since lambing in August or September would mean that the drain on energy and moisture resources of the female during lactation falls right in the critical period at the end of the dry season. A January-February lambing peak would seem to be more desirable. Temperatures are probably not cold enough in winter to be critical, although the extreme heat in summer may play a role in selecting against a lambing peak at this time.

Thus it seems that the klipspringer has a variable breeding season which is partly determined by local conditions.

Gestation and weaning

There is little published information on the gestation period of klipspringer or any other small antelope. Cuneo (1965) recorded periods of 7-7½ months for klipspringers bred in zoological gardens, but this seems extraordinarily long for a small antelope, since even the much larger springbok has a gestation period of only 5½ months (Sclater and Thomas 1896). During the present study the approximate date of mating was known for the young ram at Augrabies Falls. This gave a gestation period of 155-160 days or five months. Even though this individual seemed to show unusual growth characteristics and may possibly have been born a few weeks prematurely, this indicates that the gestation period of klipspringers is unlikely to be more than six months.

Klipspringer neonates are hidden for the first two to three months after birth, then they spend progressively more time accompanying their parents. Weaning occurs at about four to five months. In two different groups, one in each study area, young klipspringers of about this age were chased away by their mothers, or else allowed to suckle for only a short while and then chased away.

Growth

Figures 29 and 30 show the growth in body mass, shoulder height and horn length of the semi-tame young klipspringer rams at Springbok and Augrabies Falls. The most noteworthy feature of the graphs is that there is a marked difference between the growth curves for the ram at Augrabies and the one at Springbok. In addition the few readings from the second youngest ram at Augrabies agree more closely with those of the ram at Springbok than with his own younger brother. Manipulation of the curves to see if they would fit better if the Springbok study animal's age had been underestimated made little difference. An explanation may be that the youngest ram at Augrabies Falls was at the lower end of the range for growth in this species. This could have been due to disease or other effects of stress resulting from captivity. The growth curve for the ram at Springbok and the few measurements for the second youngest ram at Augrabies Falls were therefore regarded as more typical of the klipspringer growth pattern.

In spite of the difficulties in assessing the shoulder height of klipspringers accurately, this measurement was the most useful for field assessment of a wild juvenile's age. The measurement for the foetus from Franschhoek (Appendix E) is probably a slight underestimate, since it was in the partly

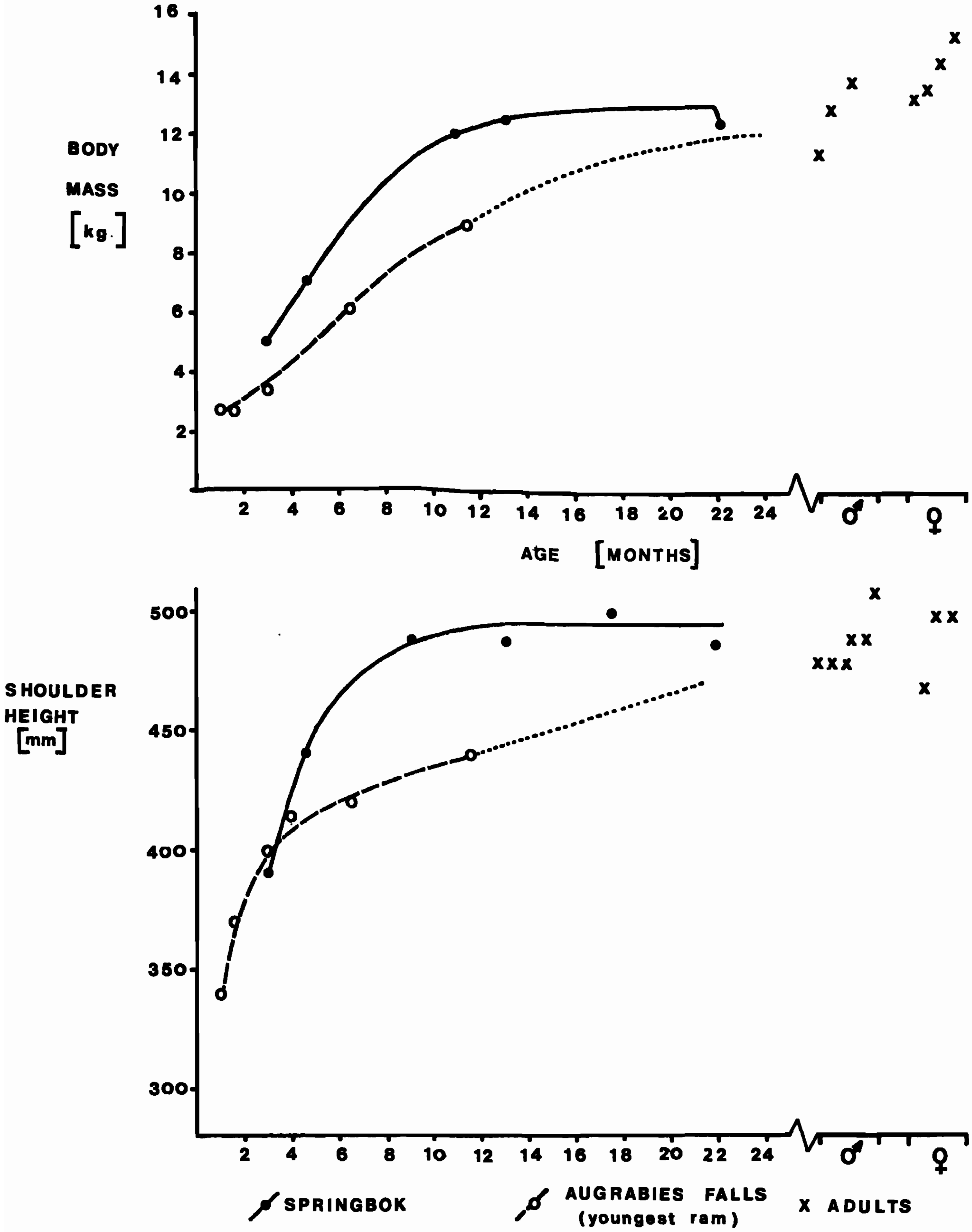


Fig. 29: Growth in body mass and shoulder height of tame young klipspringers at Springbok and Augrabies Falls, in relation to measurements from tame and shot adults.

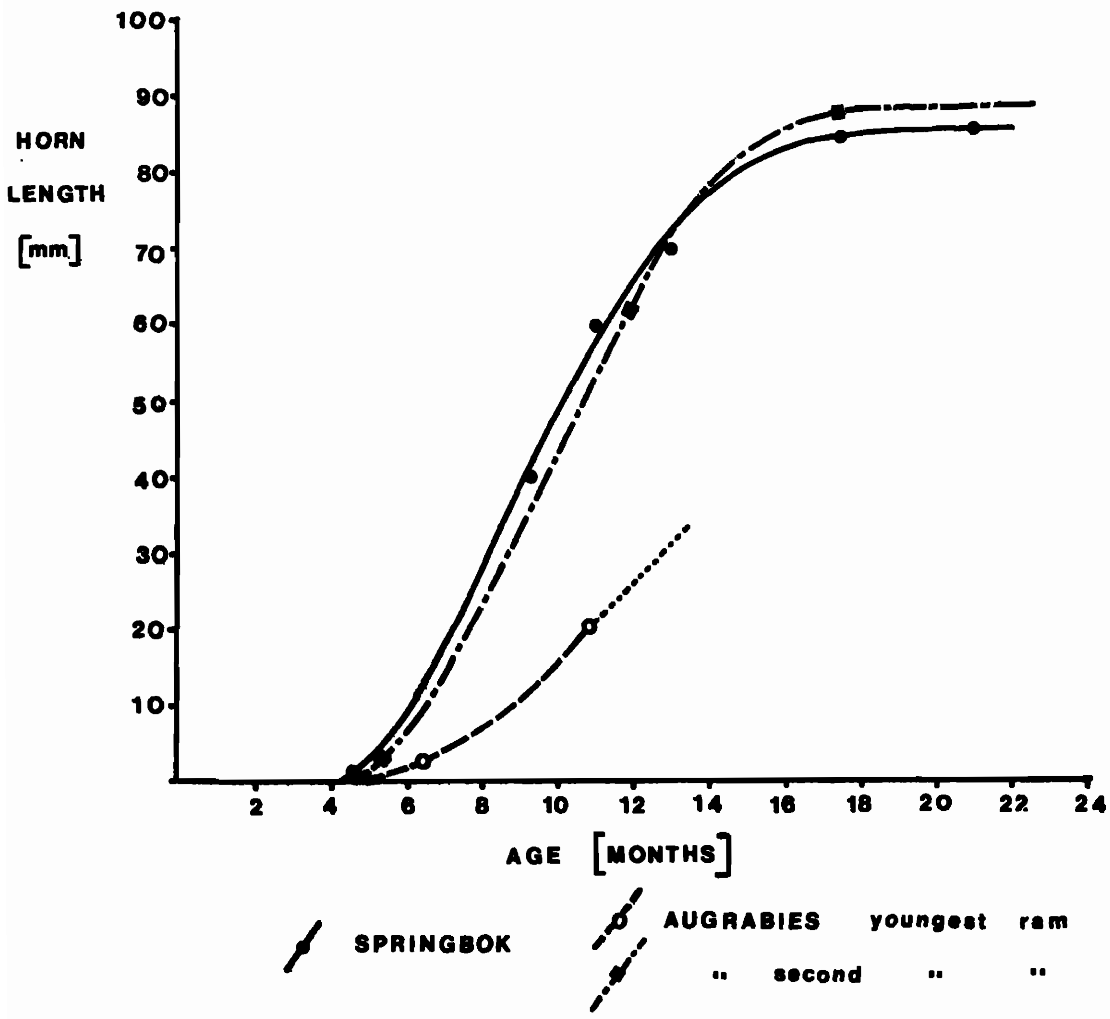


Fig. 30: Growth in horn length of tame young klipspringers at Springbok and Augrabies Falls.

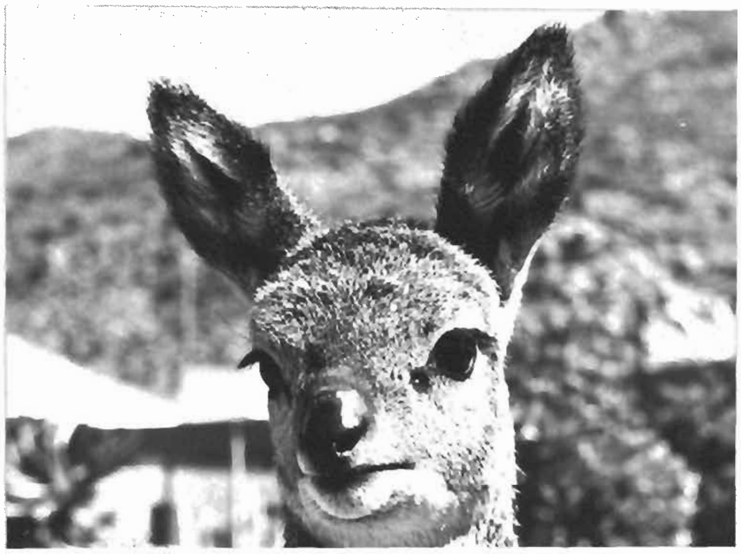
curled foetal position, so the growth curve for shoulder height in klipspringers can be taken as starting from just less than 300mm at birth and increasing more or less linearly until about six months, then flattening out so that full adult height is reached at about eight to ten months. The shoulder heights of all adults measured during the study were between 470 and 520mm (Fig. 29, Appendix E) which are very similar to the records of Wilson and Child (1965). A young ram of about three months with a shoulder height of 390mm is illustrated in Fig. 31.

Difficulty in handling the young klipspringers made it impossible to take regular measurements of mass, but the graph for body mass shows a similar growth curve to the shoulder height curve, although the asymptote is only reached after more than a year. Skeletal growth is therefore complete several months before growth in body mass, which explains why adult offspring could be distinguished with some certainty from their parents while they were still accompanying them.

Horn growth was first noticed at about four months with small buds forming on top of the skull. These only protruded above the hair on the head at about 5½ - 6 months, but from there on grew quite rapidly (Fig. 32). Growth was almost linear until about 12 months, then gradually slowed until they reached near adult size at about 17-18 months. However, there seems to be a great variation in the length of adult horns which is further accentuated by the fact that the tips are often broken off, presumably in fighting. This led Wilson and Child (1965) to say that, as shown for duiker (Riney and Child 1964), horn length does not seem to be a reliable criterion for ageing wild klipspringers, except for the classification of very young animals. This is supported by the present study, although this parameter was very useful in identifying young rams of 12-18 months that had reached full adult body size but not yet adult horn length.

Fig. 31: The tame klipspringer ram at Springbok at the age of about three months.

Fig. 32: Horn growth of the tame klipspringer at Springbok. Note also ante-orbital scent gland.



a) 3 months

b) 6½ months

c) 11 months

CHAPTER 4 : ANATOMICAL AND PHYSIOLOGICAL ADAPTATIONS

There are several ways in which the structure and functioning of the klipspringer's body have adapted to cope with the extreme conditions of the mountainous terrain it prefers. Factors such as great fluctuations in temperature, exposure, scarcity of water at certain times of the year, and the difficulty of moving on rocky substrate have all selected for unusual adaptations. Thus the klipspringer possesses an unusually thick pelage to cope with extremely hot and cold conditions, as well as the cooling effect of wind, an efficient water conservation system, and a unique hoof structure which enables it to run very swiftly on rocky terrain.

METHODS

Pelage

To assess the importance of the pelage as an insulator for hot and cold conditions the thickness of the hair layer and conductance of pelts of shot klipspringers was measured. The hair layer was measured on the flat skins in a dorso-lateral position on the ribs, just posterior to the scapula. Hofmeyr* (pers. comm.) has found that this area is the most representative for ungulate skins and is least affected by special adaptations such as "thermal windows", "manes" or rump flash organs. The skins of seven adult and one sub-adult klipspringers were measured in this way, as well as two blue duikers, four dik-diks, two vaalribbok, and three grey duiker for comparison.

Although a good correlation exists between the thickness of the hair layer and the thermal conductivity of the pelage of ungulates (Hofmeyr in prep.), the unusually coarse texture of the klipspringer's hair may show extraordinary properties. Therefore the conductance of a pelt was measured directly using a heat flux apparatus similar to the one described in Hammel (1955). The pelt measured had a thickness of 25mm and was from a female klipspringer shot at Springbok in June 1978. To determine the effect of wind on the insulation of the pelage the conductance and conductivity was measured for wind speeds of 0 ms^{-1}, 1 ms^{-1}, 2 ms^{-1}, 3 ms^{-1}, 4 ms^{-1}, 4,3 ms^{-1}.

Water metabolism

It is very difficult to assess the efficiency of the water metabolism of wild animals without laboratory experiments under controlled conditions. Nevertheless, an idea of the potential moisture conserving ability of the

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* Mrs. M.D. Hofmeyr, Zoology Dept., University of the Western Cape.

animal can be gained by testing the urine concentration and examining the kidney structure of freshly killed specimens. Thus blood and urine samples were taken from all the shot klipspringers and their kidneys were removed and frozen for later analysis.

The blood samples were placed in sealed tubes and cooled in a refrigerator within a few hours. Due to the lack of suitable apparatus in the field they could only be centrifuged two to five days after the animal had been shot. After centrifugation the serum was placed in small sealed tubes and deep-frozen. Urine samples were placed in sealed containers and deep-frozen as soon as possible, which was usually 3-24 hours after shooting.

The blood and urine samples and the kidneys were sent to the Zoology Department of the University of Cape Town for analysis and measurement. For the blood and urine osmolality and urea concentrations were measured. Osmolality was determined by the freezing point depression method using an automatic osmometer (Advanced Instruments). The urea concentration was determined enzymatically using urease and the method of Richterich (1968).

The kidneys were measured according to the methods described by Sperber (1944). The kidney size was calculated as the cube root of the product of the dimensions of the kidney and the relative medullary thickness was calculated by the formula

$$\text{Relative Medullary Thickness} = \frac{\text{medulla thickness}}{\text{kidney size}} \cdot 10$$

RESULTS AND DISCUSSION

Pelage

The klipspringer has an unusual pelage of a thick layer of coarse hair (Fig. 33). The springy texture of the hair, which is actually hollow inside, has been well-known for many years, and the early colonists used to hunt klipspringers especially to obtain hair for stuffing saddles (Harris 1840, Inverarity 1899). This led early naturalists to believe that the texture was for cushioning when the klipspringer bumps against sharp edges (Harris 1840, Shortridge 1934). Though this may be important, it is unlikely that it was the primary factor in the evolution of the unusual hair because it falls out very easily. Since it takes several weeks to grow back to normal length, it is improbable that a system has evolved to leave the most vulnerable parts exposed after even a minor collision.

Fig. 33: The coarse hair of the klipspringer pelage.

The more acceptable hypothesis for the development of such a pelage is that it is needed for insulation against the extremes of temperatures associated with mountainous habitat. A thick pelage is characteristic of many mountain ungulates, such as the thar (Hemitragus jemlahicus) and chamois (Rupicapra rupicapra), and is an adaptation to not only the lower absolute temperatures resulting from the increased altitude, but also the greater fluctuations associated with mountainous areas due to factors such as exposure to the wind and shading on the southern slopes. In addition it insulates the animal against extremes of heat, thereby aiding water conservation.

The mean pelage depth for klipspringers measured was 24 mm (range 15-28, n = 8). Figure 34 shows how the thickness of the klipspringer's hair covering compares to that of other antelopes. All except one of the values for klipspringers came from individuals that were shot in winter, which undoubtedly has an effect on the mean pelage depth, but none of the pelts of the other species measured had values higher than that of the klipspringer shot in summer, which measured 16 mm. Thus, although one expects the smaller antelope to have a thicker pelage simply because of their greater surface to body mass ratio, it is apparent that the klipspringer has a far thicker coat than it would need if it was subjected to the same conditions as other antelope of similar size. This is probably because it is less able to make use of more stable micro-climate conditions, as do grysbok, steenbok, duiker and other small antelopes.

a) Use of micro-climate

Shelter is commonly used by mammals to decrease heat loss in cold conditions, and klipspringers may use micro-climate to a certain extent. However, in the rocky, low shrub environments at Gamka and Springbok and, indeed, of most mountainous areas inhabited by klipspringers, suitable shelter is scarce.

Few observations during the study suggested that they do use such shelters to any extent. Although on several occasions klipspringer groups were seen to move to parts of their territories that afforded some protection from the main force of the wind in cold conditions, they seldom seemed to make use of shelter on the micro-climate scale. In fact, their anti-predator vigilance behaviour (Chapter 5) caused them to spend a very large proportion of the time in prominent sites of good visibility. In addition, the activity study (Chapter 7) showed that their basic activity pattern was hardly affected by cold and windy conditions.

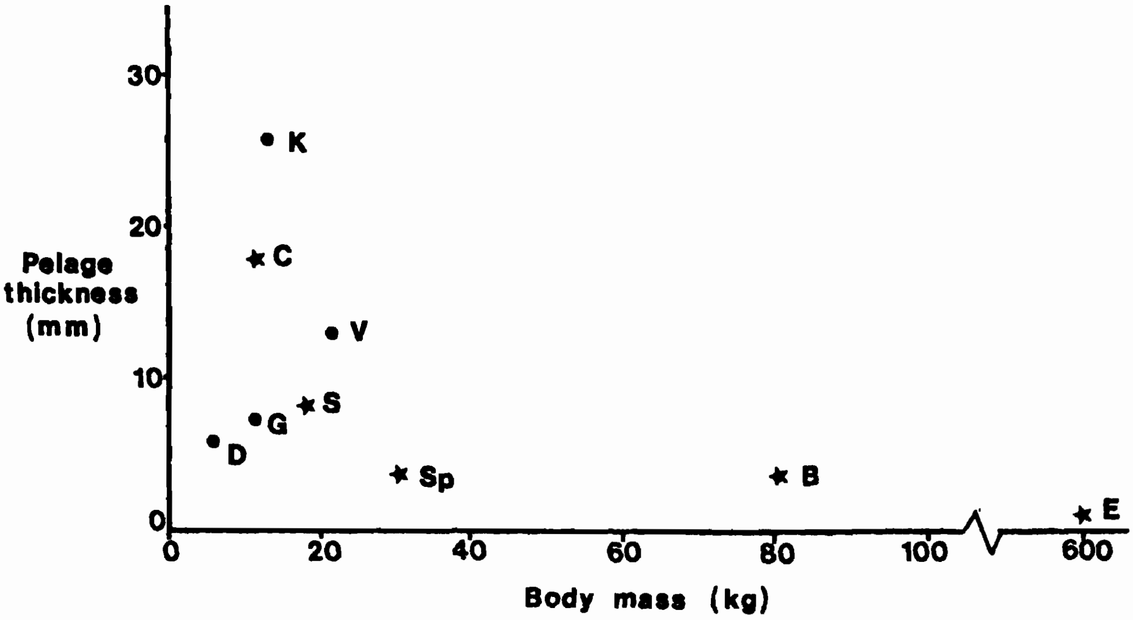

Fig. 34: Pelage thickness in relation to body mass of some South African antelope.

Sources: ★ Hofmeyr (in prep.) ● Present study

K - Klipspringer	*Oreotragus oreotragus*	(n = 8)
C - Cape grysbok	*Raphicerus melanotis*	
V - Vaalribbok	*Pelea capreolus*	(n = 2)
S - Steenbok	*Raphicerus campestris*	
G - Grey duiker	*Sylvicapra grimmia*	(n = 3)
D - Dikdik	*Madoqua kirki*	(n = 4)
Sp- Springbok	*Antidorcas marsupialis*	
B - Bontebok	*Damaliscus dorcas dorcas*	
E - Eland	*Taurotragus oryx*	

Thus klipspringers probably rely on the insulative properties of their thick pelage to protect them from excessive heat loss under cold conditions.

b) Conductivity and conductance of the klipspringer pelage

The conductivity and conductance of the klipspringer's pelage at different wind speeds is shown in Table 5 and Fig. 35. It is clear that, as the wind speed increases, the conductance rises in a linear fashion. This means that the insulative properties decrease in direct proportion to the wind speed so that the pelage is only about 60% efficient at a speed of 4,3 ms^{-1} (15,5 km h^{-1}).

The effectiveness of the pelage as an insulator can be used to calculate the approximate "thermoneutral range" of the animal concerned. This is defined as the range in temperatures in which the animal can maintain body temperature at the basal metabolic rate of heat production (Moen 1973). That is, if the temperature drops below a certain level, the "critical hypothermal environment" (Moen 1968), the animal will have to use energy at a faster rate than the basal metabolic rate if it is to maintain body temperature. Since free-living wild animals probably spend very little time at the basal metabolic rate, the basic thermoneutral range is seldom applicable, but active thermoneutral ranges can be calculated at various levels of metabolic activity to work out how active the animal must be to maintain body temperature.

Since detailed physiological data and body measurements are available for only a few wild animals, there are several basic assumptions that have to be made for these calculations. The most important are that the surface area of the klipspringer is proportional to its body weight in the relationship shown for most mammals, and that the basal metabolic rate follows the Brody-Kleiber relationship to body mass. Two other assumptions are that the pelage is uniform in thickness and conductance over the whole body, and that the body temperature is constant throughout. Since the legs and belly have a far thinner hair covering than the back and neck, the first is strictly not true, but is partly compensated for by the second, since the extremeties are able to drop in temperature while the core body temperature is maintained. In addition, the thinner pelage on the stomach and under the legs may be balanced to some extent by the restriction of air flow over these body areas under windy conditions. In any case, the error involved in having a thinner pelage than that measured on the shoulder is likely to have the effect of raising the lower level of the thermoneutral range rather than lowering it, which is important in this discussion.

Table 5: Thermal conductivity and conductance values for a klipspringer pelt of 25 mm pelage thickness at different wind speeds.

Wind speed ($m\ s^{-1}$)		Conductivity ($W\ m^{-1}$)	Conductance ($W\ m^{-2}\ {}^{o}C^{-1}$)
0		0,0544	2,17
		0,0569	2,28
		0,0565	2,22
		0,0538	2,15
		0,0549	2,18
	Mean	0,0553	2,20
1		0,0612	2,55
		0,0576	2,40
2		0,0672	2,80
		0,0651	2,71
3		0,0726	3,03
		0,0746	3,11
4		0,0815	3,40
		0,0820	3,42
4,3		0,0852	3,55
		0,0835	3,48
		0,0855	3,56
	Mean	0,0847	3,53

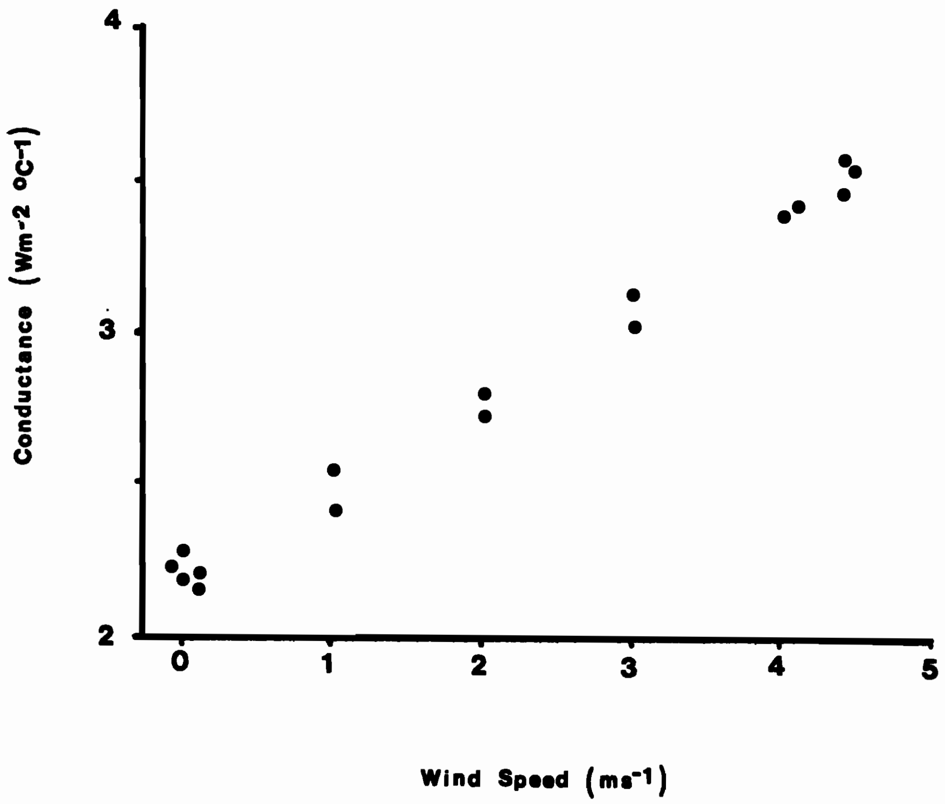

Fig. 35: The conductance of a klipspringer pelt in relation to wind speed.

The surface area of mammals has for some years been known to show a good correlation with the two-thirds power of the body weight. Thus the klipspringer's surface area can be calculated by the following formula (Campbell 1977):-

$$A = 0{,}1m^{0{,}67}$$

where A is the area in m^2, and m is the mass in kg. At an average body mass of 13,0 kg (Table 33, Appendix E) the surface area of the klipspringer is calculated to be 0,56 m^2.

The most universal approximation of the Brody-Kleiber relationship between basal metabolic rate and body weight is the formula (Campbell 1977):-

$$BMR = c\ m^{0{,}75}$$

where BMR is the basal metabolic rate in kcal hr^{-1}, c is a constant and m is the mass in kg. According to this author a value of 3,0 for the constant seems to be the most accurate for large mammals, so the BMR of the klipspringer is calculated to be 20,55 kcal hr^{-1}, which is equivalent to 23,90 Watts.

Thus to maintain body temperature, the maximum allowable rate of heat loss for the klipspringer at basal metabolic rate is 23,90 Watts which corresponds to a flow of $\frac{23{,}9}{0{,}56} = 42{,}6\ W\ m^{-2}$ over its surface.

The heat flow across an animal's body surface is defined by the following formula (Herreid and Kessel 1967):-

$$Q = c\ (T_b - T_a)$$

where Q is the heat loss in W m^{-2}, c is the conductance in W m^{-2} $°C^{-1}$ and $(T_b - T_a)$ is the temperature gradient from the body temperature (T_b) to the ambient temperature (T_a).

To work out the ambient temperature at which heat loss is balanced with heat gained from the metabolic rate, this formula can be changed round to give

$$T_a = T_b - \frac{Q}{c}$$

The body temperatures of three shot klipspringers were 39,1°C, 39,0°C, and 38,7°C within a few minutes of shooting. Since these individuals had been active, the temperature of resting klipspringers is taken to be about 38°C, which is typical for most African antelope (Hofmeyr in prep.). Thus the critical hypothermal environment is calculated to be

$$38 - \frac{42,6}{2,20} = 18,6^{\circ}\mathrm{C} \text{ at } 0 \text{ m s}^{-1} \text{ wind speed, and}$$

$$38 - \frac{42,6}{3,53} = 25,9^{\circ}\mathrm{C} \text{ at } 4,3 \text{ m s}^{-1} \text{ wind speed.}$$

This means that, if a klipspringer is resting at basal metabolic rate, the ambient temperature has to be at least 18°C with no wind, or at least 25°C in a wind of about 15 km h^{-1}, to maintain body temperature.

The active metabolic rate or "ecological metabolic rate" (Moen 1973) of an animal, that expresses the energy "cost of living" for the normal daily activities, is extremely variable, depending on factors such as its activity, diet, thermoregulation, reproductive condition, predator evasion strategies and social behaviour. Moen (1973) found that the ecological metabolic rate of white-tailed deer varied from 1,23 to 1,98 times the basic metabolic rate for five different activity regimes, with a female at the peak of lactation feeding two fawns using energy at 2,30 times the BMR. This author calculated values of 1,44 to 1,86 times the BMR for pronghorn antelope showing a normal activity regime. There are no such data available for African ungulates, but these values for widely differing American ungulates suggest that the rate for most African ungulates is unlikely to be much more than twice the BMR.

Table 6 shows that at twice the BMR the calculated critical hypothermal environment of a klipspringer with a 25mm hair covering is -0,7°C in windless conditions and 13,9°C with a wind of 4,3 m s^{-1}. Even at three times the BMR the critical temperature is just above freezing in a wind of 15 km h^{-1}. Since temperatures at both Springbok and Gamka drop to freezing or below (Fig. 3), it is reasonable to expect that their ecological metabolic rate increases in winter due to cold conditions. This supposition is supported by the fact that the above values were calculated for the average metabolic rates, whereas the coldest temperatures occur at times when the metabolic rate is below average. This is because klipspringers seem to be less active at night than during the day, and the coldest temperatures are in the very early morning. The metabolic rate needs to be increased for only a few hours per day to cause a noticeable increase in the daily rate of energy consumption.

In addition, the wind strength in the study areas was often considerably higher than the maximum used for the conductivity measurements. Although the klipspringers may have been able to avoid the full strength of the wind,

Table 6 : Calculation of "critical hypothermal environments" of klipspringers at different levels of activity and at different wind speeds.

Activity state	Wind speed (m s^{-1})	Critical hypothermal env.
Pelage 25 mm BMR = 23,9 W	0	18,6°C
	4,3	25,9°C
BMR x 2 = 47,8 W	0	- 0,7°C
	4,3	13,9°C
BMR x 3 = 71,7 W	0	- 20,1°C
	4,3	1,8°C

If pelage is 30 mm Conductance = $\frac{\text{conductivity}}{\text{thickness}}$

$= 1{,}84\ W\ m^{-2}\ °C^{-1}$ at 0 m s^{-1}

$2{,}82$ " at 4,3 m s^{-1}

Activity state	Wind speed (m s^{-1})	Critical hypothermal env.
BMR = 23,9 W	0	14,8°C
	413	22,9°C
BMR x 2 = 47,8 W	0	- 8,3°C
	4,3	7,8°C

several territories were so placed that it would have been impossible to avoid a high degree of wind-cooling. The linear relationship between wind speed and conductance (Fig. 35) suggests that heat loss would be increased even further if the wind speed was higher than 4,3 m s^{-1}.

Since there is some variation in the pelage thickness of klipspringers, the critical lower temperatures were also calculated for a far thicker pelage than the one measured with an average thickness of 30 mm (Table 6), where the conductance is decreased according to the average conductivity of the klipspringer pelt. Even with the thicker pelage the critical limit in windy conditions is well above 0°C at twice the BMR.

Thus the thickness and coarse texture of the klipspringer pelage make it an effective insulator for reducing heat loss in cold conditions. However the insulative properties are unlikely to be sufficient to prevent an increase in metabolic rate to maintain body temperature in the coldest conditions occurring in the study areas.

Water metabolism

Table 7 gives the results of the plasma and urine analyses. The low osmolality figures show that the klipspringers were under no particular water stress at the time they were shot. This is most likely because they were shot in winter, when the temperatures are lower and therefore the evaporative water loss for thermoregulation is negligible. In addition, most of the animals had succulent vegetation in their stomachs, and may have gathered early morning dew from the vegetation shortly before being shot. Because of these factors the urine to plasma concentration ratios are low (Table 7).

However, measurements of the kidneys indicates that the concentrating ability of the klipspringer's kidney may be comparatively high. This is suggested by the high value for the relative medullary thickness (mean 7,6; range 6,5 - 8,8; Table 8) which shows that the medulla makes up a large proportion of the kidney. Since the medulla consists mainly of the loops of Henlé which are the regions of the nephrons involved in active concentration of salts, a high relative medullary thickness should represent a high concentrating ability. A good correlation between these two was found by Sperber (1944). The figures from more recent studies (Table 9) suggest that klipspringers should be able to concentrate their urine to a urine : plasma ratio of at least eight or nine, but this needs to be tested under laboratory conditions.

Table 7: Osmolality and sodium, potassium and urea concentrations in the plasma and urine of shot klipspringers.

PLASMA

Area	No. of Animal	Osmolality (m Osm)	Urea (m mol/l)
Springbok	♀ K1	288	3,48
"	♂ K2	330	2,62
Gamka	♀ K3	265	3,68
"	♂ K4	380	4,68
"	♀ K5	352	3,86
Franschhoek	♀ K6	339	4,03
Mean ± S.D.		326 ± 42	3,73 ± 0,68

URINE

	No. of Animal	Osmolality (m Osm)	Urea (m mol/l)
	♀ K1	-	-
	♂ K2	-	20,0
	♀ K3	724	17,0
	♂ K4	1280	16,0
	♀ K5	1251	-
	♀ K6	-	-
Mean ± S.D.		1085 ± 313	17,67 ± 2,08

URINE : PLASMA RATIOS

No. of animal	Osmolality	Urea
♀ K1	-	-
♂ K2	-	7,63
♀ K3	2,73	4,62
♂ K4	3,37	3,42
♀ K5	3,55	-
♀ K6	-	-

Table 8: Kidney dimensions of shot klipspringers measured according to Sperber (1944).

	N.	Mean	S.D.	Range
Weight (g)	12	25,68	± 5,05	22,14 - 37,80
Size (mm)	12	30,00	± 0,23	27,0 - 34,9
Medulla %	10	77,98	± 2,73	72,9 - 81,7
Cortex %	10	22,02	± 2,73	18,3 - 27,1
Relative medullary thickness	10	7,62	± 0,75	6,53 - 8,85

Table 9: Relative medullary thickness and maximum urine/plasma osmotic ratios in selected mammals.

Animal	Relative medullary thickness	Urine/plasma osmotic ratio
Beaver (_Aplodontia rufa_)	1,3	2,7
Man (_Homo sapiens_)	3,0	4,2
Bontebok (_Damaliscus dorcas dorcas_)	4,9	5,4
Springbok (_Antidorcas marsupialis_)	5,5	8,3
White rat (_Rattus rattus_)	5,9	8,9
Klipspringer (_Oreotragus oreotragus_)	7,6	---
Gerbil (_Gerbillus gerbillus_)	10,5	14,0
Ground squirrel (_Xerus inauris_)	12,4	14,9
Desert mouse (_Psammomys obesus_)	12,9	17,0

Sources : Chew 1965, Gordon 1968, Hofmeyr and Louw * (unpubl.), Marsh, Louw and Berry 1978, Van Zyl 1978.

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* Mrs. M.D. Hofmeyr and Prof. G.N. Louw, Dept Zoology, University of Cape Town.

Unfortunately there are very few values for relative medullary thickness for African mammals in the literature, but it is interesting to note (Table 9) that the value for klipspringers is considerably higher than both the bontebok and the springbok, though it is not as high as some of the desert rodents.

Schoen (1972) and Maloiy (1973) did extensive tests on captive dik-dik and found that they are able to concentrate their urine to over 4200 mOsm and a urine to plasma ratio of up to 11 under stress conditions. This shows that the Neotragine antelope are able to evolve very efficient water conservation mechanisms. Although klipspringers are probably not as efficient as dik-dik, their high relative medullary thickness suggests that their urine concentrating ability is considerable.

The insulative properties of the klipspringer's specialised pelage are also important in this context. Because of their small body size and therefore their low thermal inertia, small antelope are less able to exploit adaptive hypothermia under conditions of heat stress than are larger antelope. However the klipspringer's coat raises the body's thermal inertia by insulating against the heat, and thus less water evaporation is necessary to maintain body temperature under hot conditions than in antelope with thinner pelages which absorb heat more readily.

Since all of the small antelope are territorial (see Chapter 5), the ability to utilise moisture efficiently and to survive without free surface water is a great advantage for dispersal in semi-arid areas. The klipspringer's adaptations in this direction must have been important in allowing it to become so specialised to rocky mountainous areas in such a wide range of rainfall regimes.

Digit structure

In the klipspringer the digits and hooves are uniquely adapted to running on rocky terrain. The main feature is that the articulation of the interphalangeal joints has rotated posteriorly so that the buck walks on the tip of its hooves.

