Factors influencing productivity in sympatric populations of Mountain Reedbuck and Grey Rhebok in the Sterkfontein Dam Nature Reserve, South Africa

By

William Andrew Taylor

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By William Andrew Taylor

Supervisor: Professor J.D. Skinner
Veterinary Wildlife Unit
Faculty of Veterinary Science
Onderstepoort
Co-supervisor: Professor R.C. Krecek
Department of Zoology and Entomology
Faculty of Natural and Agricultural Sciences
University of Pretoria

ABSTRACT

Productivity of grey rhebok and mountain reedbuck was studied at Sterkfontein Dam Nature Reserve (eastern Free State) between September 1999 and May 2002. Within a study area of 550 ha, all herds of grey rhebok and all territorial male mountain reedbuck were identified, and general population dynamics were monitored. Lambs of both species were born seasonally between September and February, while most deaths occurred between June and November. Population levels appeared to be controlled in both species mainly by the eviction of young males, but the effects of extreme weather conditions were significant, being demonstrated by the deaths of 27 % and 51 % of the grey rhebok and mountain reedbuck populations respectively during heavy snow in September 2001. Disease and predation played no role in population control. Grey rhebok formed stable harem herds with home ranges varying between 23 ha and 104 ha (95 % MCP), with an average of 57.9 ha. Home ranges in areas with extensive steep slopes tended to be smaller than those in flatter areas. The ecological density was 1/15.7 ha. Territorial male mountain reedbuck were often solitary, and only accompanied by females when these moved into their territories. Home ranges of males varied between 7 ha and 21 ha (95 % MCP), with an average of 14.8 ha, and all had areas of steep slopes within. Females showed strong preference for steep slopes and used much greater areas than males. The ecological density was 1/8.7 ha.

Grey rhebok rested less than mountain reedbuck, but did not feed for longer. Grey rhebok were active intermittently all day and night, but tended to be more active in the early morning and late afternoon than in the middle of the day. During the day, mountain reedbuck were most active in the late afternoon, rested for longer periods in the middle of the day, but were also very active at night. Body condition was investigated seasonally in mountain reedbuck at Sterkfontein and also Tussen die Riviere Nature Reserve. Kidney fat indices and leg fat percentages were lowest at the end of winter before the rains started and when the nutritive value of the veld was at its lowest. Endoparasites were investigated in both antelope species, but primarily in mountain reedbuck. Seventeen species of helminths, including fifteen nematodes, one trematode, and one cestode were recovered from mountain reedbuck at Sterkfontein and TdR. The most prevalent and abundant species were *Cooperia yoshidai*, *Longistrongylus schrenki* and *Haemonchus contortus*. Five nematode species were recovered from four grey rhebok at Sterkfontein.

Key words: Grey rhebok, *Pelea capreolus*, mountain reedbuck, *Redunca fulvorufula*, productivity, population dynamics, home ranges, behaviour, body condition, nematodes.

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Chapter 1

INTRODUCTION

Grey rhebok (*Pelea capreolus*) and southern mountain reedbuck (*Redunca fulvorufula fulvorufula*) are two similar sized and similar looking antelope species found in South Africa. Both use rocky hillsides and mountain slopes that form marginal habitat for most other ungulate species as well as domestic livestock. In many areas of South Africa they are sympatric (Figure 1).

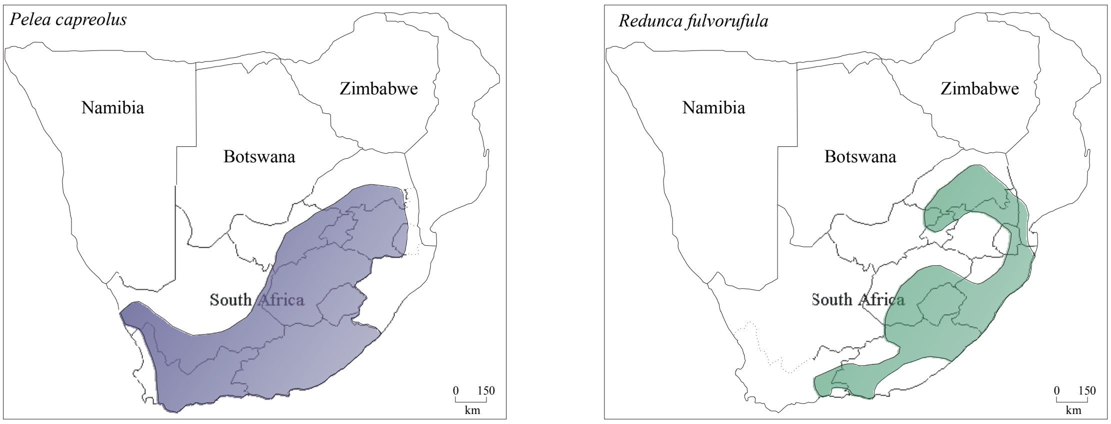


Figure 1. The geographic distribution of grey rhebok and southern mountain reedbuck within South Africa.

The favoured habitat of grey rhebok is steep grassland at high altitudes (Rowe-Rowe, 1983, 1994), where they feed selectively and almost entirely on forbs (Ferreira & Bigalke, 1987; Beukes, 1988). Only two social groups have been recorded, these being solitary males and harem herds (Esser, 1973; Ferreira, 1983; Beukes, 1984), while bachelor groups have not been observed. Harem herds are small, numbering up to 12 individuals, and comprise one adult male, several females and accompanying young.

The living requirements of mountain reedbuck are also steep grasslands (Rowe-Rowe, 1983, 1994), where they are selective grazers, feeding only on certain grass species (Irby, 1976). Social organisation consists of territorial males, non-territorial males, female herds with young, and bachelor groups (Irby, 1976; Skinner & Smithers, 1990). Female herds are normally small, comprising 3-8 individuals in unstable groups that change size and composition frequently. These females regularly move between territories of different males (Irby, 1976; Dunbar & Roberts, 1992).

The present study was conducted within a research theme at the Faculty of Veterinary Science that was aimed at the improvement in quality of life for local disadvantaged communities. These people were intended to be the recipients of reduced meat prices under the South African Governments Reconstruction and Development Program (RDP). Improving levels of production of game species would logically be beneficial to this scheme, so one of the goals of the present study was to increase ecological and biological knowledge of mountain reedbuck and grey rhebok that could be used to improve management practices related to productivity. This would not only benefit such RDP schemes, but also private game farmers and Nature Reserve managers that are involved in hunting and ecotourism ventures.

The game ranch and ecotourism industries in South Africa have been expanding rapidly over the past decade, and are predicted to continue growing at a fast rate (Rudder, 2000). Although there has been a vast amount of research conducted on wildlife within southern Africa in the last 50 years, which has resulted in the acquisition of considerable knowledge for application to game management, there is still a need for increased knowledge of individual species ecology for areas and species where this knowledge is lacking. Game ranching and ecotourism seek optimal use of space by antelope species because there is a lot of money to be made in hunting, sale of live animals, and game viewing. The more animals that can be removed in a sustainable manner, the higher the financial return, while tourists generally want to see as many animals as possible within a given time.

Optimising management practices requires sound knowledge of a wide range of biological and ecological factors including the following:

1) Optimal stocking/population densities. This is affected by social structures, home ranges and territory sizes, as well as resource availability and carrying capacities of the habitat;
2) Reproductive patterns. This is important because there are periods in the year when cropping animals would be counter-productive (e.g. removal of pregnant or lactating females would result in the loss of foetuses or young as well, and this would reduce the population growth rate);
3) Population dynamics. Knowing when changes in populations normally occur allows removal of animals before they are lost naturally (whereby they provide no income), and knowing the causes of change allows possible prevention of losses;
4) Seasonal variation in body condition. This is useful to assess the time of year when animals will provide the most meat.

Both grey rhebok and mountain reedbuck are popular game ranch species, and are increasingly being sold at game auctions and translocated between nature reserves and other game areas. In most cases, however, only a limited amount of ecological knowledge, such as habitat suitability or social structure, is put into practice when moving game between different areas. Home range and territory requirements are generally not considered, while male spacing patterns and hierarchies are often ignored. Considerable time and money invested in new animals intended for increased genetic variability would be wasted if there were not enough resources and space for them, while the success of translocations would increase if species ecological knowledge was better known and put into practice.

Mountain reedbuck are commonly hunted for trophies and meat/biltong production, and could potentially provide a considerable secondary form of income in both game and domestic livestock areas where there is marginal habitat that is not optimally utilised. Moreover, they could do this without competing with other antelope species or domestic livestock for precious grazing resources. In contrast, grey rhebok are hunted primarily for trophies, while their flesh is generally not sought after because of a perception that it is not good to eat and is often riddled with worms (Skinner & Smithers, 1990). Although optimising meat production output is unlikely to be important in the management of this species in the future, good ecological information is still needed for more efficient trophy hunting and ecotourism practises.

Relative to some other South African antelope species, such as impala (*Aepyceros melampus*) and springbok (*Antidorcas marsupialis*), grey rhebok and mountain reedbuck have not been as extensively studied. Of the latter two, mountain reedbuck have been studied most, with Irby (1975, 1976, 1979, 1981, 1982) reporting on aspects including growth and ageing, meat production, reproductive patterns, population parameters, habitat requirements and use, and potential population controls. Norton (1989) comprehensively covered the population dynamics of mountain reedbuck by examining population census data, cull figures, reproduction, age structure, recruitment and mortality. Roberts & Dunbar (1991), and Dunbar & Roberts (1992) investigated territory quality and activity patterns of Chanler's mountain reedbuck (*Redunca fulvorufula chanleri*) in Kenya. Despite these wide-ranging investigations, some aspects were not covered in great detail, and there still remain gaps in knowledge.

Grey rhebok ecology is less well known, but aspects that have been investigated include habitat requirements (Beukes, 1984), feeding behaviour (Ferreira, 1983; Beukes, 1984, 1988; Ferreira & Bigalke, 1987), body condition (Beukes, 1984) and a few other lesser aspects of their biology (Esser, 1973).

AIMS

The primary aim of the present study was to investigate factors that influence productivity in grey rhebok and mountain reedbuck that might be useful in management practices. These factors were broken down into five categories, all of which were considered important for understanding productivity. There are other aspects of ecology that are relevant to this topic, but these were not within the scope of the study. The five categories were as follows:

1) ***Population dynamics***. Knowing how and why population's change with time is a critical part of understanding and potentially exerting some control over productivity. It is also important for the management of free ranging populations. Population dynamics studies generally investigate rates of increase and decrease in population size, but rarely find or even look for the causes of changes resulting in deaths. Predation may be considered, but disease and parasites generally are not, even though these factors can exert dramatic influences (Wilson *et al.*, 2002). Understanding the causes of animal losses in more detail would have obvious benefits for managing populations because of the possibility of using the knowledge to improve survival rates;

2) ***Home ranges/territories***. Knowing spacing patterns and area requirements of animals is important when managing population sizes and stocking densities. Although home ranges of both species have been determined before, they were not investigated rigorously, while the present study allows a comparison between the two in an area where they occur together;

3) ***Behaviour***. There is a connection between behaviour and productivity whereby the time spent feeding is correlated with the amount of food eaten, which in turn is correlated with body condition (assuming constant food supply and quality). Seasonal changes in veld condition are well documented, so the main purpose of the behavioural study was to investigate seasonal differences in feeding behaviour and compare this with known veld condition variation. Additionally, due to the differences in food types of the two species, there should be differences between them in time spent feeding;

4) ***Body condition***. Mountain reedbuck are cropped for meat and biltong production, and may be marketed to a limited extent at subsidised prices to disadvantaged communities. Little is known, however, about their meat production potential and how this varies seasonally. With the other investigations being conducted concurrently during the present study, the additional information provided by a seasonal index of body condition can be used in the analysis of population dynamics;

5) ***Endoparasites***. Endoparasites can have significant affects of the health of animals (Wilson *et al.*, 2002), either by competing for ingested nutrients within the gastro-intestinal tract (GIT), or by causing disease. Moderate endoparasitic infections can reduce productivity, while extreme loads may prevent reproduction and even kill animals. The endoparasites of mountain reedbuck have been investigated to a limited extent (Irby, 1976; Boomker *et al.*, 2000), but only by looking at species occurrence (no seasonal effects were searched for), while the effect of parasite loads on productivity were not considered. Endoparasites of grey rhebok are less well known (Boomker & Horak, 1992).

The intention of the present study was not only to investigate productivity separately in the two species, but also to make comparisons between them. This was done in the population dynamics, home range and behaviour sections. Unfortunately, while mountain reedbuck were culled during the study, grey rhebok were not, so body condition and endoparasitic loads were only investigated systematically in the former, while investigations of parasites in grey rhebok were confined to a small number of carcasses from natural mortalities.

Chapter 2

STUDY SITES

Sterkfontein Dam Nature Reserve

The majority of the study was conducted at Sterkfontein Dam Nature Reserve (hereafter Sterkfontein) (S 28° 24’, E 29° 02’), situated approximately 20 km south-west of the town of Harrismith in the eastern Free State of South Africa (Figure 2). It has a total area of 17770 ha, of which 6940 ha are covered by water when the dam is full. Altitudes vary from 1 700 m around the dam to 2325 m in the hills at the south end of the Reserve. Sterkfontein has a mild climate with summer rainfall (Figure 3). Extreme maximum and minimum temperatures recorded are 38° C and -11° C respectively with an overall average of 17° C. Annual rainfall averages 680 mm in the northern part of the Reserve, but may reach 1400 mm on the high ground of the south. Occasional snow and frequent burning have a major influence on the vegetation.

Sterkfontein is a relatively new Provincial Nature Reserve and was created as a result of the dam construction. In the early 1960’s it was determined that the capacity of the Vaal Dam would not be sufficient to cater for the water needs of the Gauteng region. As a result, the Tugela-Vaal scheme was developed to pump water from the Tugela River via the Sterkfontein Dam to the Vaal Dam. Sterkfontein Dam was to act as a reservoir for the Gauteng industrial area. The Dam, a joint project of the Department of Water Affairs and Escom, was completed in 1986 and is included in the international register of the world’s largest dams. On completion it was the world’s second largest earth wall and the largest without a spillway. The Dam and land area around it, owned by the Department of Water Affairs, was mandated to the Free State Conservation Department and proclaimed a Provincial Nature Reserve in 1989.

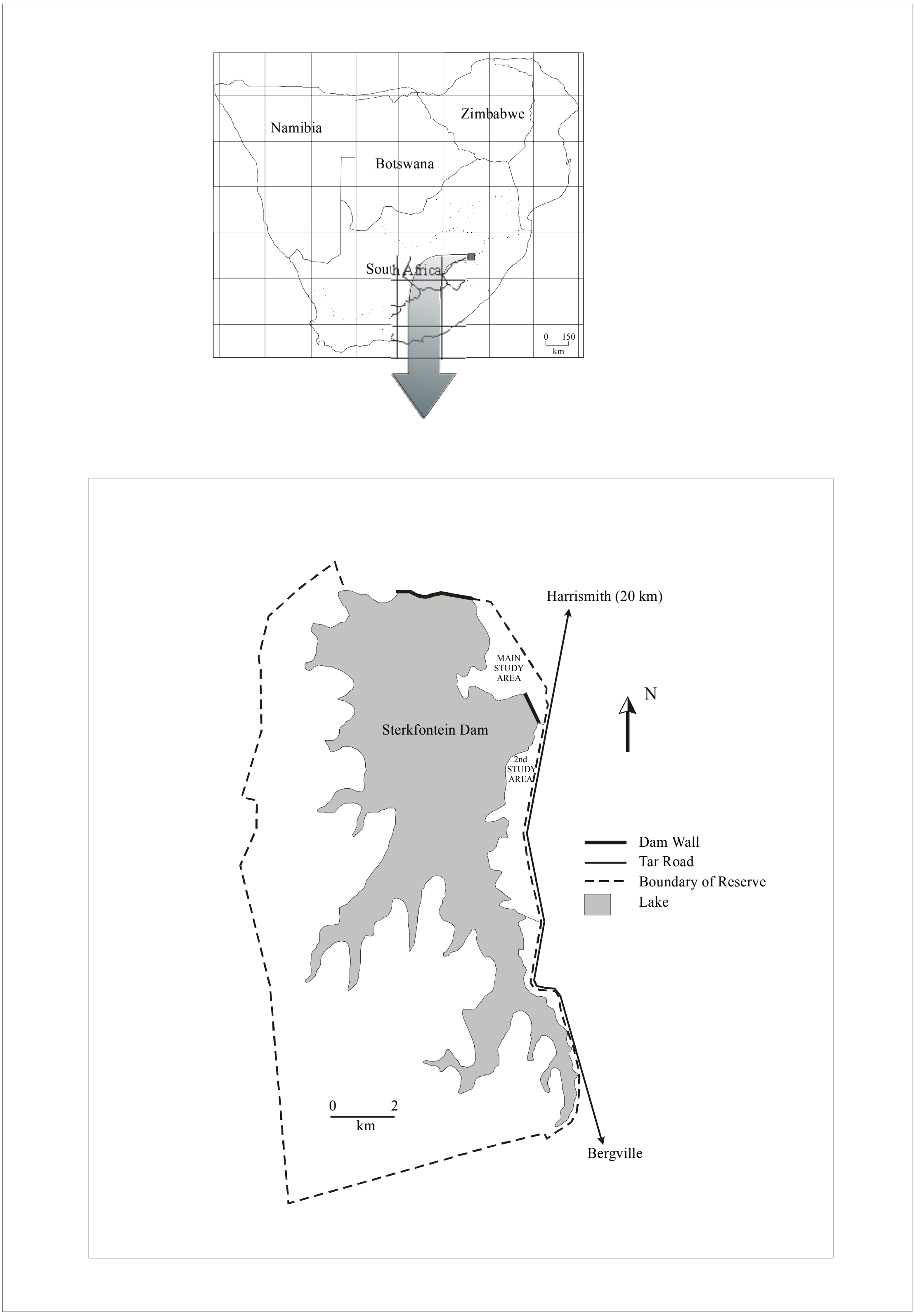


Figure 2. Sterkfontein Dam Nature Reserve.

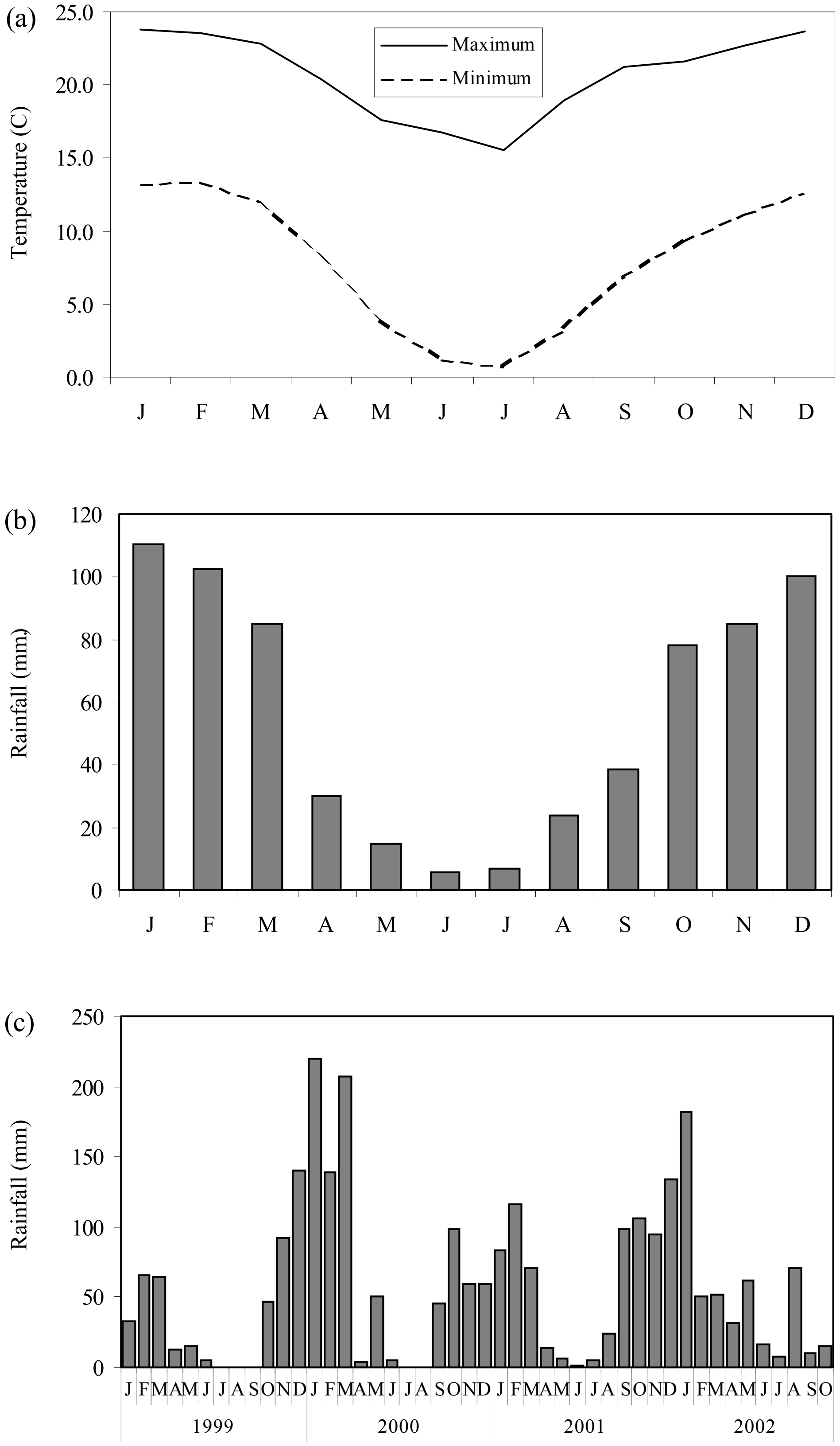


Figure 3. Climatic variables of Sterkfontein Dam Nature Reserve: (a) Maximum and minimum temperatures; (b) Average rainfall over 25 years between 1977 and 2002; (c) Rainfall in main study site during the study period.

Sterkfontein falls within the Grassland Biome, and has been split into two vegetation types: Moist Cool Highveld Grassland in the north (Bredenkamp & van Rooyen, 1996) and Wet Cold Highveld Grassland in the south (Bredenkamp, van Rooyen & Granger, 1996). In pristine condition, the former is dominated by *Themeda triandra*, with other grass species encountered including *Eragrostis superba, Brachiaria serrata, Heteropogon contortus, Cymbopogon plurinodus, Setaria sphacelata* and *Tristachya leucothrix*. There are many dicotyledonous forbs including *Tephrosia semiglabra, Ipomoea obscura, Sutera atropurpurea, Helichrysum* spp., *Crabbea acaulis, Hermannia depressa* and *Rhynchosia totta*. Deep, red (Hutton) and yellow (Clovelly) soils occur mostly on Karoo Sequence sediments but also on shale (Witwatersrand Supergroup) and andesitic lava (Ventersdorp Supergroup).

Structurally, Wet Cold Highveld Grassland is grassland, but a woody layer between 3 and 5 m may form dense thickets in places. This woody layer comprises *Leucosidea sericea, Euclea undulata, Diospyros whyteana, Myrsine africana and Rhus dentata*. North facing slopes are dry and poor in grass species, being dominated by *Hyparrhenia hirta* and *Aristida diffusa*. Other grass species include *T. triandra, Eragrostis curvula, C. plurinodus* and *T. leucothrix*. South facing slopes are relatively moist, where species rich, dense thickets with a sparse undergrowth are dominated by a non-grassy herbaceous layer. Characteristic species are the grass *Poa annua*, and forbs *Sutera polelensis, Stachys kuntzei* and *Clematis oweniae*. This is mountain grassland, with the typical cool, wet Drakensburg montane climate and severe frost. Soils, typical of a mountain landscape, are shallow lithosols, mainly representative of the Glenrosa and Mispah soil forms. Sandstones and mudstones of the Elliot and Molteno Formations (Karoo Sequences) and the Beaufort Group are predominant rock types.

The main study site comprised an area of 550 ha in the north-eastern sector of Sterkfontein, between the main wall and small eastern wall (Figure 2). The area was enclosed on three sides by 2.4 m high game fencing and the remaining boundary was set by the water level of the dam. The populations were, therefore, self-contained with limited influx of new genetic material. The average annual rainfall during the study was 682 mm (Figure 3c), and altitudes varied between 1700 m and 1900 m. Within this area all population studies, behavioural studies and home range investigations were conducted. Also, in May and August 2001, two culls removed 12 mountain reedbuck, and a further two animals were collected in February 2002.

The land on the northern boundary of the study area belonged to the Department of Water Affairs. It formed steep hillsides and contained herds of grey rhebok and mountain reedbuck at densities thought to be similar to those on the side of Sterkfontein (pers. obs.). The land adjacent to the north-eastern boundary was used for commercial cattle grazing, where there were relatively low densities of grey rhebok and mountain reedbuck (pers. obs.), while that to the east was used for arable crops. There was no game on this area.

South of the main study area was a separate section of Sterkfontein, which formed the second but less extensively used study site. Although adjacent to the main study area, it was isolated from it by a game fence. This second site was situated on the south side of the small eastern wall (Figure 2) and comprised an area of approx 800 ha. Weather conditions and altitudes were very similar to those of the main study area. This section was used for culling mountain reedbuck, and between March and December 2000 four culls removed 20 animals. A further five animals were collected from this area in November 2001 and February 2002.