In most antelope the main axes of the first and second phalanges lies at about 20° - 25° from the vertical (Fig. 36). This m ans that the lower surface of the triangular third phalanx lies flat on the ground. Thus a large area of the horny sub-unguis and the rounded edges of the unguis

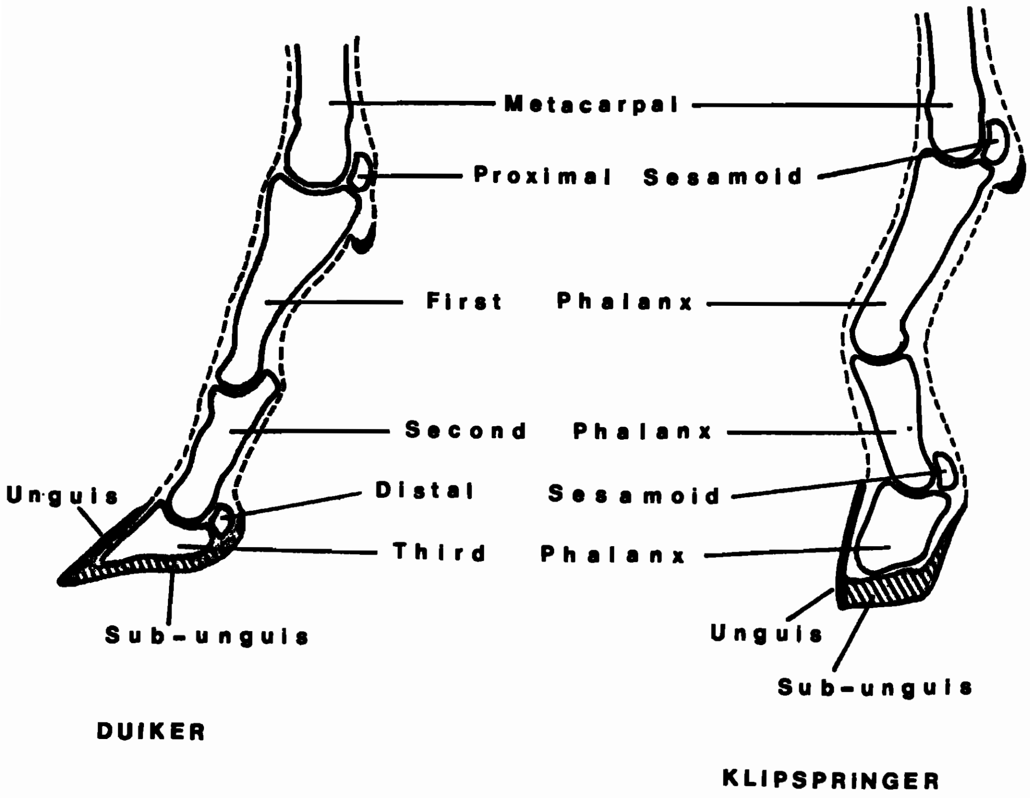


Fig. 36: Digit structure of the klipspringer as compared to that of the grey duiker.

come into contact with the substrate, but the narrow-angle anterior sloping edge of the harder unguis gives little grip on irregularities of hard surfaces.

However, in the klipspringer the proximal inter-phalangeal articulation has rotated about 30° in a posterior direction so that the main axis of the second phalanx slopes posteriorly at about 10° from the vertical (Fig. 36). This means that the articulating surface of the third phalanx is roughly parallel to the ground and the main axis of the bone is pointing almost straight downwards. Instead of being pointed, the lower end now becomes rounded so that the third phalanx is square rather than triangular in cross-section.

The advantage of this adaptation is that the young klipspringer walks on the tip of its hoof (Fig. 37). Since the unguis wears down gradually, the adult klipspringer has a cylindrical hoof (Fig. 38) with the hard edges of the unguis vertical to the substrate, which is the best angle for gripping on to slight irregularities in the rock without chipping the edges. In addition the slightly softer sub-unguis moulds itself to the rock to anchor more firmly.

This digit structure, together with the buck's strength and agility, enables it to move with remarkable rapidity on rocky terrain and to make phenomenal leaps on the cliffs it inhabits.

Fig. 37: Digit structure of a three month old klipspringer. The hoof has the typical antelope shape, but the animal stands on the tip of it.

Fig. 38: Digit structure of an adult klipspringer. The hooves have worn down to a more cylindrical shape.

CHAPTER 5 : SOCIAL ORGANISATION

METHODS

During all observations for the feeding and activity studies all social interactions were noted or recorded on tape and later transcribed. In addition several important interactions were seen during the search for klipspringer groups for the population studies.

The data for visibility, alertness and inter-individual distances were recorded during every 4 min scan of the activity study, which covered more than 300 h of observation in the two study areas. Visibility was recorded subjectively on a 1-4 scale, where "visibility 1" was when the buck seemed to have specially raised itself on to a prominent point for good all-round visibility, such as a rock or termite heap, "visibility 2" was a normal clear vision but with no special selection for a surveillance post, and "visibility 3 and 4" were increasing degrees of obscured visibility.

Alertness was difficult to classify, so only three classes were used, where "alertness 1" was when klipspringer was standing attentive looking in a particular direction with its ears facing forwards, "alertness 2" was a normal relaxed position with ears back, and "alertness 3" was when the individual was completely relaxed with its eyes closed, its head often lying flat on the ground.

For distance apart the distance from the nearest adult of the opposite sex or, in the case of juveniles, the distance from the nearest parent, was estimated. The classes used were less than 2m, 2-5m, 5-15m, 15-50m and greater than 50m, though for the first visit to each of the study areas the distance class of less than 5m was not divided into two.

All these data were recorded straight on to computer sheets for later analysis with the activity study data.

Dung sites were located by traversing the area and plotting them on an aerial photograph. A dung site was recorded if a buck had defaecated in that place more than once, but fairly recently so that the droppings were still dark brown in colour. At Springbok the whole main study territory was mapped, but at Gamka a region of known boundaries between four territories was chosen since the other limits of the territories were not clear, and the similarity of grysbok and klipspringer droppings meant that the recording of middens in habitat frequented by grysbok, such as the south-facing slope and plateau, was of little value.

Scent-marking sites were not mapped since they require a very much more intensive search, as outlined by Walther (1978), and this was beyond the scope of the study. Dunging and scent-marking were recorded whenever they were seen during the activity study.

RESULTS

Group composition and inter-individual distances.

As shown in chapter 6 the average group size for klipspringers is 2,5, but they occasionally form groups of up to five animals. The most common grouping was a mated adult pair, usually with a single offspring (Fig. 39), but occasionally accompanied by the previous year's offspring as well. During the study the male and female of each known group remained constant, so klipspringers are considered to be monogamously mated. This is confirmed by Tilson (in press).

The strength of the pair bond is illustrated by the amount of time that the male and female klipspringers spent close together. Table 10 shows that during the study the klipspringers spent 40% of the time within 2m of each other, 77% within 5m and 97% within 15m, leaving only 2-3% of the time further than 15m apart. On several occasions individuals of known pairs were seen on their own without the other nearby, so klipspringers do spend a certain amount of time completely apart, but this is a very small portion of the daylight hours. On at least one occasion the female had wandered off on her own to suckle an infant, so this may explain some of the observations of temporary absence.

The differences between the values for males and females in Table 10 are due to the presence of more than one adult female in some of the study groups. In the early phases of the study it was not clear whether both of the females were mates of the male or not as suggested by Dunbar and Dunbar (1974), so the readings for the male were taken to the nearest adult female, while those of each of the females were taken to the group's adult male.

The readings for juveniles were rather irregular, since young infants were usually hidden out of sight and mature offspring sometimes wandered off on their own, completely out of sight of the group. Thus the readings are

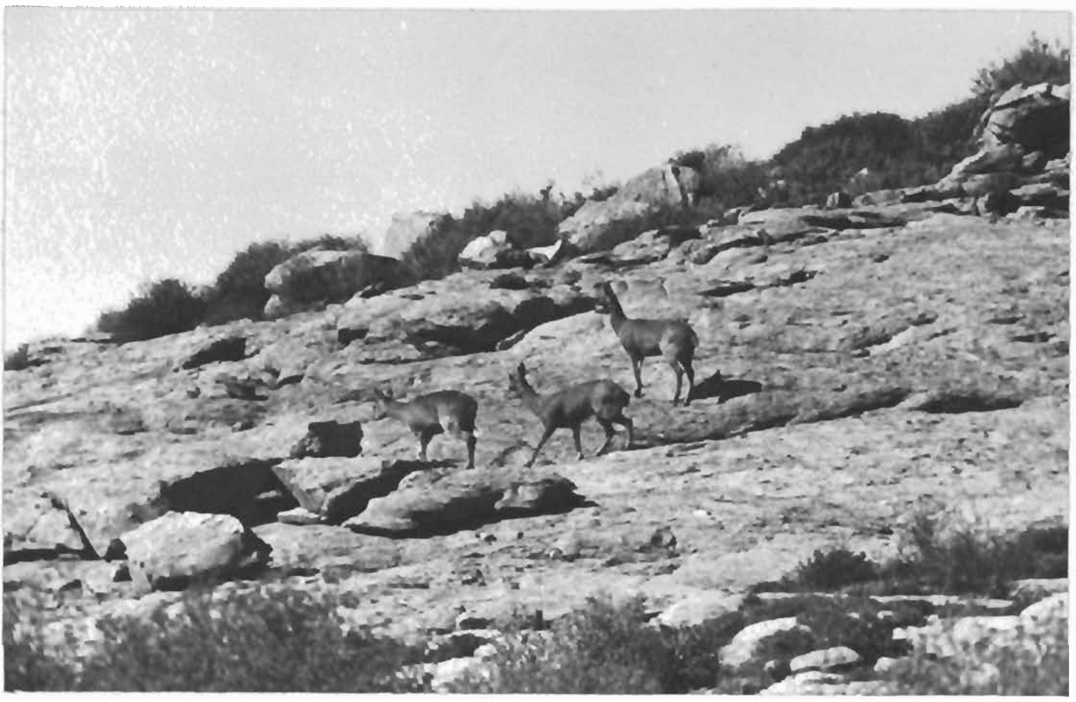


Fig. 39: A typical group of klipspringers at Springbok. The nearly full-grown offspring (right) is distinguishable from its mother (left).

Table 10: Inter-individual distances of klipspringers expressed as the percentage time spent in different distance classes.

	MALE				FEMALE				JUVENILE			
	<2	2-5	5-15	<15	<2	2-5	5-15	<15	<2	2-5	5-15	<15
			(m)				(m)				(m)	
SPRINGBOK												
May-July	71		28	1	71		29	1	72		25	3
Aug-Sept	38	36	24	3	38	36	24	3	47	23	29	2
November	37	46	17	0	37	46	17	0	54	34	11	1
Feb-Mar	53	35	12	0	53	35	12	0	59	33	8	0
GAMKA												
April	77		16	7	69		21	10	79		14	7
July-Aug	24	42	30	3	21	42	33	5	19	51	28	3
October	50	40	8	1	45	42	10	2	44	39	11	5
January	44	31	25	0	41	29	25	5	67	21	13	0
Mean* <2m	41%				38%				48%			
<5m		78%				76%				80%		
<15m			98%				97%				97%	
>15m				2%				3%				3%

* Overall mean of sum of totals in each season.

only for occasions when the youngster was accompanying its parents. However the figures show that when the offspring were very young (October to March) they spent a large proportion of the time very close to the parents, illustrated by the high proportion of the time less than 2m apart, but later in the year when they were older they spent less time close by.

Role differentiation

Dunbar and Dunbar (1974) showed that klipspringers display a noticeable role differentiation between the sexes, where the male spends more time as "look-out" than the female. During the present study this role differentiation was analysed in two different ways, by noting first the amount of time that the male spent on a prominent "look-out" point compared to the female, irrespective of whether he was alert or not, and second, the amount of time that each sex was alert, whether on a prominent point or not.

The surveillance behaviour of klipspringers from a prominent position on top of a rock has been termed "vigilance" by Tilson (in press) who found that the male spent far more time in vigilance than the female (Fig. 40). The same was found at all times during this study. Table 11 shows that the male spent significantly more time in sites of "visibility 1" than females ($t = 4{,}50$; $p < 0{,}01$), and the females spent more time in such sites than the juveniles ($t = 3{,}24$; $p < 0{,}05$). In addition females spent more time in sites of poor visibility (visibility 3 and 4) than the males ($t = 3{,}44$; $p < 0{,}01$). Although the table does not show any significant trend for juveniles to be more often in sites of poor visibility than the females, there would be a large difference if all instances when juveniles were completely out of sight were counted.

Thus male klipspringers spent an average of 47% of the daylight hours in a prominent position with good all-round visibility, while the females spent only 35% of the time in such a position.

The analysis of different classes of alertness yielded an even greater difference between the sexes. Table 12 shows that males spent significantly more time alert (class 1) than females ($t = 5{,}33$; $p < 0{,}001$) and females spent more time alert than juveniles ($t = 4{,}26$; $p < 0{,}01$). Thus the male spent an average of 19% of the daylight hours alert, while the female was alert only 11% of the time and juvenile 7%.

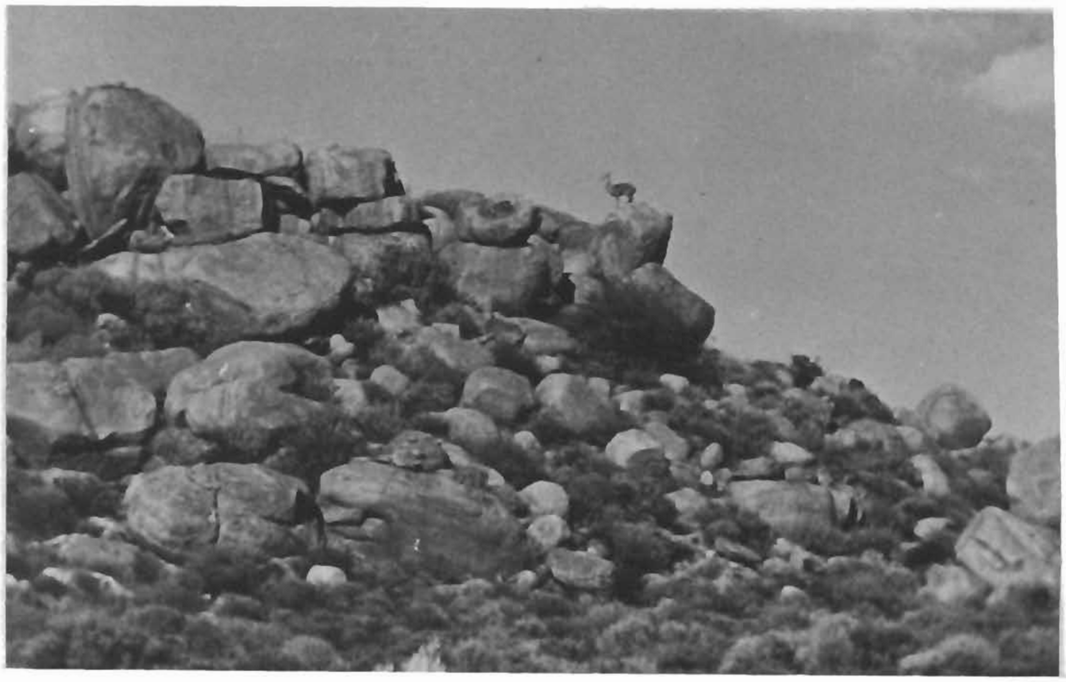


Fig. 40: A male klipspringer showing "vigilance" behaviour at Springbok.

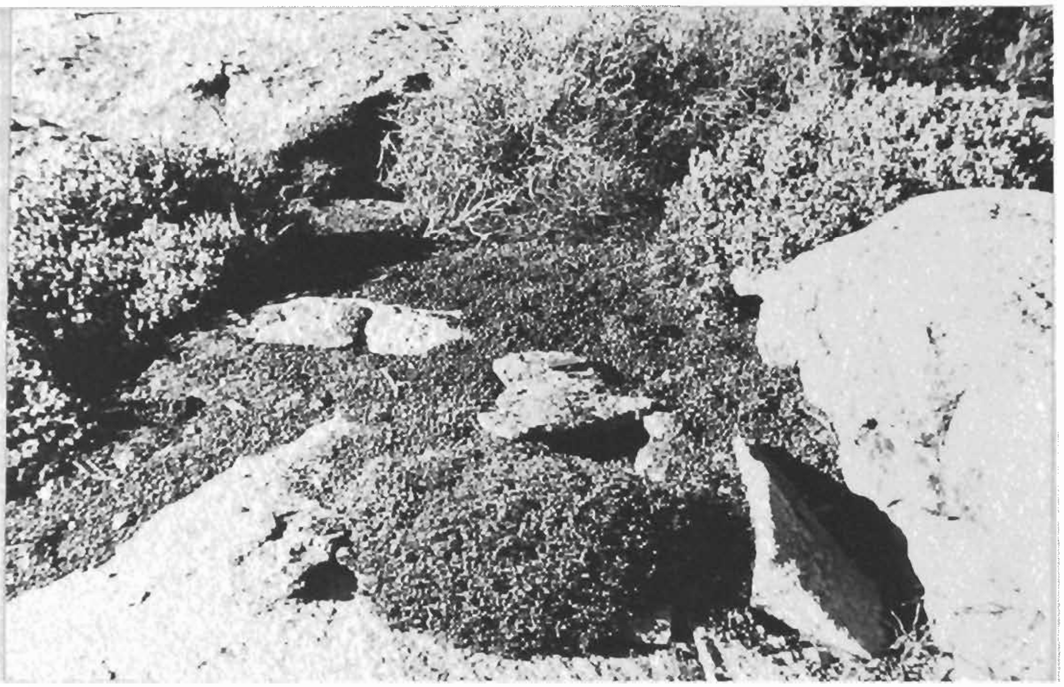


Fig. 41: A large klipspringer midden at Springbok.

Table 11: Percentage time spent in different visibility classes by male, female and juvenile klipspringers.

	1			2			3 & 4			Total records		
	♂	♀	J	♂	♀	J	♂	♀	J	♂	♀	J
GAMKA												
April	46	34	23	41	47	55	14	20	22	365	530	222
July-Aug	45	32	21	42	50	57	13	18	21	500	546	340
October	60	63	64	39	34	36	1	2	0	519	629	140
January	36	24	5	64	57	90	0	20	5	512	561	39
SPRINGBOK												
May-July	48	33	34	45	56	55	7	11	11	381	407	257
Aug-Sept	75	53	40	24	33	42	1	14	18	371	371	62
November	39	29	21	50	53	59	11	18	21	430	424	462
Feb-Mar	42	38	34	57	59	62	1	3	4	566	575	518
ZACCHARIASHOEK												
All seasons	29	7	-	57	75	-	14	18	-	320	272	-

Table 12: Percentage time spent in different alertness classes by male, female and juvenile klipspringers.

	1			2			3 & 4			Total records		
	♂	♀	J	♂	♀	J	♂	♀	J	♂	♀	J
GAMKA												
April	25	13	9	71	82	88	4	5	3	363	519	221
July-Aug	28	18	9	67	76	87	1	1	3	496	569	323
October	14	11	6	82	72	92	3	17	1	518	627	140
January	19	10	3	80	86	97	0	4	0	498	474	36
Mean	21,5	13,0										
SPRINGBOK												
May-July	21	9	9	79	86	88	1	5	4	381	407	257
Aug-Sept	15	15	5	81	78	95	4	7	0	367	327	42
November	17	11	7	82	88	92	1	1	1	408	386	237
Feb-Mar	16	9	7	83	90	91	0	1	2	538	558	491
Mean	17,3	11,0										
ZACCHARIASHOEK												
All seasons	19	5	-	81	93	-	0	2	-	320	272	-

Dunbar (in press) puts forward the theory that the male spends extra time alert only because he spends more time resting than the female and that both sexes spend the same proportion of resting time alert. However in the present study this was definitely not the case. Analysis of the alertness of resting klipspringers (Table 13) showed that the male was alert when resting significantly more often than the female ($t = 5,48$; $p < 0,001$).

The importance of alertness as a mechanism for predator avoidance is shown by increased alertness in situations where the animals are more vulnerable to predation. Table 14 shows that when the one member of the pair was feeding, the other showed a significantly greater tendency to be alert than the average daily value ($t = 6,72$; $p < 0,001$ for males and $t = 2,98$; $p < 0,05$ for females). This was confirmed by many observations of feeding bouts where there seemed to be a co-ordinated sharing of vigilance. For example, the male would stand in vigilance looking around while the female fed continuously, then the female would stop and climb on to a lookout post. Almost immediately the male would climb down and start feeding and continue undisturbed for up to 20 min without raising his head, then the two would exchange places again and the male would be continuously alert while the female fed.

Another situation where the buck were more vulnerable to predation was on the plateau at Gamka where there were few rocks to act as look-out posts and the sandy substrate would have given fleeing klipspringers no advantage over a predator. Again the proportion of time spent alert for all records on the plateau was significantly greater than the mean value for both sexes ($\chi^2 = 7,32$; $p < 0,01$ using all records as expected). In spite of the fact that this figure includes <u>all</u> activities on the plateau, the mean percentage was even higher than the mean for feeding which illustrates the importance of alertness in this terrain. However, this difference was not statistically significant.

One could expect the animals at Gamka to spend more of the time alert than at Springbok due to the greater population density which should support a greater predator population, thus increasing the chances of a predator being in the vicinity of a klipspringer group. In addition the smaller territory size should increase the chances of another klipspringer group being within sight and near enough to need watching in case of any territory violations.

The results on Table 14 do show a considerably greater value for Gamka, but

Table 13: Percentage time spent alert by resting (activity classes 2, 3, 4, 5, 6, 8) male and female klipspringers.

	Alertness class 1 (%)		Total resting records	
	Male	Female	Male	Female
SPRINGBOK				
May - July	29	15	349	311
August - September	17	16	322	297
November	21	14	334	309
February - March	21	12	420	412
GAMKA				
April	32	19	281	356
July - August	35	27	395	374
October	17	14	414	480
January	22	11	439	414
ZACCHARIASHOEK				
All visits	23	7	265	207

Table 14: Percentage time spent by klipspringers in alertness class 1 in more vulnerable situations, when the other of the pair was feeding and when the study group was on the plateau region at Gamka, compared to the means for all records.

	MALE				FEMALE			
	all records		other feeding		all records		other feeding	
	%	total	%	total	%	total	%	total
SPRINGBOK								
May-July	21	381	28	218	9	407	13	178
Aug-Sept	15	367	25	72	15	327	26	47
November	17	408	28	108	11	386	29	87
Feb-Mar	16	538	24	142	9	558	13	137
Mean	17,3		26,0		11,0		20,3	
GAMKA								
April	25	363	31	109	13	519	11	114
July-Aug	28	496	41	151	18	559	24	112
October	14	518	17	112	11	627	30	120
January	19	498	24	113	10	474	13	68
Mean	21,5		28,3		13,0		19,5	
Gamka - Plateau								
	♂ 32,8% of 472				♀ 21,6% of 533			

the variation between visits in each area was so great that the difference shows no statistical significance. The variation between different visits is probably due to the small sample of three day's study and the chance selection of particular conditions, rather than a marked seasonal trend in alertness behaviour. A far more intensified sampling procedure would be needed to elucidate this.

Territorial defence

Several workers have suggested that klipspringers are territorial (Tinley 1969, Dunbar and Dunbar 1974, in press, Choate 1975, Tilson in press), and the results from the present study support this hypothesis.

Territorial defence by males, and possibly also by females, was seen during the study. In the whole period only six chases were observed, which suggests that active defence of the territory is a rare occurrence and the buck must rely more on other methods of discouraging intruders.

Of the six chases observed a male klipspringer was the aggressor in five instances, although in three of these the female accompanied him without actively chasing the intruder. In only one instance was a female the aggressor and this was against another female. From conventional theory on territoriality one would expect the animals to chase only conspecifics of the same sex (see for example Leuthold 1977). However three of the cases involved males chasing females. In at least one of these the female was almost certainly not the offspring of the male that chased her (see incident on 77-04-16 in Appendix F) which suggests that territories are defended against intruders of both sexes. In four of the six chases the individuals being chased were single animals, and these may have been young unmated individuals that had just left their parental groups (see "Dispersal").

In none of the encounters was body contact made, though one cannot expect a female, which has no horns, to fight a male with horns. In the tame group at Augrabies Falls the adult males would sometimes confront each other with heads lowered almost to the ground and horns pointing forward. The horns are very sharp and are wielded with a strong stabbing action, but no fresh wounds on either the tame or wild animals were seen and only a few old scars showed that they do occasionally make contact.

A rare instance of intense fighting was witnessed in April 1978 by a farmer in the Bonnievale area, Steenkamp* (pers. comm.), who saw two males attacking each other violently while a female looked on. The loser had horns only slightly smaller than the winner and chose to fight rather than move away, but was so badly wounded in the process that he could no longer escape and backed into a bush absolutely exhausted. When the farmer put him out of his misery he found so many horn wounds all over the body that much of the meat was inedible. However, serious injury is probably uncommon in klipspringers, and they would seem to rely more on chasing of young animals rather than fighting between mature, almost equal males.

Dunbar and Dunbar (in press) recorded seven chases in about 80 h of observation and calculated that klipspringer groups can expect roughly two encounters with intruders during the course of 24 h. This is probably a rather exaggerated figure, first because one would not expect klipspringers to move as much during the night as during the day, thus reducing the chance of encounters, and second because the Dunbars made their observations from November to July which is the time of year that lambs are born (Dunbar and Dunbar 1974) and the previous offspring are most likely to be evicted from the group. Thus the high frequency of chases that they observed is more likely to represent expulsion of wandering youngsters than encounters with other territorial individuals.

However, one can expect the frequency of encounters to increase with increasing population density, since the individual groups are nearer together and for the same distance of movement there is a greater chance of coming near to the border of a neighbouring territory. Of the chases observed during the present study only one was at Springbok while five, including two chases during one encounter, were at Gamka. With more than 150 h of observation in each area this gives a maximum of one chase every 30 daylight hours at Gamka and one every 150 h at Springbok. This illustrates the pattern clearly and compares favourably with the Dunbars' figure especially if the latter is taken to be slightly exaggerated.

Territorial marking.

Since klipspringers do not seem to spend very much time chasing intruders off their territory there must be some other method of laying claim to their piece of ground and there are some indications that dunging and scentmarking have a direct or indirect effect.

a) Dunging

Tinley (1969) mentioned that klipspringers, like dik-dik use large communal dung-heaps that may function to demarcate a territory. During the present study several large middens were found in each territory (Fig. 41) but the study animals did not seem to be confined to regular use of large heaps. Many heaps had collections of dung that could not have come from more than five to ten defaecations.

Figures 42 and 43 show the distribution of klipspringer dung-heaps in parts of each study area. In both cases there was some tendency to place the heaps near territorial boundaries, but a large proportion of them were scattered more or less randomly through the territory. In some places at Gamka large sections of territorial boundaries had very few dung-heaps. However the larger dung-heaps were normally placed on prominent sites with good visibility, such as spurs, outcrops or the plateau edge. Since territorial boundaries tended to follow these geomorphological features, a more detailed analysis recording size of the heap as well as its location may well show a preponderance of the large established dung-heaps nearer the territorial boundaries.

To assess the significance of marking behaviour it is necessary to examine how it fits into the animal's daily activity pattern. Figure 44 shows how the number of observations of dunging was distributed through the day. While one could expect the klipspringers to defaecate at any time of the day, there were peaks in this activity in the late morning and mid-afternoon. When compared with the daily activity patterns illustrated in Figs. 47 and 48 one can see that peaks in defaecating seemed to come just after peaks in feeding activity. This supports the subjective impression obtained in the field that the study animals were most likely to defaecate at a transition between periods of activity and resting, especially just after the main morning feeding bout and before the main afternoon feeding bout. According to Walther (1978) it is common for mammals to defaecate after a long rest, which explains the afternoon peak, but the reasons for the morning peak are not so obvious.

The study animals rarely moved very far from their resting places to defaecate. Since these resting places seemed to be situated randomly throughout the territory wherever a suitable vantage point was available, the dung-heaps are distributed throughout the territories.

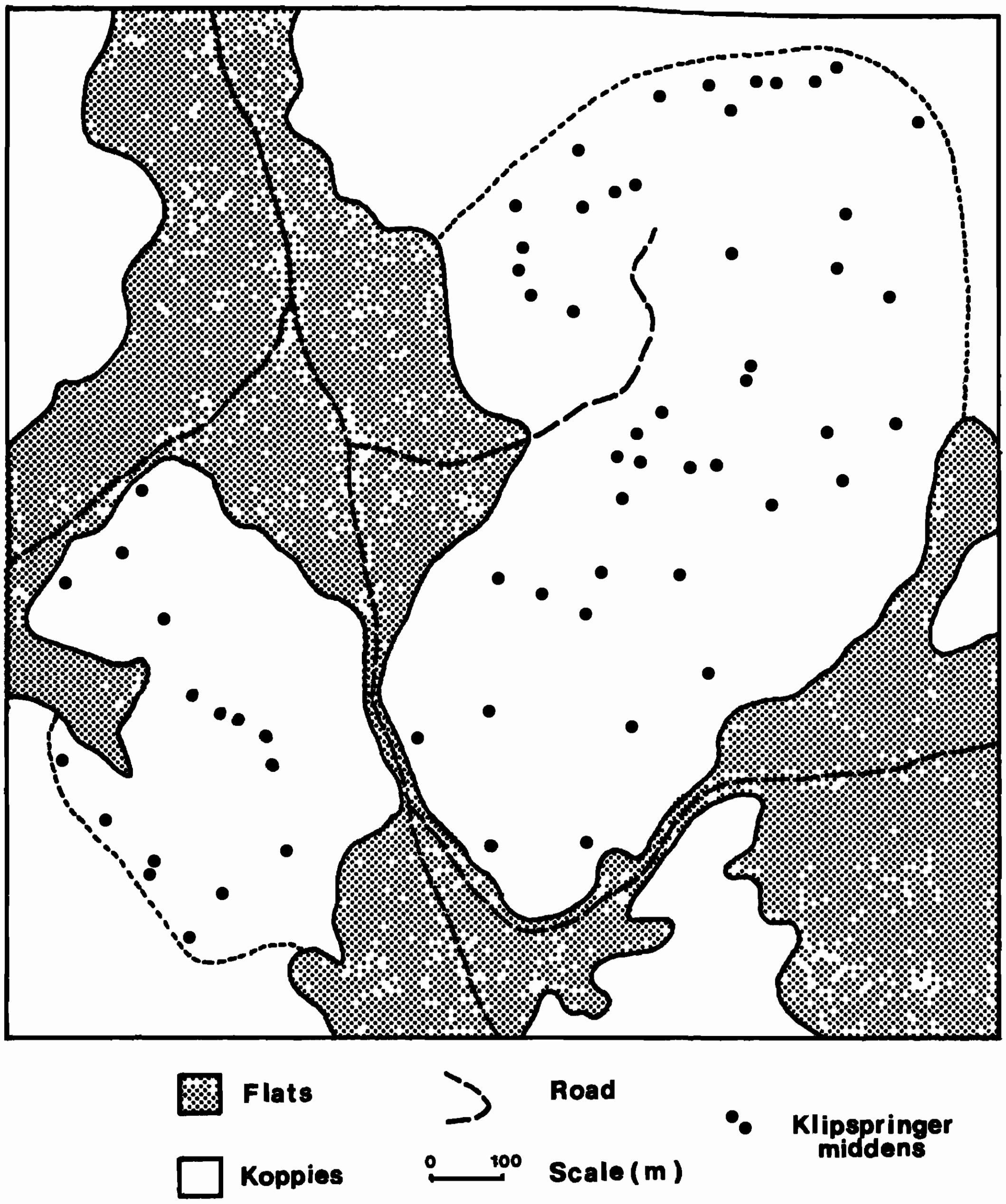


Fig. 42: The distribution of klipspringer middens in the main study group's territory at Springbok.

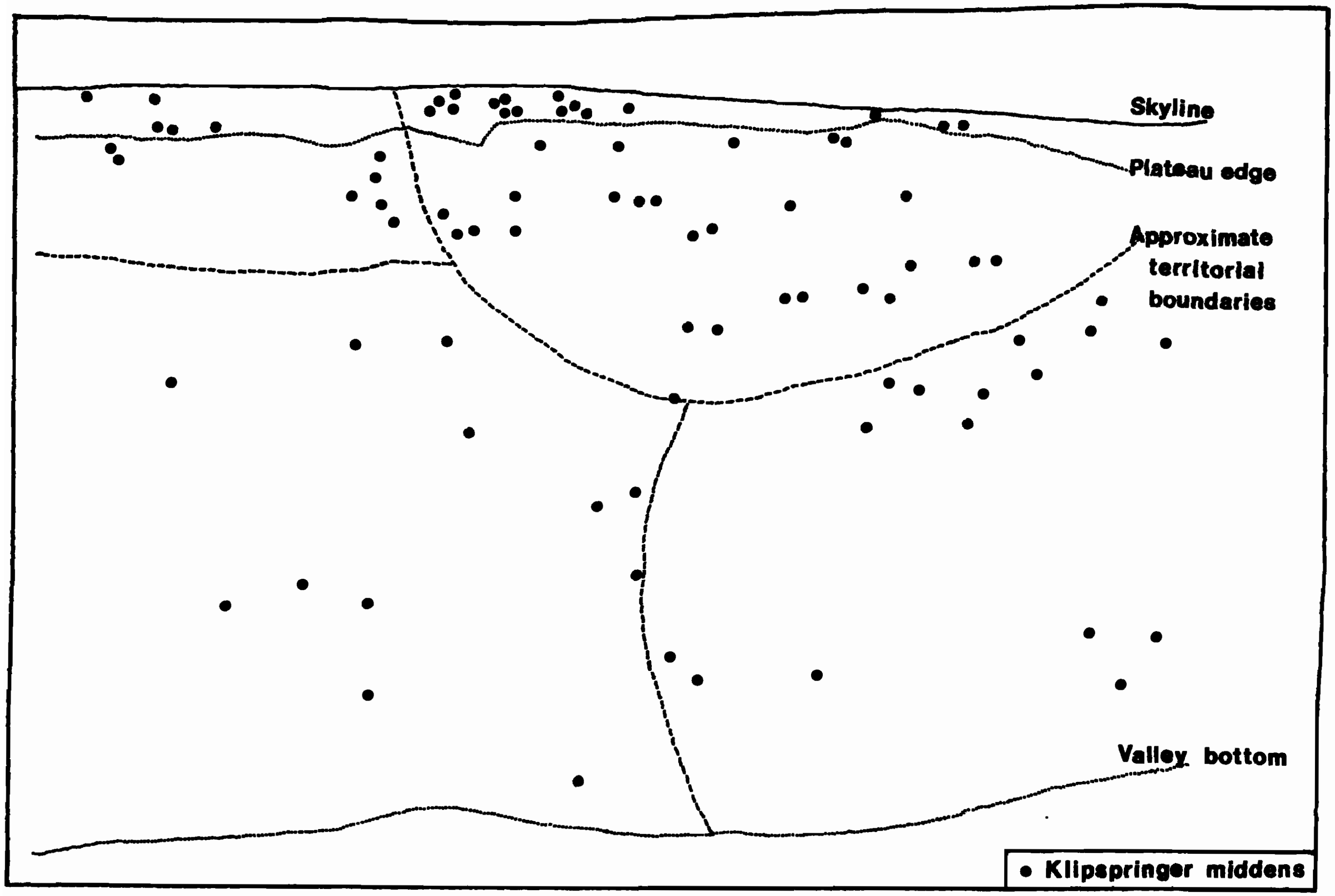


Fig. 43: Distribution of klipspringer middens in relation to territorial boundaries on the north= facing slopes of Tierkloof at Gamka (oblique aspect from the other side of the valley).

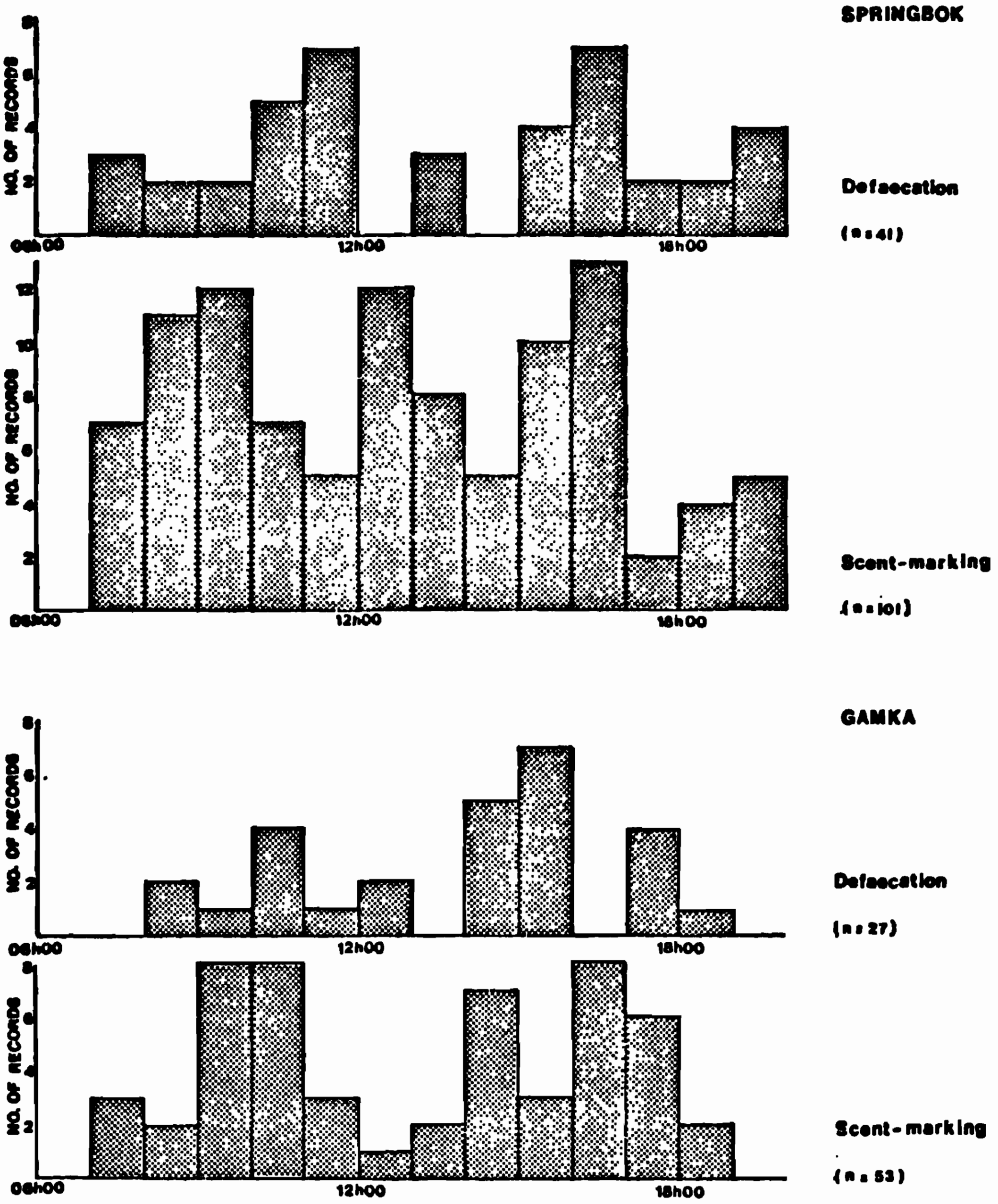


Fig. 44: The frequency of defaecating and scent-marking by klipspringers during one hour periods through the day.

b) Scent-marking

Scent-marking with the ante-orbital glands is the other important method of marking used by klipspringers. This involves inserting the end of a twig into the gland (Fig. 45), leaving a deposit of a black tar-like substance (Fig. 46). During the study the frequency of scent-marking was at least twice that of dunging. The frequency recorded would have been higher if the study animals had been watched continuously, since the marking takes only a few seconds and many records were probably missed.

The distribution of marking records through the day shows peaks very similar to those of the dunging records. This illustrates the same tendency for marking to occur most frequently during a transition between resting and active conditions. The main reason is that dunging was nearly always associated with scent-marking. In all cases where the study animals were watched continuously while dunging the male or female would always scent-mark after defaecating, and sometimes before as well.

One of the most conspicuous features of klipspringer scent-marking behaviour was that when the female of a group marked, the male nearly always marked afterwards on the same twig. This suggests that scent-marking plays an important role in the maintenance of the pair-bond, as well as serving to demarcate a territory. At Gamka, when the female marked on a bush, in at least 74% of the cases the male marked on top soon afterwards, while at Springbok there were no records of the female scent-marking on her own.

Further evidence for the importance of scent-marking in the maintenance of the pair-bond is the fact that only the dominant male and female of the group would mark. Although younger individuals often sniffed the secretion on a bush, especially after defaecating, they were never observed to scent-mark. At Augrabies Falls only the dominant male and the female were seen to scent-mark, and never the young males which were fully adult and at least three years old. However when the dominant male was removed from the camp the oldest son soon took over the dominant role and scent-marked regularly.

In contrast, the tame young male at Springbok started scent-marking at about four months old, and marked regularly after that, even though he was completely dominated in chases by a full-grown male that lived near the house. On 4 August 1978 during observation of a group of five klipspringers, including three full-grown males, one of the males defaecated and then sniffed at a scent-mark on a bush and may even have marked lightly himself,

Fig. 45: A klipspringer ram scent-marking with his ante-orbital gland.

Fig. 46: Ante-orbital gland secretion on the end of a twig near a dung heap.

but almost immediately the dominant male moved several metres to where he had been and scent-marked elaborately, seeming to assert his dominance over an inferior.

Thus scent-marking appears to be a method for the male to mark his territory as well as to lay claim to his mate and to assert dominance over any younger animals. Both the olfactory message of the scent-gland secretion and the visual message of the scent-marking display are probably important.

c) Other marking methods

Another two methods may be important in territorial marking in klipspringers, "horning" and "static optic marking".

On four occasions during the study, twice at Springbok and twice at Augrabies, the dominant male was seen to attack a small shrub or branch with his horns. He did not go down on his knees as David (1970) has described for bontebok, but, as suggested by this author, the behaviour is likely to be a visual display of aggression to deter intruders.

The concept of "static optic marking" (Hediger 1949), or the slightly better "static optic advertising" (David 1970), is that animals "mark" their territory merely by being there and making themselves conspicuous. The importance of this as a primary selection factor for behaviour patterns is debatable, but the klipspringer's vigilance behaviour almost certainly benefits it in this context. However it is most likely that predator detection is the main motivation for vigilance.

Eviction of offspring

Very few studies on African antelope have yielded useful results on the mechanism of dispersal of young animals once they leave the family group. Since no young animals were marked during the present study no results were obtained to show how far a youngster disperses, how it finds a mate and a territory etc. Nevertheless a number of incidents and sightings during the fieldwork yield clues to the mechanism by which youngsters are evicted from the group (Appendix F).

The expected pattern of eviction is shown by observations on two well-known groups, where a full-grown youngster was seen during one visit to the study area, but by the next visit it had disappeared and its place was taken by a very young infant. In both instances the previous offspring was never seen with the group again. This suggests that the full-grown offspring is actively kicked out when a new lamb is born and explains the mild aggression shown by the mother to her full grown offspring during the observation on 77-06-02 at Springbok, which can not have been more than about six weeks before she gave birth.

However the observations on "Group 1" at Gamka show that the pattern is sometimes more complex since the youngster does not necessarily leave the group suddenly, but rather comes and goes over a long period, slowly becoming more and more independent. The young female that was presumed to be the offspring born in 1975 seemed to take more than six months to become totally independent of her parents. This is in spite of a certain amount of aggression from her mother who chased her violently on 77-04-24, but later tolerated and even groomed her.

Further evidence for the tolerance of full-grown and mature offspring is the number of sightings at Springbok of groups with two or more males with full-size horns. However, it is likely that dominance is maintained by fighting or advertising displays such as scent-marking, as outlined in the "Territorial Marking" section above.

Several observations of single full-grown, but young, males with fairly short horns suggest that young adults wander around when they have left the group. They readily venture into other pairs' territories, as shown by the sightings of the strange young male in the main study territory at Springbok in September 1977. However, they are probably chased if seen by the pair, as indicated by the two records of young females being chased on 77-04-16 at Gamka and 77-09-05 at Springbok, though the latter could have been a case of evicting offspring from the group.

At this stage of their lives the young klipspringers are rather vulnerable to predation (see Chapter 6) and probably either wander around until they find a vacated or new territory and a mate, or else are harrassed by territorial groups until they lose condition and die of starvation or succumb to predators.

DISCUSSION

The klipspringer in relation to other antelope

As pointed out by Tilson (in press) the klipspringer does not fit the basic antelope pattern that links body and group size to habitat preferences and predator evasion strategies. The principle has been laid out in slightly different ways by Jarman (1974) and Estes (1974), but both authors suggest that the gradation from closed to open habitats is accompanied by a similar gradation from small body and group size to larger animals forming larger herds, and a change in predator evasion strategy from one of silence and concealment to one of rapid flight and herd cohesion. In addition, the food requirements associated with body size are linked with a trend from a territorial system in stable habitats to a more flexible social organisation that allows exploitation of fluctuating environmental condition in less stable habitats.

While the literature shows that klipspringers are small-bodied, occur in small groups and are territorial, they are unusual in that they are adapted to an open mountain habitat, which has resulted in a rather different predator evasion strategy and some unusual features in their social organisation.

Group size

There seem to be two main factors influencing the group size of klipspringers; the selection for a decrease in group size because of the distribution of suitable food, and the selection for an increase for predator detection.

Jarman (1974) gave particular attention to the relationship between feeding styles and the social organisation of antelope. His discussion is based on the idea that small antelope need high energy food because their small body size necessitates a higher metabolic rate than larger antelope. Therefore they eat the most nutritious plant parts available which are the growing shoots, flowers and fruits of dicotyledonous plants. These are widely dispersed in space and time, since they form but a small part of the total plant biomass and are only available at particular times of the year, depending on the plant species. This prevents the formation of large aggregations of the antelope and selects for as small a group as possible, usually a male-female pair.

Most small antelope that live in closed habitats rely on silence and concealment to escape predation. Therefore the male and female of a group form a fairly loose association which allows them to move about singly for most of the time and thereby reduce the chances of detection by predators. However klipspringers live in open rocky habitats and show a very different predator evasion strategy, as outlined by Dunbar and Dunbar (1974) and Tilson (in press). Instead of relying on concealment, they trust to their superior fleetness on rocky terrain and actually make themselves more conspicuous by climbing to a vantage point to watch out for predators. More individuals in the group mean that vigilance can be shared and the chances of early detection of a predator are increased. Therefore, in contrast to most other small antelope where predator evasion breaks up the basic family unit even further, in klipspringers the predator evasion strategy selects for an increase in group size.

Thus, under the influence of these two conflicting selective pressures, modified by other factors such as territoriality and juvenile dispersal, klipspringers have evolved a closely-knit family group of the mated pair and one or two offspring.

Territoriality

Continuing with Jarman's (1974) discussion of the distribution of nutritious plant parts and its utilisation by antelope, it can be argued that the best way for a buck to exploit the resources efficiently is for it to be familiar with the distribution and seasonality of food in its area. Therefore, in areas that can support a population of antelope throughout the year, it is best for the individual to remain in one place and become thoroughly familiar with the distribution of food items, so that a minimum of energy is wasted in searching for food. However, to avoid intraspecific competition, it is necessary for the individual to defend its resources from conspecifics, and this has given rise to territoriality.

Geist (1974) has summarised a number of hypotheses that explain aspects of the social evolution and ecology of ungulates. His tenth hypothesis states that "habitats stable in space and time select for territoriality.....". Mountainous areas are generally fairly stable habitats, mainly because changes in temperature and rainfall do not bring about large-scale habitat changes over the whole area, but merely shift the zone boundaries up and down the mountain. Thus the klipspringer's preference for mountainous terrain has encouraged the evolution of a strongly territorial system.

In such a system there are two alternatives open to antelope. Either each sex must defend its own territory, or else there must be a role differentiation whereby the male defends the territory while the female conserves energy for reproduction and the rearing of offspring. In an antelope where predator evasion strategies require more than one animal in a group the second alternative is the obvious choice. Thus the male klipspringer is able to take on the burden of territorial defence, as well as a large proportion of the anti-predator vigilance, and thereby maximise the female's chances of successfully raising offspring.

In such a territorial system there are a number of other selective forces in operation which explain some characteristics of klipspringers. Geist (1974) suggest that territoriality in stable habitats selects for reduced sexual dimorphism. The advantages of male mimicry by the female are that conspecifics intruding in the territory or watching from afar cannot easily tell the difference between male and female, so they have to be more cautious. An easily distinguished female would be more harrassed by other male and female intruders, but a male-like female cannot be identified quickly in a chase. In addition, the strength of the "static optic advertising" message of a territorial male is reinforced if the female can be mistaken for a male at a distance.

Geist (1974) also explains why a male should be intolerant of other females and have a strong pair bond with his mate. Since he can defend a small territory more effectively than a large one, the optimum size is one that contains sufficient resources for himself, his mate, and their dependent offspring. Another female would compete with his female for food and thus reduce her chances of breeding successfully or else, if he mated with both of them, he would have to defend a larger more unwieldy territory throughout the year. This explains why males were seen to chase off strange females on several occasions during the present study.

Geist predicts that the male must be very selective in his choice of a mate, since it is important for his own reproductive success that she is a good mother. Thus one does not expect a klipspringer to find a new mate, or replace a lost one, very quickly. This is difficult to determine without long term monitoring of well-known groups, but is probably the case with klipspringers. Hendrichs and Hendrichs (1971) found that dik-dik, Madoqua kirki , took several months to replace a lost mate.

Therefore the best way for klipspringers to exploit the food resources in the stable mountain habitats that they prefer appears to be active defence of a territory by similar-looking males and females.

CHAPTER 6 : PREDATION

METHODS

Ecological studies on large herbivores rarely yield much quantitative data on the effect of predation on the populations without detailed predator-based feeding studies. The reason for this is that actual attacks are very seldom seen during field studies, especially if the predators are mostly nocturnal in habit. This is particularly true where the potential prey animals are widely dispersed in small groups, as occurs in the klipspringer. Therefore a more indirect approach is usually necessary.

During the present study several small bits of information from the field work, as well as scattered observations from the literature, were pieced together to give some idea of the most important interactions between klipspringers and their predators.

All skulls of klipspringers found in the course of the study and others found by departmental field staff were collected and notes were made on the situation and probable cause of death. Since no known-age skulls were available, these skulls could not be aged properly, but division into the age classes used by Wilson and Child (1965), based on tooth eruption, was sufficient to differentiate between young and old animals.

Observations of alarm responses, usually elicited by the observer, were made during all fieldwork.

RESULTS AND DISCUSSION

Alarm response

As with most small antelope, klipspringers avoid predation by rapid flight. However, they differ from other species in that they do not try to hide, but rather make themselves conspicuous by standing on top of a boulder to watch the source of alarm. The alarm response reported by Dunbar and Dunbar (1974) and Tilson (1977) was similar to that seen during the present study. The reaction depends on the distance of the group from the intruder, and can be summarised as follows:-

(i) If the intruder is far away and does not seem to constitute an immediate danger, the klipspringer gives an "attention response" (Dunbar & Dunbar 1974), that is, it freezes and turns its head toward the source of alarm with both ears facing forwards. If it is in terrain with low all-round visibility it will often move to a vantage-point nearby. The other members of the group are usually undisturbed unless the alert individual gives a single alarm call which draws their attention to danger. If the intruder keeps still the klipspringers will eventually relax, but movement will usually induce flight.

(ii) If the intruder is close enough to pose a threat to the group's safety the first individual to see it will give a single alarm call and all members of the group will run a short way to a good vantage point, the distance run depending on the proximity of the intruder. Then they give further alarm calls, usually in the form of a duet between the male and female, but sub-adults may also be involved. Any movement of the intruder towards the group induces immediate flight. If the klipspringers have a good view when they first see the intruder they may call without moving away. After fleeing a short way they often stop and reinspect the source of alarm so that energy is not wasted on false alarms. If the intruder keeps moving the klipspringers normally carry on running until they are out of sight.

(iii) If the intruder is very close the klipspringers usually run to some distance away with no alarm call, but from then on the pattern is the same.

The presence of an alarm call duet is very rare among mammals. Tilson (1977) has described the klipspringer's duet in detail, and considers it a mechanism to reinforce the pair bond. In a later paper (Tilson in press) this author analysed the situations where alarm calls were uttered and concluded that a large proportion (78%) of the calls were in response to a predator and only 22% could be termed false alarms where the caller was frightened by other ungulates or even gusts of wind.

The alarm call of klipspringers is unusual in that it is very loud, being audible at least 700m away in some situations, and showing strong directional properties (Tilson 1977). Norton and Tilson (in prep.) argue that this loud alarm call has evolved to communicate with the predator rather than with other klipspringers, and that it has been permitted to evolve by the bucks' fleetness on rocky terrain. Since they are so well adapted to running on rocks they are probably faster than any predator under th se conditions, and therefore predators have to rely on surprise or catching them on unsuitable ground. Thus natural selection has worked towards minimising the chances of surprise, but also towards preventing the wastage of time on unnecessary vigilance. For this reason the call is loud to incite the predator to react, whether positively or negatively, and this causes the least overall waste of energy, even if a short fruitless chase ensues.

Thus the klipspringer's predator evasion behaviour is to maintain effective vigilance at the expense of making itself conspicuous and, once the predator has been seen, to incite it to react so that the minimum of energy is wasted by both the predator and its potential prey.

Felids

In the mountains of the Cape Province the most important predators of klipspringers, at least of the adults, are undoubtedly the larger cats. Of these the leopard (*Panthera pardus*) and caracal (*Felis caracal*) show the greatest range overlap with klipspringers. The leopard's preference for rocky mountainous terrain makes it very important in the high mountains of the south-western and southern Cape, while the caracal is more common in the open koppie terrain of the karoo regions.

The other large cats are also potential predators of klipspringers. Pienaar (1969) shows two records of lions (*Panthera leo*) killing klipspringers in the Kruger National Park, but their preference for plains and savanna habitats prevents them from coming across many klipspringers in areas where they occur together. Lions are extremely rare in the Cape, so their effect on klipspringer populations in this area is negligible. Cheetahs, *Acinonyx jubatus*, are also capable of killing klipspringers, but it is unlikely that they prey on them except under very unusual circumstances, since these cats hunt by a short sprint on flat terrain where klipspringers rarely venture.

Pienaar (1969) recorded 35 klipspringers killed by leopards in the Kruger National Park, which constituted 85% of all records of klipspringers killed by predators in this area. In the Rhodes Matopos National Park Grobler and Wilson (1972) and Smith (1977) found that klipspringers formed a fairly constant proportion of the leopard's diet, at 9-13% relative frequency. However, in one of the few feeding studies of the leopard in the Cape, Manson (1974) found that klipspringer remains occurred in only one out of 54 scats collected in two reserves in the western Cape mountains.

During the present study several instances of predation on klipspringers by leopards and caracals were recorded. Four of the carcases of klipspringers found lying in the veld at Springbok showed distinct signs of predation by a large cat. Since the caracal is the only large felid occurring in the reserve, this species must have been responsible. One freshly killed full-grown klipspringer ram had fresh caracal spoor around it and another very young ram had a caracal scat containing klipspringer hairs lying nearby.

At Gamka two very old carcases showed signs of chewing on the bones, and hair lying around, which could have been due to predation by caracals or leopards. Lawson* (pers. comm.) found a leopard scat in Tierkloof containing a pair of klipspringer hooves.

During an investigation by the author of leopard damage to domestic livestock in the mountains east of Ceres, spoor showed that a leopard had killed and eaten a full-grown klipspringer ewe.

Birds of prey

The importance of large raptors in predation on klipspringers is less clear, as different observations in the literature and during the present study support conflicting arguments. There is little doubt that large raptors are able to take quite large prey and several of the large eagles seem to be capable of killing small antelope. Boshoff and Palmer (in press) cite a number of records of eagles of different species killing fairly large ungulates in different parts of the world. For example some deer fawns taken by golden eagles (*Aquila chrysaëtos*) in America weighed more than 20kg. In South Africa prey remains from crowned eagle (*Stephanoaetus coronatus*) nests in the Cape suggested that these eagles catch young bushbuck of considerably more than this weight (Jarvis, Currie and Palmer in press). Therefore it seems that even full-grown klipspringers are potential prey for the larger raptors.

However, while there is some evidence that eagles pose a threat to young klipspringers, it is likely that adults are only killed under special circumstances and do not form a regular part of any raptor's diet. Most of the encounters recorded between raptors and klipspringers involve black eagles (*Aquila verrauxi*), which is predictable because both species are more or less restricted to rocky habitats.

In August 1978 van der Westhuizen* (pers. comm.) found a young klipspringer at Springbok that had probably been killed by a black eagle. The evening before he had seen a pair of eagles active in the vicinity and in the morning he found a dead klipspringer, a young female weighing 7 kg. A small amount of the carcase had been eaten but there was no mammal spoor in the vicinity. Therefore the loose hairs scattered around and a few scratch marks, that could have been made by an eagle's claw, suggest that the eagles had killed it but were unable to carry it away.

Gargett (1970, 1971) records two instances of predation on young klipspringers by black eagles. One record is of the hooves of a very young buck being found in an eagle pellet below a nest. In the other instance a black eagle was seen "flying rather heavily" carrying what was presumed to be a very young klipspringer, but could possibly have been a duiker or a steenbok. However it is noteworthy that these are the only records out of a total of 1892 black eagle prey items recorded during the period 1964-1976 in the Motopos study area, even though klipspringers are very common there (Gargett 1977).

During the present study adult klipspringers showed very little reaction to black eagles, even if dassies were uttering loud and urgent alarm calls nearby. On one occasion at Springbok a pair of klipspringers was feeding peacefully when a young eagle swooped down to land on a rock not more than 15m away. Apart from looking up briefly as it flew overhead the buck showed no fear response at all. A few days earlier van der Westhuizen (pers. comm.) saw what appeared to be two pairs of black eagles fighting, with one pair on the ground and the other stooping on them repeatedly from a considerable height. For two klipspringers standing on a rock about 20m away it must have seemed as if the eagles were stooping on them, but again they showed no alarm.

In spite of these observations it appears that black eagles do occasionally manage to frighten klipspringers enough to cause them to fall and kill themselves. This has been witnessed by several farmers around the Cape. A reliable sighting of black eagles chasing klipspringers was made by a scientist studying vultures in the Mariepskop area of the Transvaal Drakensberg (Mundy+ pers. comm.). As he was walking along a narrow grassy band above a steep cliff in thick mist, the mist cleared and he noticed a pair of black eagles soaring above, as well as a group of adult klipspringers

* Mr P. van der Westhuizen, Officer-in-charge, Hest r Malan Nature Reserve.

\+ Mr P. Mundy, Vulture Study Group, Johannesburg.

that were cut off from their escape along the grass ledge. As they started alarm calling and running about in confusion the eagles suddenly dived on them and stooped repeatedly until the researcher moved out of the way to let the klipspringers pass. This suggests that the eagles were capitalising on an alarm situation to try to cause one of the klipspringers to fall and kill itself.

Gargett (1971) records a sighting of a black eagle feeding on a klipspringer that was lying at the base of a steep incline of granite, which suggests that it may have fallen off the rock, possibly after being chased by the eagle.

There are very few records of other large raptors feeding on klipspringers. Pienaar (1969) wrote that a martial eagle (Polemaëtus bellicosus) was seen feeding on a klipspringer in the Kruger National Park. Boshoff (pers. comm.) has found remains of three klipspringers among bones gathered below a crowned eagle nest in the George area. A skull and a femur were from adult klipspringers and another femur from a sub-adult. It is quite possible that these klipspringers were killed by the eagles, though the remains may have come from scavenging. However, crowned eagles hunt mostly in forests and martial eagles prefer savanna, so it is unlikely that these two raptors have very much effect on klipspringer populations.

Predation and its effect on klipspringer populations

From the above it appears that the main predators of the klipspringer in the Cape Province are the leopard and the caracal, with large raptors, especially the black eagle, taking the occasional juvenile.

However, the stability of the klipspringer populations and the slow turn-over of territorial animals suggest that the mechanisms they have evolved to avoid predation are successful enough to reduce predation to a very low level. Thus it is likely that few of the mated territorial individuals are taken by predators, and that predation acts as a controlling factor to remove the "surplus" of young and old animals.

As outlined in Chapter 5, once the young adults are evicted from the group they move around on their own for some while looking for a mate and a territory. If most of the territories in suitable habitat are occupied, the youngsters will be chased until they lose condition and either die of starvation or succumb to predators. In addition, if old rams are displaced from their territories by younger, more vigorous rams, they will fall under the same stresses and die in a similar manner.

Thus, as with any system where the ungulate population is intricately balanced with the predator population, one would expect the "surplus" young and old animals to be the segment of the population that is most preyed on. Since very young infants of any antelope are especially vulnerable to predation, it is inevitable that some very young klipspringers will also be taken.

From the present study there is some evidence that this pattern is followed. In all, ten klipspringer skulls were found lying in the veld during the study period, eight at Springbok and two at Gamka. Although these animals could have died from any one of a number of causes, at least six showed signs of having been preyed on, with three leaving little doubt that they had been killed by predators. The other skulls were too old to diagnose the cause of death.

Of these ten skulls, seven were sub-adult according to Wilson and Child's (1965) tooth eruption classes (Table 15), and one of the three remaining seemed to be a very old male with battered horns. By comparing these classes with the horn length of known-age males the young animals could be roughly classed as either less than six months or older than six months but still sub-adult. Table 15 shows that four of the sub-adults fell into the latter category.

Since youngsters appear to be evicted from the group at around 9-12 months (Chapter 5), this category would include these animals. If one takes the average life span of klipspringers to be at least seven or eight years, this figure of 40% of the skulls found for an age class spanning less than a year, suggests that this is the age when klipspringers are most likely to die of sickness, starvation or predation.

Thus predation may be an important factor in klipspringer populations if it maintains the population in a healthy state by removing sick and old animals as well as excess young adults that cannot find a territory.

Table 15: Approximate age of klipspringer skulls picked up in the veld, calculated by comparing Wilson and Child's (1965) tooth eruption classes with horn length of known-age males.

Study area	Date	Sex	Horns (mm)	Tooth eruption class	Age class (months)
Gamka	Aug 77	♂	69	4	6 - 12
"	Jul 78	?	?	2/3	6 - 12
Springbok	Aug 77	♂	93	Adult	Adult
"	"	♂	85	Adult	Adult (old)
"	"	♂	82	4	6 - 12
"	Jun 78	♀	-	2	<6
"	"	♂	64	3	6 - 12
"	"	♂	7	1/2	<6
"	Jul 78	?	-	1	<6
"	Jul 79	♂	90	Adult	Adult

CHAPTER 7 : ACTIVITY

METHODS

The most widely used method for quantifying the daily activity of ungulates is that originally described by Harker, Taylor and Rollinson (1954) on Zebu cattle in East Africa. This consists of noting the activity of each individual in a group at 4 min intervals. A number of activity classes are used and the activity at the exact time is recorded, irrespective of what it has been doing before.

This method has been used on waterbuck (Spinage 1968), elephant (Wyatt and Eltringham 1974), impala (Jarman and Jarman 1973), and warthog (Clough and Hassam 1970) and for a comparison between eland, oryx, buffalo and zebu cattle (Lewis 1977). Waser's (1975) work on the bushbuck and Joubert's (1972) on Hartmann's zebra used 5 min intervals for the same type of study, and Dunbar and Dunbar (1974) noted the activity of their klipspringers every 10 min.

Harker *et al* (1954) and Rollinson, Harker and Taylor (1956) did tests which showed that noting the activity of cattle at 1 min and 2 min intervals did not substantially reduce the error in the major activities recorded, and Jarman and Jarman (1973) found the same with impala. This 4 min interval gave the best return of reliability of results for the amount of effort put into gathering the data. The error for klipspringers may differ since only one group of two to four individuals can be watched at a time, as compared to the large herds of these species. However, the 4 min interval was kept to allow comparison with other studies. The 5 min interval, which was used by some workers to simplify timing from a wristwatch, was rejected because a 20% decrease in sample size for each half-hour period could have reduced the significance of the results.

During each visit to the main study areas a minimum of three days of continuous activity study data was gathered. The nature of the terrain and conditions of observation often made it impossible to keep the study group under observation continuously for the whole day, so the three day period for each study area was usually made up of one or two almost complete days, with some half days or periods of a couple of hours in the early morning or late evening. This means that some accuracy was lost with different individuals and slightly different weather conditions, but it does give a general picture of activity for the species in that area.

The activity data were coded straight on to a form for later computerisation. The activity classes used were feeding, ruminating (standing or lying), resting (standing or lying), "resting - ?" (for the few records where it was impossible to see whether the animal was ruminating or not), directional movement and "other". The last class included all activities such as grooming, defaecating, urinating and sexual behaviour, which did not occur frequently enough to produce significant percentages in the computer analysis. These activities were recorded and analysed separately.

Except for the "resting - ?" category, where it was difficult to see whether the klipspringer was ruminating or not due to an obstruction or distortion of the image through the telescope by heat shimmer, all the categories are mutually exclusive. Directional movement was noted only when the individual was moving purposefully, although not necessarily rapidly, from one site to another some distance away, and not just moving a few metres from one feeding station to another.

Every half-hour during the activity study environmental parameters were recorded. The factors noted were:-

(a) Weather conditions - sunny, partly cloudy, overcast, rain, mist, etc.

(b) Wind strength and direction - strength estimated on the Beaufort scale.

(c) Temperature - in 5°C classes. This was measured with a thermometer in the shade at the observation post or vehicle and broad classes were used due to the distance of observation and concomitant inaccuracy in predicting the actual air temperature around the klipspringers.

(d) Heat - a subjective estimate of thermoregulatory stress, later replaced by a more objective combination of absolute temperature and wind strength to give a rough "discomforture rating" in the classes very cold, cold, normal, hot, very hot (Table 16). In this way conditions of very cold temperature but no wind could be classed with less cold temperatures, but with a stronger wind, that would give a similar cooling effect. The same principle could be applied to hot conditions where wind could reduce the animal's temperature by evaporative cooling.

Table 16: Classes for hot and cold conditions, based on a combination of temperature and wind strength to give a realistic "discomforture rating".

	Temperature	Wind strength
Very cold	Class 1 (< 5°C)	all classes
	" 2 (5-10°C)	Classes 4,5,6 (>11 knots)
Cold	" 1 (< 5°C)	all classes
	" 2 (5-10°C)	Classes 2,3,4,5,6 (>3 knots)
	" 3 (10-15°C)	" 4,5,6 (>11 knots)
Hot	" 5 (20-25°C)	" 1 (< 4 ")
	" 6 (25-30°C)	" 1,2,3,4 (<17 ")
	" 7 (> 30°C)	all classes
Very hot	" 6 (25-30°C)	Classes 1,2 (< 7 ")
	" 7 (> 30°C)	all classes

(e) Sun or shade - and whether the individual seemed to have specifically selected a shady area.

(f) Aspect-N, NE, E, SE, etc.

(g) Slope-in 10° estimates.

(h) Rock - a subjective estimate of rock size and abundance in broad classes.

(i) Vegetation - height and cover in broad classes.

(j) Formation - plateau, rocky slope, outcrop, valley floor, etc.

A total of over 300 hours of activity study on the main klipspringer groups yielded nearly 10 000 activity records after incomplete records and data for periods less than two hours had been omitted. The difficulty in finding the klipspringers and keeping them under observation at Zacchariashoek made it impossible to gather sufficient data to describe their activity through the day in this area. However, records during different weather conditions helped to fill in gaps and were included with the data for these conditions from all areas together.

The data were analysed by a digital computer which presented the results as the percentage frequency of activity for each half hour period through the day. The variable and irregular total number of records for each period would have caused an analysis of total records to be misleading, so the results are presented on a percentage basis to give a more meaningful comparison between different periods through the day. The data were analysed in several different ways, first to show the typical activity pattern for all klipspringers during each visit to each of the main study areas, then for each sex, and then for all visits together but with extreme weather conditions, to determine the effect of these on their behaviour.

Since the activity of juveniles was age-dependent and they spent most of the time concealed during the first few months, data for this age group were not analysed separately, although the records were used in the analysis for all klipspringers if they were with their parents.

There are several sources of bias inherent in a project of this nature where conclusions are drawn about a species "typical" daily pattern from only three days of observation. However, the klipspringers' basic movements were fairly predictable and the computer analysis largely confirmed patterns that had already been recognised subjectively. Variation in behaviour between individual groups is a source of error that cannot be ignored, but the fact that clear patterns emerged in spite of the use of data from two or three different families in each area supports the conclusion that these patterns were typical for the species in that area. There was an obvious bias in favour of the more static resting activities, since a feeding or moving klipspringer could easily disappear from view, but it is unlikely that this would have affected the basic activity patterns to any great extent.

The use of the "resting - ?" activity class meant that all rumination values should be regarded as minima, but the small proportion of records in this category could not have affected the pattern very much.

To estimate the total time spent feeding per day the feeding bouts were timed with a stopwatch. However, it proved difficult to gather data for complete days (Table 17), so this was later abandoned in favour of extracting values from the computer analysis. Since the number of records for each half-hour is irregular and some periods, particularly in the early morning, have lower values, the use of the absolute number of feeding records would give unwanted weighting to some periods. Therefore an estimate was arrived at by manipulating the percentages in the manner best illustrated by the following example:-

<u>Example</u>: For a $\frac{1}{2}$ hour period 30% of the records are for feeding.
$\equiv$ 30% of the time is spent feeding
$\equiv$ 30% of 30 minutes is spent feeding
$\therefore$ 9 minutes is spent feeding

Thus the total time spent feeding for the average day during that season is the sum of all the percentages for each half-hour period multiplied by a factor of 0,3 to express it in minutes. This estimate makes use of all the activity study data for that period and compensates for periods that have a low number of records.

RESULTS

Basic activity pattern

The basic activity pattern of klipspringers during different seasons in the two study areas is illustrated by figs. 47 and 48. It can be seen that

Table 17: Feeding time of individual klipspringers measured by stop-watch.

	Time (min)	
SPRINGBOK	♂	♀
77-09-07: 07h20-19h00	48	74
77-11-06: 06h50-19h00	140	199
78-02-13: 07h45-19h30	154	125+
78-02-16: 07h30-19h00	163	180
78-03-01: 07h40-15h00	93+	92+
GAMKA		
77-10-17: 07h30-17h30	136	124
77-10-19: 07h00-19h00	127	169
78-01-21: 06h30-19h30	70	152
78-01-25: 07h15-19h20	59	114
78-01-29: 07h30-19h50	98+	175

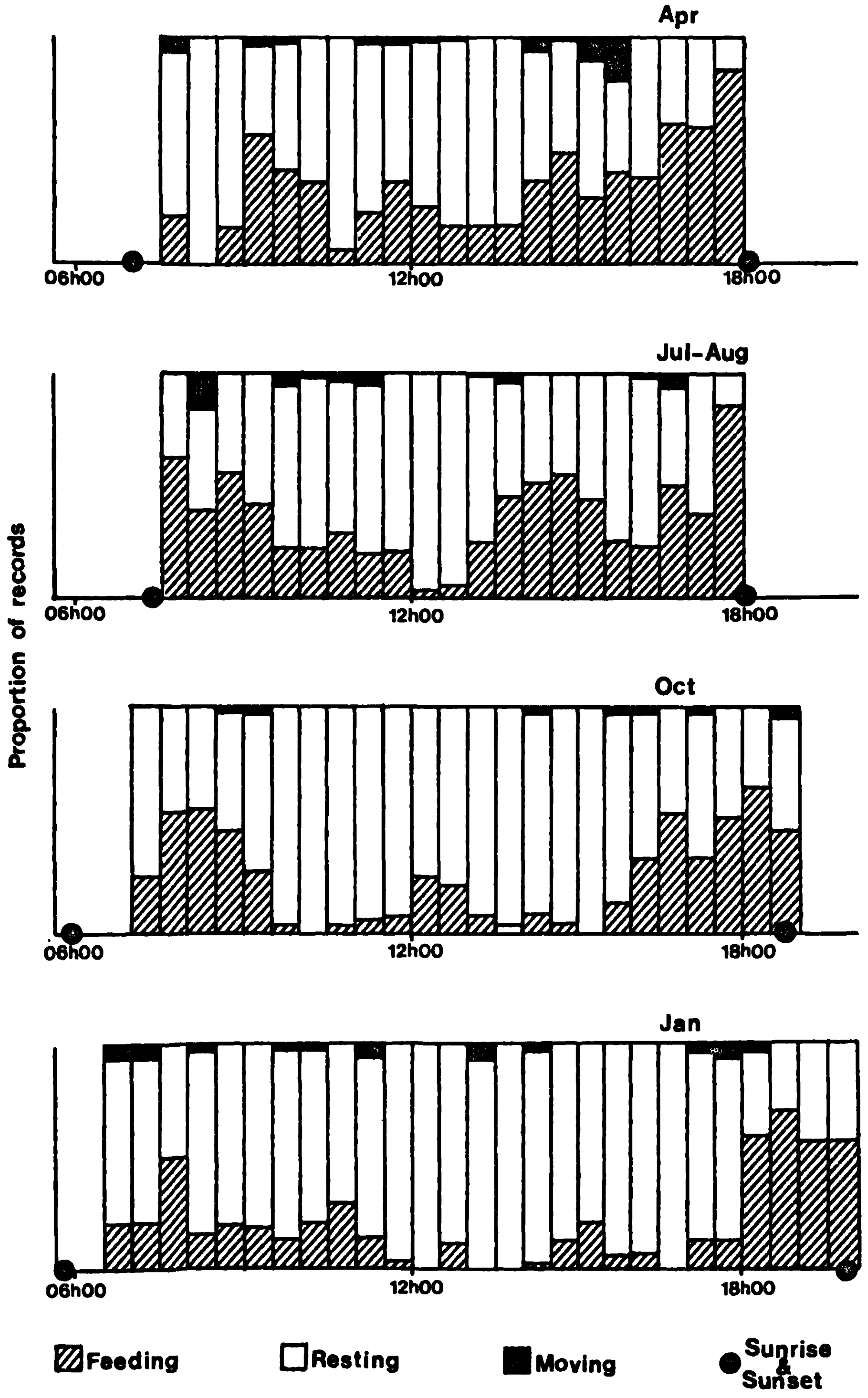
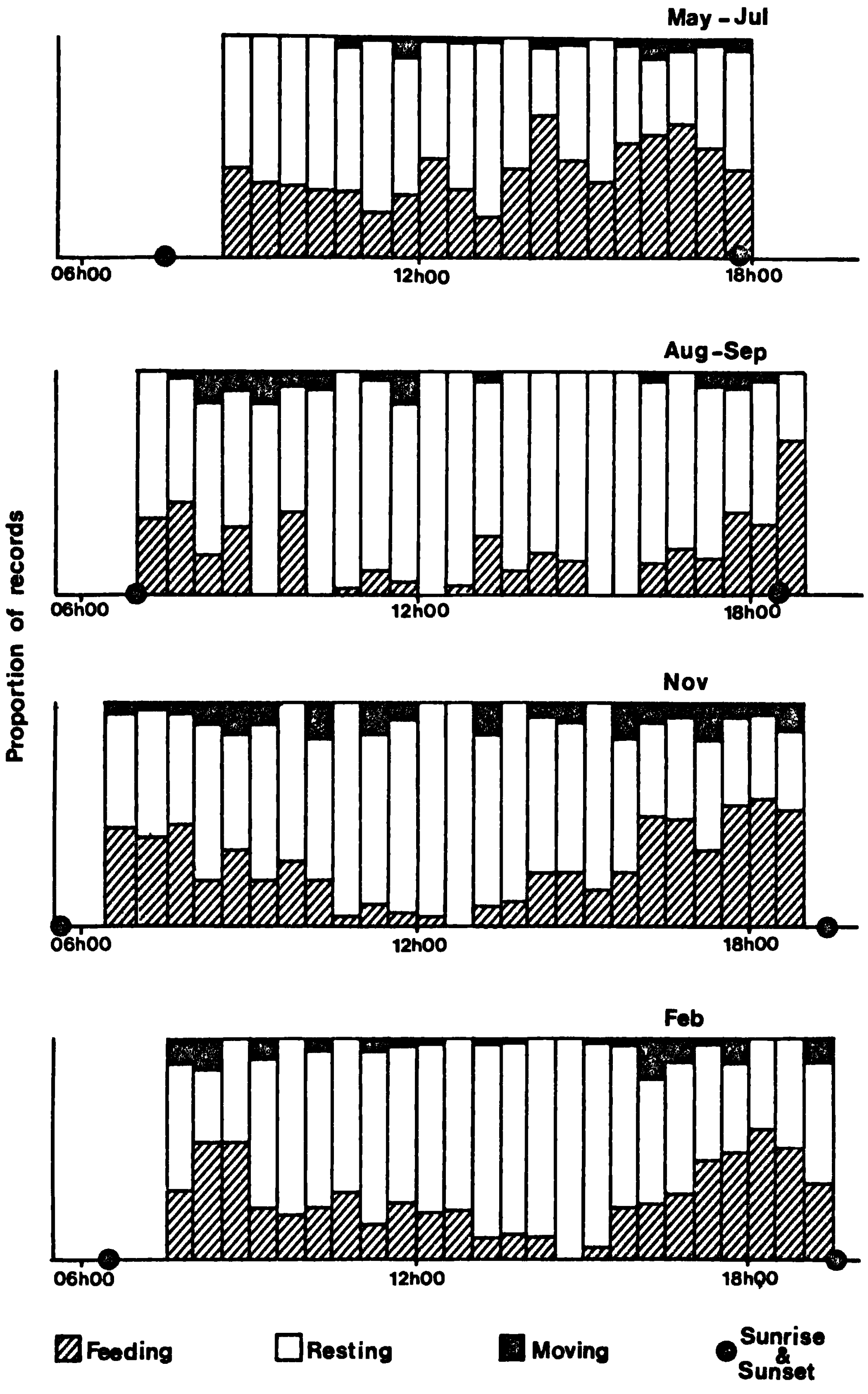


Fig. 47: Activity of klipspringer at different times of the year at [illegible].