Tussen die Riviere Nature Reserve

Tussen die Riviere Nature Reserve (hereafter TdR) (S 30° 30’, E 26° 07’) is situated approximately 20 km east of the town of Bethulie in the southern Free State of South Africa (Figure 4), at the confluence of the Gariep (formerly Orange) and Caledon Rivers. The total area of the reserve is approximately 22 000 ha and the altitude varies between 1200 and 1500 m. The climate is defined as arid (steppe), cold and dry, with a mean average temperature of 18° C (Werger, 1973). Annual rainfall averages 420 mm per year (Figure 5). TdR falls in the Eastern Mixed Nama Karoo, part of the Nama Karoo Biome (Hoffman, 1996), previously the False Upper Karoo (Acocks, 1988). Although this was considered the most degraded of all vegetation types in South Africa (Acocks, 1988), Werger (1973) recorded a marked recovery of the veld after the withdrawal of farming and the creation of TdR in 1967.

TdR has a complex mix of grass and shrub dominated vegetation types. Common shrubs include *Pentzia incana, Eriocephalus ericoides, E. spinescens* and *Hermannia* spp., while dominant grass species include *Aristida* spp., *Eragrostis* spp. and *Themeda triandra*. Tree species, including *Acacia karoo* and *Celtis africana*, are commonly found along the rivers, but are not abundant elsewhere. Beaufort Group sandstones and shales dominate the landscape, with the flat-topped landscape shaped by many dolerite dykes and sills.

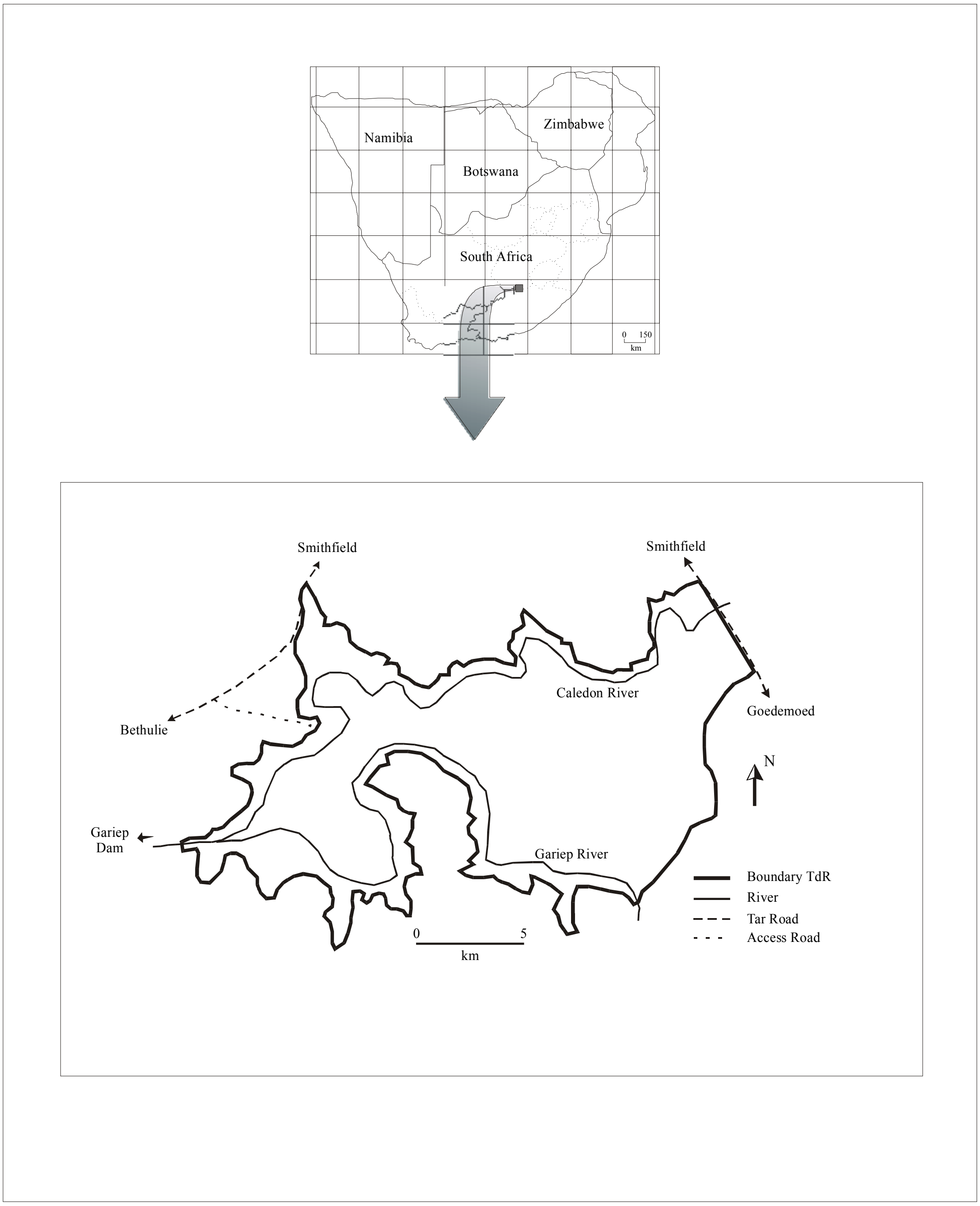


Figure 4. Tussen die Riviere Provincial Nature Reserve.

Mountain reedbuck are regularly hunted and culled at TdR and biological material was obtained from 41 animals collected between December 1999 and June 2001. No observations were made on live mountain reedbuck at TdR, while grey rhebok do not occur there.

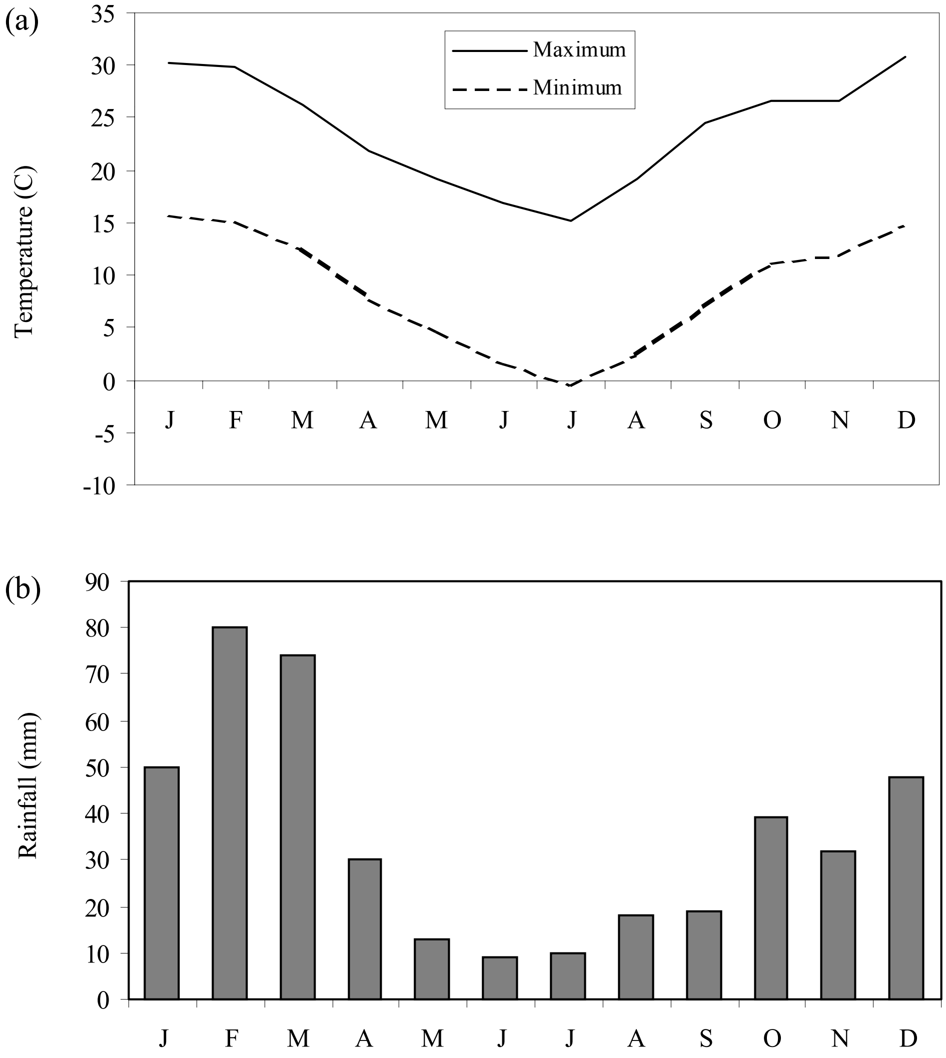


Figure 5. Climatic variables of Tussen die Riviere: (a) Maximum and minimum temperatures, (b) average rainfall for 23 years. Recorded at Goedemoed.

Chapter 3

POPULATION DYNAMICS

Introduction

Population dynamics is the study of temporal changes in the number and composition of individuals in a population, and the factors that influence those changes. It is important for successful management and conservation, and involves four basic components of interest to which all changes in populations can be related: births, deaths, immigration and emigration (Caughley & Sinclair, 1994).

Birth rates are affected by age at first reproduction, birthing intervals, average number of young produced, and the quality and quantity of food available when there are new lambs. The death rate is normally age-specific and sometimes sex-specific, and is related to survival and longevity. The mating system and degree of territoriality of a species, as well as the suitability of the surrounding habitat affect dispersal, which is the movement of an animal from its natal area of birth to a new area, where it breeds (Caughley & Sinclair, 1994). This is an understudied and poorly understood component of wildlife population dynamics but is critical to the long-term persistence of a species. Sex ratios, mating systems and age structures also affect how many animals within a population are able to breed.

Some of the basic components of population dynamics have been described for grey rhebok (Esser, 1973; Ferreira, 1983; Beukes, 1984, 1988; Rowe-Rowe, 1994). This antelope either forms social herds in which an adult male maintains a small harem of between two and five females as well as the young born that year, or males remain solitary (Ferreira, 1983). In the former, the mating system is female defence polygyny, while solitary males do not get the opportunity to mate. Also, because one male sires offspring with more than one female, there is strong competition amongst males for females. Groups containing up to 10 females may occur, but larger herds are rare, and temporary aggregations of two groups are only likely to occur if one male is absent. This is because territoriality is very strong and males do not tolerate rivals within their home ranges (pers. obs.). Adult males without a harem do not generally form bachelor herds, although yearling males may form temporary associations after they have been evicted from their natal groups. Grey rhebok are seasonal breeders, with females producing a single lamb between November and January in the Free State and Kwa-Zulu Natal (Ferreira, 1983; Rowe-Rowe, 1994) and during August in the Western Cape (Beukes, 1984). Little has been recorded about the age at first reproduction and birthing intervals, while death rates (Oliver, Short & Hanks, 1978) and dispersal (Esser, 1973) have not been well investigated. For the latter, young males leave their natal herds just before new lambs are born.

The population dynamics of mountain reedbuck in the Karoo, South Africa have been covered comprehensively by Norton (1989). Social organisation consists of territorial males, non-territorial males, herds of females with young, and bachelor groups (Irby, 1976). Female herds normally consist of small groups of 3 - 8 individuals, but congregations of over 30 animals may occur under certain circumstances (pers. obs.). All female groups are unstable, with females and young moving from herd to herd (Irby, 1976). The mating system is resource defence polygyny. Territorial males occupy their territories all year while females move from one male’s territory to another. These males generally do most of the breeding (Irby, 1976), but have no control of females once they move out of the males’ territories. There is then a greater chance for opportunistic mating by non-territorial male mountain reedbuck than for solitary male grey rhebok. Although mountain reedbuck are considered aseasonal breeders and single lambs may be born at any time of year, there is a distinct birth peak between November and January in South Africa (Irby, 1979; Norton, 1989). Age at first reproduction in females is approximately 15 months (Irby, 1979; Norton, 1989) while birthing intervals are eight months to one year. Mortality rates are relatively high in juvenile animals, particularly immature males, low in young and middle age classes (with no differences between sexes), and relatively high again in older age classes ≥ 7.5 years. Adult sex ratios vary from 1 M: 1.64 F to 1 M: 3.3 F (Irby, 1979; Norton, 1989). Young males are evicted from their natal areas between nine and 15 months age.