[illegible]: Activity of klipspringer in different times of the year at Spr[illegible]n bu[illegible].

most of feeding was done in the morning and evening, but there were also one or two smaller peaks during the early afternoon.

In the study areas under discussion the feeding period was usually quite long, being interrupted by long resting spells, which differs rather markedly from the situation in the Kuiseb Canyon, South West Africa, where the klipspringers showed a concentrated feeding bout of about one hour in the late morning (Tilson pers. comm.). Moving occurred at any time of the day but was more common in the morning and evening and a peak in moving usually preceded a peak in feeding, showing that the klipspringers sometimes moved a short distance away from their resting places to feed.

The pattern for resting and the different activities during resting was predictable (Figs. 49 and 50). It can be seen that the klipspringers lay down mostly in the middle of the day and that lying was negatively correlated with feeding. Standing resting occurred throughout the day with slightly higher values in the early morning and late afternoon, that is, it was more positively correlated with feeding. This is because the buck that was acting look-out while the other fed seldom lay down, but usually stood on a vantage point looking around. They did not always lie down during the heat of the day and on some very hot days gave the impression that they were purposefully standing up on a vantage point to get the maximum air flow round their bodies.

Ruminating showed no clear pattern, apart from being negatively correlated with feeding, meaning that whenever they were resting they spent a fairly constant proportion of the time ruminating, and did not show a preference for any particular time of the day. Ruminating standing and lying followed the proportion of resting made up by standing and lying during the day, so that they ruminated lying down mostly in the middle of the day and they ruminated standing early and late in the day.

Effect of weather conditions

Figure 51 shows that the activity during hot and cold conditions differed very little from the basic activity pattern. In spite of the scarcity of data for cold conditions in the afternoon the pattern was very similar, with a peak in feeding early in the day, one or two peaks around the middle of the day, and a major feeding peak in the late afternoon.

For hot conditions the pattern was somewhat different, since there was an overall reduction in activity during the hottest part of the day. However,

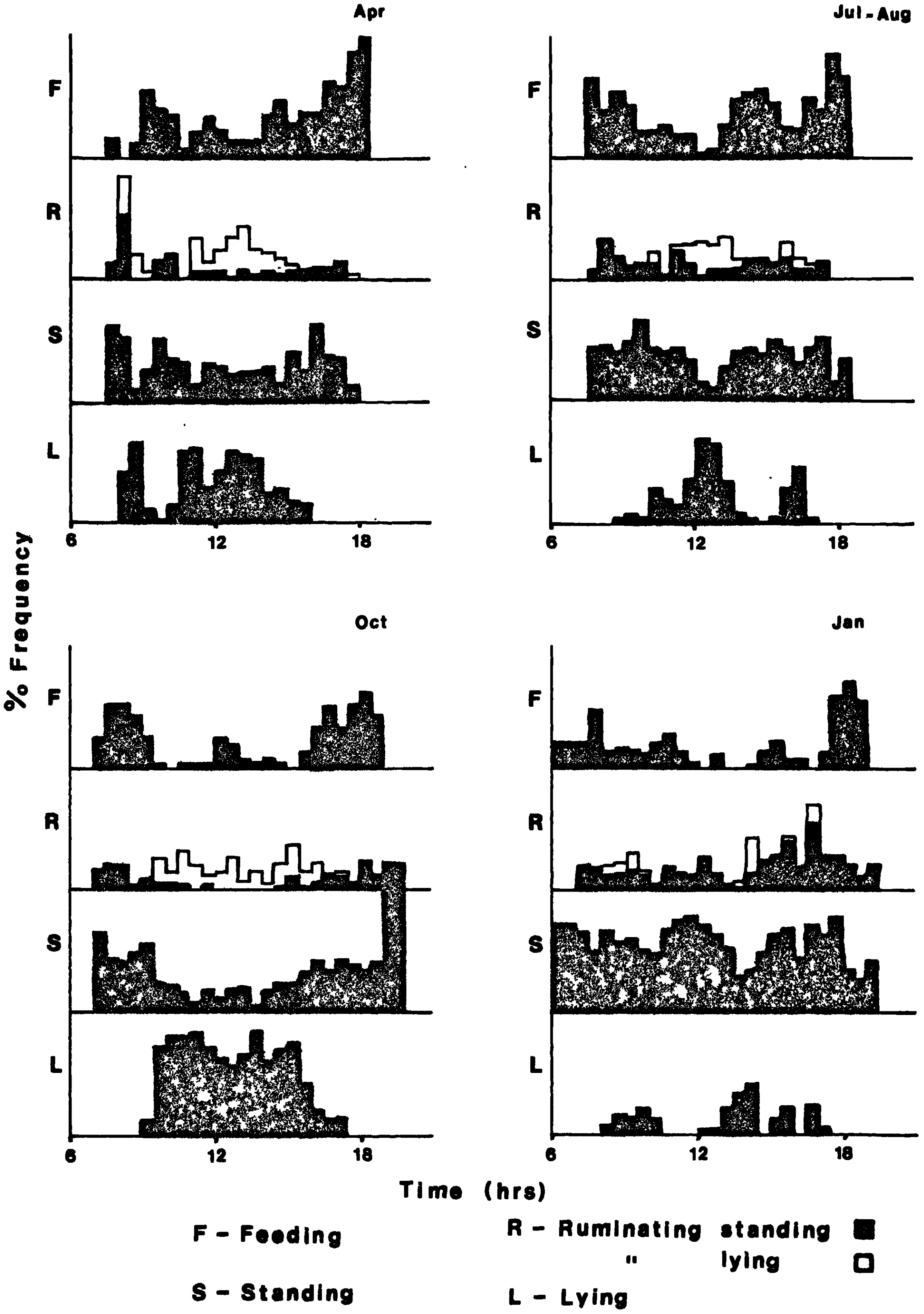


Fig. 49: Resting activity of klipspringers at different times of the year at Gamka.

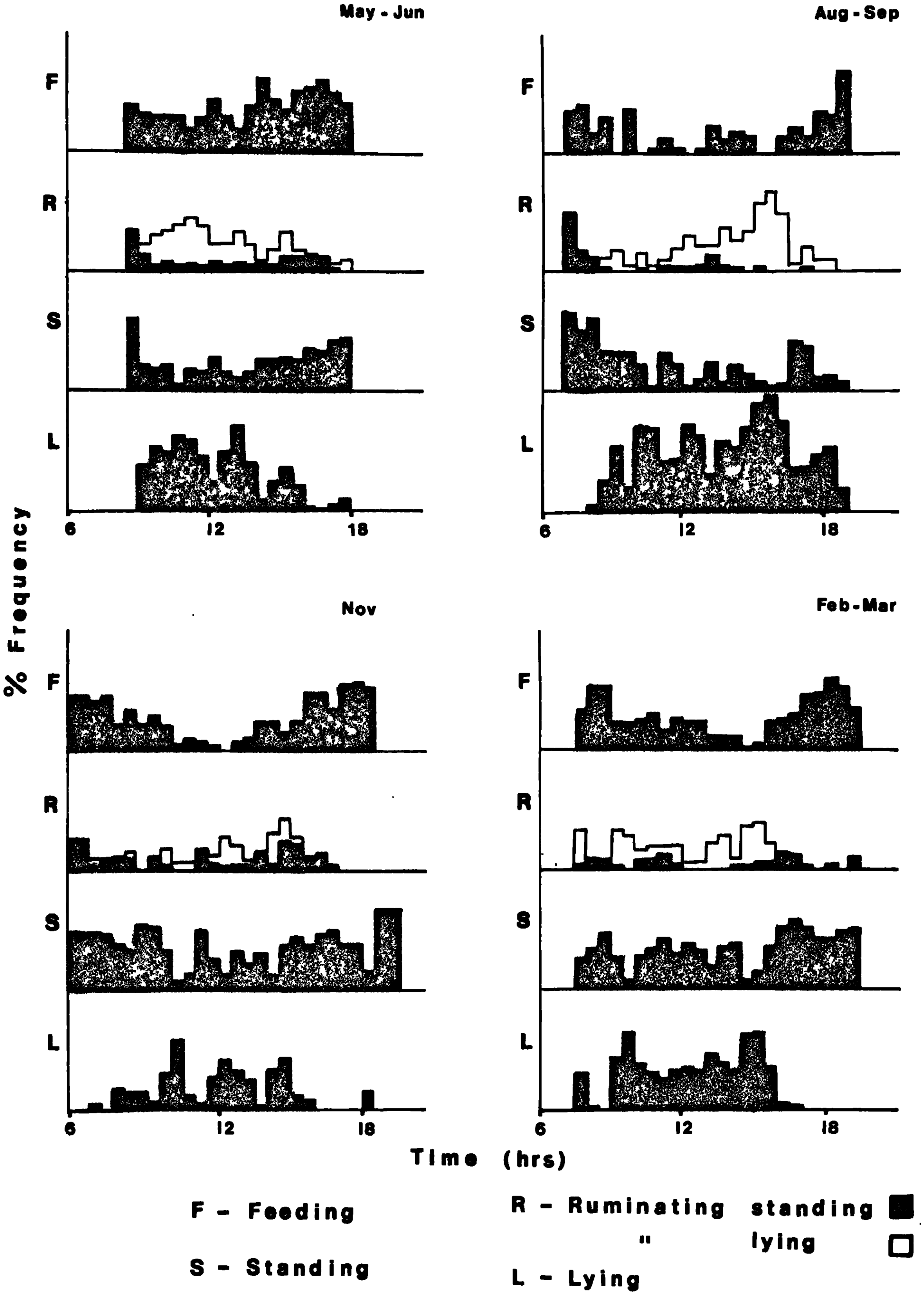


Fig. 50: Resting activity of klipspringers at different times of the year at Springbok.

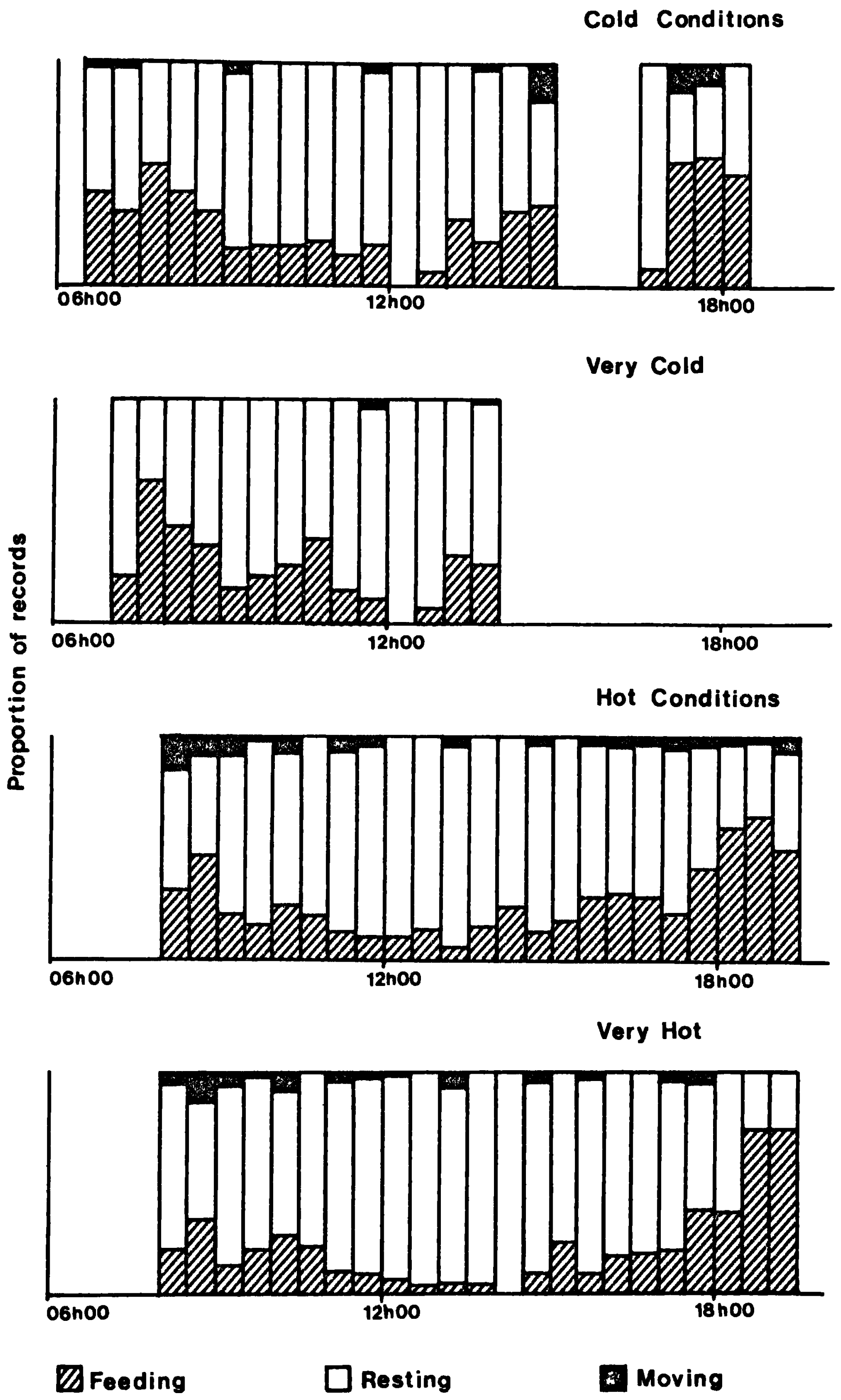


Fig. [illegible]: Activity of klipspringer [illegible] all areas under [illegible] [illegible] conditions.

it is interesting to note that feeding did not cease altogether, as the records for only one half hour period in the "hot" category showed less than 10% feeding. Even under "very hot" conditions during the middle of the day there was a noticeable proportion of the records for feeding. This supports the idea that klipspringers are well adapted to coping with hot conditions (see Chapter 4). Further evidence comes from field observations where on several occasions during the study the klipspringer group was resting in the hot sun and suddenly got up, with no apparent stimulus, to feed for half an hour or so before lying down again.

Few records were gathered under rainy conditions, but Fig. 52 shows that the klipspringers carried on feeding when it was raining. Subjective impressions gained during the fieldwork confirmed that their activity was not noticeably affected by rain.

Strong winds also had little effect on the basic activity pattern (Fig. 52). Even when the wind was Force 5 or more (about 30 km h^{-1}) they spent a large proportion of the early morning feeding, with a peak just after midday. However, wind strength did affect the site selection within their territories, as on several windy days the groups were found up side valleys or behind koppies that were at least partially sheltered from the wind.

Although wind did not noticeably affect the basic pattern, a change in wind often precipitated a change in the klipspringers' behaviour. This was most noticeable at Springbok where a well-known metereological phenomenon is the cool westerly wind that blows up from the coast between midday and 13h00. The oppressive heat of a windless summer's morning would often be changed by the sudden appearance of the breeze which would cause an immediate drop of two or three degrees in temperature. On at least four occasions the klipspringer group under observation started feeding within 10 min of the appearance of the breeze. Therefore, without affecting the basic pattern of activity, this change in wind did affect the timing of the change in activity.

Variations in activity patterns

The proportion of the day that the animals spent moving seemed to show seasonal trends in both areas (Table 18), but it is likely that these are artificial since the sample size was so small, and the number of records on a particular day depended on whether they disappeared out of sight quickly or not. What is significant is that there was a marked difference between the overall proportions of time spent moving in the two study areas

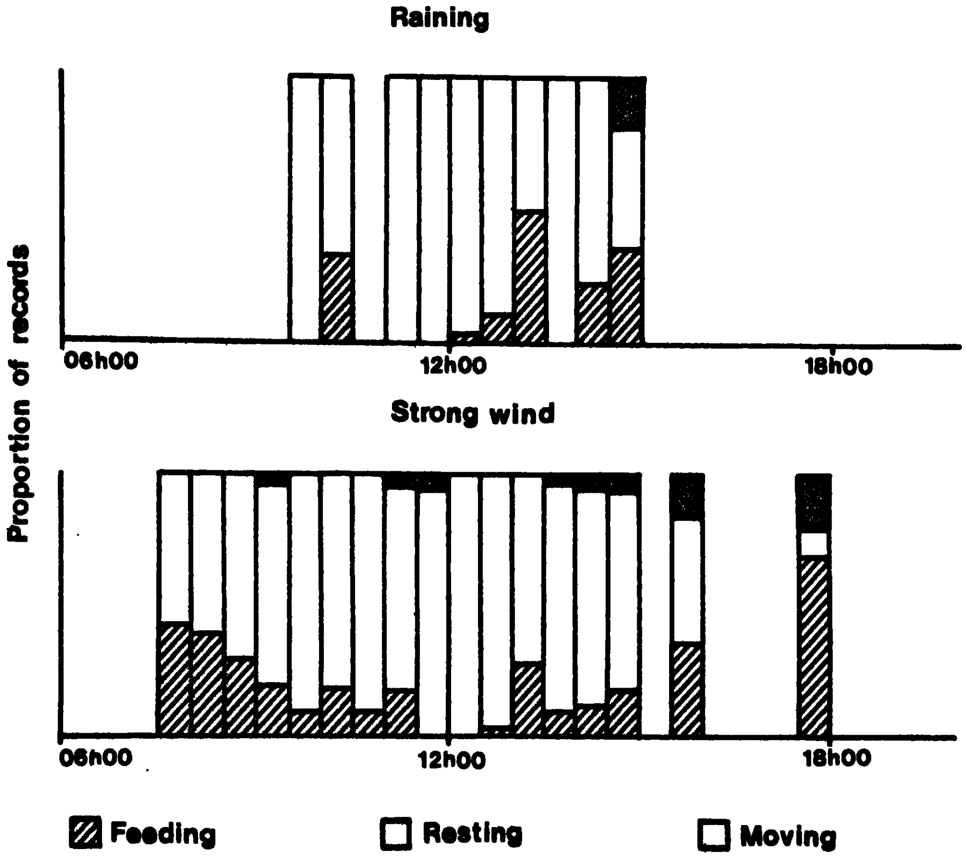


Fig. 52: Activity of klipspringers in all areas under rainy and windy (Force 5 and above) conditions.

($t = 3{,}52$; $p<0{,}05$). This clearly reflects the difference in territory size between the two areas. While territories at Springbok covered about 50 ha, those at Gamka were less than 15 ha (see Chapter 3). This meant that at Gamka the klipspringers did not need to spend so much time moving to cover their territories and exploit the food available.

Table 18: Proportion of time spent moving by klipspringers in the main study areas.

SPRINGBOK		GAMKA	
May-July	3,0%	April	2,4%
Aug-Sept	4,5%	July-Aug	1,7%
November	7,0%	October	0,6%
Feb-Mar	4,6%	January	1,6%

The sexual and seasonal variation in feeding and ruminating times is shown in Table 19. There is a highly significant difference ($t = 6{,}15$; $p<0{,}001$) between the times spent feeding by males and females at all times of the year. This suggests that the energy requirements of the female klipspringer are considerably higher than those of the male.

The total time spent feeding varied considerably through the seasons in each area, with the highest values in the middle of winter, dropping to lower values in summer, and an unusually low figure for the August-September visit at Springbok. This variation differs significantly from a uniform distribution around the mean in each area ($\chi^2 = 27{,}9$ and $18{,}4$ for Springbok and Gamka respectively; $p<0{,}001$). It may be noted from Figs. 47 and 48 that some of the half-hour periods just after sunrise have no values for feeding, which would raise the feeding totals for some visits, but this would only increase the seasonal variation even further.

The total time spent ruminating through the day varied seasonally, being negatively correlated with feeding. That is the more time the klipspringers spent feeding, the less time they spent ruminating, and vice versa. While one would expect a seasonal variation in ruminating time related to the fibre content of the food, the most likely explanation for the pattern in diurnal ruminating times is that only a portion of the ruminating is done during the day while the rest is done at night. This suggests that the observed differences reflect the time available for ruminating during the day, of which the klipspringers utilise a certain proportion, and not the ruminating total

Table 19: Total time (min) spent feeding and ruminating by klipspringers at different times of the year.

	Feeding			Ruminating
	♂	♀	Total	
SPRINGBOK				
May-July	180	233	223	136
August-September	105	150	129	173
November	186	218	204	107
February	187	202	208	120
GAMKA N.R.				
April	149	208	206	133
July-August	157	231	246	119
October	161	189	179	130
January	120	205	167	177

for the whole 24 hours. The breakdown of resting activities illustrated in Figs. 49 and 50 shows no obvious seasonal variation from the basic pattern described above.

DISCUSSION

Feeding activity and food availability

If a selective feeder, such as any of the smaller antelope, spends more of the day feeding we can expect that either it is spending more time searching for food or else it is actually ingesting a greater quantity of plant material. With the klipspringer it is likely that both of these factors are important in explaining the differences in feeding times between the sexes and between seasons.

As with all antelope, the female klipspringer needs extra energy to develop a foetus or suckle a lamb. Studies on the energy requirements of domestic stock have shown that during the last third of the gestation period the female ruminant uses up considerably more energy than is predicted from her total body weight, and this is necessary for the accelerated synthesis of foetal tissue at this stage of pregnancy (Moen 1973). Earlier in the pregnancy the energy requirements are only increased in proportion to her total body mass, including the foetus.

Lactation is an even greater draw on the energy resources of a female antelope than gestation. Moen (1973) has shown that the energy requirements of lactating deer are up to 2,3 times the basal metabolic rate, and that the peak is roughly one third of the way between parturition and weaning.

Thus the energy requirements of a female klipspringer should be higher than those of the male for nine to ten months of the year, since they appear to have one offspring a year (Chapter 3), and are pregnant for 5½ - 6 months, then lactate for about four months. The peak in energy requirements will be from roughly four months after conception to six weeks after parturition.

In antelope such as the klipspringer, that do without drinking water for most of the year, the effect of lactation on the water balance of the female is also likely to play a very important role in the feeding requirements, since the water content of the milk must be a considerable drain on her moisture resources.

Therefore the greater requirements for both energy and moisture explain the longer daily feeding times of female klipspringers in relation to the values for the males shown in Table 19. Whether the female is fulfilling these requirements by being more selective for only the most nutritious and succulent plant parts, or else that she is consuming a greater quantity, is not clear. However, the subjective impression gained was that there was no conspicuous difference in feeding rate between male and female klipspringers, and the difference in feeding times is considerable, so the ingestion of a greater quantity of food probably accounted for some of it.

Table 19 shows a marked increase in diurnal feeding times of klipspringers in winter. In fact, they more than made up for the shorter day length at this time of the year. Although it is possible that klipspringers feed at night, it is likely that the proportion of time spent feeding is minimal, since klipspringers probably follow the usual pattern for diurnal antelope where they spend most of the night resting, ruminating and sleeping (Jarman and Jarman 1973, Lewis 1977). Since selection of plant parts seems to be largely by sight, it would in any case be difficult to feed selectively in the dark.

The most likely explanation for the longer feeding times in winter is that more energy is utilised due to an increased metabolic rate to combat the cold (Chapter 4), and that extra energy is needed by the pregnant female. Since most lambs are born in August or September (Chapter 3), in the months just before this the energy required by the foetus must be at its highest.

The phenology and seasonality of the vegetation in a klipspringer's territory have a great effect on the amount of time spent feeding at different times of the year. That is, the more food of suitable quality available, the less time the animals will have to spend searching for food to fill their stomachs. Thus, if there is a very seasonal production of plant parts suitable for utilisation, in this case the shoots, fruits and flowers, we can expect that the food searching time will vary considerably through the year.

In Chapter 1 it was shown that at Springbok the rainfall is more limiting in quantity, as well as being more seasonal in occurrence, than at Gamka. Figs. 53 and 54 illustrate how this affected some of the important klipspringer food-plants in the two areas. It can be seen that, while at Springbok flower and fruit formation occurred almost entirely in the middle of the year from autumn to spring for all the plants, at Gamka there was always at least one of the major food plants in flower or fruit. This means that the vegetation

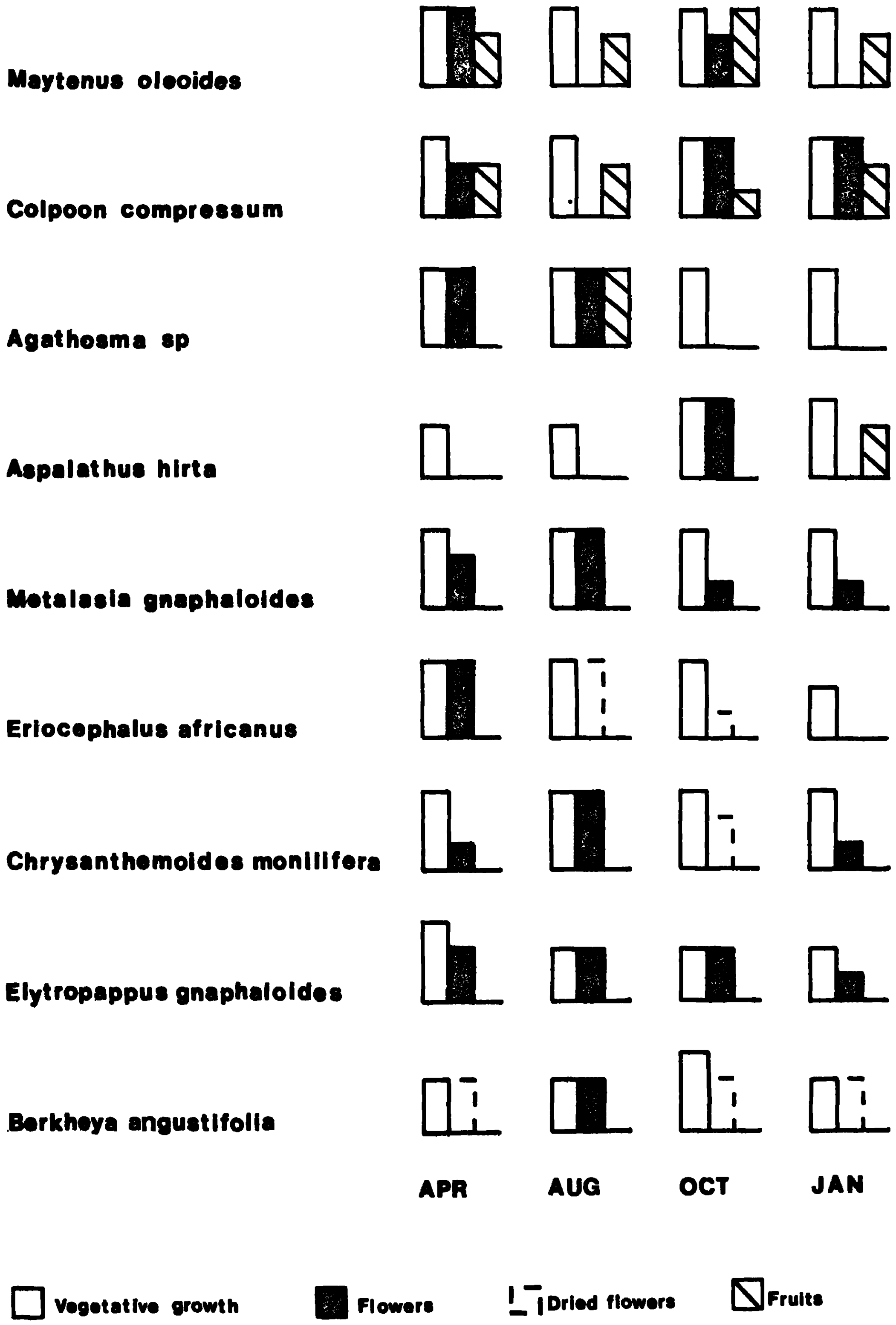


Fig. 53: Phenology of some important food-plants of the klipspringer at Gamka.

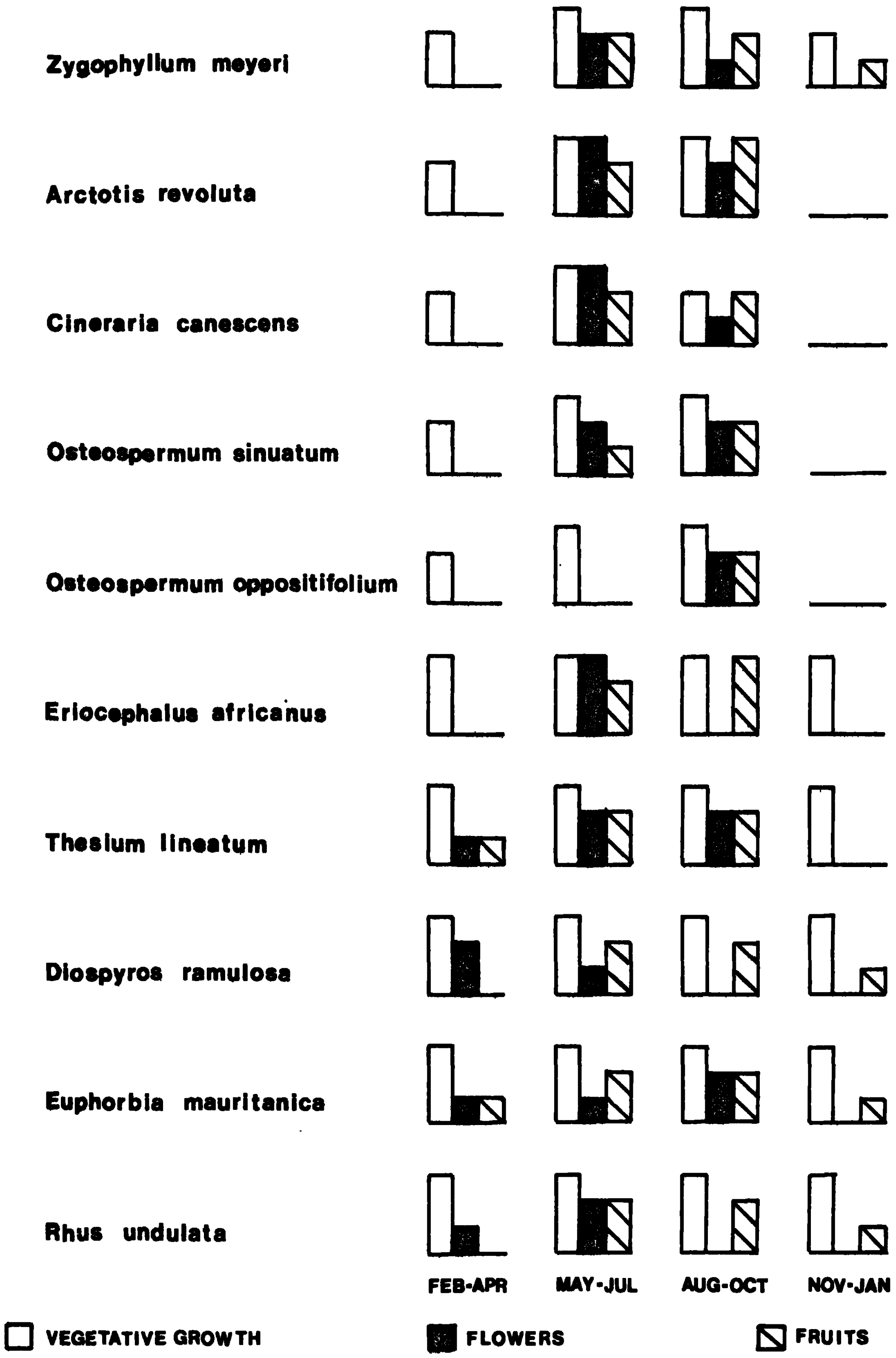


Fig. 54: Phenology of some important food-plants of the klipspringer at Springbok (adapted from Rösche 1978).

variation in food searching time and therefore in total feeding time. Table 19 shows that the variation in total feeding time at Springbok (94 min) was considerably greater than at Gamka (79 min), although the difference was not large enough at this small sample size to be statistically significant.

The great variation in feeding times at Springbok is caused by the extremely low value for the August-September visit, which can be explained by the phenology of the vegetation and the searching time necessary to find suitable food. Spring in the Namaqualand is a well-known natural spectacle with not only the famous Namaqualand annuals, but also most of the shrubs, in flower at this time. Feeding observations showed that klipspringers utilised this fully, with a large proportion of their diet being made up of flower heads. With an abundance of suitable food the klipspringers wasted very little time in searching for food, so the feeding time was far lower than for other times of the year. This was in spite of the high energy demand on the female while she was suckling a young lamb.

An alternative suggestion for the low spring feeding time is that the klipspringers actually ingested a smaller quantity of food because of its higher protein content. However, most theories on rumination indicate that there is little variability in overall volume of the content of a ruminant's stomach. Therefore, reduced food searching time is the more likely hypothesis.

CHAPTER 8 : FEEDING ECOLOGY

METHODS

The feeding of klipspringers was monitored by direct observation of the main study groups in the two study areas as well as by analysis of the stomach contents of dead animals.

Direct observation

During the activity study the klipspringers were watched as they fed and the precise locality of the feeding station was recorded on tape. Later that day or on the following day the station was checked and a food record was counted if there were clear, fresh bite marks on the bush. It proved necessary to use this laborious method of checking the bushes individually since, from the long range and lack of depth of field when looking through the telescope, it was not often obvious exactly which plant the animal had fed on. In the low dwarf-shrub communities of both study areas, the vegetation is complex and young plants growing up inside established bushes of other species were often the most sought-after food. Therefore a record of the larger, more obvious shrub would have given a very misleading picture.

A food record was counted when an individual fed from a single bush for one continuous space of time. If he moved his position but remained feeding on the same bush no new record was counted. Thus two individuals feeding from one bush would count as two records, and one individual standing in one spot feeding from a single bush, then turning his head to a bush nearby, and after a while coming back to feed on the original bush, would yield a total of three records. In addition, each record was given a rating of 1, 2 or 3, where "1" meant the klipspringer had taken only one bite off the bush, "2" was feeding with several bites and "3" was when he fed for more than 1 min. During the calculation of feeding record totals records of "feeding 3" were counted as two records to give a small amount of weighting to the plants that were most popular, and therefore to give a more realistic picture of the proportion of the diet made up by the different plants. This weighting underrated some records as, for example, on one occasion where only a single record of "feeding 3" could be counted when a klipspringer ram spent more than 35 min eating the fruit of a single *Maytenus oleoides* bush at Gamka.

The system of recording feeding minutes at each plant was rejected as it was impossible to combine it with the activity study. Continuous observation through the telescope for more than about 20 minutes at a time caused too much eye strain to allow monitoring of the several hours of feeding each day by this method.

Since a number of plant genera occurring in both study areas contain very similar species that can only be differentiated when flowering, or else show such small differences that one has to get involved in detailed botanical taxonomy to tell them apart, several species were grouped together for the analysis of food records. The species comprising each taxon are listed in Appendix A and B.

In all over 500 feeding records were collected in each of the main study areas. This number is too low to allow detailed statistical treatment of the results and to make valid conclusions as to seasonal changes in feeding patterns, but the accumulation of records was so time-consuming that these data were considered sufficient to illustrate the main trends in klipspringer feeding preferences.

Stomach analyses

The stomachs of the shot animals were analysed macroscopically in the same way as the dassie stomachs (see Chapter 9). All recognisable plant parts were identified and a subjective assessment of abundance made on a 1-5 scale for each plant as follows:-

1 - only one piece of the plant present (< 1%)
2 - several pieces " " " " (1-3%)
3 - a substantial proportion of the content (3-10%)
4 - a large proportion of the content (10-25%)
5 - very large proportion of the content (> 25%)

Due to the large proportion of the stomach contents that was made up of unidentifiable plant material it was impossible to attach a meaningful percentage value to each species, but the figures in parenthesis give an approximate percentage value to each of the abundance classes. The results are presented as abundance class totals, which is a simple addition of the numerical values of each class, e.g. 3 + 1 + 0 = 4.

Plant species abundance

The plant species abundance values for the rocky slope and plateau edge were calculated from the habitat analysis plots (see Chapter 2). Since the cover values for each plot were originally assigned to Braun-Blanquet cover classes which do not allow means to be calculated, each class was given an average percentage cover value as follows:-

Braun-Blanquet class + = 1%
1 = 3%
2m = 5%
2a = 10%
2b = 20%
3 = 35%

Because these classes were assigned according to the proportion of the vegetation cover that they made up, and not the total cover, the mean percentage for each species for all the quadrats can be considered as the proportion of the vegetation made up by that species, irrespective of the relationship between vegetation, rock and bare ground in the different plots.