Population dynamics is a key factor in the investigation of productivity and forms an integral part of the present study. Sterkfontein offers a different type of habitat to those areas of past research and has a low density of predators, simplifying interpretation of results. Additionally, the presence of both mountain reedbuck and grey rhebok together allows for a comparative study that has not been done before. The aims of this component of the study were to investigate population dynamics in grey rhebok and mountain reedbuck by determining rates of birth, death, immigration and emigration, and to compare and contrast the two species. To accomplish these aims, the following questions were considered:

a. What are the levels of fecundity in the two species and how do they compare?
b. What time of year are lambs born, what are the sex ratios of lambs, and what are the survival rates of lambs?
c. What are the levels of mortality in the two species and how do they compare?
d. What are the causes of death amongst the populations?
e. What time of year do deaths occur, and which animals die?
f. Does disease play a role in mortality?
g. How much immigration and emigration occurs?
h. Which animals emigrate and when?
i. How often do changes in male territorial ownership occur?

Methods

Study site and animals

This component of the study was conducted in the main study site at Sterkfontein, in an area of approximately 550 ha (see Chapter 2). This area was enclosed on three sides by 2.4 m game fencing, while the remaining boundaries were set by the water level of the dam. Although a small number of animals were known to enter the site from surrounding farmland or reserve land, possibly through improperly shut gates, most animals could not escape and were confined to the area. The populations were, therefore, self-contained with limited influx of new genetic material. The land on the northern boundary of the study area contained herds of grey rhebok and mountain reedbuck at densities thought to be similar to those on the side of Sterkfontein (pers.

obs.). The land adjacent to the north-eastern boundary was used for commercial cattle grazing, where there were low densities of grey rhebok and mountain reedbuck (pers. obs.), while that to the east was used for arable crops. South of the study area was a separate section of Sterkfontein.

Grey rhebok were monitored within the main study area between October 1999 and July 2002, while mountain reedbuck were monitored between February 2000 and April 2002. The only breaks of longer than two weeks during this observation period were February to April 2001 and three weeks in August 2001. At the beginning of the study there were 35 grey rhebok within the area, comprising six herds and one solitary male, and there were approximately 66 (± 5) mountain reedbuck.

Six herds of grey rhebok were monitored within the study area, and these were identified numerically as Groups 1 through 6 according to their geographic position within the study area. Within each herd a male maintained a harem of females plus the current year's offspring. It was possible to differentiate herds by identifying these harem males because they all had characteristic horn shapes. Group identification was facilitated by their habit of sticking rigidly to home ranges, rarely venturing into another group's territory. Each time a group was encountered, the number of adult males, adult females, juveniles and lambs were recorded. This was done approximately five days a week, but only once a day per group, and always at the first observation to avoid observer interference. Changes in population structure were then easily established.

In contrast, mountain reedbuck did not remain in rigid groups. Males were territorial but defended an area without maintaining a harem. They generally excluded other males and could thus be identified by their geographic positions as well as horn shape. Their presence or absence was recorded approximately five days a week and the number of attending females and young noted. Female mountain reedbuck and their young roamed freely and moved between territories of different males, but without the aid of distinguishing physical characteristics or well-defined home ranges, they were impossible to identify. Moreover, yearling females cannot be reliably differentiated from adult females in the field (Irby, 1976; Norton, 1989). Although they were counted daily, even when unattended by males, full counts were only made once every two weeks by traversing the entire area on foot and in a vehicle. It was not possible to count mountain reedbuck lambs because their hiding behaviour made them extremely difficult to see or flush out.

Helicopter counts of mountain reedbuck and grey rhebok were carried out at Sterkfontein in July 2001 and July 2002. These were compared with actual numbers known from direct long term ground observations.

Changes in population size

Changes in grey rhebok numbers were easily detected and any incoming or outgoing animals were immediately noticed. Most lambs were born at the same time of year, and when it was time for females to give birth, they moved away from the herd and remained in a small area away from possible interference. These sites were most commonly areas of long grass or herbaceous vegetation, often in areas of low human activity. Such females were monitored frequently until new lambs were sighted and this allowed infant survival rates to be determined.

Changes in adult male mountain reedbuck populations were easy to establish, but this was not the case for females and lambs, for reasons discussed above, and they could only be monitored on a very rough population level. Infant births and deaths could not be monitored at all. However, as 20 adult mountain reedbuck females were culled during the study, and 12 fresh carcasses of adult females that died in snow were examined, pregnancy rates and foetus weights could be established. From the latter, dates of birth could be extrapolated using the Hugget & Widdas (1951) formula adapted by Norton (1989) for mountain reedbuck.

Using a gestation period of 240 days and a body mass at birth of 3.0 kg, the following formula was used:

$$t = (w^{1/3} /a) + t_0$$

where t = age of foetus, w = mass of foetus, a = a constant (0.075), and t_0 = “intercept where linear part of the plot cuts the time axis” (48 days).

Additionally, lambs under three months age were recorded when sighted and the approximate month of birth estimated. This was not a systematic method because there was no way to determine what proportion of lambs were encountered, but it was a means of sampling in a random manner.

Monitoring deaths and disease

As grey rhebok numbers were monitored regularly and precisely, no animals could have died or emigrated without being noticed. When an individual could not be found, a thorough search was conducted in its home range, concentrating in the area where it was last sighted. The terrain was, however, difficult and carcasses were not easily located if the animal did not die in an open area. On most occasions when an animal was unaccounted for, it usually had been temporarily separated from the herd and returned within a day.

Territorial male mountain reedbuck were also monitored in this way, but adult females and lambs could not be; so any disappearance of the latter was not noticed during normal observations. To overcome this problem, large areas within the study site were searched on a weekly basis for possible carcasses. This was carried out both actively and passively between February 2000 and April 2002 (excluding February to April 2001 and August 2001). Experience showed that certain areas were more likely than others to contain carcasses so they were traversed on foot once a week for this purpose. Such areas included the shoreline of the dam, where the majority of dead animals were located, as well as areas of patchy long grass and steep rocky slopes. Long grass and boulders regularly provided shelter for mountain reedbuck so it was considered likely that they might also be used as hiding places for sick animals. Additionally, large areas within the main study site were walked every day while following live animals, and other areas were scanned with binoculars during behavioural observations. Although carcass location was not the primary aim at these times, such activities improved the chances of locating dead animals.

A very important addition to the investigation of disease came from the material provided by 41 mountain reedbuck culled for management purposes. These animals were used for research on body condition and parasitic infections (see Chapters 6 &

7), but were also examined for signs of disease at the same time. During each of eight culls, two adult males, two adult females and one juvenile animal were randomly shot and should, therefore, have been representative of a thorough cross section of the population.

When fresh carcasses were located, necropsies were performed immediately, following guidelines set by the Section of Pathology at Onderstepoort (Faculty of Veterinary Science, University of Pretoria). On one occasion an emaciated, sick looking female grey rhebok was shot for necropsy. It was not left to die on its own due to the high probability of failure to recover the carcass in good time. Before dissection, sex, age (by examination of teeth) and body condition were determined, and obvious signs of injury such as broken limbs or flesh wounds searched for.

After skinning, the subcutis was examined for lesions and abnormalities. The abdominal cavity was then opened and the topography of the abdominal organs examined. Again, the presence of abnormal abdominal content and lesions were assessed. The diaphragm was pierced to check thoracic negative pressure, the rib cage cut away and the topography of the thoracic organs inspected to determine the presence of lesions. Before removal of entire organs, the following structures were examined *in situ*: the thoracic aorta was cut open longitudinally and examined for abnormalities and parasites; the pericardial sac was opened and its contents inspected; the gall bladder and bile ducts were checked; and the pancreas's surface examined and incisions made to check for lesions.

Abdominal organs were then removed. The spleen was palpated thoroughly and incised at regular intervals for the presence of lesions. The forestomach was tied at both ends with double ligatures before removal. The serosal surface, lymph nodes and mucosa were examined, followed by the contents of the rumen, reticulum, omasum and abomasum (examination for, and collection of any parasites were carried out at the same time). The mesenteric vessels around the intestines were examined for the presence of parasites or lesions before being cut away from the intestinal wall. The kidneys and adrenal glands were removed and the former examined for symmetry, the fat stripped off and then cut along the long axis to expose the cortex, medulla and pelvis. After removal of the liver, incisions were made across the large bile ducts and into the parenchyma for detection of lesions.

The tongue, oesophagus, heart and lungs were removed together and examined. Thyroids and parathyroids were inspected superficially and then incised to expose the parenchyma. The heart was opened to expose the chambers and valves for examination. The lungs were then examined by palpation and incision, and finally the brain was extracted. Samples from all organs and tissues were collected (especially those with suspected lesions) for histopathology (5 x 15 x 15 mm blocks stored in 10% buffered formalin), and examined later at the Section of Pathology, Onderstepoort.

Results

Births

Over three lambing seasons 91 % of grey rhebok lambs were born between November and February with the majority of births occurring in December and January (Figure 6). Out of 43 lambs, only three were born out of season (one in March 2000, one in April 2000 and one in July 2002).

Over three breeding seasons an average of 74 % of adult females produced lambs at a ratio of 22M: 19F (Table 1). The genders of two lambs born in 2002 were not determined. Taking the fecundity rate as the number of female live births per female per year (Caughley & Sinclair, 1994), the average fecundity rate was 33.3 %. If the fecundity is taken as the total number of births per female per year, the average fecundity rate was 74 %. In all cases females had single lambs.

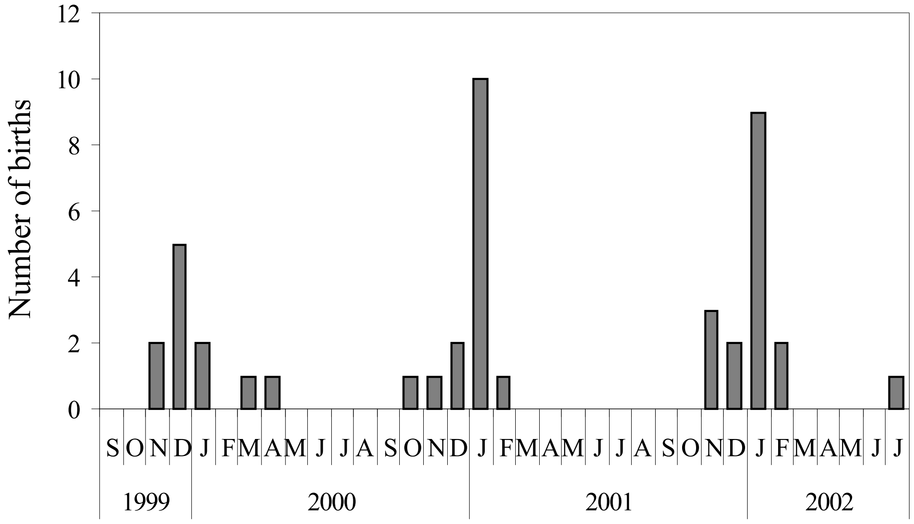


Figure 6. Grey rhebok births for three lambing seasons at Sterkfontein between September 1999 and July 2002. Data were from direct observations of live animals.

Table 1. Grey rhebok birth records, lamb sex ratios and adult female numbers separated into herds between 1999 and 2002.

Grey rhebok group	Number of adult females 1999	Number of lambs born in 1999/ 2000	Number of adult females 2000	Number of lambs born in 2000/ 2001	Number of adult females 2001	Number of lambs born in 2001/ 2002
1	3	1 (1M,0F)	3	3 (1M,2F)	1	1 (0M,1F)
2	3	2 (2M,0F)	3	3 (1M,2F)	5	4 (1M,3F)
3	3	3 (2M,1F)	3	3 (1M,2F)	4	4 (3M,1F)
4	3	2 (2M,0F)	2	1 (1M,0F)	-	-
5	2	1 (1M,0F)	2	2 (1M,1F)	5	4 (2M,1F,1?)
6	5	2 (1M,1F)	5	3 (1M,2F)	5	3 (1M,2F)
Total	19	11(9M,2F)	18	15(6M,9F)	20	16(7M,8F,1?)

Out of the original 19 adult females from 1999, one produced four lambs in three years (two of which were out of season), six produced three lambs, seven produced two lambs, four produced one lamb, and one produced no lambs over three consecutive breeding seasons. Two females that had two lambs died before the third breeding season, while one female that had one lamb also died before the third season. This female and the female that had no lambs appeared to be too old to maintain pregnancy in the second and third seasons. In addition, the two females born during the 1999/2000 lambing season each produced their first lamb during the 2001/2002 season, indicating that they reached sexual maturity before the age of 16 months.

Assuming that these original females represented a random cross section of ages when the study began, i.e. from newly sexually mature females through to animals too old to breed, adult females at Sterkfontein produced an average of 0.7 lambs for every year between sexual maturity and death.

Extrapolated birth dates of mountain reedbuck foetuses for 2000 and 2001 found that all lambs would have been born between September and January (Figure 7). Observations of lambs in the field also indicated a peak in births between November and January, but there were occasional lambs born in other months. In all cases single lambs were observed.

Sixty nine percent of culled and snow killed adult female mountain reedbuck were pregnant and 12 % were lactating (Table 2). However, the fact that these culls were conducted at different times of year should be taken into account when interpreting the results. In calculating fecundity, the culls performed during December 2000, November 2001 and February 2002 have been excluded because they took place when females would not normally have been pregnant (see Figure 7). The females sampled from the snow deaths have also been excluded. Using the Caughley & Sinclair (1994) definition of fecundity (the number of female live births per adult female per year) the average fecundity rate was 31 % (bearing in mind that two foetuses were not sexed and may have been females – this would have increased the fecundity). If the fecundity is taken as the total number of births per adult female per year (including both male and female lambs), the average fecundity rate was 92 %. The overall sex ratio of foetuses was 12 M: 8 F, while two foetuses were too small for macroscopic sex determination.

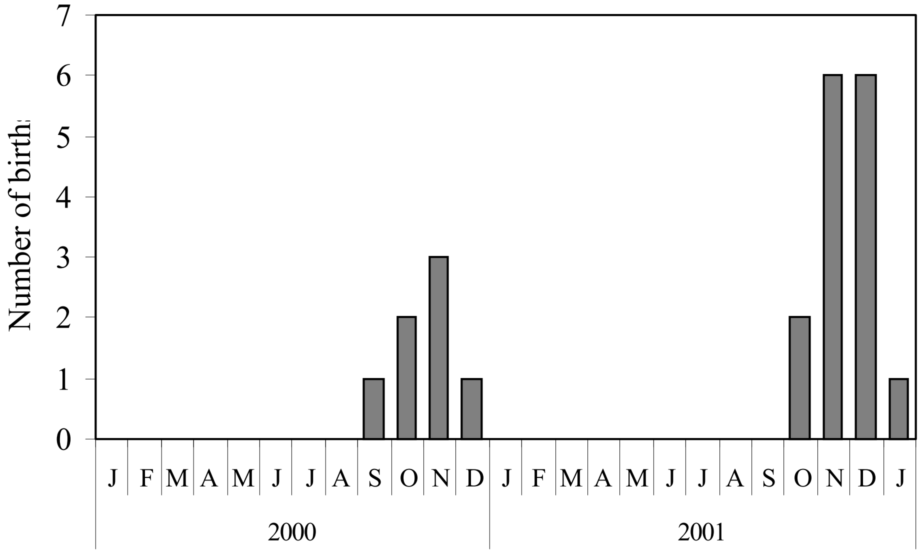


Figure 7. Mountain reedbuck birth months at Sterkfontein, obtained by extrapolation of foetus masses using the Hugget & Widdas (1951) formula, adapted for mountain reedbuck by Norton (1989).

Deaths

Between October 1999 and April 2002 there were exactly 16 grey rhebok deaths in the study population (Table 3), with ten of these resulting from hypothermia during a single snowfall in September 2001. These animals had no perirenal fat deposits (see Chapter 6) and showed atrophy of the liver and spleen, indicating poor body condition. Nephrosis had also occurred, and this was probably the result of renal shutdown caused by a failing circulatory system.

Table 2. Pregnancy records of mountain reedbuck from culled females and females that died of hypothermia (*) at Sterkfontein in 2000 and 2001.

Date of sampling	Number of mature females sampled	Number of mature females pregnant	Number of mature females lactating	Sex ratio of foetuses
March 2000	1	1	1	1M
June 2000	3	3	0	1M, 1F, 1?
September 2000	3	3	0	2M, 1F
December 2000	2	0	1	-
May 2001	3	2	1	0M, 1F, 1?
August 2001	3	3	0	2M, 1F
September 2001*	12	9	-	5M, 4F
November 2001	3	1	2	1M
February 2002	2	0	0	-
Total	32	22	5	12M, 8F, 2?

Before the snowfall there were 37 grey rhebok; afterwards there were 27. Ratios of adult males (AM), adult females (AF), juvenile males (JM) and juvenile females (JF) before the snow were 6AM: 19AF: 5JM: 7JF. Ratios killed during the snow were 1AM: 3AF: 2JM: 4JF. A χ^2 test (applying Yates's correction) was used to test whether the ratio of male and female deaths differed from that expected if they had an equal chance of dying. A second χ^2 test (applying Yates's correction) was used to test whether the ratio of adult and juvenile deaths differed from that expected if they had equal chances of dying. Expected values were estimated using the numbers of animals in each category while assuming that each had an equal chance of surviving. Due to the small number of animals, data had to be pooled and the four categories separating age and sex could not all be tested at once. The ratio of male and female deaths did not differ from that expected ($\chi^2 = 0.11$, df = 1, p = 0.99), while there was a marginal difference between the observed and expected death rates when comparing age classes, with adults surviving better than juveniles ($\chi^2 = 3.14$, df = 1, p = 0.063).

Table 3. Mortality records of grey rhebok in the main study area at Sterkfontein between October 1999 and April 2002.

Date	Age & gender	Numbers	Cause of death
October 1999	Adult female	1	Unknown
November 1999	Adult male	1	Hit by car
November 2000	Adult male	1	Stress caused by fighting
November 2000	Yearling male	1	Wounded by adult male
June 2001	Adult female	1	Old age, and possibly hypoproteinaemia due to renal amyloidosis
August 2001	Juvenile female	1	Unknown
September 2001	Adult male	1	Hypothermia due to snow
September 2001	Adult female	3	Hypothermia due to snow
September 2001	Juvenile male	2	Hypothermia due to snow
September 2001	Juvenile female	4	Hypothermia due to snow

During the rest of the period only five natural mortalities occurred amongst adults and yearlings, and there were no deaths of lambs. There was also no evidence of infectious disease or predation. All of the deaths occurred between June and November, which was mostly before the rains started.

Between February 2000 and April 2002 there were 43 deaths recorded within the mountain reedbuck study population (Table 4). It is possible that a small number of mortalities were overlooked, particularly amongst lambs. Thirty-two deaths were caused by hypothermia resulting from a single snowfall in September 2001, so only 11 deaths, from other causes, occurred during the rest of the study. Of these, only one carcass was fresh enough for autopsy, but no aetiological diagnosis could be made. In five cases, where the remains were not too damaged, there was no evidence of predation. All mortalities occurred between June and November.

Table 4. Mortality records of mountain reedbuck in the main study area at Sterkfontein between February 2000 and April 2002. * = animals that had been introduced from Caledon Nature Reserve.

Date	Age & gender	Numbers	Cause of death
June 2000	Sub-adult male	1	Unknown
June 2000	Adult (?)	1	Unknown
June 2000	3 month female	1	Unknown
July 2000	Adult male	1	Unknown
July 2000	Adult female	1	Unknown
August 2000	Adult male	1	Unknown
August 2000	Adult female *	1	Unknown
October 2000	Adult male *	1	Unknown
November 2000	Adult female	1	Unknown
June 2001	Juvenile (?)	1	Unknown
August 2001	Adult female	1	Unknown
September 2001	Adult male	3	Hypothermia due to snow
September 2001	Adult female	16	Hypothermia due to snow
September 2001	Sub-adult male	2	Hypothermia due to snow
September 2001	Juvenile female	6	Hypothermia due to snow
September 2001	< 3 month male	3	Hypothermia due to snow
September 2001	< 3 month female	2	Hypothermia due to snow

Fifteen carcasses of animals killed in the snowfalls were examined for perirenal fat deposits (see Chapter 6) and all were found to have none. This fact, combined with the results of five necropsies, indicated that they probably had inadequate fat reserves to mobilise against resultant hypothermia. As with the grey rhebok, liver and splenic atrophy indicated poor body condition, and nephrosis had also occurred. There was no evidence of underlying disease in the five animals.

Before the snowstorm there were approximately 53 mountain reedbuck in the study area (this figure does not include lambs under three months old). Twenty-seven adults and juveniles died, representing 51 % of the population. The sex ratio of adults and juveniles before the snow was 17M:36F (32 % males), while the sex ratio of animals that died in the snow was 5M:22F (19 % males). The apparent difference in survival rates between males and females was tested using a χ^2 test, with Yates's correction applied. The ratio of male and female deaths did not differ from that expected if they had an equal chance of dying ($\chi^2 = 2.54$, df = 1, p = 0.13). The data from adult and juvenile animals was pooled and no attempt was made to test for differences between age groups. This was because the ratio of adults to juveniles was not known accurately before the snow due to difficulties of differentiation, especially in females. Nine out of 11 adult females examined (three of the original 16 were never found and two had been scavenged by predators) were pregnant and one had been nursing a small lamb.

Numbers of the other ungulates that died in the study area as a result of snowfalls in September 2001 were also estimated and the mortality rates determined (Table 5). No attempt was made to age or sex them or investigate pregnancy or body condition.

Table 5. Mortality rates of ungulates in the main study area during the snowfall of September 2001. Numbers do not include lambs less than three months age.

	Numbers before snow	Numbers dead as a result of snow	% mortality
Oribi	6	6	100 %
Common reedbuck	16	11	69 %
Mountain reedbuck	53	27	51 %
Zebra	7	2	29 %
Grey rhebok	37	10	27 %
Blesbok	45	5	11 %
Black wildebeest	10	1	10 %
Springbok	40	3	8 %

The most useful data for the investigation of disease in mountain reedbuck came from the carcasses of animals killed in the snow and from examination of culled animals. There was no evidence of disease in any of these individuals; in fact the five necropsies revealed very healthy animals aside from the low body fat. Carcass location by systematic searching was unsuccessful at most times, but rather than highlighting deficiencies with the location technique, this was probably more indicative of a genuinely low mortality rate. Disease, therefore, appeared to be of very little significance in the mountain reedbuck population at Sterkfontein.

Immigration and emigration

In the grey rhebok population, herd size either varied as a result of movement of animals between herds within the main study area, with no overall change in the local population numbers, or as a result of the movement of new animals into, or resident animals out of the study area, resulting in an overall local population change. The former was easy to detect but only recorded three times. Two adult females moved from Group 1 to Group 2 in August 2001, and four females moved from Group 2 to Group 3 in June 2002. In September 2001 the harem male from Group 4 moved into the home range of Group 5 and took over the females after the male from Group 5 died.

Inward movement of new animals was also uncommon, and only recorded twice. In March 2002 an unknown young adult male appeared within the home range of Group 2, but was only present for one day. After an aggressive interaction with the resident male the intruder disappeared. In April 2002 two young males of approximately 15 months age appeared within the home range of Group 5. They remained for the final month of the study without being evicted, but only one was observed when the area was resurveyed in July 2002. This male was still present in November and December 2002 and in fact appeared to have acquired a small herd of his own.

Outward movement was suspected to be common in yearling males but impossible to confirm because once out of the study area they could not be found. Between mid October and mid December every year the most recent batch of young males (approximately 11 months age) were aggressively evicted from their natal groups by the harem males. For up to two months after this they were sometimes seen on the peripheries of their previous home ranges, where they avoided contact with the herd. Harem males regularly searched for these yearlings and chased them around trying to stab them with their horns. The young males were not able to join other groups either because the resident males of those herds attacked them as well. After two months or less all the evicted males had disappeared and it was assumed that most had moved out of the study area looking for territories of their own. On two occasions young males were seen with injuries that appeared to have been inflicted by horns of harem males, and these animals probably died.

An unexpected occurrence observed four times was that of young females between eight and 12 months age being aggressively evicted by the harem males. Two of these females were allowed to return to their herds after about two months, but before being allowed back they remained on the peripheries of their home ranges and avoided contact with their natal groups.

Only two changes in territorial ‘ownership’ were observed. First, a car killed the male from Group 2 accidentally, so the largest young male took over. Second, the male of Group 5 died of hypothermia and the male of Group 4 took over his harem and territory. A number of antagonistic interactions were observed between harem males, and every time the victor was the animal that was within his own territory at the time. Generally, intruding males were immediately and very aggressively chased back to where they came from. On only one occasion did two males briefly lock horns and fight, but this involved a new male to the area, not a resident, and the interaction was short lived with the intruder being chased off. No incidents of evictions of harem males by other males via aggressive interactions were observed.

In July 2002, four grey rhebok were captured, collared and translocated from the west side of the dam into the main study area on the east side. They all came from the same herd and comprised two adult females, one 8 month old female, and one 6 month old male. The purpose of the experiment was to see whether they would integrate themselves into pre-existing herds. Within 24 hours of release, the two adult females had disappeared, while the two young animals stuck together in an area not usually frequented by any of the established herds. In October and December 2002 the two adult females and young male could not be located, but the young female had joined a different young male that was first observed in the study area in April 2002 (see above).