Preference ratings

The preference rating for each species was calculated as follows:-

$$\text{Preference Rating (PR)} = \frac{\text{\% of food records}}{\text{\% of vegetation}}$$

The percentage of food records was the proportion of the total number of feeding records in that habitat type, and the percentage of the vegetation was the mean percentage cover of that species for all plots in that vegetation type.

Due to the low number of feeding records that was collected from the moist south facing slopes and the valley bottom at Gamka, meaningful preference ratings could not be calculated from these areas. Because of the variation in vegetation between Tierkloof and Klippe se Kloof "dry rocky slope" habitats only the 16 quadrats in Tierkloof were counted in the vegetation percentages. For the plateau edge there was less difference between the two valleys, so all eight plots were used, but these were all situated on the ecotone between the dry north facing rocky slopes and the plateau, and plots outside this narrow band were disregarded.

At Springbok only the 16 plots on the transect line through the main klipspringer territory were used, so that several important food species that occur only in areas of slightly different micro-habitat, obtained no preference ratings. In both areas preference ratings from plant species that made up less than 0,5% of the vegetation were rejected as unreliable.

Thus the preference ratings in each area contained many inaccuracies due to the low number of feeding records, the low number of vegetation plots, and the siting and location of the plots, but they do give an idea of the relationship between frequency of occurrence and feeding pressure for the most important plant species, and provide a more quantitative basis for dividing the vegetation into groups according to food preference and not just abundance.

Browsing pressure

When each feeding record was checked a subjective assessment of the browsing pressure on the plant was made, and the symbols listed represent the most common state found for that species throughout the study period. The classes used were:-

+ - little browsing - few bites taken and the plant showing very little effect from browsing pressure.

M - medium browsing - several bites and the plant showing some loss of parts to browsing.

H - heavy browsing - many shoots bitten off and the plant's shape markedly affected by browsing.

vH - very heavy browsing - a large proportion of the plant eaten and only a few protected shoots surviving.

Aromatic compounds and spininess

To look for a correlation between the preference ratings of the food plants and the presence of strong-smelling aromatic compounds the leaves of most of the important shrubs on the dry rocky slopes at Gamka were crushed between the fingers and subjectively assigned a rating of 0-4, with "0" recording almost no smell detectable to the human nose, and "4" denoting a very strong and pungent smell.

In addition, the plants were given a rating on the same 0-4 scale to record subjectively the presence of spines on the leaves and shoots. This was done to assess the importance of spines in discouraging herbivory.

Micro-nutrients

The livers of the shot klipspringers were analysed for some essential trace elements to examine the possibility that they may be suffering from defi=

ciencies in micro-nutrients in their diet. The livers were frozen soon after shooting and sent to the Regional Veterinary Laboratory, Stellenbosch where concentrations of copper, iron, zinc and manganese were determined by standard flame-photometric methods.

RESULTS

Tables 20 and 21 show the results of the feeding study by direct observation in the two main study areas, with the plants arranged according to the total number of feeding records during the study. The results of the stomach analyses of animals shot and found dead (Tables 22 and 23) show a good correlation with the observational data in spite of the small sample size.

These results show that in the Cape klipspringers are almost exclusively browsers and feed mostly on a wide range of perennial shrub species, with a small proportion of annual and biennial herbs. The single record of grazing, on an inflorescence of Themeda triandra at Gamka, out of a total of more than 1000 feeding records, illustrates the low significance of grass in the diet of klipspringers in these areas. While a few more records could have been over-looked, there is little chance that grasses could make up even one percent of the plants eaten while the animals were under observation.

Selection for plant species

That klipspringers feed rather unselectively on a wide range of plant species within the shrub and herb community is supported by several lines of evidence.

From direct observation at Gamka at least 37 taxa (including 41 species) were fed on, while at Springbok definite records were obtained for 45 taxa (62 species). These figures can be considered as underestimates since many of the smaller and less obvious plants that had been fed on were unavoidably overlooked when the feeding sites were checked. In addition, the main study groups occupied territories that covered only a small proportion of the total areas available to klipspringers in each locality, and several plant species that are likely to be eaten by klipspringers in that habitat type did not occur in these territories.

Though in each area only six taxa make up half of the feeding records, only one taxon at Springbok and three at Gamka gave values of over 10% of the

Table 20: Feeding records by direct observation of klipspringers at Gamka, showing season totals, parts eaten and number of "feeding 3's" (question marks show where a part was possibly eaten, and small letters denote parts that were fed on but formed a small proportion of the records).

Plant taxon	Part eaten	Species totals	Season totals APR	JUL	OCT	JAN	"Feeding 3's"
Agathosma sp.	S	62	17	3	13	29	6
Maytenus oleoides	F	53	2	5	44	2	3
Aspalathus hirta	F s?	52			51	1	11
Phylica purpurea	SI	33		19		14	9
Cineraria sp.	ISL	25			15	10	5
Metalasia gnaphaloides	I s	25		25			5
Eriocephalus africanus	S i	25	8	8	8	2	
Chrysanthemoides monilifera	FS	23		21		2	7
Montinia caryophyllacea	S f	20		12	1	7	3
Solanum tomentosum	SIF	19			8	11	2
Colpoon compressum	FI	18	4			14	3
Berkheya angustifolia	I s?	14	3	1		10	1
Elytropappus gnaphaloides	S	13		9		4	1
Muraltia alopeçuroides	SIL	13		13			1
Pelargonium spp.	SI	10	4	3		3	3
Polygala fruticosa	I s	9	2		3	4	
Thesium nigromontanum	SI	9		8	1		
Asparagus capensis	S	8	6	2			
Diospyros dichlorophylla	F s	8	8				
Hermannia spp.	SI	8	6		2		
Dodonaea viscosa	S f?	7		1		6	
Metalasia langebergensis	I s	7				7	2
Dioscorea elephantipus	SL	6	3			3	
Muraltia ericaefolia	SI	5		3	1	1	
Cliffortia pulchella	SL	5	1			4	
Cliffortia ramosissima	S	4				4	2
Felicia filifolia	S i?	3	1			2	
Manochlamys albicans	FS	2	2				
Carpobrotus sp.	L	2				2	1
Elytropappus adpressus	S	2				2	
Rhus tomentosa	S	2			2		
Euphorbia sp.	SL	1			1		
Pentzia dentata	S	1		1			
Rhus lucida	F s?	1	1				
Relhania squarrosa	S	1				1	
Leucadendron salignum	S	1	1			1	
Themeda triandra	I	1			1		
Totals 37 spp.		498	69	134	150	145	

I = Inflorescence or flower, F = Fruit, S = Young shoots, L = Leaves, St = Stems

Table 21: Feeding records by direct observation of klipspringers at Springbok, showing season totals, parts eaten and number of "feeding 3's" (question marks show where identification of species or parts eaten was not certain, and small letters denote parts that were fed on but formed a small proportion of the records).

	Part eaten	Species totals	Season totals				"Feeding 3's"
			JUN	SEPT	NOV	FEB	
Zygophyllum spp.	SLI	85	42	24	2	17	20
Galenia fruticosa	SL i	58	20	12		26	9
Indigofera spinescens	FS	47	3	8	12	24	14
Euphorbia mauritanica	St I	40	2			38	9
Tetragonia spp.	SL f	38	27	5		6	1
Rhus undulata	FI s	32	14	4	2	12	5
Osteospermum spp.	IS	27	6	13		8	4
Euphorbia decussata	St IF	23	13	2	1	7	5
Ruschia/Leipoldtia spp.	I fs	23	3	18	2		2
Asparagus aspergillus	L	23	23				9
Pentzia incana	SI	21	11	1		9	1
Pelargonium dasyphyllum	S	20	19	1			3
Arctotis revoluta	I di	18	1	4	10	3	1
Diospyros ramulosa	FS	16	6		1	9	4
Dodonaea viscosa	t f?	16	6			10	7
Eriocephalus africanus	S	15	10	3		2	2
Cineraria canescens	LI	12	3			9	2
Drosanthemum albens	I s	9?		3		6?	1
Moquiniella rubra	F s	6	6				3
Eriocephalus ericoides	SL	6	2	2		2	
Amoebophyllum angustum	SF	5	1			4	
Crassula brevifolia	SL	5				5	
Lotonis longiflora	SL	5			5		2
Pelargonium grandicalcaratum	S	5	4	1			1
Polymita albiflora	I l	5	2	1	2		
Pharnaceum spp.	SI	5		1		4	
Thesium lineatum	S St	5	2	1		2	
Antizoma miersiana	SL ?	4		1		3	
Hermannia spp.	SI	4	2	1		1	
Nenax dregei	S	4		1		3	
Veltheimia capensis	L	4	4				1
Galenia africana	I s?	3	1	1		1	
Lycium oxycarpum	S	3	3				
Montinia caryophyllacea	F s	3			3		1
Pteronia spp.	S	3	1	1		1	
Othonna spp.	S	3	3				
Albuca altissima	I l	2		1	1		
Asparagus asparagoides	L	2	2				
Hebenstreitia crassifolia	SI	2		2			
Mesembryanthemum karroense	F l	2				2	
Solanum burchellii	SF	1				1	
Asparagus capensis	L	1	1				
Berkheya spp.	SI?	1	1				
Didelta spinosa	I s?	1		1			
Manochlamys albicans	L f	1				1	
Totals 45 spp.		614	244	113	41	216	

I = Inflorescence or flower, F = Fruit, S = Young shoots, L = Leaves, St - Stems.

Table 22: Klipspringer food-plants at Gamka from stomach analysis of three shot animals (July 1978). For abundance classes see text.

	Part eaten	Species totals	Individual ratings		
			♀3	♂4	♀5
Agathosma sp.	SI	10	4	3	3
Chrysanthemoides monilifera	ISL	6	3	-	3
Pelargonium spp.	SL	5	1	4	-
Dodonaea viscosa	LS	4	2	-	2
Cliffortia pulchella	L	3	-	2	1
Clutia alaternoides	SLF	2	-	2	-
Aspalathus hirta	Is	1	-	-	1
Montinia caryophyllacea	L	1	1	-	-
Cliffortia ramosissima	L	1	1	-	-
Thesium sp.	L	1	1	-	-
Muraltia ericaefolia	S	1	1	-	-
Number of species			8	4	5

I = Inflorescence or flower, F = Fruit, S = Young shoots, L = Leaves

Table 23: Klipspringer food-plants at Springbok from stomach analysis of two shot animals (July 1978) and one animal found dead (Oct 1978). For abundance classes see text.

	Part eaten	Species totals	Individual ratings		
			♀1	♂2	Juv. 6
Zygophyllum spp.	SL	10	3	4	3
Euphorbia mauritanica	St	8	3	2	3
E. decussata	St	6	3	2	1
Ruschia/Leipoldtia spp.	SL	3	2	-	1
Maytenus oleoides	L	3	-	-	3
Boscia foetida	L	3	-	3	-
Galenia fruticosa	SL	2	1	1	-
Indigofera spinescens	S	2	1	1	-
Polymita albiflora	L	2	-	2	-
Asparagus aspergillus	L	2	-	2	-
Moquiniella rubra	F	2	-	2	-
Crassula spp.	SL	2	-	1	1
Zygophyllum divaricatum	S	1	-	-	1
Didelta spinosa	S	1	1	-	-
Galenia africana	S	1	-	-	1
Eriocephalus africanus	S	1	1	-	-
Lycium oxycarpum	LS	1	-	1	-
Rhus undulata	S	1	-	1	-
Antizoma miersiana	L	1	-	1	-
Cheirodopsis sp.	S	1	-	-	1
Albuca altissima	L	1	-	-	1
Number of species			8	13	10

F = Fruit, S = Young shoot, L = Leaves, St = Stems feeding records. Petrides (1975) suggests that a species that constitutes 10% of the diet is a "principal food" regardless of whether it is a "preferred food" or not. So, by his definition, klipspringers have few principal foods, and these species only just qualify. If one takes 5% as the cut-off point, there are six taxa of principal foods at Springbok, and seven at Gamka, but at Springbok 20 taxa (44% of the total) and at Gamka 25 taxa (68% of the total) made up more than 1% of the food records.

The stomach analyses of dead klipspringers showed a few extra plant species that were not recorded by the observation method, but the general pattern for the more important species was very similar. The extra species were not very common in either area, but it is interesting that Maytenus oleoides, which is common and heavily utilised by klipspringers at Gamka but rare at Springbok, was found in one of the stomachs from this area. Although the sample of stomachs was very small for each area and all the specimens were shot at the same time of the year, the order of the more important species shows a surprising similarity to the observation data, and in each area the most important plant, Agathosma and Zygophyllum for Gamka and Springbok respectively, was the same using both methods.

In addition to utilising a wide range of species through the year, the klipspringers fed on several different species during the day. Tables 22 & 23 show that the mean number of plant species that could be identified per stomach was 8,0 (range 4 - 13) suggesting that a klipspringer is unlikely to fill its stomach with food from only one or two species of plants, even though a large proportion of the content may consist of one species. Further evidence for the use of a number of plants at a time is the high ratio of the number of species fed on to the number of food records for each day that food records were gathered (Table 24). The days that showed less than 10 records were discarded as unreliable which left a mean value of 2,8 and 3,3 species per 10 feeding records for Gamka and Springbok respectively.

Table 24: Average number of plant species per 10 feeding records of klipspringers, on days when 10 or more records were gathered.

SPRINGBOK	Number of days	Mean No. of spp.	GAMKA	Number of days	Mean No. of spp.
May-Jul	7	3,2	Apr	3	3,6
Aug-Sep	3	4,0	Jul-Aug	3	2,3
Nov	2	3,2	Oct	2	2,5
Feb	6	3,2	Jan	3	2,8
Overall mean		3,3			2,8

Selection of plant parts

Selectivity for plant parts is hard to quantify from long distance observatior because it is often not clear exactly which part has been bitten off when the plants are checked. However, it was obvious that in nearly all cases the part eaten was at the tip of a branch, either a young growing shoot, a flower or a fruit. Tables 20 and 21 show that a large proportion of the food selected was growing shoots, with flowers and fruits of most species eaten when they were available. Mature leaves of only a few species were eaten and these were mostly species where the older leaves do not become hard and leathery. The only stems that were eaten were the two Euphorbia species and Thesium lineatum at Springbok, and Montinia caryophyllacea and T. nigromontanum at Gamka, all of which have photosynthetic green stems that take over the function of leaves.

Further evidence for selectivity for plant parts is a description of the species' feeding behaviour. Klipspringers never stood in one place and fed heavily on one section of a plant until it was completely eaten back, but rather moved around taking a bite here, a bite there and then moving to another plant or the other side of the same plant. If a bush had flowers or fruits, they spent a long time picking off just these nutritious parts, but hardly touching the vegetative parts. When particular plant species were in flower or fruit they would feed almost entirely off these species with only the occasional bite from other plants that were not in this growth stage. An example of this is spring at Gamka where 95 out of a total of 150 records were for feeding on the flowers of Aspalathus hirta and the fruit of Maytenus oleoides. However these two species were seldom utilised at other times of the year (Table 20).

Table 25: Number of records of "feeding 3" in the klipspringer feeding records from plants with flowers or fruits as compared to those without.

	Flowers or fruits			Flowers or fruits	
SPRINGBOK	Present	Absent	GAMKA	Present	Absent
May-Jul	14	30	Jul-Aug	21	2
Aug-Sep	15	2	Oct	33	0
Nov	7	1	Jan	9	13
Feb	17	22			
Total	53	55	Total	63	15

The tendency to feed for a long time on plants with flowers or fruits is shown by Table 25, which gives the number of records of 'feeding 3" on plants with flowers or fruits as opposed to those without. In spite of the scarcity of flowering or fruiting plants at some times of the year in the study areas, nearly two thirds (62%) of all "feeding 3" records were from plants with flowers or fruits.

Large bushes with popular fruits, such as *Rhus undulata*, *Indigofera spinescens*, and *Euphorbia mauritanica* at Springbok and *Maytenus oleoides* at Gamka, often lost all the accessible fruit to browsing, so that there was a clear browse line at about 1,2 m and below this height only fruit right inside the bush were left untouched. Observations on the captive klipspringers at Augrabies Falls showed that they can learn to stand up on their back legs (Fig. 55), but only a few individuals in the group did this, and no evidence of it was seen in the main study areas.

The stomach analysis showed a higher proportion of feeding on leaves than one would expect from the observation data, but this is because the animals were shot in winter when there were not many flowers and fruits available, especially at Springbok where 1978 was considered to be a drought year.

Seasonal changes in feeding patterns

Whenever there are seasonal changes in the phenology of the vegetation in an area, there must be seasonal changes in the availability of food for highly selective herbivores such as klipspringers. In Chapter 7 it was suggested ~~that~~ the seasonal changes in the amount of time spent feeding during the day are related to the availability of food and the amount of time spent searching for desired high-energy or succulent food.

While klipspringers are highly selective and live largely off succulent and nutritious food such as fruits and flowers when these are available they must be adaptable enough to cope with dry periods when there is little succulent food on the plants. Thus the stomach analyses of klipspringers shot in winter showed that under dry conditions they eat more mature leaves.

Although it was difficult to quantify exactly what the buck had eaten for each observational feeding record, it was obvious during the study that they fed largely on flowers or fruits when they were available and at times, like spring at Springbok, flowers or inflorescences made up a large proportion of the diet. The only way to quantify the food that was available to the buck

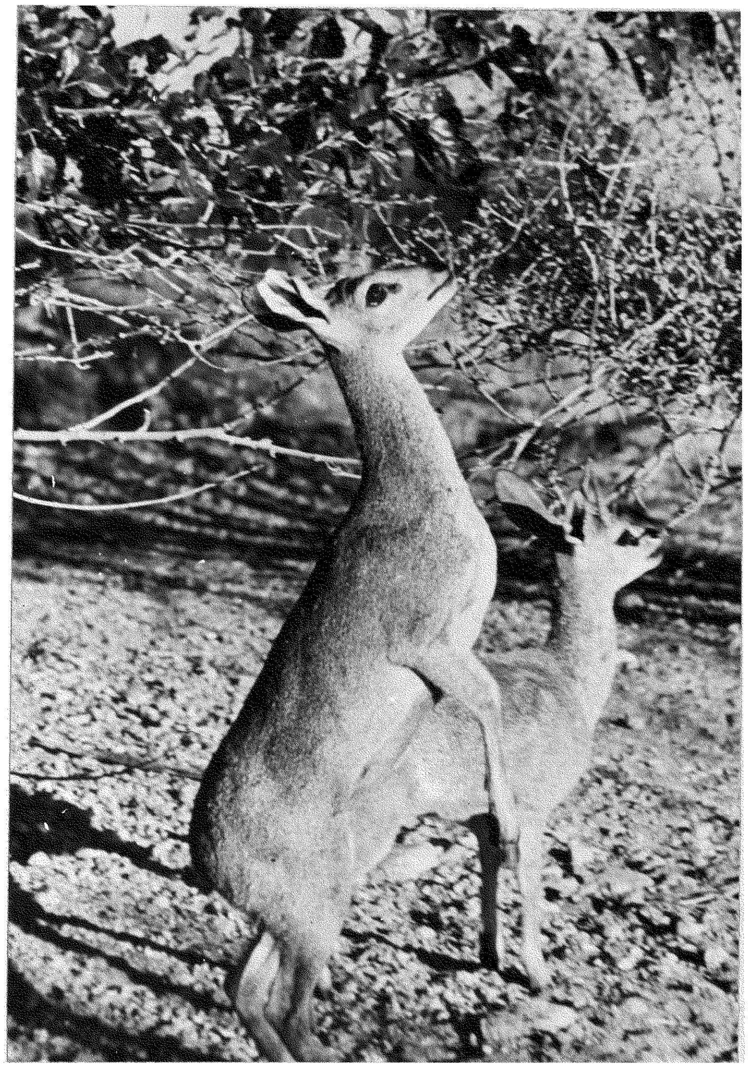


Fig. 55: A klipspringer ewe feeding by standing on her back legs at Augrabies Falls.

is to look at the number of feeding records from bushes that had either flowers or fruits on them (Table 26). Although this ignores the fact that the buck may have selected some bushes for the young growing shoots, even if they did have fruit on them, and that there may have been very few fruits or flowers on the plants, the data do show strong seasonal trends and give an idea of what was available at different times of the year in the two study areas.

The most striking feature is the difference in seasonality between the two areas, as suggested in Chapter 7 and Figs. 53 and 54. In Table 26 the range in percentage of records from flowering bushes of 3,2 to 79,8% is exactly three times the range at Gamka (from 27,5 to 53,0%). This supports the impression given by Fig. 53 that there is always one of the main food plants flowering at Gamka, while the plants at Springbok show a marked seasonality. The figure for September at Springbok indicates that up to 80% of the food of the klipspringers in spring could have consisted of flowers.

The presence of fruit on plants that were fed on was less important than that of flowers, although the high value for October at Gamka reflects the heavy utilisation of Maytenus oleoides fruits mentioned earlier. At Springbok the occurrence of fruits on the plants in late summer and winter, as shown by the higher February and June values, probably represented an important contribution to the klipspringers diet when flowers were scarce. The most important fruiting species at these times were Rhus undulata and Indigofera spinescens, which were so heavily utilised that only a few inaccessible fruit usually survived to the end of winter.

Table 26: Percentage of klipspringer feeding records from plants with either flowers or fruits, at different times of the year.

SPRINGBOK	Flowers	Fruits	GAMKA	Flowers	Fruits
May-Jul	4,1	14,5	Apr	53,0	6,8
Aug-Sep	79,8	7,2	Jul-Aug	38,8	18,6
Nov	43,9	14,6	Oct	49,6	40,7
Feb	3,2	20,5	Jan	27,5	10,5

Feeding preferences

Studies on the feeding of African ungulates have usually resulted in long lists of plant species utilised, sometimes with a simple preference index, but seldom with any discussion on possible relationships between the herbivore and the vegetation it feeds on. In the present study the food-plants of klipspringers were subjectively assigned to groups according to such factors as importance in the diet, selection for plant parts and browsing pressure on the plant. The vegetation plots for the habitat analysis yielded percentage cover values for the most important plants in the two main feeding areas at Gamka, the dry rocky slope and the rocky slope - plateau ecotone, and for the more uniform rocky habitat at Springbok, which allowed preference ratings to be calculated for some species of food plants. While these were not used as the only basis for dividing the plants into the five groups, they do serve to confirm the placing of most of the more common species.

The five groups can be separated as follows:-

A. Species that are highly selected for particular plant parts, usually fruits or flowers, but where the vegetative parts are rarely utilised. The plant may be completely stripped of flowers and fruits, but its shape shows little effect of browsing.

B. Plant species that are preferred by the klipspringer, the shoots and at least the young leaves are eaten, and the plant's shape is noticeably affected by herbivore browsing pressure. If the plant is not heavily browsed the feeding records include several of "feeding 3" or else a large number of records from that species for a particular day.

Group B (i) contains plants that are important in the klipspringer's diet, and

Group B (ii) plants that are not very common but do not seem to be neglected.

C. Succulents with thick fleshy leaves or stems as adaptations for storing water. They show varying degrees of utilisation but are succulent even during the dry season, so they are probably selected for moisture content with little regard for their nutritional value or the presence of inhibitory compounds.

D. Plant species that are generally neglected or partially avoided. They are occasionally fed on, but very rarely with records of "feeding 3" and seldom more than one or two records on any one day. Feeding records are often "feeding 1" and the plant's shape is hardly affected by browsing pressure.

E. Plants that are fairly common in the koppies and rocky terrain, but appear to be avoided by klipspringers altogether.

The plants occurring in both study areas can be sorted into these classes quite easily (Tables 27 and 28) although, as with any classification of units showing overlapping characters, several species may on further investigation prove to be placed in the wrong groups. Uncertain species are indicated with question marks in the tables.

The analysis of preference ratings show that the two groups of preferred and common plants, Groups A and B(i) have high values, that few values were obtained for Group B(ii) due to the small percentage of the vegetation made up by these species, and values are less than 0,5 for the neglected species of Group D. By definition Group E has preference ratings of zero and Group C hows variable ratings depending on the abundance of the species and the klipspringers' moisture requirements.

Most of the records of "feeding 3" came from species in Group A and B(i), which attracted much attention from the klipspringers at certain times of the year. Records of "feeding 3" are almost absent from Group D, although the records from Eriocephalus africanus at Springbok were from a plant that had fresh young buds that were just about to flower, and this suggests that plants of this group may be eaten at particular times of the year. Eriocephalus africanus is a striking example of a species that is very common in both study areas but is hardly utilised at all. The total number of records is high, but the preference rating of only 0,4 shows that this is only because of its abundance, and it is generally selected against. In addition, a subjective impression gained during the fieldwork was that only a very small quantity of food was ingested during each bite, which reduces its importance even further.

Predictably the majority of records of "feeding 1" come from species of Group D. The occurrence of several records in Group A seems anomalous but can be explained by the fact that it often needed only one bite to ingest a single flower and, with the number of plants flowering together, the klipspringer

Table 27: Grouping of the most common plants available to klipspringers at Gamka according to the degree of utilisation and possible defence mechanisms. Availability is shown by the percentage of the vegetation cover (% veg) in each habitat type, and utilisation by browsing (see methods), total feeding, "feeding 3's and 1's" (F_3, F_1) and preference rating (Pref. - see text) in "dry rocky slope" (R.SL.) and "plateau edge" (Plat) habitats. The "smell" and "spines" values are on arbitrary 1 - 4 scale.

		smell: spines	Part eaten	Browsing	F_3	F_1	Total feed	% Veg.	Pref. R.SL.	% Veg.	Pref. Plat.
A.	Maytenus oleoides	1.0	F	+(HF)	13		53	6,1	2,3	2,2	2,6
	Aspalathus hirta	1.3	Is?	M(HI)	12		52	3,3	4,6	15,4	0
	Colpoon compressum	1.0	FI	+(HI)	3		18	5,4	1,0		
	Berkheya angustifolia (B?)	1.4	Is	M(HI)	1		14	8,5	0,5	2,2	0
B.i)	Agathosma sp.	3.1	S	M-H	6	1	62	16,4	1,1		
	Phylica purpurea	1.0	SI	M-H	9		33			18,4	2,0
	Metalasia gnaphaloides	1.2	Is	M-H	5	1	25				
	Cineraria sp.	0.0	ISL	H-vH	5		25				
	Chrysanthemoides monilifera	1.0	FS	M-H	7		23			13,2	1,3
	Montinia caryophyllacea	1.0	Stf	H-vH	3		20	3,6	0,4		
	Solanum tomentosum	0.1	SIF	M(HF)	2	1	19	4,2	1,3		
	Muraltia alopecuroides	2.0	SIL	M	1		19				
	Elytropappus gnaphaloides	3.0	S	M	1		13	2,2	2,6		
	Pelargonium spp.	3.0	SI	M-vH	3		10	1,8	1,1		
	Polygala fruticosa	3.0	Is	M-H			9	3,4	0,8		
	Thesium nigromontanum	2.0	StI	H-vH			9				
ii)	Metalasia langebergensis	0.3	Is	+-M	2		7			2,9	2,7
	Dioscorea elephantipus	0.0	SL	+-M			6	1,7	1,1		
	Dodonaea viscosa	4.0	Sf?	+-M			7			3,7	1,5
	Muraltia ericaefolia (D?)	2.4	SI	M			5	2,3	0,4	1,3	1,7
	Cliffortia ramosissima	2.0	S	+-M			4	2	0	5,9	0,8
	Euphorbia sp.	2.0	SL	vH			1				
	Manochlamys albicans		FS	H			2				
	Relhania squarrosa		S	M-H			1				
	Asparagus capensis	1.3	SL	+			8	2,3	1,0		
	Clutia alaternoides	2.0	SL								
C.	Carpobrotus	0.0	L	M-H							
D.	Eriocephalus africanus	3.0	Si	+		2	25	13,2	0,4	14,7	0,2
	Diospyros dichlorophylla	1.0	Fs	+			8	8,0	0,3		
	Hermannia sp.	1.0	SI	+			8	4,9	0,4	3,5	0
	Cliffortia pulchella	2.0	SL	+			5				
	Felicia filifolia	3.0	Si?	+			3	5,0	0,2		
	Elytropappus adpressus	3.0	S	+			2				
	Rhus tomentosa	3.0	S	+			2	0,7	0,1		
	Rhus lucida	3.0	Fs?	+			1	3,0	0,1		
	Pentzia spp.	3.0	S	+			1	2,7	0	2,2	0,4
	Leucadendron salignum	1.0	S	+		1	1				
E.	Erica spp.	3.0									
	Protea arborea	1.0									
	Crassula spp.										

I = Inflorescence or flower, F = Fruit, S = Young shoots, L = Leaves, St = Stems.

Table 28: Grouping of the most common plants available to klipspringers at Springbok according to the degree of utilisation and possible defence mechanisms. Availability is shown by the percentage of the vegetation cover (% veg), and utilisation by browsing (see methods), total feeding, "feeding 3's and 1's" (F_3, F_1) and preference ratings (Pref. - see text).

		Part eaten	Browsing	F_3	F_1	Total feed	% Veg.	Pref.
A.	Arctotis revoluta	I	M(HI)			18	2,0	1,5
	Ruschia/Leipoldtia spp.	Ifs	+(MI)	2	2	23	12,2	0,3
	Moquiniella rubra	Fs	+(HF)	3		6		
	Rhus undulata	FIs	+(HF)	5	2	32	7,0	0,8
	Drosanthemum albens	Is	+(MI)	1		9	2,7	0,6
B. i)	Zygophyllum spp.	SLI	M-H	20		65	7,3	2,0
	Galenia fruticosa	SLi	(v)H	9		58	6,4	1,5
	Indigofera spinescens	FS	M-H	14		47	4,7	1,7
	Tetragonia spp.	SLf	vH	1		38	1,3	4,8
	Osteospermum spp.	IS	vH	4		27	1,8	2,5
	Asparagus aspergillus	L	H	9		23		
	Pentzia incana (D?)	SI	+-M	1	1	21	6,1	0,6
	Pelargonium dasyphyllum	S	vH	3		20		
	Diospyros ramulosa	FS	H	4		15	0,7	3,8
	Cineraria canescens	LI	vH	2		12		
	Dodonaea viscosa (D?)	Lf?	+-M	7		16		
ii)	Amoebophyllum angustum	SF	H			5	1,4	0,6
	Pelargonium grandicalcaratum	S	M	1		5		
	Manochlamys albicans	Lf?	vH			1		
	Nenax dregei	S	H			4	0,6	1,2
	Lotononis longiflora	SL	H	2		5		
	Lycium oxycarpum	S	H			3		
	Montinia caryophyllacea	Fst	M-H	1		3		
	Pharnaceum spp.	SI	M-H		1	5		
	Thesium lineatum	Sst	M-H		1	5		
	Veltheimia capensis	L	H	1		4		
	Hebenstreitia crassifolia	SI	+-M			2		
	Albuca altissima	Il	H			2		
	Solanum burchellii	SF	M			1		
	Didelta spinosa (D?)	Is?	M(I)			1		
	Maytenus oleoides							
	Boscia foetida							
C.	Euphorbia mauritanica	St I	H	9	-	40	-	-
	E. decussata	St IF	H	5	-	23	1,4	2,7
	Ruschia/Leipoldtia spp.	Ifs	+-M	2	2	23	12,2	0,3
	Mesembryanthemum karroense	Fl	+	-	1	2	-	-
	Crassula brevifolia	SL	M	-	-	5	-	-
	Cheiridopsis sp.							
D.	Eriocephalus africanus	S	+	2?	3	15	6,7	0,4
	Antizoma miersiana	Sl?	+	-	-	4	-	-
	Asparagus asparagoides	L	+	-	1	2	-	-
	Berkheya ferox	SI?	+	-	1	1	-	-
	Eriocephalus ericoides	SL	+	-	2	6	5,3	0,2
	Polymita albiflora	Il	+	-	4	5	5,6	0,1
	Hermannia spp.	SI	+(M)	-	1	4	8,3	0,1
	Othonna spp.	S	+	-	-	3	2,8	0,2
	Galenia africana	Is?	+	-	-	3	2,2	0,2
	Pteronia spp.	S	+	-	-	3	3,3	0,2
	Asparagus capensis	L	+	-	-	1	-	-
E.	Salvia dentata	-	-	-	-	-	2,7	0
	Mentha longifolia	-	-	-	-	-	1,4	0
	Euryops spp. (C?)	-	-	-	-	-	1,2	0
	Ballota africana	-	-	-	-	-	-	-
	Stachys flavescens	-	-	-	-	-	-	-
	Melianthus pectinatus	-	-	-	-	-	-	-

I = Inflorescence or flower, F = Fruit, S = Young shoots, L = Leaves, St = Stems.

often moved to another plant nearby.

The presence of a strong smell in the leaves of klipspringer food-plants at Gamka shows no apparent correlation with their preference grouping, with high and low ratings being spread throughout the groups. Spines are not common in many of the plants, although it is probably significant that two of the four Group A species are very spiny and in both of them only the inflorescences and very young shoots were eaten.

Unusual feeding behaviour

On several occasions during the study unusual feeding behaviour of both wild and tame klipspringers was observed.

Osteophagia was recorded twice at Gamka where the study klipspringers spent some time chewing on old bones lying around in the veld. At Gamka geophagia was also recorded when a klipspringer nibbled some of the soil from a termite heap and on another occasion a lump of partly digested grassy material was eaten, which looked as if it could have come from the stomach of a hare caught by a predator.

At Springbok the tame young klipspringer ram was seen to nibble at just about every plant available in the garden, as well as old rags, dog food, paper, and other objects completely foreign to his natural diet. Once, when he was only a few months old, he became very ill and almost died, probably due to his habit of chewing on some poisonous crassulas growing on the rockery. At the age of 14 months he died after being very sick for several days with convulsions and vomiting, and a possible reason for his death is that he had eaten a considerable amount of material from an exotic Aptenia cordifolia plant in the garden. This species comes from Natal and is known to contain quantities of the poison mesembrine (Herre 1971).

Micro-nutrients

Table 29 shows the results of the analysis of the livers of the shot klipspringers. Although little is known of the trace element needs of wild animals, experience from sheep suggests that these values show that the klipspringers were not suffering from deficiencies in iron, zinc or manganese while the levels of copper are bordering on a deficiency (Zumpt* pers. comm.). Sheep with levels lower than 50 p.p.m. tend to show effects of copper

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deficiencies, so these levels in the klipspringers are probably just adequate.

Table 29: Concentrations of some micro-nutrients in the livers of shot klipspringers

Area	No.	Concentration (p.p.m. dry basis)			
		Cu	Fe	Zn	Mn
Springbok	♀ K1	53	406	112	10
"	♂ K2	69	357	118	11
Gamka	♀ K3	57	307	110	11
"	♂ K4	157	253	107	12
"	♀ K5	383	261	137	15

DISCUSSION

Jarman's (1974) synthesis of ideas on the social organisation of antelope in relation to their ecology provides a good basis for explaining the klipspringer's feeding habits. The main factors involved are the species' small body size and the relatively high energy requirements associated with this.

Because of the Brody-Kleiber relationship between body mass and metabolic rate in mammals, the klipspringer's rate can be expected to be higher than that of larger antelope. This means that its energy requirements per unit body mass are higher. To compensate for this there are two alternatives to follow. Either the klipspringer must increase the amount of food ingested, or else it must increase the food quality. Since roughage feeders need large stomach to allow slow breakdown of coarse food particles (Hofmann 1968, Hofmann and Stewart 1972), the small body size of klipspringers obliges them to follow the second alternative to increase their energy intake. Thus they select fruits, flowers and growing shoots, which are low in fibrous structural material and high in nutrients and moisture content.

Jarman points out that grasses are on average far more homogeneous in food value than browse plants, which range from the extremely nutritious growing tips to the highly lignified and inedible woody stems. There is not necessarily much difference in food value between the choice growing shoots of grasses and those of browse plants, but the growing season for browse plants tends to last for a greater proportion of the year than for grasses.

Since smaller ungulates are obliged to select only nutritious plant parts, it is better to select plants that have high energy shoots for a greater portion of the year, even if these shoots are relatively less abundant. While the results of the present study show that klipspringers are almost entirely browsers, as was found by Wilson and Child (1965) in Rhodesia, the Dunbars' (1974) work in Ethiopia indicates that they are able to utilise a greater proportion of grasses under certain conditions.

The advantage in not being too selective for plant species is that a wider range of plants fed on gives a greater chance of finding suitable nutritious plant parts at any particular time of the year, due to inter= specific variation in shooting and flowering times.

Factors which aid klipspringers in their highly selective browsing are a small mouth size in relation to the selected plant parts, the higher propor= tion of the daily intake that the selected plant part makes up, and the species' sedentary nature which enhances familiarity with its food resource.

As outlined by Jarman (1974) the small antelope have narrow muzzles which make it easier to select small plant parts than it is for larger antelope. Although their muzzles are the same width relative to their body size, the larger antelope find that the plant parts are proportionately much smaller, so that selective browsers such as kudu have to use their prehensile lips and tongues to pull off only the nutritious parts.

Since small antelope require a lesser total amount of food per day than large antelope, the rate of ingestion of plant material need not be as great as for large antelope. Because of this klipspringers can spend more time and effort searching out an individual fruit, flower or shoot, as this will make up a larger proportion of their daily food intake.

The social organisation of smaller antelope, where they occur singly or in pairs in fixed territories, allows them to become familiar with the distribu= tion and phenology of the principle food plants, which reduces the amount of time spent searching for plants in the right growth stage.

DEFENCE MECHANISMS

Plant growth in extreme habitats

The mountainous and rocky areas that klipspringers prefer are rather extreme habitats where environmental conditions impose limitations on the amount of new growth the vegetation can produce each year. This low primary production can be attributed to limitations in either water or nutrients or a combination of the two. In the arid conditions of the Springbok region the most apparent limiting factor is water, while at Gamka and in most of the fynbos the scarcity of nutrients, especially phosphorous, is severely limiting, sometimes being compounded with low water availability.