In mountain reedbuck males there were occasional changes in territorial ownership, but eviction events were never witnessed. These changes all appeared to be the result of dynamics within the existing population because the influx of new adult males was not detected. Generally, males that lost territories were not seen again, and the lack of carcasses, as noted above, made it difficult to determine whether such males had died or emigrated out of the study area. In February 2002, a territorial male was shot as part of the culling program and within two days another male that had previously held a neighbouring territory moved in and took over. Emigration or mortality of young males that can be inferred from the skewed adult sex ratio was very difficult to detect because they were not individually identifiable.

In female mountain reedbuck there were no fixed groups and movement of females between herds and male territories was the norm. Neither immigration nor emigration could be inferred for females.

During August 2000, seven mountain reedbuck were translocated from Piet Retief Nature Reserve in the central-southern Free State, to Sterkfontein. Among these animals were three adult males and four adult females, all marked with coloured collars. After release within the study area, three females and one male were sighted, but the male subsequently disappeared. The carcass of one of the males was found but was unidentifiable because the collar had lost its colour strip. The whereabouts of the remaining two males were unknown. Also, one of the females was recovered dead from unknown causes about two weeks after release. In total, three of the females survived and remained in the study area, while none of the males remained (they possibly all died).

Overall population dynamics

The most important factor in the dynamics of the grey rhebok population was the eviction of yearling males between October and December every year (Figure 8).

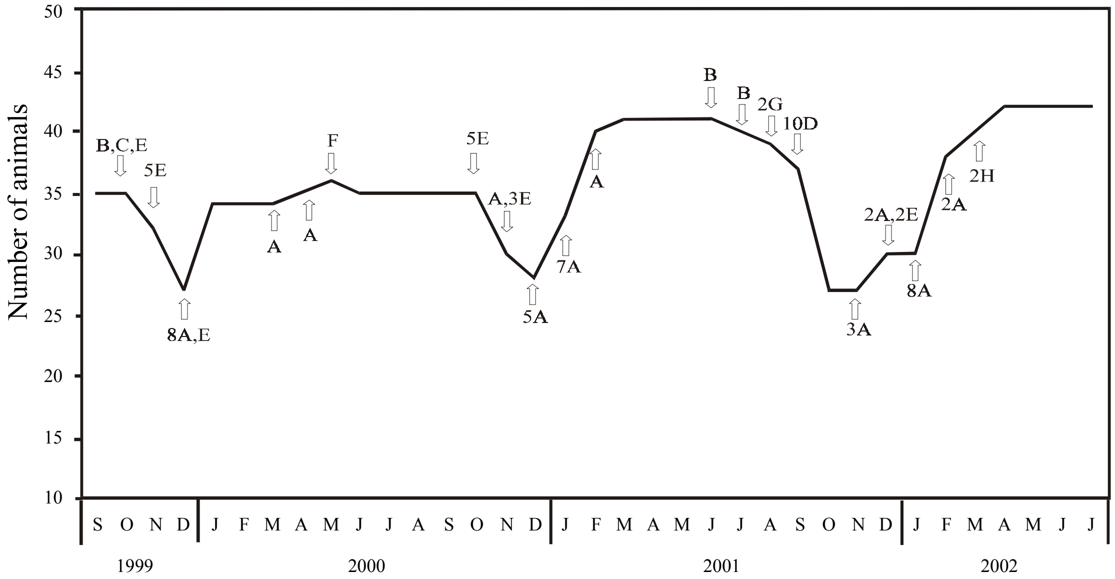


Figure 8. The population dynamics of all grey rhebok within the main study area at Sterkfontein between September 1999 and July 2002. Up arrows indicate increases in population; down arrows indicate decreases. Letters indicate reasons for change: A = birth, B = natural death, C = accidental death, D = snow death, E = eviction of young male, F = eviction of young female, G = disappearance of animal for unknown reason, H = immigration.

Although mountain reedbuck population numbers were not known as accurately as they were in grey rhebok, there was no clear pattern of decreased numbers at specific times of year, except possibly a continuous but slight reduction at the end of winter and early spring (Figure 9).

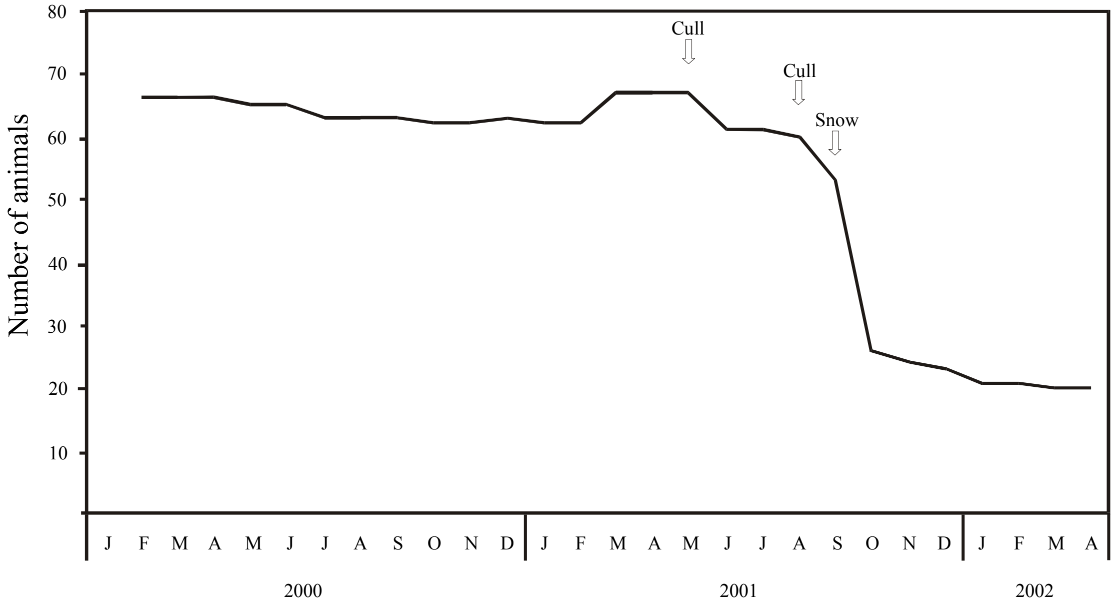


Figure 9. Population dynamics of mountain reedbuck within the main study area at Sterkfontein between February 2000 and April 2002. The numbers are approximations from counts taken every two weeks.

Helicopter counts

Helicopter counts of grey rhebok were exact in 2001, but less accurate in 2002, while counts of mountain reedbuck were very inaccurate (Table 6).

Table 6. Comparison of counts of grey rhebok and mountain reedbuck using two different techniques: helicopter counts and long term ground counts.

Date	Counting method	Grey rhebok	Mountain reedbuck
July 2001	Ground	39	53
	Helicopter	39	25
July 2002	Ground	42	29
	Helicopter	29	14

Discussion

Births

Grey rhebok bred seasonally at Sterkfontein, with 91 % of births occurring between November and February, and 70 % occurring between December and January. This is consistent with previous findings in Natal by Rowe-Rowe (1994) and Oliver *et al.* (1978). Beukes (1984) also found that grey rhebok were seasonal breeders at Bontebok National Park in the Western Cape Province, although the birth peak occurred in August. This difference in breeding is due to a different timing of the flowering of forbs at Bontebok NP, which results from winter rather than summer rainfall. The condition of the veld is better for feeding at a different time of the year to most other areas of South Africa.

Depending on the definition of fecundity used (either the number of female lambs per adult female per year, or the total number of lambs, including males, per adult female per year), fecundity for grey rhebok females was found to be 33 % for female lambs, and 74 % for all lambs. However, there was a marked difference in the percentage of lambs born to females in the first year of study (58 % in 1999/2000) compared to the following two years (83 % in 2000/2001 and 80 % in 2001/2002), so there may have been undetected early mortality. Taking this into account, overall fecundity would have been 81 % (assuming that 80 % of adult females gave birth every year).

Captive births of 23 grey rhebok at the National Zoological Gardens, Pretoria showed a peak between September and March, and a gap between April and August (Skinner, Moss & Skinner, 2002). Although this was a fairly small sample, it indicated that grey rhebok remained quite seasonal despite having access to good quality nutrition throughout the year.

During the present study two female grey rhebok started breeding at the age of 16 months and gave birth for the first time at two years. Unfortunately only two females were born in the first year and this kept the sample size for age at first breeding very small. Females born at a later date were not old enough to breed before the end of the study. The birthing interval for adult females was generally one year, although one female demonstrated an average birthing interval of nine months. On average females at Sterkfontein produced 0.7 lambs for every year after sexual maturity, up to and including old age. Longevity has not been determined for wild grey rhebok, so the average number of offspring produced per female in a lifetime cannot be accurately determined. However, if they have a similar lifespan to mountain reedbuck (Norton, 1989) they might live for an average of five to seven years. This will give an average number of offspring per female of between 2.8 and 4.2 lambs, assuming they have their first lamb at two years and all lambs are born singly.

Although a few mountain reedbuck lambs were seen at different times of the year during the present study, extrapolated birth months from 22 foetuses indicated a birth peak between October and December. Irby (1979) estimated birth months of mountain reedbuck at Loskop Dam Nature Reserve (hereafter Loskop) in Mpumalanga, using field sightings of lambs and the reproductive condition of 24 culled females. The cull material supported the summer peak found in the present study, while lambs were sighted in most months of the year. Estimated birth months of lambs sighted in other areas of South Africa, including Ohrigstad Nature Reserve (Mpumalanga), Giant’s Castle Nature Reserve (Drakensberg, Kwa-Zulu Natal), Umfolozi National Park (Kwa-Zulu Natal), and the Kruger National Park also indicated a peak in births during the wet summer months (Irby, 1979).

Using field observations, Norton (1989) recorded a few mountain reedbuck births throughout the year at Rolfontein and Doornkloof Nature Reserves in the Northern Cape Province, but examination of reproductive status of culled females (81 and 89 females respectively) indicated a distinct birth peak in November. The standard deviation of the mean birth dates was one month, suggesting that mountain reedbuck in the Karoo fell within the “birth pulse” population category (Norton, 1989). Els (1991) found a similar birth peak at Rolfontein using separate cull material.

Results from the cull studies are congruent with fairly strict seasonality in mountain reedbuck in South Africa. The only evidence for year round breeding came from field sightings, while the foetuses collected provided no back up for this. The proportion of lambs born out of season must have been very low relative to the numbers born between November and January. However, as these studies were all carried out in

South Africa, lambing periods were probably influenced by photoperiod and the seasonal nutritional cycle that is characteristic of these latitudes. In Kenya, Irby (1979) found that mountain reedbuck had no birth peaks and suggested they were capable of year-round breeding. Captive birth records of 53 mountain reedbuck from the National Zoological Gardens, Pretoria, where the animals were not subject to seasonal variations in nutritional quality, seem to confirm this (Skinner *et al.*, 2002). There they bred throughout the year, although there was still a slight birth peak between December and January.

In the present study some of the females were culled in November, December and February. This is a time between parturition and mating for many animals, so the percentage of pregnancies among sampled females was probably an underestimate. Thus the fecundity was determined by excluding these data and was found to be 92 % overall, or 31 % using the Caughley & Sinclair (1994) definition. The latter fecundity for female lamb births may be an underestimate because the sex of two foetuses could not be determined. These results are corroborated by culls at Rolfontein and Doornkloof (Norton, 1989) where 95 % of adult females sampled in August 1984 and June 1985 were pregnant or lactating. Fecundity in females from these two reserves decreased in the oldest age classes (Norton, 1989), but even very old females were sometimes pregnant. Yearling females were able to become pregnant, but not all did (Irby, 1979; Norton, 1989).

As females were not individually identifiable during the present study, birthing intervals could not be monitored in the same way as they were in grey rhebok. Determination of pregnancy from culled animals is a one off event and nothing can be gleaned about the times of previous pregnancies. However, the high percentage of pregnant females in the present study and those of Irby (1979) and Norton (1989) imply that most females are pregnant within any given year and, therefore, lambing intervals must be approximately one year.

Deaths

At Sterkfontein all carcasses of grey rhebok and mountain reedbuck were found in the second half of the year, between June and November. This period corresponded mainly with winter and spring when conditions were cold and dry, and when their food supply was reduced. This agrees with Irby (1976) who recorded a consistent pattern of increased mountain reedbuck deaths between August and November at Loskop. Norton (1989) found mountain reedbuck carcasses throughout the year, but there were peaks in late winter to spring at Rolfontein, and late summer and early winter at Doornkloof. The reason for the disparity at the latter site was unknown. Oliver *et al.* (1978) recorded more deaths of grey rhebok and mountain reedbuck in Natal between July and October.

The vegetation at Sterkfontein falls within the sourveld (Acocks, 1988), and grasses lose nutritional quality in the cold dry months. At such times the animals would have been relatively nutritionally stressed and this would have negatively affected their body condition. Indeed, body fat indices determined in mountain reedbuck indicated that they were in their worst condition in August and September (see Chapter 6) and would have been most vulnerable to adverse environmental conditions at these times. This was well demonstrated by the deaths of half the mountain reedbuck and a quarter of the grey rhebok during heavy snowfalls in September 2001. These conditions came at the worst time when animals were struggling to survive. Unable to feed because of the snow, they would have used up the last of their remaining body fat before quickly exhausting their glycogen stores. Examination of 15 mountain reedbuck and three grey rhebok that died found no kidney fat deposits.

Although the proportion of male mountain reedbuck that survived the snow was higher than that of females, it was not greater than would have been expected if both sexes were equally likely to die. At this time of year males and females had similar levels of body fat (see Chapter 6), so the similarity in survival rates was as expected. Male and female grey rhebok also had survival rates that would have been expected if their chances of survival were equal, but juveniles died in greater numbers than expected. This would probably have been because they had lower fat reserves than adults. As animals grow, the carcass becomes an increasing proportion of their live weight (Ledger, 1990). The ratio of muscle to bone increases and progressively more adipose tissue is laid down. Juveniles would, therefore, have been in poorer condition than the adults as a result of their young age.

Fifty one percent of mountain reedbuck died in the snow, compared to 27 % of grey rhebok. Only oribi (100 %) and common reedbuck (69 %) were worse affected, while springbok (8 %), blesbok (11 %) and black wildebeest (10 %) survived relatively well. The reason for this difference was not established, but was unlikely to be poor adaptation to cold on the part of the mountain reedbuck. Excluding the oribi and common reedbuck, all these species, including mountain reedbuck, are well adapted to living in cold areas (Skinner & Smithers, 1990). The body condition of springbok, blesbok and black wildebeest was not tested, but all should have had low body fat reserves at the time of the snow.

One factor that does seem to correlate with the death rate but that appears counter-intuitive was the behaviour of the different species in the snow. Springbok, blesbok and black wildebeest frequent the open plains (Skinner & Smithers, 1990) and remained exposed and active in the snow (pers. obs). In contrast, all the mountain reedbuck that died were found in very sheltered sites out of the wind, often huddled in groups (pers. obs.). Possibly animals that kept moving may have maintained higher body temperatures, but the chance that springbok, blesbok and black wildebeest were simply in better condition cannot be ruled out.

In adult females there was no evidence that pregnancy influenced survival in the snow. Nine out of 11 that died were pregnant and one was lactating. These proportions were consistent with normal rates of pregnancy for this time of year.

Irby (1976) reported a slightly higher death rate among male mountain reedbuck than females at Loskop, and it was suggested that immature males were subjected to greater stresses, probably resulting from aggressive behaviour of territorial males. Sex ratios of animals older than one year were between 1 M: 1.64 F and 1 M: 2.38 F. Norton (1989) found that adult mortality was similar in both sexes, but differential gender mortality occurred in immature animals. The reasons for this have not been tested, but young evicted males tend to move into peripheral areas, and this may lead to nutritional stress or increased predation (Norton, 1989). Adult sex ratios at Rolfontein were between 1 M: 2 F and 1 M: 3.3 F.

The small number of carcasses located during the present study, other than during the snowfalls, made it difficult to determine whether there was differential gender mortality. However, the fact that there were slightly more male foetuses than females extracted during the culls, but twice as many adult females than males in the study area, suggests that young males were lost from the study area at a greater rate than females, either from mortality or dispersal. Moreover, the greater survival of males during the snow implied that they were more resistant to the extreme conditions than females. Unfortunately it was not known what proportion of young males emigrated out of the study area and what proportion died.

No studies have reported on gender mortality among grey rhebok, and too few died during the present study for any meaningful comparisons to be made. Grey rhebok sex ratios (adults and sub-adults) in Natal were 1 M: 1.72 F (Oliver *et al.*, 1978). At Sterkfontein the average sex ratio of adults was 1M: 3 F, but if the juveniles were included before young males were evicted, it was 1M: 2 F. The sex ratio of lambs born during the present study was 1M: 0.86 females.

There was no evidence of disease within the grey rhebok or mountain reedbuck populations at Sterkfontein. In grey rhebok, few natural deaths occurred, and most of those that did were accounted for. There have been no other studies of mortality rates in grey rhebok, except a limited one by Oliver *et al.* (1978), and no investigations of disease. In fact, population dynamics studies on wild ungulates that incorporate disease are rare. In mountain reedbuck, although the causes of death in the majority of carcasses could not be ascertained, results from necropsies of six natural deaths and 41 culled animals, showed no indication of disease within the population.

No evidence of disease outbreaks was noted at Loskop (Irby, 1976). In Natal, Oliver *et al.* (1978) recorded 21 deaths in 18 months out of the population of mountain reedbuck, grey rhebok and oribi. Sixteen of these were of unknown causes. One grey rhebok and two mountain reedbuck were caught in snares, and one mountain reedbuck died in a snow drift. There were no direct observations of predation by jackals, and only one death was a suspected jackal kill. No predation took place at Sterkfontein amongst the grey rhebok, even among the 43 lambs. There was also no evidence of predation on the mountain reedbuck, although lambs were not identified, and it is possible that it did occur. During 2.5 years, jackals were only sighted on three occasions, while other predators capable of taking lambs, such as caracal, were not seen.

Dispersal

Dispersal is an aspect of ecology often mentioned, but rarely investigated in population dynamics studies because it requires an intimate knowledge of the animals that is not within the scope of many research projects.

Movement of grey rhebok between herds turned out to be a rare occurrence because they formed very stable groups. The harem males appeared to keep their groups in check by rounding them up when they strayed. The limited amount of movement between groups would still, however, have been beneficial in mixing the gene pool and reducing inbreeding. Under normal circumstances, this movement was restricted to females, and harem males only moved around if another male died and left a vacancy. Although it was not recorded during the study, changes in territorial ownership must also occur as a result of antagonistic interactions between resident males and intruders. The one interaction observed resulted in the intruder being chased out.

In adult females no immigration was recorded, possibly because the fencing around the study site precluded this. Even without the fencing, immigration of adult females would have had little impact on population dynamics because movement between groups within the study area was very limited. The eviction of young females would have increased the numbers available for emigration, but the re-admittance of approximately half these to their natal groups would then reverse this.

The low degree of female dispersal between grey rhebok herds, and the permanent defence of females within herds by single males within specific territories, results in a social structure that is very unusual for antelope. The only other African species that is similar in this regard is the tsessebe (*Damaliscus lunatus*), where harems of females remain permanently associated with their territorial male (Skinner & Smithers, 1990). A second ungulate species that has a similar social structure is the vicuña (*Vicugna*

vicugna), a member of the Family Camelidae from South America. This species inhabits the high grasslands and scrublands of the Altiplano region of Bolivia, Chile, Peru and Argentina. Vicuñas form stable family groups with one male, two-four females and offspring, as well as variable groups of bachelor animals (Vilá, 1992). Males defend year round areas where females and calves live.

The timing of dispersal of yearling male grey rhebok was quite predictable. They were tolerated within their natal herds for approximately eleven months, while at the same time becoming increasingly submissive to the harem male (see Chapter 5). Sometime between late October and early December, or at about the time that new lambs were due, the harem male suddenly evicted them. The actual event was observed twice, and on both occasions the adult male started pushing the young male around slowly, then grew progressively more aggressive until there was a flat out pursuit. After this the young male could not return to the group without being pursued. On other occasions harem males appeared to search for and chase previously evicted males that were hiding on the peripheries of their home ranges. One young male was chased along a fence into the dam and had to swim around the fence, which protruded 25 m into the water, to escape the adult male. The adult remained at the water line to make sure the young animal did not return, so if the fence had not been there, the yearling would have drowned.

Two possible reasons for the eviction of yearling males were the elimination of competition and incest avoidance. Dispersal of individuals from their natal group or site, especially of one sex, is widespread among mammals (Pusey & Wolf, 1996), and serves to separate close relatives and thus prevent inbreeding. The question of whether it has evolved as an inbreeding avoidance mechanism, or whether it results from intra-sexual competition or resource competition, remains contentious (Pusey & Wolf, 1996). The importance of each of these factors undoubtedly varies among species, but it is difficult to measure their relative contribution to dispersal patterns. In the case of grey rhebok, yearling male dispersal fits with the elimination of competition theory because harem males are intolerant of all males and are equally aggressive towards yearling males that have been evicted from separate herds. The latter are unlikely to be closely related to females from a separate herd (unless they had a sister that dispersed to the neighbouring herd – this was not observed during the present study) and do not pose a problem of inbreeding. Evidence for inbreeding avoidance might then come from the measurement of dispersal distances, and these could be tested to see whether yearling males moved further than would be expected on the basis of competition alone (Pusey & Wolf, 1996). Unfortunately, as the destinations of evicted yearling males were never determined, this could not be done.

The aggression of harem males was so marked that all young males were pushed out of the study area and effectively lost from the local population. They had no chance of taking over their own territory at that stage because they were too small, while it was also difficult for them to find places of safety elsewhere. Yearlings that escaped from the main study area simply moved into the home ranges of other males where they would have come up against the same aggression. It is possible, therefore, that most males do not survive to the stage when they are strong enough to gain their own harems. To investigate this properly, however, young males would have to be followed after eviction using radio telemetry.

In the case of the eviction of young female grey rhebok from their natal herds, inbreeding avoidance is more probable than elimination of competition. Harem males were never observed showing aggression to females from other groups when in close proximity, and with their social system, any female that remained in her natal herd would most likely have to mate with her father (unless he was forced out or died). However, two previously evicted young females returned to their natal herds during the present study, and one of these mated with her father.

Investigating dispersal in the mountain reedbuck population at Sterkfontein was more difficult because of the lack of fixed groups. Neither immigration nor emigration could be inferred for females, except in the case of five individuals that were marked with colour collars. One of these died, while the rest remained within the study area. They moved over quite large distances within the site, but did not emigrate.

In males, occasional changes in territorial ownership appeared to be the result of dynamics within the existing population because the influx of new adult males was not detected. Two animals lost their territories and were not seen again, but it was unclear whether they emigrated or died. It appeared that the rate of turnover was low.

However, an idea of the strength of competition for good territories was given by the speed (less than two days) at which an adult male moved into and took over the territory of his neighbour after the latter was shot.

The skewed sex ratio of adult mountain reedbuck, as mentioned earlier, implies that males were lost from the study site at a greater rate than females. The lack of carcasses of young animals suggests that most of them emigrated from the area, probably to escape aggression by territorial males, although the fencing around the area would have made this difficult. However, it was impossible to ascertain whether such young males had dispersed out of the study site. Irby (1976) found that aggressive interactions between adult and juvenile males started as early as six months, and that most juvenile males were evicted from the group at the age of 9-15 months. Norton (1989) concurred with this and observed that testis development began at the age of nine months. Young males were then perceived as competition by the territorial males and were evicted. A number of chases were observed during the present study, but these only occurred when the juvenile was clearly in the resident male's territory.

Translocations

The translocation of grey rhebok was quite unsuccessful, while that of mountain reedbuck was only moderately successful. Although in both cases it was only attempted once under observation, it indicated that considerable care should be taken when deciding what animals to translocate. In the case of the grey rhebok, it was hypothesised that the females would join another group. This did not happen because the adult females disappeared. It was unfortunate that their whereabouts were not determined, but the implication was that random translocations do not necessarily have the desired effect of increasing the population size in the area where they are being introduced. Moreover, it is likely that the release of an adult male would have resulted in an antagonistic interaction with another harem male, and one of the animals would have been forced out. Again, no population increase would have been achieved.

In the case of the mountain reedbuck translocation, there was no room for additional males within the study area. Even the largest male that was introduced was not able to find a territory of its own even though it was larger than most of the resident males. The adult females did better, and this is probably a result of their different social structure, whereby females do not have strict groups and are not herded in harems by a male.

Aerial counts

Many publications exist on accuracy of helicopter counts and the effect of various factors such as flight speed and height (Botha *et al.*, 1990). Reilly & Emslie (1998) published data on power and precision of such techniques for counting ungulates in South Africa and suggested that all counts should be replicated to allow statistical analysis of each data set. Varying degrees of power were attained for different species, indicating that a general aerial count for all species is inadequate and each species must be considered individually.

Aerial counts at Sterkfontein concurred with the latter statement because considerable differences were observed in accuracy for the two species. Grey rhebok counts were more accurate than mountain reedbuck counts, and the likely explanation for this was the difference in behaviour of the two species. Grey rhebok usually run away and stay in the open when they feel threatened (Ferreira, 1983; pers. obs.), so are easy to count, but mountain reedbuck often hide in long grass or rocks, even when closely approached, and this makes them difficult to see. Because of this, it is impossible to know what proportion of the population has been counted, and this leads to low precision.