Janzen (1974) discusses the effect of deficient nutrients on the vegetation in tropical blackwater - white sand areas where the conditions are very similar to the mountainous areas of the southern and western Cape. His ideas on the relationship between herbivores and the vegetation seem to be applicable to the fynbos, as well as to other areas of low primary production, such as the semi-desert at Springbok.

Janzen's thesis is that, owing to the scarcity of nutrients in the soil, the roots can only absorb them at a very slow rate, so the uptake by the structural and growing parts of the plant is restricted. Thus the plant cannot tolerate a large annual loss of its parts to browsing as it does not have the reserves of nutrients to replace them. For this reason it is worthwhile for the plant to have a considerable portion of its energy channelled into discouraging feeding by herbivores. This can be either by an increase in the structural part of the plant to allow the growing shoots to be raised above the reach of ground-dwelling herbivores (about 2 m for most antelope), or else by making these parts inedible. The first alternative, which is applicable to the tropical rain forest, would not work in the more exposed mountain areas because of the increased risk of loss to wind damage. Therefore many fynbos and semi-desert plants seem to have energy invested in defensive mechanisms such as spines, that make feeding unpleasant, or secondary compounds, that may be distasteful or inhibit the basic metabolic or reproductive processes of herbivores when eaten in large quantities.

The principle is not necessarily that utilisation is prevented altogether but more that it is reduced to a level that can be tolerated by the plant. In many cases the amount of extra energy needed to cut out feeding altogether, rather than to allow a low level of utilisation, may be greater than the energy saved, although this depends on just how costly that plant's compounds are to manufacture. This is particularly true of plants that rely on oils and resins to reduce herbivory, since it would be difficult to accumulate these compounds in the growing tips, as the cells around the apical meristems are extremely small and largely undifferentiated. It would be much easier to allow the oils and resins to be slowly deposited as the leaves mature, especially if the differentiation process results in the formation of special oil and resin secreting cells, known as idioblasts and laticifers. Furthermore, the presence of secondary compounds in the young differentiating cells would probably retard their development. This may explain why some shrubs cannot afford to have inedible shoots, even though these are the parts most selected by the herbivores because of their high protein content.

Examination of the possible ways in which the secondary compounds work sheds some light on the pattern of feeding shown by klipspringers in the two study areas.

Herbivore feeding strategies

In their discussion of the role of plant secondary compounds in mammal feeding strategies Freeland and Janzen (1974) outline the ways in which secondary compounds can inhibit digestion by herbivores, and how the herbivores break them down and modify their feeding to cope with an array of plants all showing varying amounts of different compounds. The most important points are that nearly all plants do contain secondary compounds, that each plant species has its own type or combination of types, and that herbivores can tolerate a small amount of almost any of them. Thus the herbivore regulates its feeding to fulfil its energy and nutrient requirements, but also to keep the accumulated amounts of each of the different compounds below the levels where they become toxic. This means that some plants can be utilised to only a very small extent, while others can make up a considerable proportion of the animal's diet. However it is important to the herbivore that its detoxification mechanisms should allow it to ingest at least a small amount of any plant, and thus allow sampling behaviour.

Freeland and Janzen propose a system where herbivores feed largely on a selected number of familiar foods, but must keep sampling small amounts of all foods available to enable them to cope with seasonal changes in food availability, as well as onger term changes in the vegetation of the area. In addition, the detoxification of some compounds requires higher concentrations of particular nutrients, so the herbivore may sample unusual plants in search of the required nutrients, even if those species are of little food value or have other inhibitory substances which can also be tolerated only up to a certain level.

The authors suggest that the sampling process entails taking a small mouthful of the new or unfamiliar plant and waiting to see if it has any harmful effect on its body, implying that the individual's ability to associate ingestion of a particular food with a later physiological upset is well-developed.

Smells and taste also play a part in food selection, but actual ingestion must remain the most important testing method, or else over the years the plants would have evolved to lose the harmful secondary compounds in the leaves and thereby save energy, or even to mimic the smells of other plants containing powerful defensive compounds. Furthermore, it would be easier for the plant to develop the smells, which need very low concentrations, in the young growing parts than to supply the differentiating cells with the high concentrations of compounds necessary to make them inhibitory. By testing properly the herbivore would find that the young shoots are quite edible, even though they may smell the same as the inedible mature leaves.

Defence mechanisms and the feeding of klipspringers

Unfortunately the detailed chemical analyses that would be necessary to determine the occurrence of secondary compounds in the different plants of the study areas, and the feeding trials with tame klipspringers that would prove that they react to the compounds, were beyond the scope of the present study. However, some of the results of the klipspringer feeding study assume more significance if they are interpreted in the light of the above hypotheses, and several observations support the application of these theories to the plant-herbivore relationships of the study area.

The species of Group A plants shown in Tables 27 and 28, which have plant parts that are highly selected by klipspringers, probably have well-developed defensive mechanisms in their vegetative parts. While the spines of *Berkheya angustifolia* and *Aspalathus hirta* at Gamka are obvious deterrents to heavy utilisation of the leaves, all of the other plants have no visible defensive mechanisms, so we must conclude that secondary compounds are important. Allowing herbivores to feed on mature fruits is of obvious benefit for seed dispersal, and must represent a positive selection pressure in the evolution of species such as *Maytenus oleoides*, *Rhus undulata* and *Moquiniella rubra*. However, there can be little advantage in allowing heavy browsing of flowers which have not yet set seed, and this probably represents a major loss of protein and nutrients to the plant. It would be difficult for the plant to build up the required concentrations of secondary compounds in the parts that are still differentiating, so they have to rely on other mechanisms to reduce loss to herbivores. The presence of large numbers of flowers on all plants of Aspalathus hirta in October at Gamka, as well as the general blooming of flowers in spring at Springbok suggests that "swamping" (see Janzen 1974) is important, even though the winter rainfall and the onset of warmer conditions in spring are likely to be the primary factors affecting flowering times.

Group B plants may have defensive compounds, but not in sufficient quantities to prevent klipspringers from utilising at least the shoots and young leaves. They have probably evolved to make do with very low concentrations of nutrients, so that they can tolerate a fair amount of loss to browsers and do not need to invest a large amount of energy in defensive mechanisms. In other words their physiological adaptation to environmental conditions has lowered the level at which it becomes uneconomical to invest energy in defensive mechanisms that prevent further browsing. That plants of this group do channel at least some energy into defensive mechanisms is illustrated by the spiny leaves of Muraltia ericaefolia and the Metalasia species at Gamka. However plants such as these may actually show a closer affinity to group A species, but are not considered as highly selected foods in this study due to their low frequency in the feeding areas sampled. The figures for the number of plants in each klipspringer stomach sampled and the minimum number of plants fed on on any one day support the idea that, even though the plants fed on may be preferred foods, the klipspringer is unable to feed entirely on them, possibly due to the presence of secondary compounds.

Group C plants are those that are very succulent and are probably fed on mainly for their water content. In the browsing of herbivores it is difficult to differentiate between selection of plant parts for succulence and selection for nutrient value, since the two are usually closely linked. In young leaves there is little structural material, which means that both nutrient and moisture content are high, but in mature leaves the structural component increases at the expense of the moisture and nutrients. However, some plants, particularly members of the Mesembryanthemaceae, have developed the leaves as organs of water storage, which means that their water content is very high. Thus, in the dry season when the klipspringers are under severe water stress, they eat mature leaves of these plants, which are the only succulent food available. But in the "wet" season, the small number of records for feeding on these Group C plants (Tables 27 and 28) suggests that they are largely ignored in favour of the more nutritious young shoots of other plants. This is in spite of the fact that their moisture contents are higher than many of the preferred foods, as shown by some of the results of Dieckmann's (in prep.) analysis of gemsbok food-plants at Springbok (Table 30).

The presence of secondary compounds in Group C plants is open to speculation, but most of them have an unpleasant taste, with bitter white latex being characteristic of Euphorbias and high concentrations of oxalic acid being found in most of the Mesembryanthemaceae (Naude* pers. comm.). The fact that the klipspringers at Springbok ate large quantities of Euphorbia mauritanica, which is known to be poisonous to sheep (Terblanche, Adelaar and van Straten 1966), suggests that these wild ungulates may have evolved special mechanisms to detoxify high dosages of these compounds. This ability would be of considerable selective advantage to herbivores that are deprived of drinking water for most of the year.

Group E plants, which are avoided altogether, must have the highest level of inhibitory compounds. They may have been sampled only once or twice by the klipspringers, but would have had such an unpleasant taste or adverse effect on the digestion that they would be remembered and seldom touched again. These are probably the plants that find it economical to develop such high concentrations of secondary compounds that they cut out browsing altogether. In some cases very strong and pungent smells indicate that the plants are inedible, such as the members of the family Lamiaceae at Springbok, but other plants, such as the proteas, have little smell. Thus some of the plants must have inhibitory compounds that are odourless, but are distateful or affect the digestion and other physiological processes after they have been ingested.

Group D plants probably contain high levels of inhibitory compounds, since only small quantities of plant parts can be tolerated by klipspringers. Even though the plants may be common and make up a considerable total number of feeding records, for example Eriocephalus africanus, they never form very much of the animal's daily intake. Some parts at particular growth stages may be acceptable food, but generally the presence of feeding records is probably due to sampling behaviour, when the klipspringer is looking for particular nutrients.

Possible nutrient deficiencies

The observations of osteophagia and geophagia at Gamka support the theory that klipspringers may be suffering from nutrient deficiencies, and that these

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Table 30: Moisture content of some plant species fed on by both klipspringers and gemsbok at Springbok (Selected from Dieckmann, in prep.).

Plant species	Moisture content (%)			
	Feb-Apr	May-Jul	Aug-Oct	Nov-Jan
"Group C" plants				
Euphorbia decussata	-	73	65	68
E. mauritanica	-	80	81	-
Leipoldtia pauciflora	-	79	75	67
Mesembryanthemum karroense	96	89	-	96
Ruschia brevibracteata	-	79	73	68
"Group B" plants				
Zygophyllum meyeri	61	95	83	60
Tetragonia spp.	-	74	72	54
Pelargonium dasyphyllum	-	66	63	-
Nenax dregei	45	60	52	43
Osteospermum sinuatum	49	73	76	53

may cause unusual feeding behaviour. It has been known for more than 50 years that large areas of the western Cape have very low levels of phosphorous in the vegetation, and that this has a marked effect on the breeding of cattle (Du Toit and Bisschop 1929). In addition, the soils of the western Cape have been found to contain low levels of copper and cobalt (Van der Merwe and Perold 1967). Joubert, Stindt and Perold (1969) showed that in the Mountain Rhenosterbosveld and False Macchia vegetation of the southern Cape levels of phosphorous and calcium are universially low, with manganese and copper low in some areas.

However, it is known that browsers such as sheep are affected by these deficiencies far less than cattle (Zumpt pers. comm.), and it is likely that wild ungulates that browse are affected less than grazers. The levels of copper in the livers of the shot klipspringers (Table 29) suggest that they are able to assimilate just enough from the vegetation, in spite of the very low concentrations in the plants, but may suffer slight deficiencies in certain areas or at particular times of the year.

The ability to assimilate micro-nutrients may vary with age, since the first klipspringer shot at Gamka was a young female (K3) and she had considerably less copper in her liver than the mature male (K4), and much less that K5, which was an old female.

Thus, although occasional observations of osteophagia and geophagia are not conclusive evidence of deficiencies, the length of time spent chewing on the bones suggests that the klipspringers were aware that something was lacking in their diet and were testing unusual foods to try to satisfy this need.

Development of feeding habits

As Leuthold (1977) points out there is a lot of information in the literature on what plant species and plant parts many ungulates feed on, but there has been almost no research on the ontogeny of food selection patterns. While no direct data were gathered in the present study, some observations on wild and tame klipspringers can be construed as circumstantial evidence for a basic pattern. In spite of the lack of useable data it is important to consider the possible mechanisms, since adaptation to a change in vegetation type is a fundamental factor in antelope translocations.

Leuthold (1977) suggests that from birth ungulates know instinctively which type of food to select, and this is then modified by learning. The basic instinct consists of an innate "screening" mechanism based on olfaction and taste. He cites examples of tame animals living with older animals of different species, which learned from their foster mother to eat plants that were not normally eaten in the wild by their own species, but were eaten by wild animals of the foster mother's species.

On several occasions during the November field trip at Springbok, the main study group of a male, female and a young male of about three months was watched as they fed. The juvenile was not yet weaned, but seemed to take considerable interest in the plant food available. He would stand right next to the female while she was feeding busily, and seemed to be investigating the plants she had fed on, often moving to exactly the same spot. He would "mouth" and sniff at the flowers and shoots, with only the occasional jerk of the head to show that he had actually broken off a piece to eat. He could not have been very hungry, since on at least two occasions he had suckled from his mother shortly before. Most of the time he stayed very close to his mother, although sometimes he would wander off on his own for a short way and nibble at other bushes.

These observations suggest that the young klipspringer learns what food to eat by following its mother around, and becoming familiar with the smell and taste of the best food-plants in this way. The learning process must be a gradual one started long before the juvenile has to rely on plant food for most of its energy requirements. This idea is supported by observations of unusual feeding behaviour shown by the tame young male klipspringer at Springbok. His rather disorganised sampling of potential food items suggests that he was born with some basic instinct about what to eat - he was particularly keen on the flowers of all sorts of plants - but further learning had to be by a process of trial and error, since he did not have his mother's example to follow.

One can hypothesize that the selection for the instinctive versus the learning components in the evolution of a species' feeding behaviour must depend on the variability of the vegetation and the need to adapt to changing food availability. The significance of this in the management, and particularly translocation, of ungulate species is that species that range widely over a number of different habitat types under natural conditions are more likely to adapt to a new area than species, such as klipspringer, which are highly specialised for a particular habitat. This is especially true where the habitat is relatively stable, such as in mountain catchment areas. Although klip=springers show considerable variability in feeding habits throughout their range, the geographical isolation has ensured a gradual evolution of these feeding habits in each particular area, so the klipspringer cannot be regarded as a highly adaptable species. This means that special care should be taken to avoid translocating klipspringers into very different habitats.

CHAPTER 9 : COMPETITION

In any ecosystem where more than one species of herbivore occurs one can expect a certain amount of resource partitioning to reduce competition between them. Although klipspringers are more or less restricted to rocky terrain they are not the only large mammalian herbivore to be found in this terrain, so some idea of the amount of overlap with the others is essential for management of the populations.

At Springbok competition for food between klipspringers and other antelope is probably limited, since the gemsbok and springbok spend most of their time in the flats or plateau areas where klipspringers seldom venture. Hartmann's zebras Equus zebra hartmannae spend more of their time in rocky areas, but are almost entirely grazers and occur in very low numbers (five at the last count). Grey duikers may overlap with klipspringers to a certain extent, but they are also very rare in the reserve (less than 10 in total). However, one of the most striking aspects of the landscape around Springbok is the large number of dassies Procavia capensis on all rocky areas. Since dassies are at least partly browsers (Sale 1965, Smithers 1971, Lensing 1978), a certain amount of food partitioning can be expected. The other herbivore that occurs in large numbers in rocky areas at Springbok is the red rock hare Pronolagus rupestris, but this species seems to be largely a grazer (Smithers 1971, own records) and its nocturnal habits make it very hard to study.

In the mountainous terrain at Gamka the situation is more complex, since the presence of a rocky substrate is of varying importance in the different habitat types, which the antelope use to different extents, and some degree of overlap can be expected. The common antelope are vaalribbok, Cape grysbok and steenbok. Occasionally duikers have been seen in the bottom of the kloof, but so rarely that they can be disregarded. About 10 Cape Mountain zebra Equus zebra zebra occur in the reserve, but this species is principally a grazer, so they are unlikely to compete with klipspringers.

Dassies are not as numerous as at Springbok, but are still common and their restriction to steep rocky terrain assures a certain amount of overlap.

Thus to find how competition is avoided it was necessary to work primarily on the relationships between klipspringers and dassies at Springbok, and klipspringers and the three small antelope species, as well as dassies, at Gamka.

METHODS

For the assessment of competition between two or more species of animals the most important aspects to study are spatial overlap in ranges, relative biomasses, and overlap in feeding. Within the scope of the present project the habitat preferences of the antelope species and the spatial overlap and feeding competition with the dassie were investigated.

Plotting antelope records at Gamka

To get some idea of the habitat preferences of the small antelope at Gamka a small portion of the reserve around the main klipspringer study site, that included all the habitat types mentioned in Chapter 4, was selected for study. Fig. 8 shows the distribution of these habitat types and the presence of the road from which most observations were made. Regular and systematic sampling was not done, but during all movements within the area, whether for klipspringer observation, checking the weather station, vegetation sampling, or shooting dassies, the exact locality of every sighting of small antelope was marked on an enlarged 1 : 3800 aerial photograph. The group size, sex and age structure of the animals was noted wherever possible, although the long range of observation often made this difficult.

All dassie colonies were plotted in the same way, although each colony or group of dassies was plotted only once on a particular spot to avoid repetition of plots of regularly seen groups. This method gives no indication of the numbers of dassies sighted in each locality, but it does show their habitat preferences clearly.

Habitat preference values were calculated by dividing the percentage of sightings of that species in that habitat type by the percentage of the study area made up by that habitat. Thus values greater than one show preference for that habitat type, while values less than one show avoidance.

Since the terrain was not covered systematically, seasonal trends in numbers and stocking rates could not be determined. However, to give some idea of the relative numbers of the different antelope species, a beat was carried out in February 1979 with seven people spaced approximately 100 m apart. Only the southern portion of the study area was covered. The approximate position and sex of each antelope seen was plotted, with careful checking between observers to obviate possible overlap in sightings. Due to the ruggedness of the terrain and the confusion as some of the antelope ran from the plateau down into the valleys, the sweep was not carried on to the steep rocky slopes of Tierkloof and Klippe se Kloof. Thus the numbers of antelope seen give an idea of the relationship one can expect between the different species on the plateau and upper drainage basin in summer.

This method was considered too coarse to give a reliable estimate of the number of dassies to be found in the area. Therefore dassie sightings were merely plotted on the aerial photographs for analysis of habitat preferences.

Dassie biomass and dung sites at Springbok

With the extremely high densities of dassies at Springbok and the large rounded boulders which made them conspicuous when sunning themselves in early morning, it was possible to estimate the numbers present in the study area. Thus the approximate biomasses of klipspringers and dassies in the main klipspringer study group's territory were calculated to give an idea of the degree of competition that can be experienced under extreme conditions.

On one day, 24 February 1978, all the dassies that could be seen between 09h00 and 10h00 were counted and plotted on an aerial photograph. The whole territory was covered by counting from different vantage points. The ratio of juveniles to adults was estimated to be approximately 1 : 1, and the shot sample showed that the average body mass for adults was about 2,5 kg ($\bar{x}$ = 2,422 kg; S.D. ± 0,484; n = 18) while the juveniles weighted approximately 0,75 kg ($\bar{x}$ = 0,743 kg; S.D. ± 0,093; n = 7). From this the total biomass of dassies could be determined.

To study spatial relationships between the dung sites of dassies and klipspringers the whole klipspringer territory was searched on two days in February 1978 and the location of all middens was plotted on an aerial photograph of the area.

Dassie stomach analysis

Since both dassies and klipspringers seemed to be largely restricted to rocky slopes and both are known to be mainly browsers, it was regarded as important to gather some information on the degree of overlap between the food-plants utilised by the two species.

The analysis of feeding habits by direct observation is very difficult with a herbivore as small as the dassie. Therefore a sample was shot for analysis of stomach contents. Twenty-two stomachs from Gamka and fourteen from Springbok were used. They were collected during the middle of the day after the main morning feeding spell, at all times of the year. Most dassies were collected in areas adjacent to the main klipspringer study territories, since hunting within these territories might have disturbed the klipspringers.

Soon after being shot the dassies were measured and weighed and the stomach contents were fixed in 10% formalin. Later in the laboratory the contents were sieved and washed, and all recognisable plant parts were sorted and identified.

A reference collection of small pieces of all plants found around the dassie colonies was made, with a dry pressed specimen and a wet specimen in 10% formalin for each plant taxon. Plant parts were identified on macroscopic features by comparison with these specimens. In some cases identification was only to the level of genus as it was difficult, and indeed relatively unimportant, to distinguish between closely related species. No attempt was made to differentiate between grasses, as these are hardly ever utilised by klipspringers in the study areas.

Once all the recognisable plant parts in a stomach had been identified a subjective estimate of abundance was made on the 1 - 5 scale described in Chapter 8 for klipspringer stomach analysis. As with klipspringer stomachs a large proportion of the contents was too finely chewed to be recognisable, so the percentage values are very approximate. The results were analysed according to abundance class totals and frequency of occurrence in the stomachs to give a clear picture of the importance of the different plants in the diet of dassies.

Dung analysis

To assess the relative efficiencies of the klipspringer and dassie digestive tracts in breaking down food to a small particle size, pellets of both species were analysed. Several samples of 7 - 14 g of pellets were collected from each area, crushed and dried in an oven. After weighing they were shaken through a sieve of mesh size 1,2 mm, and the residue was weighed again.

RESULTS AND DISCUSSION

OVERLAP WITH OTHER ANTELOPE

Table 31 gives the densities of vaalribbok, grysbok, steenbok and klip=springers determined for the plateau and upper drainage basin areas at Gamka. Although the density of klipspringers in this region is low, it is much higher on the rocky slopes (Chapter 3). These figures show that the concentration of all small antelope in the mountainous area at Gamka is relatively high. Therefore there must be some competition for food resources where the ranges of the different species overlap.

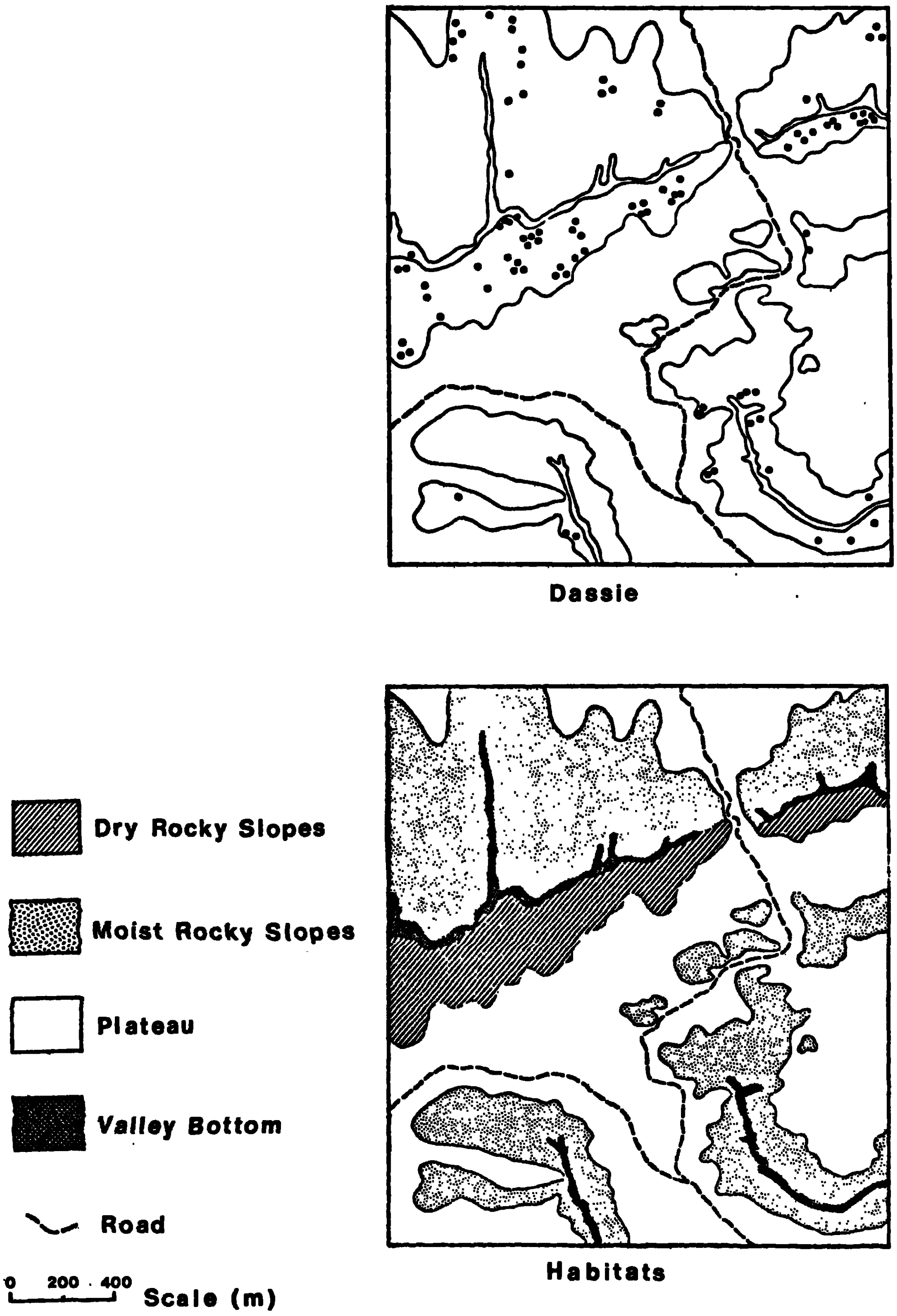
Table 31 : Densities of small antelope on the plateau and moist rocky slope habitats at Gamka, from a count on 5 February 1979.

	Vaalribbok	Grysbok	Steenbok	Klipspringer
Minimum total counted	16	21	6	2
Total area covered	205 ha	205 ha	205 ha	205 ha
.˙. densities	0,08/ha = 8/km²	0,10/ha = 10/km²	0,03/ha = 3/km²	0,01/ha = 1/km²

Figure 56 indicates that there is a certain amount of spatial overlap between klipspringers and the other species of small antelope at Gamka. However, an analysis of habitat preferences according to frequency and percentage of sightings in the different habitats (Table 32) shows that klipspringers and dassies strongly prefer the dry rocky slopes while the other three antelope show low preferences for this habitat and higher ratings for the plateau region which klipspringers and dassies tend to avoid. Thus most of the overlap between the species is in the moist rocky slope and valley bottom habitats.

Steenbok were the least often seen and never occurred on areas of more than about 15° slope, so that competition with klipspringers must be minimal.

Vaalribbok were far more numerous and several groups were seen on the moist slopes. However, these were mostly groups of up to five young bachelor males which, contrary to what Esser (1973) found, seemed to remain associated for some time. The relegation of non-breeding animals to these habitats suggests that the steep rocky slopes are not prime vaalribbok habitat.



Dassie

Habitats

Grysbok

Steenbok

Klipspringer

Vaalribbok

Fig. 56: Sightings of small ungulates in the different habitats of the main study area at Gamka.

Table 32: Habitat preference of small ungulates from sightings in the different habitat types at Gamka, showing number and percentage in that habitat type, and preference rating (PR = $\frac{\%\text{ of sightings}}{\%\text{ of total area}}$).

		Dry rocky slopes	Moist rocky slopes	Plateau	Valley bottom	Total sightings
% of study area		8,9	40,5	47,6	2,7	
Vaalribbok	No.	2	17	51	2	72
	%	2,8	23,6	70,8	2,8	
	PR	0,31	0,58	1,49	1,03	
Grysbok	No.	1	21	50	8	80
	%	1,3	26,3	62,5	10,0	
	PR	0,15	0,65	1,31	3,70	
Steenbok	No.	0	3	26	0	29
	%	0	10,3	89,7	0	
	PR	0	0,25	1,88	0	
Klipspringer	No.	39	25	9	2	75
	%	52,0	33,3	12,0	2,7	
	PR	5,84	0,82	0,25	1,00	
Dassie	No.	52	40	0	2	94
	%	55,3	42,5	0	2,1	
	PR	6,21	1,05	0	0,78	

Grysbok showed a lower proportion of records from the plateau region, with a number of sightings on the moist slopes and a high preference for the valley bottom habitat, which occupies only a small percentage of the total area.

The best way to explain these habitat preferences and to get some idea of how the different species avoid competition is to analyse the characteristics of the habitats they appear to be selecting for, and how they are physiologically and behaviourally adapted to these conditions. The most important characteristics are:-

i) Cover, which plays a part in anti-predation strategies.
ii) Shelter, and its role in temperature regulation.
iii) Substrate, and the antelope's ability to run on different surfaces.
iv) Vegetation species composition, and the selection of food plants.

Cover

When frightened by a potential predator the four species of mountain antelope show very different evasive responses.

The largely nocturnal grysbok spends most of the day lying up in a cool shady spot from which it "explodes" when a predator is very close, and zig-zags off to lose itself amongst the bushes. It is almost entirely solitary and does not utter any alarm call.

The steenbok occurs more often in pairs, although the male and female may be widely separated. Their evasive behaviour is similar to that of the grysbok, although the flight distance is greater and they show less tendency to hide, but stand and look at the potential predator from a distance. A single sharp alarm snort is very occasionally heard (Dorst and Dandelot 1970).

The evasive behaviour of vaalribbok is very different from the other two, since it is a larger antelope and occurs in groups of up to eight individuals, which makes it hard to hide from a predator. For this reason these buck are very alert and during the study they often started running when the observer was still far away, sometimes more than 500 m. The loud alarm snort and white patch under the tail, which is lifted when the animal runs, may well be an adaptation to communicate with the predator, rather than just with members of the group (see Chapter 6).

Thus bush cover is an important factor in the habitat preference of grysbok, since they rely almost entirely on concealment to evade predators, but is less important for steenbok. The number of records for grysbok in the valley bottom is probably because of selection for the increased bush cover, as shown by the large proportion of bushes over 1 m in height in this habitat type in Chapter 2. Vaalribbok are similar to klipspringers in that they need good visibility to keep watch for predators. While the klipspringer prefers rocky terrain for this purpose, the greater head height of the vaalribbok enables it to maintain good visibility in plateau grassland or low scrub conditions.

Shelter

Little work has been done on temperature regulation of antelope in mountainous areas. The exceptional tolerance of extremes by klipspringers has been discussed in Chapter 4, but the other species may not show such versatility.

Figure 34 shows that the grysbok and vaalribbok have relatively thick pelages, which must give a degree of insulation against extremes of temperature, but the thickness is considerably less than that of the klipspringer. However, the grysbok is usually found in thick cover where it can utilise the more stable micro-climate under bushes to avoid extremes. In addition, its nocturnal habit means that more heat is generated by activity during the coldest part of the day, and therefore heat loss is not as critical. The vaalribbok may need less insulation due to its greater body mass and the lower surface to mass ratio associated with this.

The steenbok is able to tolerate very hot conditions, as is shown by the climate in its distribution area, which includes semi-desert regions. However, its relatively thin pelage (Fig. 34) is unlikely to give sufficient insulation in very cold conditions. The fact that only one sighting of the total of 29 was during the winter months, and that a well-known group that could usually be found near the fork in the road was never seen in winter, suggests that this species may move down off the colder plateau regions in winter.

Substrate

The uniquely adaptated hoof of klipspringers was discussed in Chapter 4. This is probably one of the primary factors in the avoidance of competion with the other small antelope, since the other species all lack special adaptations for running on rocky substrate. The subjective impression gained during field work was that fleeing grysbok ran awkwardly and cautiously in rocky terrain. Although they will no doubt take to rocky areas under duress they showed little of the fleetness of klipspringers, and never moved to the more rocky outcrop areas as the latter do.

The vaalribbok that were seen on rocky terrain were mostly young bachelor males, which managed to move quite rapidly but also did not give an impression of agility as klipspringers do, and seemed to rely more of fleeing when the predator was still far away.

Vegetation species composition

Jarman's (1974) ideas on the feeding of antelope in relation to their body size and social organisation lead one to expect little difference in food selection between the four species of small antelope at Gamka. These solitary or pair bonded species are small-bodied and therefore probably utilise high energy food, and can be expected to be highly selective for plant parts and less selective for plant species. The vaalribbok which occurs in small family groups (Jarman's group B) have slightly larger bodies and should be a bit more adaptable in their feeding.

The early literature on the feeding of these small antelope is rather confused, with various authors describing them as anything from entirely grazers to entirely browsers. However, the few more detailed studies that have been carried out recently suggest that they are all predominantly browsers, but may eat some grass at certain times of the year.

Manson (1974) analysed 23 grysbok stomachs from Darling and Stellenbosch and found that grasses made up less than 2% of the contents in 22 of them. However, one stomach contained more than 80% grass.

Manson also analysed four steenbok stomachs from Darling and found 17% grass, which supports Hofmann and Stewart's (1972) classification based on their stomach structure that steenbok are intermediate feeders preferring forbs and shrub foliage. However, Huntley (1972) found that a semi-captive steenbok utilised very little grass even when starving.

Esser (1973) does not give a quantitative analysis of vaalribbok feeding records, but he refutes Dorst and Dandelot's (1970) classification of them as "entirely grazers", showing that only seven species of grasses were grazed out of a total of about seventy food plants, and these only during the summer months. More recently Ferreira's (in prep.) analysis of vaalribbok stomachs showed that, even though this species fed almost entirely in "grassland", shrubs and forbs made up more than 90% of the food.

In Chapter 8, it was mentioned that the klipspringers in the present study hardly utilised grass at all, as was found by Wilson and Child (1965) in Zambia, but Dunbar's (1978) study showed 17% grass in the diet.

Thus it is unlikely that the ratio of grasses to dicotyledonous plants in the vegetation is a major factor in habitat selection of small antelope at Gamka. Whether they reduce competition by selecting different species of food-plants is not clear, although the klipspringer seems to eat most of the dicotyledonous food available that falls within its nutritional requirements. Since the klipspringer, steenbok and grysbok are roughly the same weight (Table 33), their metabolic rates, and therefore energy requirements, must be similar. The vaalribbok is about 10 kg heavier, which means that its energy requirements are likely to be slightly lower, but the effect of this on food selection should be minimal.

The greater head height of the vaalribbok is unlikely to be important in stratification of feeding on plants, since only a very small proportion of the shrub layer is higher than one metre, as shown by the values for class 3 in Appendix C. This means that most parts of all plants are within reach of all the antelope species.

Thus it seems that selection for substrate and cover are the most important factors in the reduction of competition between the small antelope at Gamka, and that these ensure a degree of spatial separation of feeding areas. Because of their preference for rocky substrate and good visibility, klipspringers feed mostly in or near rocky areas, while the other small antelope select more level plateau areas, with steenbok and especially grysbok preferring denser vegetation cover for predator evasion.

FOOD PARTITIONING BETWEEN KLIPSPRINGERS AND DASSIES

Early studies on habitat preferences suggested that dassies are largely restricted to rocky terrain (Sale 1960, Turner and Watson 1965). This was confirmed during the present study and a considerable overlap in habitat selection by klipspringers and dassies was apparent. At Springbok almost all dassies sighted were in the rocky koppie habitat type, which is also highly preferred by klipspringers (see Chapter 2).

Table 33: Body mass of antelope occurring at Gamka, showing mean, range and sample size (where applicable), and source.

Antelope	Body mass (kg)	Source
Klipspringer	mean (range ; sample size)	
adult ♂	10,9 (9-15 ; n = 10)	Wilson & Child 1965
" ♀	12,3 (9-16 ; n = 11)	" "
♂	9,7 (9-11 ; n=3)	Smithers 1971
♀	11,5 (10-13 ; n=3)	"
adult ♂	12,8 (11-14 ; n=3)	Present study
" ♀	14,4 (12-16 ; n=4)	" "
	(14-18)	Dorst & Dandelot 1970
Grysbok		
♂	10,3 (9-12 ; n=17)	Manson 1974
♀	11,0 (9-12 ; n=15)	"
	(11)	Dorst & Dandelot 1970
	(11)	Maberly 1963
Steenbok		
♂	10,9 (9-13 ; n=37)	Smithers 1971
♀	11,3 (9-13 ; n=39)	"
	(14)	Dorst & Dandelot 1970
	(11-15)	Maberly 1963
Vaalribbok		
♂	20,2 (19-30 ; n=2)	Esser 1973
♀	22,1 (19-30 ; n=2)	"
	(23)	Dorst & Dandelot 1970

At Gamka the dassie and the klipspringer showed very similar habitat preferences (Fig. 56, Table 32). The analysis of preference ratings gave comparable values for both species, with ratings of over five showing that the dry rocky slope habitat is highly preferred. A number of sightings were made in the moist rocky slope habitat, but this habitat is not particularly preferred or avoided, with values close to unity. Few sightings were made in the valley bottom habitat, and the ratings suggest that this region was avoided to a small extent. On the plateau the low number of sightings shows that both species avoided this area almost entirely.

With such similar habitat preferences of two browsing herbivores, it is likely that a degree of partitioning of food exists. The calculation of relative biomasses of klipspringers and dassies at Springbok (Table 34) shows that under extreme conditions the biomass of dassies can rise to more than four times that of klipspringers (Fig. 57). Because of this discrepancy the main klipspringer study group's territory at Springbok was selected to look for possible mechanisms whereby partitioning of food is achieved. The most likely mechanisms are either that klipspringers and dassies select for different plant species, or that they select different plant parts, or else that they avoid each other by separation of feeding sites according to their different predator avoidance strategies.

Table 34: Relative biomasses of klipspringers and dassies in the main klipspringer study group's territory at Springbok on 2 March 1978.

	DASSIE		KLIPSPRINGER
	Adult	Juvenile	
Mean body mass (kg)	2,5	0,75	13,4
Sample size	18	7	6
Number in territory	± 60	± 60	3
Total mass (kg)	±150	± 45	
	± 195		40
Ratio Dassie : Klipspringer		4,7 : 1	

Selection for plant species

Tables 35 and 36 show the occurrence of different food plants in the stomachs of dassies collected from Gamka and Springbok. These results tend

Table 35: Important food-plants identified from the stomachs of 22 dassies shot at Gamka, showing abundance class totals and frequency.

(x denotes species not present in klipspringer feeding records)

	Abundance class totals	Frequency
Chrysanthemoides monilifera	69	21
Grasses	55	22
x Brunsvigia	18	7
Mesemb spp.	8	3
Eriocephalus africanus	6	6
Agathosma sp.	6	5
x Aspalathus peduncularis	6	4
Montinia caryophyllacea	6	4
Maytenus oleoides	6	2
x Oxalis spp.	5	3
Muraltia ericaefolia	4	3
Aspalathus hirta	4	3
Metalasia spp.	4	2
x Restio spp.	4	2
Polygola fruticosa	3	3
Pelargonium spp.	3	2
Rhus spp.	3	2
Berkheya angustifolia	2	2
Aspalathus sp.	1	1
x Chrysocoma sp.	1	1
x Helichrysum sp.	1	1
Hermannia disermifolia	1	1
x Lebeckia sericia	1	1
x Senecio juniperinus	1	1
Solanum tomentosum	1	1
x Struthiola sp.	1	1
x Sutera sp.	1	1
Phylica purpurea	1	1
x Phylica paniculata	1	1
Relhania squarrosa	1	1

Table 36: Important food-plants identified from the stomachs of 14 dassies shot at Springbok, showing abundance class totals and frequency.

(* denotes species not present in klipspringer feeding records)

	Abundance class totals	Frequency
Zygophyllum spp.	28	13
Ruschia/Leipoldtia spp.	11	6
*Grasses	6	4
Arctotis revoluta	6	2
*Oxalis sp.	5	3
Galenia fruticosa	5	4
Albuca altissima	4	2
Lycium oxycarpum	4	1
Euphorbia mauritanica	3	2
Lebeckia sericia	3	1
Manochlamys albicans	3	2
Osteospermum spp.	3	2
Thesium lineatum	3	2
Mesembryanthemum karroense	2	1
Drosanthemum albens	2	1
Boscia foetida	2	1
Zygophyllum divaricatum	2	2
Didelta spinosa	1	1
Pelargonium sp.	1	1
Pteronia sp.	1	1

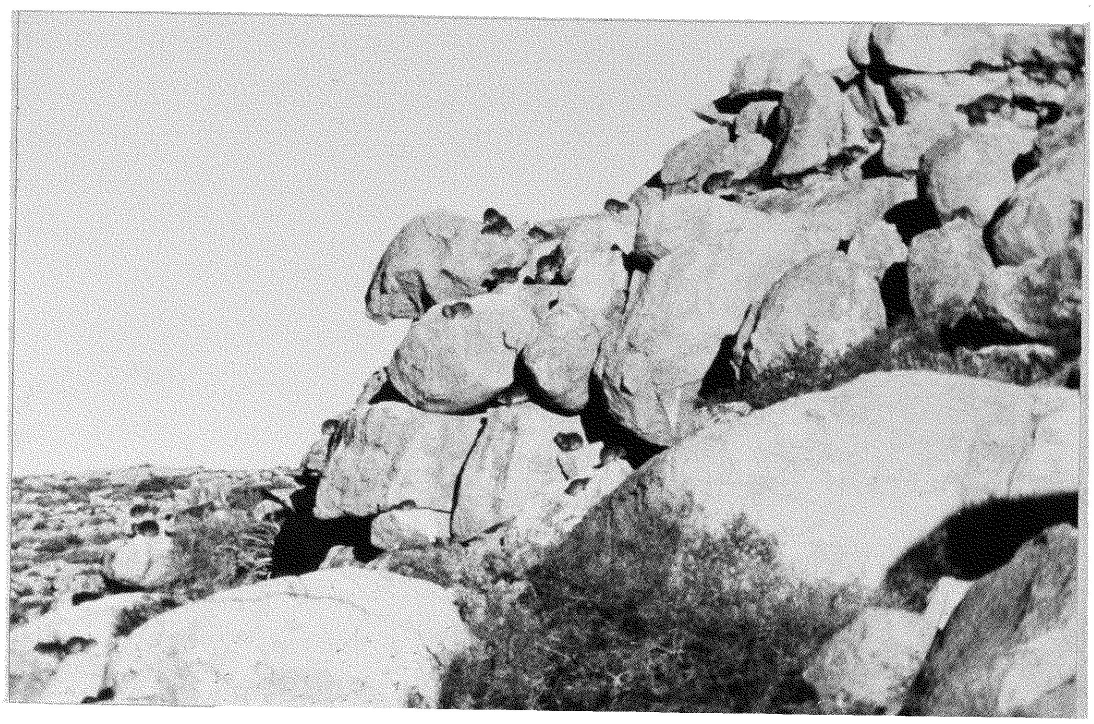


Fig. 57: A large colony of at least 30 dassies sunning themselves on rocks near suitable shelter at Springbok.

to confirm the findings of Turner and Watson (1965) and Hoeck (1975) that plant species are less important in the diet of dassies than plant parts.

The most obvious difference between the feeding of dassies and that of klipspringers is the amount of grass eaten, as shown by the proportion of grasses in the dassie stomachs from both areas. However, grasses formed less than a quarter of the food, and there was a large amount of overlap in the choice of browse by dassies and klipspringers. The tables show that at Springbok five plant taxa were among the ten most preferred food plants for both klipspringers and dassies, while at Gamka four plants were in the top ten for both.

At Gamka the leaves and flowers of Chrysanthemoides monilifera made up a large proportion of the dassies' diet and all bushes of this species were so heavily browsed that one wonders how the plant can tolerate such levels of nutrient loss (see Chapter 8). This species was also an important food-plant for klipspringers.

At Springbok the top rank of Zygophyllum in the food of dassies confirms the importance of this genus as a food plant for ungulates living on the rocky koppies. The only plants identified from the 14 dassie stomachs that were not fed on by klipspringers were grasses and Oxalis, which did not seem to be common in the main study area. In other areas of the reserve where dassies also overlap with klipspringers, dassies fed extensively on succulent plants such as Tylecodon paniculatus and Aloe spp., to the point where many Tylecodon plants were severely overbrowsed during the drought in the winter of 1978. This species is well-known to be poisonous to domestic stock (Naude pers. comm.), and must present considerable problems of detoxification. The fact that they are heavily utilised suggests that the dassies have evolved to cope with them, and that the difference in ability to detoxify secondary compounds may be important in food partitioning with klipspringers.

Therefore, while there were small differences in the selection of plant species by dassies and klipspringers during the study, the overlap seems to be considerable and other mechanisms must be looked for. The most likely way that they achieve partitioning when both prefer the same plant species is by spatial separation of feeding sites.

Selection of feeding sites

There are two possible ways in which spatial separation of feeding sites can take place. Either they can feed on different parts of the same bush, or else they can feed in different areas of the habitat.

On larger plants there is a certain amount of differentiation between those parts taken by dassies and those taken by klipspringers. Klipspringers can feed on the growing tips on the outside of a plant up to about 1,1 m, and may stand on a rock nearby to reach parts above this level. However, dassies can only feed on the outside of the bush up to about 0,3 m. It is well-known (Sale 1965) that dassies often climb up into bushes to feed, but here they are restricted to parts they can reach while standing on a branch that is thick enough to support them. Thus all growing shoots, fruits etc. on the inside of a large bush are likely to be eaten by dassies while those on the outside are eaten by klipspringers.

However, Chapter 2 showed that most of the shrubs occurring in rocky areas at both Springbok and Gamka are not much more than half a metre in height. Therefore evidence of feeding in different areas of the habitat must be sought.

Dassie dung sites are usually situated close to their rocky shelters (Sale 1960). Klipspringers do not seem to move very far from their resting and feeding sites to defaecate either (Chapter 5). Therefore we can assume that the distribution and number of middens of both species more or less represents the amount of time spent in the different parts of their home ranges.

Figure 58 shows the distribution of klipspringer and dassie middens in the main klipspringer study group's territory at Springbok. Apart from the higher concentration of middens around the edge of the territory, which is associated with territorial demarcation (Chapter 5), the klipspringer middens show a clear dissociation from those of the dassie. This means that either the dassies are avoiding the klipspringers, or else the klipspringers are spending more time away from the larger concentrations of dassies. Examination of the types of predator avoidance behaviour shown by the two species and differences in food quality selection and digestion leads one to suggest that the latter is the case.

Predator avoidance

There are important differences in the predator avoidance behaviour of klipspringers and dassies which affect their utilisation of habitat, but allow them to co-exist in the same areas. While klipspringers range widely over their territories and escape predators by outrunning them on the rocky

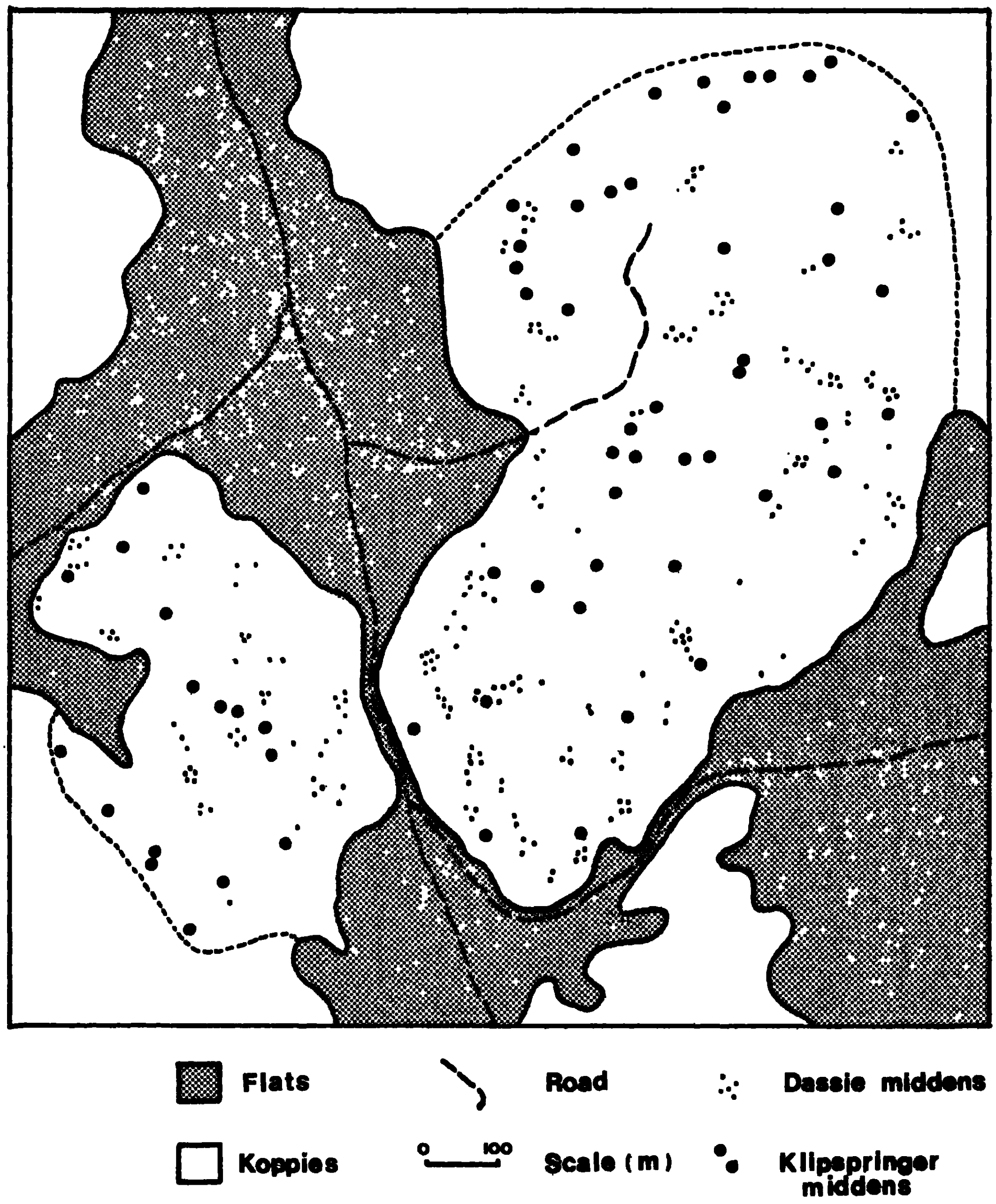


Fig. 58: Distribution of middens of klipspringers and dassies in the main klipspringer study group's territory at Springbok in February 1978.

terrain, dassies rely on hiding in rock crevices to avoid predation. Thus the further they move from their shelter, the greater is the risk from predation. Although in some areas the artificial reduction of predators has allowed dassies to grow accustomed to moving much further from their shelter, they are generally restricted to feeding within about 30-50 m of the rock crevices.

Therefore, in dassies there must have been strong selection for a mode of digestion that enables them to make the best possible use of the food available within the area where they can easily avoid predators.

Digestion and metabolism

Since dassies are not ruminants their digestive system is rather different from that of klipspringers. Examination of the particle size in the faeces shows that they break down food less completely than klipspringers, and this suggests a mechanism whereby they are able to survive on lower quality food.

Table 37 shows that about a fifth of the plant particles in the dassie faeces were too large to fit through a 1,2 mm sieve, while nearly all of the particles from klipspringer pellets were small enough to fit through the mesh. This means that the structure of the dassie digestive system must allow the passage of larger particles than those passed through the digestive system of the klipspringer.

Table 37: Percentage of large particles in the faeces of klipspringers and dassies, from mass of dried, crushed pellets before and after sieving.

	Dried pellets	Sieved	%
DASSIE	14,0 g	3,0 g	21,4
	12,0 g	2,3 g	19,2
	7,0 g	2,0 g	28,6
Total	33,0 g	7,3 g	22,1 %
KLIPSPRINGER	12,5 g	0,1 g	0,8
	7,0 g	0,2 g	2,8
Total	19,5 g	0,3 g	1,5 %

In ruminants the rate of flow of the digesta through the gut is regulated by the small size of the reticulo-omasal orifice (Campling 1970), which means that the food has to be broken down to a small particle size before it can pass to the intestine. This breakdown is achieved by grinding the food between the teeth during rumination and by microbial breakdown of the plant matter in the rumen.

However, the dassie has a simple stomach. Although there may be a small amount of microbial action in the cardiac part of the stomach (Clemens 1977, Van Engelhardt, Walter, Laurenz and Hensley 1978, Leon in press), most of the food breakdown takes place by enzymatic digestion in the glandular pyloric stomach. Extensive microbial breakdown occurs in the rather unusual large mid-gut sacculation as well as the paired caeca. Clemens (1977) has shown that food can be retained in these areas for a considerable length of time, but there is no filter mechanism that obliges dassies to retain food until it is broken down to a very small size, as occurs in the ruminant. The presence or absence of this filter mechanism may be important in partitioning of food between dassies and klipspringers.

In his discussion of a grazing ecosystem in the Serengeti, Bell (1971) suggests that the digestive system of the non-ruminant zebra allows it to utilise lower quality food than the ruminant antelope. In his hypothesis the zebra makes up for less efficient breakdown of the food ingested by processing a larger quantity of food more quickly. Thus, by digesting only a part of the food eaten and letting a lot of the structural material pass straight through, they can still fulfill their energy requirements on low quality food. However, in the ruminant food intake is limited by the amount of food in the rumen, which is in turn limited by the speed that it can be broken down to small enough size to pass to the intestines, so the only way that enough energy can be assimilated is to keep the proportion of fibre in the diet at a low level.

There are obvious differences between the digestion of horses and dassies, particularly in the structure of the teeth and sites of microbial breakdown, but the basic principle seems to be the same. Both species have large distensible stomachs lined with stratified epithelium and rely mostly on enzymatic digestion in the pyloric stomach, with some microbial fermentation in the hind gut. In both species a large amount of structural material is passed through to the faeces. This suggests that the same mechanism of being able to speed up the through-flow of plant material may allow the dassie to compete favourably with the klipspringer when the food quality drops very low.

No research has been carried out on the working of the klipspringer's digestive system and the rate of passage of food. However, it is likely that they show a similar pattern to other smaller ruminants. Studies on domestic sheep have shown that many factors affect the rate of flow of food through the gut (Blaxter, Graham and Wainman 1955), but an average digestion time for unground food is between 80 and 100 h for 80% of the food to pass through. Clemens (1977) showed that the dassie takes about two days (48 h) to process 80% of the food, and this has been confirmed by Leon* (pers. comm.). Thus the dassie may be able to process food more quickly than the klipspringer.

Dassies are far better equipped than klipspringers to feed on hard plant parts. While klipspringers have no upper incisors at all, those on the dassie are well-developed, with persistent pulps similar to rodents. Sale (1965) reported extensive use of bark as a food source, and during the present study many shrubs and trees showed signs of dassie damage. At Springbok, on the farm adjoining the Nature Reserve, several large _Pappea capensis_ trees had been completely ring-barked by dassies.

Although dassies are much smaller than klipspringers, their energy requirements do not differ as much as is predicted by the Brody-Kleiber relationship of metabolic rate to body size. This is because they have a lower body temperature than expected (Louw, Louw and Retief 1973), and conserve energy by making use of the more stable micro-climate of rock crevices and by huddling to keep warm (Sale 1970). Bartholomew and Rainy (1971) found that their oxygen consumption is 20% lower than the rate predicted by the normal mammalian scaling of respiratory variables described in Stahl (1966).

Thus dassies probably have similar energy requirements to klipspringers, but the structure of their digestive sustem may allow them to survive unfavourable conditions by browsing the vegetation near to their rocky shelters down to a very low level of food quality. If they have to range further from their shelters to feed they become more vulnerable to predation, which means that there is selective advantage in browsing the vegetation nearby close to the lowest limit of food quality that they can tolerate.

Therefore klipspringers avoid large concentrations of dassies, not only because there is no selective advantage in browsing one part of their territory preferentially, but also because the dassies may be able to browse the vegetation near their shelters to well below the lower limit of food quality that

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* Miss B. Leon, Zoology Dept., University of Cape Town.

klipspringers can tolerate without losing condition.

Tolerance of fluctuating conditions

Because of their restriction to relatively small feeding areas dassies are more susceptible to seasonal changes in the vegetation than klipspringers, so selection seems to have favoured two particular characteristics. The first is that they are able to utilise relatively coarse, low quality food, as outlined in the previous section. This means that, instead of having to range further from their shelters for food in the dry season, and thus becoming more vulnerable to predation, they are able to make the best possible use of what is available nearby.

The second adaptation to a fluctuating environment is that they are fairly prolific breeders. Although the gestation period is exceptionally long for a mammal of this size, they produce an average of about three offspring in a litter (Millar 1971, personal obs.). This fecundity means that in good years the population can increase quickly, but it can also tolerate an extensive die-off during bad years. Thus, when food quality near to the rocky shelters drops very low and they have to move further to feed, the population can tolerate a considerable loss to predation.

Therefore, in rocky areas the populations of klipspringers, dassies and predators is intricately balanced. Klipspringers avoid the parts of their territories most heavily used by dassies, because the latter are forced by their predator avoidance strategy to browse the vegetation near to their shelters to a very low quality because of the high risk of moving further afield, and the critical lower limit of food quality may be lower for dassies than it is for klipspringers. However, klipspringers can survive in the same areas because of the discontinuous distribution of suitable shelters for dassies. The difference in their tolerance of predation has important implications in the management of conservation areas, since the short-term removal of predators to attempt to boost small antelope populations may actually be detrimental because the dassies are able to exploit the situation more quickly, and therefore increase the competion for food with the klipspringers.

CHAPTER 10 : CONCLUSION

The most important components of an animal's habitat are food, water, shelter against climatic extremes, and cover for predator evasion. The habitats available in mountainous terrain show many unusual characteristics, and it is within the framework of the above four factors that the klipspringer has evolved specific adaptations which suit it to living in this terrain. These adaptations include modifications in social organisation, feeding behaviour and predator evasion strategy, as well as in anatomy and physiology. The aspects of the habitat that have had the most effect on klipspringer evolution are the rocky substrate, the climatic extremes associated with mountainous topography, and the distribution of suitable food-plants in these stable habitats.

Since the widespread occurrence of surface rocks is the character which most clearly distinguishes mountain habitats from forest, bushveld, and other habitats, the adaptations to cope with moving and evading predators on this substrate are probably the critical factors determining klipspringer habitat selection and distribution.

PREDATOR EVASION

All antelope species in Africa are susceptible to predation by large mammalian carnivores, and therefore selection for an effective predator evasion strategy is one of the strongest forces which have influenced their evolution. Thus in rocky mountainous terrain the ability to move rapidly over the rocky surface to avoid predation is of primary importance. Since the vegetation of rocky slopes is usually low-structured there is seldom sufficient cover available to provide hiding places for an animal as large as an antelope. In addition, running on a loose rocky substrate tends to be noisy as stones are easily dislodged. Therefore the klipspringer has diverged from the normal small antelope predator evasion strategy of silence and concealment to one where it stands and watches the predator, relying on its superior fleetness in rocky terrain to avoid being caught should the predator attack. The adaptations for fleetness are a unique digit structure and agility, which is partly associated with a small body size.

The digit structure of the klipspringer is very unusual amongst antelope in that the proximal interphalangeal joint has rotated posteriorly to enable it to walk on the tips of its hooves. These then wear down to a cylindrical shape which gives better grip on rocky surfaces.

There are several factors which affect the body size of ungulates, but it is likely that the loss in agility associated with an increase in body size is one of the factors that determines the size of antelope most suited to occupying this rocky montane niche. The reason for this is the scaling of the skeleton, where body mass increases according to the third power of a linear dimension, while bone strength is related to its cross-sectional area, or the square of a linear dimension (Schmidt-Nielsen 1972). Therefore smaller mammals are able to have a greater muscle-to-bone ratio than larger mammals.

With a body mass of about 15 kg the klipspringer is considerably smaller than other montane antelope, which are mostly goats of the sub-family Caprinae, where large males may exceed 100 kg. However, the subjective impressions of Greig *(pers. comm.) working on feral goats Capra hircus, and Lloyd *(pers. comm.) on the Himalayan thar, suggest that the large males of these species are far less agile than the smaller females and juveniles, which weigh less than 40 kg. This supports the hypothesis that an increase in agility in rocky terrain is associated with a decrease in body weight.

It is likely that the lower size limit of montane antelope is also affected by predation, since a smaller body size would make them more vulnerable to raptors. The results of the present study suggest that juvenile klipspringers are easily caught by raptors such as black and crowned eagles but, by the time they reach adult size, predation by birds is reduced to a very low level. This could be one of the main reasons why lambs are hidden for the first few months after birth.

The brown rock-like coloration of klipspringers prevents them from being detected easily at long range, but it is of little use in evading predators once they have been seen. The reason is that on detection of a predator they usually move to vantage points where they can watch it clearly, at the expense of making themselves conspicuous.

Group size is also affected by the predator evasion strategy. Since silence

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* Mr P.H. Lloyd, " " " " "

and concealment are no longer factors which regulate the number of individuals that can move together, the klipspringers take advantage of the increased vigilance of a family group and the role differentiation which this allows. The male and female can nearly always be found within a few metres of each other, usually with one or two offspring nearby. In such a close-knit group it is always possible to have one member maintaining vigilance from a prominent point while the others feed, which increases the chances of early detection of a predator. In addition, the male takes over a large proportion of the vigilance duty, enabling the female to concentrate on assimilating the greater quantity of energy she needs for reproduction.

This predator evasion strategy means that a minimum of energy is wasted on false alarms and unnecessary flight when the predator is not hunting. By waiting until the predator is close the klipspringers can be sure of its intentions. A further means of conserving energy is that the loud and piercing alarm call and foot-stamping behaviour either goad the predator into a fruitless chase or inform it that a chase would be pointless. Even if a short chase ensues, the overall cost in energy is less than if the klipspringer had just stood and watched the predator for a long time.

Therefore the klipspringer's fleetness and agility has allowed it to evolve an effective predator evasion strategy in rocky terrain, but also has the effect of restricting it to rocky areas or their close vicinity, since its sharp-pointed hooves become a handicap on a softer substrate.

ADAPTATIONS FOR CLIMATIC EXTREMES

The climate of mountain habitats is usually more extreme than that of surrounding lowland habitats. The most obvious variation is the decrease in temperature associated with altitude and exposure to wind. However, temperatures may also be hotter under certain circumstances, due to aspect, shelter, or long-wave reradiation from rock surfaces. Although the total rainfall is often greater due to orographic cloud formation, run-off is more rapid, and seasonal drought may be critical.

The klipspringer has evolved to cope with these climatic extremes in several ways, both with regard to behaviour and anatomy. Because of its small body size this species is affected by cold temperatures more than a larger antelope would be. In the low-structured vegetation that is typical of most rocky mountain areas there is little small-scale microclimatic variation which klipspringers can utilise to avoid temperature extremes. While large boulders may offer shade in hot weather, they do not give much protection against the cold, unless the klipspringer climbs right underneath them, but this conflicts with the necessity for vigilance for predator evasion. The only way that adult klipspringers use microclimatic variation to avoid extremes is to select side valleys to escape the main force of the wind under very cold conditions. Because of their smaller body size juvenile klipspringers are even more vulnerable to cold than adults, especially because most lambs are born in July and August. This may be another important reason why lambs are hidden for the first few months of life.

The activity pattern of klipspringers is not affected by hot and cold temperatures to any great extent. They show the usual ungulate pattern of feeding peaks in the early morning and late afternoon, with one or two minor peaks during the middle of the day. Most of the hottest part of the day is spent resting or ruminating on a vantage point, often with one or more of the group in the shade. However, during the study klipspringers were often seen lying out in very hot sun with little apparent discomfort.

Because of the necessity to tolerate very cold conditions and the observed ability to tolerate very hot conditions the klipspringer must have physical and physiological adaptations that enable it to do this. The most important of these is the unusually thick and coarse pelage, which acts as an insulator against both cold and radiated heat. The efficient insulation of this pelage not only enables the klipspringer to cope with temperature extremes, but also aids it in water conservation, since less water is needed for thermoregulation.

Klipspringers seem to be well-adapted to living in dry conditions where drinking water is scarce. The most important adaptation here is probably efficient kidney function, since the structure of the klipspringer's kidney is similar to that of mammals with a high urine concentrating ability. Although they drink when water is available they are able to assimilate enough moisture from the succulent plant parts that they eat, and thus free themselves completely from the necessity of having perennial drinking water available. This adaptation must have played an important role in klipspringer range extension, because it means that they are able to occupy many marginal mountain areas. These include both the drier parts of mountains that show great topographical variation in the amount of precipitation they receive, and mountains in drier regions of the country.

SOCIAL ORGANISATION

A perennial supply of food is the ultimate factor regulating a species' density and abundance within an environment. (Because mountains are stable habitats the abundance of plant material available to herbivores fluctuates little from year to year, although the total abundance is low due to the impoverished soils} Therefore the most effective way for a herbivore to secure adequate food to subsist throughout the year is to defend an area of land that supports sufficient vegetation.

Because they have largely dispensed with the necessity of shelter and drinking water klipspringers are able to exploit such a territorial system to the full, by demarcating such an area in any habitat that has sufficient rocky substrate to enable them to evade predators successfully.

The importance of food supply in the evolution of a territorial system is supported by the fact that the territory size of klipspringers shows a good correlation with rainfall. Since above-ground plant biomass in an area depends largely on the amount of moisture available, it is likely that the klipspringer's territory size is correlated with the biomass of vegetation available to it.

The optimum territory size seems to be one that will support a family group of a male and a female with one, or occasionally two, offspring. Since territories are defended by chasing conspecifics of both sexes, the territory for such a group is probably the largest that a male can defend adequately. Since the male klipspringer defends a territory that has just enough food to support his female and their offspring he must chase off other females as well, or else he would decrease his mate's chances of reproducing successfully. Although territory size varies greatly in different areas, the advantage in high rainfall areas of having a small territory which the male can cover easily is compensated for by the higher density of klipspringers, and therefore more frequent clashes. During the present study chases were more frequent in the small territories at Gamka than in the much larger territories at Springbok.

Thus group size seems to be regulated, on the one hand, by the advantage of having more individuals for vigilance, especially when it allows role differentiation between the male and female, and, on the other, by defendibility of the territory and its resources.

Klipspringer males and females show very little sexual dimorphism, apart from the presence of horns in the male. The most likely reason for this is that in open mountain habitats visual messages play an important part in spacing behaviour. Territories are marked by ritualised dunging and scent-marking, both of which carry an olfactory message, but the visual message of the ritual may be just as important. "Static optic advertising" is hard to prove as a factor in natural selection, but is probably also an important method of showing that a territory is occupied. In all of these the presence of a female that can be easily mistaken for a male at a distance in effect doubles the strength of the message.

FEEDING

The small body size that is best suited to predator evasion in rocky terrain affects the life-style of the klipspringer in several ways. The most important is that it is obliged to be a selective feeder. The reason for this is that the relatively high metabolic rate associated with a small body size requires a greater daily input of energy per unit weight than in the case of larger antelope. Since stomach size in ungulates is roughly proportional to body size and cannot be increased without affecting the animal's agility and mobility, the best way to assimilate more energy is to select more nutritious food.

The data on feeding support previous observations that klipspringers feed on the growing shoots, flowers and fruits of a number of dicotyledonous shrubs, and indicates that they are highly selective for plant parts, but not as selective for plant species.

The energy requirements of male and female klipspringers differ, since the female needs more energy for gestation and lactation. During the study the female spent significantly more time feeding than the male. A further variation in energy requirements is the amount of extra energy needed to survive cold conditions in winter. The conductivity tests showed that the klipspringer's pelage is a very good insulator, but it is unlikely to provide enough insulation for the coldest conditions. Therefore the metabolic rate and energy requirements are likely to increase in winter.

This was reflected in the longer feeding times recorded during this season, which more than made up for the shorter day length.

Because of the seasonal variation in the availability of suitable nutritious food, the food searching time of klipspringers also varies through the year. The most notable variation during the study was at Springbok where the feeding time in spring was little more than half that recorded in summer, and this can be attributed to the abundance of flowers and growing shoots available at this time.

The occupation of a fixed territory has an important influence on food searching time, since the klipspringers become familiar with the distribution and seasonality of the plants in their territory. With this advantage they waste a minimum of time and energy in searching when the supply of nutritious food becomes critical.

Because they have dispensed with the necessity for drinking water klipspringers have to eat succulent plant parts to satisfy their moisture requirements. Therefore succulence is probably one of the most important factors in food selection. However, it is not the only factor, since the klipspringer appears to eat large quantities of the mature leaves of succulent xerophytic plants only during the dry season, when more nutritious young growth of other plants is not available. This selection for young growth must have a great effect on the growth of the plants, and it seems that there are important relationships between the plants and herbivores in mountainous areas, especially in the fynbos.

Although there is little literature available on the subject, the plants of the fynbos are well-known to be rich in oils, tannins, and other aromatic compounds. The metabolic origins of these substances are not clear, but it is likely that they give the plants an evolutionary advantage by reducing herbivory in areas where the supply of nutrients is critical. In such circumstances it would appear to be worthwhile for the plants to invest a large amount of energy in preventing loss to herbivores.

Since the klipspringer is one of the most important herbivores in rocky areas it is likely that it has evolved in close association with the vegetation of these areas. Its habit of feeding on a wide range of plants, both through the season and on any particular day, supports the hypothesis that individuals are avoiding the accumulation of toxic quantities of the compounds present in each plant species.

COMPETITION

Several other herbivores occur sympatrically in mountainous terrain and may compete with klipspringers to a greater or lesser extent. The analysis of habitat preferences of the other small antelope species occurring at Gamka showed that they reduce competition with klipspringers by selecting flatter areas, and only occasionally feed in rocky terrain.

However, dassies showed very similar habitat preferences to klipspringers and probably overlap to a greater extent. The analysis of feeding preferences and feeding site selection suggests that both species eat very similar food, but reduce competition by feeding in different areas within the rocky terrain. This is regulated by their predator evasion strategies, since dassies need suitable small shelters to hide in while klipspringers merely run away in open rocky terrain. Although dassies tend to browse the vegetation down to a very low level of food quality, and may even be able to survive on food that is too coarse for klipspringers, the two species are able to co-exist in mountainous terrain because of the irregular distribution of suitable shelters for dassies.

Thus the unusual conditions of rocky mountainous terrain have selected for several specialised adaptations in the evolution of klipspringers. The dassie is the only other medium-sized mammal that is able to tolerate these conditions, but its predator evasion strategy and feeding behaviour have evolved in a different direction from those of the klipspringers. The latter's adaptations to evade predators on rocky terrain, to tolerate the climatic extremes usually associated with mountainous areas, and its unusual social organisation make it ideally suited to living in more open mountain habitats.

CHAPTER 11 : MANAGEMENT ASPECTS

CONSERVATION STATUS

Klipspringers do not appear to be in any immediate danger of extinction. Although they have been exterminated in some areas of the Cape, most notably the Cape Peninsula, and considerably reduced in others, they are still widespread and fairly common in many inaccessible mountainous areas. Their preference for rugged terrain, remarkable crypsis among the rocks when undisturbed, and their shy nature, mean that they are often not seen when they do occur in an area. On several days during the study many hours were spent in fruitless searching when at least three or four pairs of klipspringers must have been nearby.

Some examples of underestimates in klipspringer numbers are shown in Millar and Lloyd's (1976) questionnaire survey which gave figures of only 10 klipspringers for both the Gamka and Hester Malan Nature Reserves, while the present study yields estimates of at least 300 at Gamka and 70 at Hester Malan (Chapter 3). These figures were so low simply because the local officials seldom went into the inaccessible areas of the reserves and had no way of judging just how many klipspringers there were.

Klipspringers are relatively easy to hunt because of their habit of making themselves conspicuous on a vantage point to watch the source of danger (Chapter 6). This predator evasion strategy works well with the klipspringer's natural predators, but has led to its downfall at hands of men with guns. In addition, stray domestic dogs may have helped the decrease in numbers by predation on lambs and continual harrassment, which causes a drop in condition.

The areas where klipspringers have been most noticeably reduced in numbers are those close to large concentrations of people, with the accompanying poaching and dog problems, and in areas of more marginal habitat. In terrain such as the karoo, where klipspringers appear to have been fairly plentiful at one time, their numbers have declined drastically. The most likely explanation for such areas is that, although the terrain is suitable, it is fairly accessible for hunting and there are no undisturbed areas to act as "reservoirs" for restocking, as occurs in areas adjoining large mountain catchments. This is particularly true where farmers have no idea of cropping small game populations for sustained yield.

However, a number of farmers approached during fieldwork showed encouraging interest in the aesthetic value of conserving klipspringers. Therefore it is possible that significant numbers of klipspringers may be conserved on farms in the future, especially if farmers are made aware of the fact that the small antelope offer comparatively little competition to domestic animals. This would partially make up for the inevitable population decline that will be caused by increased use of mountainous areas for cultivation and grazing.

Since the Department of Forestry has recently started a strict conservation program for catchment areas, klipspringer populations in these habitats should be reasonably secure. Outside forestry areas the situation is less clear, but several National Parks, such as Augrabies Falls N.P., and Provincial Nature Reserves, such as Hester Malan N.R., Gamka Mountain N.R., and Vrolijkheid N.R., have adequate populations. Many local authority nature reserves have expressed interest in re-establishing populations of klipspringers, as have several members of the farming community, so there is great potential if an effective method of capturing the antelope can be found.

Thus the conservation status of the klipspringer in the Cape seems reasonably secure, although a further decrease in their populations is inevitable in marginal rocky areas that will soon be more heavily utilised due to increased agricultural and industrial activity.

HABITAT SUITABILITY

Chapter 2 outlines the habitat preferences of klipspringers. It is clear that the most important factor in klipspringer habitat selection is the presence of a rocky substrate which gives them security for predator evasion (Chapter 6). Since the species has adapted so completely to the rocky terrain, wild klipspringers are unlikely to settle down on non-rocky terrain, even if all the predators have been removed.

Thus, for reintroduction of klipspringers to areas where they once occurred, it is necessary to make sure that the rocky terrain is suitable and covers a large enough area to fulfill their needs. It is particularly important that they do not have to move out of rocky terrain in areas near human settlements where harrassment by dogs is likely to be a problem. The area required for the territories depends on the type of terrain and the average rainfall. Chapter 3 gives the approximate densities one can expect in semi-desert, medium rainfall, and high rainfall habitats, if conditions are ideal.

An important factor is the availability of food. Chapter 8 outlines the klipspringers's feeding habits and shows that they are almost entirely browsers and only occasionally take shoots of fresh green grass. Thus a large variety of edible shrubs must be present in the rocky habitat so that the klipspringers have sufficient food throughout the year. Trees and grasses may sometimes be utilised under stress conditions, but should not be considered as part of the basic food supply.

CAPTURE

Adult klipspringers have very seldom been captured in the wild, largely due to the difficulties involved in working in rocky mountainous terrain. The method most commonly used for small antelope, that of driving them into nets, presents problems in carrying the heavy nets into the mountains and co-ordinating a drive there. During the present study several weeks were spent attempting to capture klipspringers with nets, and a certain amount of experience was gained. Only one individual was caught, but once the system had been worked out time was the only factor that prevented more from being captured.

The main problem seems to be to find the right place to set up the nets and then to drive the klipspringers into them. It is important to site the nets within the rocky terrain, since klipspringers need to be extremely frightened to leave this for the flats, and in this state they have a far greater chance of dying from shock or capture myopathy. The ideal place would be on top of a ridge or in a narrow valley where the klipspringers cross regularly from side to side, but where the ground is level enough to set up the nets easily. However the work involved in carrying the nets and poles, as well as the immobilised klipspringers, makes it necessary to choose a site not too far from a point that is accessible to vehicles.

The length of netting needed depends very much on the terrain. Since klipspringers do not seem to use regular paths, a considerable length of netting is necessary, although this can be reduced if an obstacle, such as a cliff or a fence, can be used to give the animal direction. During the present study a funnel of about 200m of nets set up along a jackal-proof fence worked well.

Because of the very strong territoriality of klipspringers (Chapter 5), it is desirable to catch them near their territories, as the stress of chasing them away from familiar areas may reduce their chances of surviving the trauma of capture. Thus it will probably be necessary to set up the nets for each particular group, which makes the process very labour-intensive.

Once the klipspringers are caught in the nets, one must still exercise great care because a high proportion of small antelope caught in nets die within a couple of days from the stress of capture. During this study the single buck caught was injected with Haloperidol (R1625 Serenace : G.D. Searle) which worked very well. The dosage rate was 0,3 mg/kg, which was injected intramuscularly, as the veins in the ear proved very hard to find. In spite of using this slower route and the low dosage, the buck was fairly relaxed after 20 min, and did not need to be tied after 30 min. With a blindfold over his eyes he was easily transported and handled with no tying (Fig. 59). Lying relaxed with a good air circulation and panting easily, his body temperature rose from 41,2°C just after capture to 42,1°C when the drug was starting to take effect after 20 min, and dropped to 40,4°C half an hour later. When the blindfold was removed after 80 min, he stood up and trotted off without alarm. Several hours later, and again after two days, he was seen to be quite healthy, although he escaped from the enclosure soon afterwards and was not seen again.

Therefore driving klipspringers into nets appears to be a feasible method of capturing them, but it is unlikely that large numbers will be caught in this way. Other methods that deserve attention are boma or cage-trap methods, but these will require a lot of time to allow the animals to grow accustomed to the enclosures being used. In addition, suitable attractants will have to be found. These methods have great advantage that the trauma of capture is is reduced to a minimum, which increases the chances that the animals will survive.

Drug immobilisation using dart guns is unlikely to be a satisfactory method for capturing klipspringers, since it is likely that they will fall off the rocks and hurt themselves as the drugs start to take effect.

Several farmers in the Cape Province have acquired klipspringers as pets by catching them when they were very young and left hidden by their mothers, but this method is not recommended, as such animals have to be hand-reared, and therefore would be of little use for re-establishing "wild" populations.

Fig. 59: A captured klipspringer ram tranquillised with Haloperidol. Note the blindfold, plastic pipes covering the sharp horns, and the lack of tying round the legs.

TRANSLOCATION

Genetic considerations

Most plains and savanna antelope, such as the springbok and impala, are more or less continuously distributed within their natural range, due to the distribution of the savanna habitat. Although they are now more restricted by man's partitioning of the land with fences, they tend to show a certain amount of seasonal migration according to factors such as food and water availability and predator pressure. These species seem to show little differentiation into sub-populations because gene flow, in the form of mating between individuals from neighbouring populations is likely to take place regularly. In fact, they may have evolved to be "obligate outbreeders", which means that they would need to have a continuous interchange of genes with neighbouring populations. Because of this the populations are probably adapted to the general conditions of the distribution range, but show little tendency to specialise for the local conditions on a small scale.

However, populations of antelope that prefer a habitat which is discontinuous in distribution are likely to show different genetic characteristics. Because of the discrete nature of the "units" of their habitat type, individuals move from one unit to the other more rarely, especially if the intervening habitat is very different from the habitat they prefer. Because of this gene flow is sporadic or rare, and natural selection may be able to bring about a greater change in the different gene pools, so that these antelope tend to become highly specialised to their local conditions. In this way they may have evolved to tolerate a high degree of inbreeding, although this would not necessarily be obligatory.

It is clear that in the first situation man's partitioning of the land has interfered with gene flow to some extent, and therefore translocation of animals from one area to another nearby is acceptable, and even to be encouraged on a small scale, if the "donor" and "recipient" areas were once connected by a region of similar habitat type through which the antelope could move freely.

However, in the species that prefer a habitat which is discretely distributed, individuals would have moved from one population to the next very rarely, and therefore translocation is to be discouraged. The further the distance between the donor and recipient, the less desirable is the translocation, especially if the intervening area is of unsuitable habitat. Therefore translocations on a large scale or over long distances interfere with the natural variability of the species and the populations' specialised adaptations to local conditions. Since such a specialist will have evolved to suit the peculiar conditiohs of the area as well as the cyclical climatic and habitat fluctuations that characterise the area, mixing of genetic material tends to decrease the ability of the population to survive in the long term, even if this only becomes apparent under extreme conditions that arise at intervals of several decades.

The klipspringer is one of the most striking examples in Africa of this second type of antelope. Although it has a very wide distribution range (Chapter 2), it is highly specialised for living in rocky terrain, both in behaviour and anatomy, and only very rarely moves out into non-rocky areas. In addition, the buck are sedentary in habit, and occupy territories which are more or less fixed in time and space (Chapter 5). This means that they show little, if any, seasonal movement and the only dispersal of klipspringers outside the area will take place when all the available territories are occupied and young adults are forced to seek new terrain. Since klipspringers seem to form life-long pair bonds, gene flow will not be nearly as rapid within the population as it would with a species where new mates are sought each year.

Thus there will be a continuous slow interchange of genes within each mountain range or outcrop of rocky terrain, but little gene flow between different ranges, if they are separated by some distance of plains or forest habitat. Because of this, each population will be genetically adapted to the particular conditions of that area. Possible adaptations are the ability to conserve water very efficiently on mountains that receive little rainfall or are subjected to periodic droughts, and the ability to detoxify secondary compounds in the plants that are locally dominant (Chapter 8).

Therefore, when translocation of klipspringers is contemplated, it is particularly important to assess the differences between the donor and recipient areas very carefully. Any farmer will acknowledge that a buck from the karoo is unlikely to adapt very well to the fynbos, but it is not often realised how much relatively small differences in habitat can affect translocated animals.

For example, the local population may have a small genetic mutation to enable it to tolerate large quantities of toxins from a particular succulent plant that is common in the area. If the population on a farm within this area has been exterminated and klipspringers are brought in from an area some distance away because they are the easiest to capture, they may adapt well to the new circumstances after an initial period of familiarisation with the vegetation. However, if after a few years there is a drought, and the "local" population is able to survive by feeding on the particular succulent plant, the translocated klipspringer may not be able to cope with the toxins and most of them may die.

The above example is a hypothetical case to illustrate only one of the more extreme ways in which the chances of long term survival of a population are lowered by translocation from a dissimilar area, but it shows that the principles of genetic conservation, as outlined by Greig (in press), should be obeyed not only for philosophical reasons, but also because they are likely to have a sound practical basis.

Restocking

The first aspect to look at when restocking of klipspringers is contemplated is whether they used to occur in the area. If there is no record of previous occurrence it is highly likely that the area is unsuitable and that the operation will fail. If they did once occur there the next question is to find out how much the habitat has changed since those days, especially with respect to vegetation cover and the presence of exotic trees and shrubs.

Since translocation of klipspringers has hardly ever been attempted before, priority should be given to the restocking of areas where the operation is most likely to be successful. These areas should have a good proportion of suitable habitat where the buck can be left alone to build up a viable population free from disturbances such as traffic of visitors, poaching and, particularly, harrassment by stray dogs. Because of the logistical problems involved it will be impossible to translocate large numbers of animals, so the growth of the population will be slow initially, and even a slight disturbance may have a noticeable effect. Once reasonable numbers have built up the population should be able to withstand more disturbance, and only then can regular visits by the public and other types of "utilisation" be contemplated. Even then it would be advisable to keep an undisturbed "core" area.

Equal numbers of males and females should be translocated, because they are monogamous and a male is likely to mate with only one female, even if others are available. Thus the usual ratio of one male to two or three females, which is used for most antelope, should not be applied to klipspringers.

HUNTING

According to the Provincial Ordinance (No. 19 of 1974) klipspringers are protected in the Cape Province. This means that a permit is needed to hunt them. However, there are only two divisional councils, Calvinia and Ceres, that have an open season for klipspringers so, officially at least, very few klipspringers are hunted in the Cape. In spite of these regulations several farmers have related how klipspringers have been hunted in their areas recently.

Apart from sentimental considerations, there is very little reason why klipspringers should not be hunted if they occur in large enough concentrations in an area. In fact, less restriction on hunting could even be beneficial to the conservation of klipspringers if farmers look on them as a utilisable resource which can be cropped on a sustained yield basis. Such a relaxation of control, if backed up with the right educational programme, might encourage farmers to protect their populations more actively, instead of letting them look after themselves. However, hunting on non-agricultural land would still have to be strictly controlled.

During tsetse control operations in both Zambia and Zululand, klipspringers could not be eradicated even with intensive hunting (Wilson and Child 1965). These authors suggest that heavy hunting may actually have stimulated an increase in the population, as was shown for duiker in Rhodesia (Child and Wilson 1964).

Thus utilisation of klipspringers, whether by hunting or capture for translocation, will not necessarily be harmful to their populations, provided that size of the populations and the hunting methods are carefully considered.

In Chapter 5 it was shown how paired klipspringers spend a very large percentage of their time close together. However, young adults that have been evicted from the group may spend several months wandering around looking for a mate and a territory. From this it may be concluded that single klipspringers encountered in the veld have a good chance of belonging to this "surplus" of young adults, and can be hunted with very little effect on the population, since territories and pair bonds would not be disrupted. If a paired klipspringer is shot the effect on the population would probably be doubled, as the mate is unlikely to find a replacement and raise another offspring for that year.

It is very difficult to suggest the best open season for hunting klipspringers, since the infant is dependent on its mother for nine to ten months, with five to six months gestation and about four months of suckling. The present season in Calvinia and Ceres, May to July (Proclamation No. 313 of 1978), falls right in the lambing season. Since at any time from conception to weaning the offspring will also be lost, hunting during this period should not make too much difference, apart from the possibility that under extreme hunting stress on the population near full-term foetuses may be aborted. In fact the lambing season may be a good time to hunt them because this is when previous year's offspring are most likely to be evicted from the groups (Chapter 5) and shooting of single animals would cause little disruption.

The only time that is really important to avoid is the peak of the rutting season, from about February to April, since disturbance of the population may cause paired females to miss mating.

PROBLEM KLIPSPRINGERS

Due to their preference for rocky habitat which is largely unusable for farming, especially cultivation, klipspringers are seldom looked on as problem animals. However, their habit of feeding very selectively on the succulent growing shoots of shrubs has led to several instances of complaints. If these buds are eaten at a very early growth stage, the klipspringer may destroy what would have been a considerable weight of fruit or new growth, so farmers are understandably intolerant of individuals which return to their young orchards and vineyards regularly.

In the incident at Franschhoek mentioned in Chapter 3, a single pair of klipspringers had stripped the very young bunches from a large proportion of the vines in a vineyard of more than a hectare. Although these bunches did not weigh very much when they were eaten, they represented what would have grown into several tons of grapes. In another incident near Ladismith two groups of klipspringer stripped the shoots of a number of newly planted apricot trees, killing the young plants before they had become established.

Both of these incidents illustrate the principle that klipspringers are likely to be a problem only at critical periods in the growth of certain crops. Thus, if a farmer wants to plant crops in unfenced land adjacent to rocky areas where klipspringers occur, he will have to accept that effort must be spent in chasing them off during those critical weeks. However, while adequate watching or fencing would be the ideal, it is inevitable that requests for permits to shoot problem klipspringers will be sent in by farmers. Since the problems will be caused by groups that have learned to come down into cultivated lands, capture or shooting has to be accepted as the best short-term control method in some cases.

However, discretion should be exercised where the "damage" is a natural phenomenon, such as when complaints are made about klipspringers eating the buds of proteas in natural mountain land used for protea exploitation.

MANAGEMENT TO ENCOURAGE KLIPSPRINGER POPULATIONS

When management to encourage depleted klipspringer populations in a particular area is contemplated, a very cautious approach must be adopted, since extreme measures may actually upset the balance to the detriment of the klipspringers.

For example, even if predators are killing klipspringers occasionally, eradication of these predators may turn out to have an adverse effect on the klipspringer populations if large numbers of dassies are present. In Chapter 9 it was suggested that the dassie is the "dominant" competitor for food in areas with suitable shelter, but they are restricted by predator pressure to feeding within a certain radius of these shelters. However, in some areas where predators have been exterminated the dassies have learned to move out into the flats and to utilise shelters there that would be inadequate for protection from predators. Thus, the eradication of predators is more likely to stimulate the dassie population, which would increase their competition with klipspringers. In addition, with their greater litter size, dassies are able to exploit conditions favourable to population growth more quickly than klipspringers, which produce only one lamb per year.

In spite of the competition between dassies and klipspringers, hunting of dassies is also unlikely to have much effect, because they will soon be replaced if food is available, and the shooting may disturb the klipspringers.

Competition with other antelope is probably not very important, unless they occur in such great numbers that the vegetation in the habitats where they are more commonly found has been heavily overgrazed, with the result that they move into rocky terrain to feed.

Thus the most effective way to encourage klipspringer populations is probably to do no more than reduce disturbance as much as possible. If poachers and stray dogs are kept out and they are left alone, they will have a good chance of building up their numbers gradually.

SUMMARY

The klipspringer is an antelope that is highly specialised for living in rocky mountainous habitat. It shows adaptations in social organisation, feeding behaviour and predator evasion strategy, as well as in anatomy and physiology, which enable it to cope with the unusual conditions of montane habitats.

Klipspringer social organisation is orientated towards demarcating and defending a fixed territory with sufficient food resources to maintain a family group throughout the year. The groups usually consist of a monogamously mated pair with one, or occasionally more, offspring. The male and female spend most of the time within a few metres of each other, which permits a role differentiation where the male spends more time in anti-predator vigilance than the female, who requires more energy for gestation and lactation. A single lamb is born each year, in an extended lambing season from July to December.

Klipspringers show a unique predator evasion strategy where they make themselves conspicuous to watch the predator and avoid being surprised, rather than rely on silence and concealment. This has evolved in response to the lack of sufficient cover for hiding in rocky areas, and is permitted by the klipspringer's superior fleetness in rocky terrain. This is due to a unique digit structure and a small agile body.

The main predator of the klipspringer are the leopard and caracal, although raptors such as black and crowned eagles may take occasional juveniles and possibly adults.

Anatomical and physiological adaptations include an efficient kidney for water conservation and an unusually thick pelage for insulation. These are in response to the climatic extremes which are characteristic of mountainous areas. Efficient water conservation and selection of succulent food enable klipspringers to survive without drinking water, and thereby extend their range considerably by occupying areas without perennial surface water.

Klipspringers show the typical ungulate activity pattern with peaks of feeding in the early morning and late afternoon. Feeding times vary seasonally and between sexes, with increases due to the energy demands of

cold temperatures and gestation and lactation. They are almost entirely browsers, feeding on the shoots, flowers and fruits of shrubs and herbs, and feeding preferences may show a relationship to defensive mechanisms in the plants.

Klipspringers avoid competition with other small antelope by preferring more rocky terrain. Food separation from dassies is also important, and it is suggested that klipspringers avoid large concentrations of dassies because of the latter's tendency to browse the vegetation near their rocky shelters down to a very low food quality.

All these factors play an important role in the conservation of klipspringers and must be considered when management of their populations is contemplated.

OPSOMMING

Die klipspringer is 'n boksoort wat hoogs gespesialiseerd is om rots- en bergagtige habitatte te bewoon. Aanpassings word ondermeer getoon in sosiale organisasie, voedingsgedragspatrone, en roofdier-ontwykingstrategieë, asook anatomiese en fisiologiese aspekte, wat dit in staat stel om die besondere toestande van berghabitatte die hoof te bied.

Die sosiale organisasie van die klipspringer is aangepas om 'n vaste gebied, met voldoende voedsel om die familie groep dwarsdeur die jaar te onderhou, af te baken en te verdedig. Die groepe bestaan gewoonlik uit 'n monogamiese paar met een, of uitsonderlik meer, lammers. Aangesien die ram en ooi die meeste van die tyd 'n paar meter van mekaar af bly, is dit moontlik vir eersgenoemde om gereeld op te tree as "skildwag" teen roofdiere, wat die ooi geleentheid bied om haar hoër energiebehoeftes tydens dragtigheid en melkforming aan te vul. 'n Enkele lam word jaarliks gebore, en die uitgestrekte lam seisoen duur vanaf julie tot desember.

Klipspringers toon 'n unieke roofdier-ontwykingstrategie waar hulle hulself opvallend maak om roofdiere dop te hou asook sodoende verrassing te vermy, instede van staat te maak op verberging soos ander klein boksoorte. Hierdie gedragsaanpassing het waarskynlik ontwikkel weens tekort aan skuilplekke in rotsagtige gebiede, en word moontlik gemaak deur die klipspringer se besondere vermoë om in rotsagtige terrein vinnig te beweeg. Hierdie vlugheid word toegeskryf aan die unieke poot struktuur en klein, ratse liggaamsbou.

Die klipspringer se vernaamste roofdiere is luiperds en rooikatte, terwyl roofvoëls soos die witkruis- en kroonarend soms 'n lam of, by wyse van uitsondering, 'n volwasse individu mag vang.

Anatomiese en fisiologiese aanpassings sluit onder andere in doeltreffende niere vir die beperking van vogverlies, en 'n buitengewoon digte haarbedekking vir isolasie. Hierdie aanpassings word geassosieer met die uiterste klimaatstoestande kenmerkend van bergagtige gebiede. Effektiewe beperking van vogverlies en die selektering van sukkulente voedsel stel die klipspringer in staat om sonder drinkwater te kan klaarkom, en sodoende kan hulle dus hul verspreidingsgebied aansienlik uitbrei.

Klipspringers toon 'n tipiese hoefdier aktiwiteitspatroon bestaande uit piek voedingstye net na dagbreek en voor sonsondergang. Voedingstye varieer seisoenaal en tussen geslagte, en verleng normaalweg weens hoër energie benodighede soos tydens dragtigheid, melkvorming en met lae temperature. Hierdie boksoort is feitlik uitsluitlik blaarvretend en hulle voed op jong spruite, blomme en vrugte van struike en kruide. Voedselvoorkeure toon 'n moontlike verwantskap met die verdedigingsmeganismes van plante.

Klipspringers vermy kompetiesie met ander klein boksoorte deur hulle voorkeur vir die meer rotsagtige terreine. Voedselskeiding met dassies is ook belangrik, gevolglik word dit voorgestel dat klipspringers hoë konsentrasies dassies vermy aangesien laasgenoemde neig tot oorbeweiding van plantegroei in die omgewing van hul skuilplekke.

Al bogenoemde faktore speel 'n belangrike rol in die bewaring van klipspringers en moet in ag geneem word by die oorweging van toepaslike bestuurmatreëls.

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APPENDIX A : Gamka plant species list.

AMARYLLIDACEAE
Brunsvigia sp.

ANACARDIACEAE
Rhus lucida L.
Rhus tomentosa L.

ASTERACEAE
Berkheya angustifolia (Houtt.) Merr.
Chrysanthemoides monilifera (L.) T. Norl.
Chrysocoma sp.
Cineraria sp.
Elytropappus adpressus Harv.
Elytropappus gnaphaloides (L.) Levyns
Elytropappus rhinocerotis Less.
Eriocephalus africanus L.
Eroeda imbricata (Lam.) Levyns
Felicia filifolia (Vent.) Burtt Davy
Helichrysum sp.
Metalasia gnaphaloides Druce
Metalasia langebergensis Salter
Metalasia muricata (L.) D. Don
Pentzia dentata Kuntze
Pentzia elegans DC.
Pteronia incana (Burm.) DC.
Relhania squarrosa (L.) L'Hérit.
Senecio juniperinus L.
Stoebe microphylla DC.

CELASTRACEAE
Maytenus oleoides (Lam.) Loes.

CHENOPODIACEAE
Manochlamys albicans (Ait.) Aell.

CRASSULACEAE
Crassula sp.

DIOSCOREACEAE
Dioscorea elephantipus (L'Hérit.) Engl.

EBENACEAE
- Diospyros dichlorophylla (Gand.) de Winter

ERICACEAE
- Erica cerinthoides L.
- Erica simulans Dulfer

EUPHORBIACEAE
- Clutia alaternoides L.
- Clutia ericoides Thunb.
- Euphorbia sp.

FABACEAE
- Amphithalea ericifolia Eckl. & Zeyh.
- Aspalathus hirta E. Mey.
- Aspalathus pedunculata Houtt.
- Aspalathus rubens Thunb.
- Aspalathus sceptrum-aureum Dahlg.
- Lebeckia sericea Thunb.
- Rafnia racemosa Eckl. & Zeyh.

GENTIANACEAE
- Chironia baccifera L.

GERANIACEAE
- Pelargonium divaricatum Thunb.
- Pelargonium extipulatum (Cav.) L'Hérit.
- Pelargonium glutinosum (Jacq.) L'Hérit.
- Pelargonium myrrhifolium (L.) L'Hérit.

LILIACEAE
- Asparagus capensis L.

MESEMBRYANTHEMACEAE
- Carpobrotus sp.
- Mesembryanthemaceae sp.

MONTINIACEAE
- Montinia caryophyllacea Thunb.

OXALIDACEAE

Oxalis spp. = O. attaquana Salter
O. depressa Eckl. & Zeyh.

POACEAE

Aristida diffusa Trin.
Cymbopogon plurinodis (Stapf.) Stapf. ex Burtt Davy
Cynodon dactylon (L.) Pers.
Digitaria sp.cf. eriantha Steud.
Ehrharta calycina J.E. Sm.
Eragrostis curvula (Schrad.) Nees
Merxmuellera stricta (Schrad.) Conert
Pentaschistis angustifolia (Nees) Stapf.
Stipagrostis zeyheri (Nees) de Wint.
Themeda triandra Forsk.

POLYGALACEAE

Muraltia alopecuroides (L.) DC.
Muraltia ericaefolia DC.
Polygala fruticosa Berg.

PROTEACEAE

Leucadendron salignum Berg.
Leucospermum pluridens Rourke
Leucospermum wittebergense Compton
Protea arborea Houtt.
Protea repens L.

RESTIONACEAE

Restio spp.

RHAMNACEAE

Phylica curvifolia (Presl.) Pillans
Phylica paniculata Willd.
Phylica purpurea Sond.

ROSACEAE

Cliffortia pulchella L.f.
Cliffortia ramosissima Schltr.

RUBIACEAE

Anthospermum spp. = A. aethiopicum L.
A. ciliare L.
A. dregei Sond.
A. tricostatum Sond.

RUTACEAE

Agathosma sp.

SANTALACEAE

Colpoon compressum Berg.
Thesium nigromontanum Sond.

SAPINDACEAE

Dodonaea viscosa Jacq. var. angustifolia Benth.

SCROPHULARIACEAE

Sutera sp.

SOLONACEAE

Solanum tomentosum L.f.

STERCULIACEAE

Hermannia spp. = H. holosericea Jacq.
H. disermifolia Jacq.
H. sp.

THYMELAEACEAE

Struthiola sp.

APPENDIX B : Springbok plant species list

AIZOACEAE

Galenia africana L. var. africana
Galenia fruticosa = G. fruticosa (L.f.) Sond.
G. namaensis Schinz
G. rigida Adamson
Pharnaceum spp. = P. albens L.f.
P. auranticum (DC.) Druce
Tetragonia spp. = T. macroptera Pax.
T. reduplicata Welw. ex Oliv.
T. spicata L.f.

ANACARDIACEAE

Ozoroa dispar (Presl) R. & A. Fernandes
Rhus undulata Jacq. var. tricrenata (Engl.) R. Fernandes

ASTERACEAE

Arctotis revoluta Jacq.
Berkheya spp. = B. ferox O. Hoffm. var. tomentosa Roessl.
B. fruticosa (L.) Ehrh.
Cineraria canescens Wendl. ex Link
Didelta spinosa (L.f.) Ait.
Eriocephalus africanus L.
Eriocephalus ericoides (L.f.) Druce
Euryops spp. = E. multifidus (Thunb.) DC.
E. tenuissimus (L.) DC. subsp. tenuissimus
Osteospermum spp. = O. grandiflorum DC.
O. oppositifolium (Ait.) Norl.
O. sinuatum (DC.) Norl.
Othonna spp. = O. arbuscula (Thunb.) Sch. Bip.
O. furcata (Lindl.) Druce
Pentzia incana (Thunb.) Kuntze
Pteronia spp. = P. ciliata Thunb.
P. glauca Thunb.
P. incana (Burm.) DC.

CAPPARACEAE

Boscia foetida Schinz subsp. foetida

CELASTRACEAE

Maytenus oleoides (Lam.) Loes.

CHENOPODIACEAE

Manochlamys albicans (Ait.) Aell.

CRASSULACEAE

Crassula spp. = C. brevifolia Harv.
C. sp.
Tylecodon paniculatus (L.f.) Toelken

EBENACEAE

Diospyros austro-africana De Wint. var. austro-africana
Diospyros ramulosa (E. Mey. ex A. DC.) De Wint.

EUPHORBIACEAE

Euphorbia decussata E. Mey. ex Bioss.
Euphorbia mauritanica L.

FABACEAE

Indigofera spinescens E. Mey.
Lebeckia sericia Thunb.
Lotononis longiflora H. Bol.

GERANIACEAE

Pelargonium dasyphyllum = P. sp. cf. dasyphyllum E. Mey.
Pelargonium grandicalcaratum Kunth
Pelargonium sp.

LAMIACEAE

Ballota africana (L.) Benth.
Mentha longifolia Huds.
Salvia dentata Ait.
Stachys flavescens Benth.

LILIACEAE

Albuca altissima Dryand.
Aloe dichotoma Mass.
Asparagus asparagoides (L.) Wight
Asparagus aspergillus Jessop

LILIACEAE (cont.)

Asparagus capensis L.

Veltheimia capensis (L.) DC.

LORANTHACEAE

Moquiniella rubra (Spreng. f.) S. Balle

MELIANTHACEAE

Melianthus pectinatus Harv.

MENISPERMACEAE

Antizoma miersiana Harv.

MESEMBRYANTHEMACEAE

Amoebophyllum angustum N.E.Br.

Cheiridopsis sp.

Drosanthemum albens L. Bol.

Mesembryanthemum karroense L. Bol.

Polymita albiflora (L.Bol.) L. Bol.

Ruschia/Leipoldtia spp. = R. brevibracteata L. Bol.
R. cymosa (L. Bol.) Schwant.
R. robusta L. Bol.
R. tribracteata L. Bol.
L. sp. cf. pauciflora L. Bol

MONTINIACEAE

Montinia caryophyllacea Thunb.

OXALIDACEAE

Oxalis sp.

RUBIACEAE

Nenax dregei L. Bol.

SANTALACEAE

Thesium lineatum L.f.

Thesium spinosum L.f.

SAPINDACEAE

Dodonaea viscosa Jacq. var. angustifolia Benth.

Pappea capensis Eckl. & Zeyh.

SELAGINACEAE

Hebenstreitia crassifolia Choisy

SOLANACEAE

Lycium oxycarpum Dun.
Solanum burchellii Dun.
Solanum gifbergense Dun.

STERCULIACEAE

Hermannia spp. = H. cuneifolia Jacq. var. cuneifolia
H. disermifolia Jacq.

ZYGOPHYLLACEAE

Zygophyllum spp. = Z. meyeri Sond.
Z. morgsana L.
Z. retrofractum Thunb.
Zygophyllum divaricatum

APPENDIX C: Cover values for the plots used to classify the habitat types at Gamka, showing the proportion of the vegetation in each height class and the relative importance of the different floristic elements. Ren = renosterbos; Prot = proteoid; Eric = ericoid; Rest = restioid; Gram = graminoid; BG = bare ground; Veg = vegetation; 1 = veg.$<$0,5m; 2 = veg. 0,5 - 1,0m; 3 = veg.$>$1,0m.

Habitat type and plot number	% of vegetation cover					% of total cover					
	Ren	Prot	Eric	Rest	Gram	Rock	BG	Veg	1	2	3
DRY SLOPES											
Outcrops											
2	-	-	-	-	5	50	5	45	40	5	-
10	-	-	-	2	10	50	10	40	30	10	-
11	-	-	-	5	10	50	5	45	30	10	5
13	-	-	-	-	2	50	15	35	25	10	-
16	-	-	-	30	10	50	10	40	30	10	-
19	-	-	-	-	15	50	-	50	15	30	5
20	-	-	-	-	10	45	15	40	35	5	-
21	-	-	-	-	15	45	10	45	35	10	-
25	-	-	-	-	-	45	10	45	10	25	10
26	-	-	-	2	10	50	10	40	30	10	-
28	-	-	-	-	-	50	10	40	30	10	10
mean n=11	0	0	0	4	8	49	10	42	27	12	3
Scree slopes											
1	-	-	-	5	10	30	15	55	20	30	5
3	-	-	-	5	10	30	15	55	45	10	-
4	-	-	-	-	5	25	20	55	45	10	-
12	-	-	-	5	2	40	5	55	35	20	+
14	-	-	-	-	20	30	20	50	30	20	-
15	-	-	-	-	25	30	10	60	35	20	5
17	-	-	-	2	25	25	20	55	45	10	-
18	-	-	-	-	55	35	10	55	35	20	-
24	-	10	-	2	20	40	10	50	30	20	-
27	-	-	-	-	5	50	5	45	35	10	-
29	-	-	-	-	5	50	5	45	35	10	-
mean n=11	0	1	0	2	18	35	12	53	36	16	1
MEAN n=22	0	0	0	3	13	42	11	48	32	14	2

Appendix C continued:

Habitat type and plot number	% of vegetation cover					% of total cover					
	Ren	Prot	Eric	Rest	Gram	Rock	BG	Veg	1	2	3
MOIST SLOPES											
South slopes											
5	-	10	30	10	10	15	20	65	40	25	-
6	30	-	2	20	10	5	25	70	30	30	10
44	-	5	20	10	15	30	5	65	40	15	10
45	-	15	15	10	20	25	10	65	40	20	5
48	-	20	30	15	10	30	10	60	30	20	10
49	-	5	15	20	15	10	20	70	30	25	15
50	5	20	10	15	5	15	20	65	30	25	10
61	-	20	30	15	10	15	5	80	30	30	20
mean n=8	4	13	19	14	12	18	14	68	34	24	10
Outcrops											
51	2	10	5	15	15	35	5	60	30	20	10
52	2	20	10	20	25	20	20	60	35	15	10
53	-	5	-	15	20	45	5	50	40	10	-
54	10	5	-	25	20	25	15	60	50	10	-
60	-	-	-	5	15	45	10	45	25	10	10
46	-	5	5	15	25	40	10	50	35	10	5
59	-	-	-	-	15	40	15	45	25	10	10
64	15	5	10	15	10	50	5	45	15	20	10
73	-	15	-	10	15	30	10	60	15	20	25
74	-	5	-	10	25	45	5	50	30	15	5
mean n=10	3	7	3	13	19	38	10	53	30	14	9
Upper drainage											
62	-	20	30	10	5	5	5	90	20	30	40
63	-	25	30	25	5	15	5	80	30	30	20
69	-	20	15	20	15	25	15	60	20	30	10
76	-	20	25	20	10	10	15	75	30	30	15
mean n=4	0	21	25	19	9	14	10	76	25	30	21
Rocky plateau											
77	-	5	45	20	5	5	30	65	45	15	5
78	-	20	30	20	10	25	15	60	30	20	10
79	-	-	20	10	30	35	-	65	50	15	-
80	-	5	40	10	10	35	5	60	45	15	-
70	-	25	25	15	15	25	15	60	30	20	10
mean n=5	0	11	32	15	14	25	13	62	40	17	5
MEAN n=27	2	12	16	15	14	26	12	62	32	20	10

Appendix C continued:

Habitat type and plot number	% of vegetation cover					% of total cover					
	Ren	Prot	Eric	Rest	Gram	Rock	BG	Veg	1	2	3
PLATEAU											
Grassy plateau											
57	5	-	-	15	60	-	15	85	80	5	-
66	-	-	20	25	25	20	10	70	50	20	-
67	10	-	-	20	25	-	40	60	40	20	-
65	5	10	15	15	15	-	45	55	40	15	-
mean n=4	5	3	9	19	31	5	28	68	53	15	0
Renosterbos											
42	-	-	-	25	15	15	30	55	35	15	5
43	5	-	-	-	10	+	20	80	20	55	5
55	20	-	2	-	10	-	10	90	40	30	20
56	30	-	2	10	15	-	20	80	40	30	10
68	30	-	-	5	35	-	25	75	45	30	-
71	5	-	-	10	35	-	25	75	40	25	10
mean n=6	15	0	1	8	20	3	22	76	37	31	8
Plateau edge											
8	10	-	-	20	10	15	45	40	30	10	+
9	+	-	-	10	20	30	25	45	30	10	5
22	5	-	-	-	20	30	25	45	30	15	-
23	-	-	-	+	+	20	15	65	20	40	5
39	-	-	-	15	10	25	20	55	35	20	-
40	-	-	-	10	10	25	15	60	25	30	5
41	-	5	-	10	10	15	15	70	25	40	5
58	-	5	-	15	5	20	15	65	25	35	5
72	+	-	-	-	20	-	25	75	55	15	5
mean n=9	2	1	0	9	12	20	22	58	31	24	3
MEAN n=19	5	1	2	11	18	11	23	66	37	24	4
VALLEY BOTTOM											
7	-	-	-	5	10	15	30	55	25	20	10
31	10	-	5	2	20	20	5	75	35	30	10
32	25	5	3	5	20	25	15	60	25	25	10
33	10	-	-	-	20	20	5	75	30	30	15
34	-	-	-	-	15	20	10	70	30	15	25
35	-	-	-	10	15	25	20	55	25	20	10
36	10	-	-	-	15	10	20	70	20	20	30
37	-	-	-	10	10	25	10	65	35	20	10
38	10	10	-	20	15	25	10	65	35	20	10
47	-	-	-	-	10	35	5	60	15	10	35
75	35	-	-	10	15	15	10	75	20	25	30
MEAN n=11	9	1	1	6	15	21	13	66	27	21	18

APPENDIX D: Cover values for the habitat analysis plots in the main klipspringer study territory at Springbok, showing the percentage of total cover made up by rock, ground and total vegetation, and the three height classes of vegetation.

Plot number	% of total cover					
	Rock	BG	Veg.	<0,5m	0,5-1,0m	>1,0m
ROCKY KOPPIES						
1	40	20	40	10	25	5
2	40	30	30	15	15	-
3	30	50	20	10	10	-
4	50	20	30	5	10	15
5	40	10	50	20	20	10
6	20	30	50	30	20	-
7	75	10	15	15	5	-
8	45	30	25	15	10	-
9	5	40	55	45	10	-
10	50	30	20	20	-	-
11	20	30	50	40	10	-
12	10	30	60	35	20	5
13	5	35	60	35	20	5
14	25	30	45	35	10	-
15	40	20	40	30	10	-
16	45	15	40	35	5	-
Mean n=16	34	27	39	25	13	3
FLATS						
A	5	35	60	60	-	-
B	-	75	25	20	5	-
C	-	70	30	25	5	-
D	-	85	15	5	10	-
E	-	70	30	25	5	-
F	-	75	25	15	10	-
G	-	70	30	25	5	-
H	-	40	60	20	40	-
I	-	65	35	15	18	2
J	-	65	35	15	18	2
K	-	80	20	15	5	-
L	-	70	30	15	15	-
M	-	80	20	15	5	-
Mean n=13	0	68	32	22	10	0

APPENDIX E : Measurements from klipspringers shot during the study.

				Measurements (mm)						
No.	Locality	Date Shot	Body mass (kg)	Total length (curves)	Tail	Shoulder height	Hind foot	Ear	Horns L	R
♀ K1	Springbok	78-06-28	13,5	890	70	470	240	115	-	
♂ K2	"	78-07-06	13,0	860	70	510	230	110	90	84
♀ K3	Gamka	78-07-26	13,6	890	60	500		100	-	
♂ K4	"	78-08-01	14,0	920	50		250	108	91	92
♀ K5	"	78-08-03	14,7	880	70		250	100	-	
♀ K6	Franschhoek	78-08-29	15,6 (with foetus)	930	40		230	108	-	
Foetus	"	"	1,25	450	37	270	130	60	-	
♂	Springbok	79-02-15	11,5	850	75	490	235	120	82	90

APPENDIX F : Observations associated with the eviction of klipspringer offspring from their parental groups.

Gamka: 77-04-16 - 09h30. Group 1 of four klipspringers - 11♂, 12♀ adult ♀ 13 (probably last year's offspring) and juvenile ♂14; as 11♂ moves close to 13♀ she jumps aside out of his way ----------------10h20; 13♀ moves off on her own to over 100 m away ----------------10h35; 13♀ suddenly appears running away from adjacent ♂21, who chases her ± 200 m across the bottom of group 1's territory - then he gives up and walks back, but 11♂ comes nearer and chases him 50 m back to his own territory - both stop, and start feeding about 30 m apart (displacement activity ?) - after a while 21♂ moves off round the corner and 11♂ walks back to his ♀ 12, who nuzzles and grooms him elaborately - after about ½hr 13♀ comes back and is groomed lightly by 12♀, and 11♂ stands right next to her showing no aggression at all.

Gamka: 77-04-20. Group 1 of four klipspringers surprised from close - ♂, ♀, J♂ run off together in one direction but 13♀ runs in the opposite direction 13♀ only rejoins the others about an hour later.

Gamka: 77-04-24. Group 1 of four klipspringers - 13♀ standing on rock while 11♂ and 12♀ groom each other 10 m away - 12♀ stops grooming and moves up towards 13♀ who stands relaxed but 12♀ suddenly charges at her and chases her about 100 m away - 12♀ stands and watches 13♀ for a while, then scent-marks profusely and slowly moves back to her mate.

Gamka: 77-04-27. Group 1 seen again but without 13♀.
" 77-07-28. Group 1 - 13♀ spent whole day with them - no aggression observed.
" 77-08-04. Group 1 - without 13♀.
" 77-08-09. Group 1 - without 13♀.
" 77-10-17. Group 1 feeding together - after a while 13♀ appears some distance away and moves towards them all alert and watching her - as she approaches 12♀, 12♀ lowers head in mild threat, but 13♀ does not react - later 12♀ grooms 13♀.

Springbok: 77-06-02. Main study group of pair with full-grown ♀ offspring, both ♀♀ feeding - adult ♀ suddenly butted her daughter sharply with the side of her head, groomed her briefly, then butted her again so that she ran out of reach.

Springbok: 77-08-31. Same pair but full-grown offspring disappeared and replaced by 1-2 month old infant.

Springbok: 77-09-02 and 77-09-04. Single young ♂ with short horns. Seen twice in main study territory but well away from the study group.

Springbok: 77-09-05. Study group above house seen chasing a young ♀ across the road; ♂ was about 20 m ahead of the female; all panting heavily so must have run some way.

Springbok: 77-11-04. Two males with long horns seen together.

Springbok: 78-02-10. Group of three klipspringers, a three quarters grown juvenile and two males with long horns, no female visible.

Springbok: 78-07-04. Group of five klipspringers seen - 3 adult ♂♂, 1 ♀ and 1 juvenile ♂ - when disturbed one ♂ ran off on his own but the others stayed together, and were still together two days later.