Overall trends

The population of grey rhebok increased very little during the study period. This occurred even though there were 43 lambs born over three seasons, there was a very high survival rate of these lambs, and there were no signs of disease. The low rate of population increase had been noted prior to the commencement of the study (N.

Collins, pers. com.) and appeared to be standard for this population. Part of the reason for this during the present study was a low recruitment rate, and this was due to the eviction of all yearling males and some juvenile females before they reached maturity. In the 1999/2000 breeding season, the sex ratio of lambs was 9M: 2F, so almost all of these were evicted before they could be recruited into the breeding population. In 2000/2001 the sex ratio of lambs was 6M: 9F and the larger number of females allowed the overall population to increase by 14 %. The population declined again, however, when 27 % of the animals died in snow. Extreme climatic events can, therefore, play a major role in population control in regions of South Africa that experience similar weather patterns.

The implication of the static growth rate before the study and during the first year was that the grey rhebok carrying capacity was probably saturated. The result of the translocation experiment, where the two adult females disappeared rather than integrating into another group, supported this.

The population of mountain reedbuck appeared fairly stable in 2000 and 2001 before the snowfalls. Norton (1989) found that populations in South Africa, where food quality is relatively low in winter months, fluctuated to a small degree and were effectively in balance with their environment without causing major changes to the vegetation. He suggested that in areas where food quality was good in winter, such as in Kenya (Irby, 1976), the population would only be limited by quantity. For this to happen there would have to be substantial changes to the vegetation and this might result in greater fluctuations in animal numbers.

Similar to grey rhebok, mortality rates in adults were low and there was no sign of disease. One reason for slow population increase may have been dispersal of yearling males, or unrecorded mortality, but neither could be confirmed. Irby (1976) and Norton (1989) suggested that mortality was probably high in juvenile males because of the skewed adult sex ratio, but the lack of carcasses of young males at Sterkfontein implies that mortality rates were not high.

Chapter 4

HOME RANGES AND HABITAT

Introduction

A home range consists of a more or less restricted area within which an animal moves when performing its normal activities (Harris *et al.*, 1990). Measuring home range size, shape, and pattern of utilisation is important for ecological studies concerned with population density, foraging behaviour, habitat selection, and spacing of individuals. In species that are cropped for meat production, collection will be most efficient and economical if animals are kept at or near an optimum population density. If animals are over-stocked there may be competition, resulting in the loss of condition in many and possibly the deaths of some. With the translocation of game becoming increasingly more common, it is important to know how many animals can be introduced to an area without exceeding the ecological carrying capacity. Even when animals are conserved for reasons other than meat production, it is pointless introducing them if the resultant competition will cause the loss of animals through emigration or death.

For grey rhebok, Oliver *et al.* (1978) recorded an average home range size of 76.7 ha for eight males (range 31 to 135.4 ha) at the Highmoor State Forest in Natal, while two females had home ranges of 43.1 and 117.1 ha. In the Free State, home ranges averaged 61 ha with a range of 46 to 187 ha (Ferreira, 1983). Ecological densities were 1/42 ha in Natal (Oliver *et al.*, 1978), 1/23 ha to 1/57 ha in the Drakensburg (Rowe-Rowe, 1994), and 1/15 ha in the Bontebok National Park (Beukes, 1984). The two social groups recorded were solitary males and family parties (Ferreira, 1983; Beukes, 1984). Family groups were small, numbering up to 12 individuals, and comprised an adult male with a harem of several females and young.

Mountain reedbuck males at Loskop had a mean territory size of 28 ha while females had a mean home range of 57 ha (Irby, 1976). Males occupied their territories throughout the year regardless of the presence of females. In Kenya, male territories were smaller and varied between 3.1 ha and 5.5 ha (Dunbar & Roberts, 1992). Ecological densities varied between 1/15 ha and 1/21 ha at Loskop (Irby, 1976), and 1/11 ha and 1/32 ha in the Drakensburg (Rowe-Rowe, 1994). Social organisation consisted of territorial males, non-territorial males, herds of females with young, and bachelor herds (Irby, 1976). Female herds were unstable and normally consisted of small groups of 3 - 8 individuals, with females and young moving from herd to herd and between territories of different males.

The two species utilise similar marginal habitats and are of a similar body size, yet have different social structures and eat different foods. Although their home ranges have been determined before, the present study allowed for a comparison between the two in an area in which they were sympatric, while the previous studies were not particularly rigorous in their assessments, nor did they use modern statistical methods of determining range use. As with many ungulates, grey rhebok and mountain reedbuck are often translocated between nature reserves and onto private land, so it is important to know the spatial limitations of new areas for re-introductions or artificial population increases. There were three aims to this component of the study:

1) To determine home range areas of grey rhebok and mountain reedbuck at Sterkfontein;
2) To compare and contrast range use between the two species;
3) To investigate habitat and other environmental variables that might influence range use within both species.

To accomplish these aims, the following questions were considered:

a. What are the home ranges of both species and how do they compare?
b. Within each home range, how is the space used (i.e. is the space used evenly or are there core areas)?
c. Are there any seasonal differences in home range use?
d. How much overlap is there within and between species?
e. What are the ecological densities of both species?
f. How do the food densities vary within the study site?
g. Within and between species, what are the causes of variation in home range size?

Methods

Study site and animals

The grey rhebok herds at Sterkfontein were found to be very stable for most of the year (see Chapter 3) and females accompanied males almost everywhere. As a result, home ranges were calculated for herds rather than individuals. Six harem herds were monitored within the main study area between February 2000 and April 2002. During this time there were two breaks of longer than two weeks in which no monitoring was done on any animals. These were 12 weeks between February and April 2001, and three weeks in August 2001. The herds were identified numerically as Groups 1 through to 6 and this was based on identification of harem males, certain females, group size and geographic position within the study area (because herds used exclusive home ranges). Five of these (Groups 1, 2, 3, 4 & 6) were monitored for the entire period, while Group 5 was only observed until September 2001. After this it ceased to exist. There were no other grey rhebok herds within the study area.

Mountain reedbuck herds were unstable and males did not maintain harems (Chapter 3), so males were treated individually in the calculation of home ranges. Ten territorial male mountain reedbuck were monitored within the main study area between February 2000 and April 2002, excluding the two periods mentioned above. Only one male was present for the entire period, while the others came and went at different times. The adults were identified as Males 1 through to 10 according to their horn shapes and geographic positions. There were other males present within the study area, but these were considered non-territorial and were difficult to identify. They were not included in the study. Female mountain reedbuck were not systematically monitored for home range analysis because it was difficult to identify them. However, three females were collared and were monitored to a limited extent.

Geographic positions

Geographic positions of grey rhebok herds were recorded in a discontinuous manner (Harris *et al.*, 1990) approximately four times a week. Their positions were only fixed once a day per group to ensure independence of data points and these were always recorded at the location of first sighting to avoid observer interference. This generally occurred at different times on different days because of variability in the order in which groups were located. Animals were located by sight and positions determined by triangulation using compass bearings from two known landmarks. These comprised telephone poles, large boulders, trees, etc., and the geographic positions of these were determined using a GPS (5 m estimated positional error). Groups 4, 5 and 6 occurred in hilly terrain and it often took longer to find them than Groups 1, 2 and 3. This meant that they were not always located if time was limited and the total number of positional fixes for them was, therefore, less.

Mountain reedbuck males were located discontinuously and their positions fixed in the same way as grey rhebok. They were located approximately three times a week, and the number of fixes varied between animals because of the different lengths of time over which they were in the study area and the degree of difficulty of location.

Triangulated bearings were transformed into Universal Transverse Mercator (UTM) coordinates using a mathematical equation written by the author, and these were entered into the software package CALHOME (U.S. Forest Service, Pacific Southwest Research Station) for home range estimation.

To assess the accuracy of the triangulation, coordinates of 20 positions were estimated from varying distances to landmarks, and these then compared with GPS coordinates of the same positions. Distances of 400 m between the animals and landmarks yielded errors of up to 30 m, while distances over 2 km were found to be unreliable, occasionally giving errors of 200 m. As a result, triangulation was carried out using the closest possible landmarks and these were never more than 400 m away. This meant that the maximum positional error of the coordinates used was 30 m. The 5 m GPS errors of landmarks were not taken into account because they were fixed for the entire study and did not vary every time a group of animals was located.

Home range estimation

Studies have suggested that because many home-range analytical techniques have a number of disadvantages, no one method is likely to be entirely satisfactory and at least two should be used in any study (Worton, 1989; Harris *et al.*, 1990). The two methods chosen for the present study were minimum convex polygon (MCP) and adaptive kernel (AK). The MCP method was selected because it has been frequently used by other studies and generally allows comparisons of results. Its faults include the tendency to incorporate areas that are not visited by the subject animals (Harris *et al.*, 1990) and an inability to indicate intensity of range use that can be used to visualise core areas (Gallerani-Lawson & Rodgers, 1997). While nothing can be done about the latter, the first problem can be reduced by using a 95 % MCP, whereby 5 % of positions that lie furthest from the centre of the home range are removed from the analysis (Harris *et al.*, 1990). However, when analyses are run with less than 100 % of the fixes, results between different software programmes are less comparable (Gallerani-Lawson & Rodgers, 1997).

The more recent AK method is being used more frequently in ecological studies (Harris *et al.*, 1990; Gallerani-Lawson & Rodgers, 1997) and is an elegant and powerful technique representing range configuration (Cresswell & Smith, 1992). It is an approach to home range analysis based on probability density estimations, so that the home range is described in terms of a probabilistic model. It is very useful for estimating the utilisation distribution density because there are no constraints placed on the form of the utilisation distribution (Worton, 1989). Due to the non-parametric statistical approach of its calculation, the method makes no assumptions about the distribution of the data (Gallerani-Lawson & Rodgers, 1997), although each point should be independent. Isopleths of 95 % and 50 % are generally used to estimate home-range areas and core areas respectively, and it was the intent to investigate the latter that motivated the use of this technique. During analyses, the number of grid cells was set at 30 cells x 30 cells, while the programme was set to select its own optimal bandwidth or "smoothing parameter" (Worton, 1989) using a least-squares cross validation (LSCV) score, which is a measure of how well the bandwidth fits the data

To ensure that enough positional fixes were collected to estimate home ranges reliably, accumulative home range areas were plotted against the number of positions fixed, and the point determined when an asymptote was reached. This was defined as the point after which additional locations resulted in a minimal increase in range size

(Harris *et al.*, 1990). After an asymptote is reached, additional positions still cause the home range area to fluctuate slightly above and below an average value (Harris *et al.*, 1990) and, because the number of positions differed between the groups, the home range area estimated for the final position may have been slightly above or below average, depending on whether it was increasing or decreasing at the time of the final fix. To reduce this problem an average home range area was calculated for each group using values from every 25th position after the asymptotic number was reached.

Vegetation surveys

Ten vegetation surveys were carried out between October 2001 and March 2002. Five surveys were done on steep slopes (>10°) while five were done on flat or gently sloping ground. They were done in pairs so that each steep slope had a corresponding flat area close by. Surveys were carried out using the step point method adapted from Barnes (1976), whereby observations were made every 1 m along transects of 200 m. At every point the nearest grass and nearest edible forb species were recorded and at every fourth point the distances to these plants were measured. Edible forbs were those that grey rhebok had fed on during the present study (pers. obs.). The aim of the surveys was to determine the plant species densities in different parts of the study area.

Investigating causes of variation in home range sizes

There are a number of ecological parameters that could influence home range size in antelope species. Those thought to be relevant to grey rhebok and mountain reedbuck in the present study were assessed and values assigned to them for each home range. These values were then incorporated into a Backward Stepwise Regression analysis with the aim of determining which parameters were the best predictors of home range size. The parameters selected differed between grey rhebok and mountain reedbuck because of their different social structures and ecological requirements.

For grey rhebok the variables selected were the following:

1) The average number of animals in each group, calculated from monthly counts;

2) The area of steep slope (>10°) within each home range, calculated using aerial photographs and knowledge of the terrain. Slope gradients were determined using a clinometer. This parameter was included because steep slopes are considered a standard requirement for grey rhebok habitat (Skinner & Smithers, 1990), and it appeared that herds with greater amounts of steep slope available had smaller home ranges;
3) The average distance to safety, defined as the distance that an animal had to move to get out of sight from a threat. This was calculated using aerial photographs and an overlay grid, whereby escape distances were estimated from 10 grid positions within each home range. This parameter was selected because grey rhebok do not hide when they feel threatened, but rather run out of sight or to a position far from the danger (Ferreira, 1983; pers. obs.). It was, therefore, thought to be a good measure of evasive behaviour.

There were other parameters that might influence home range sizes of grey rhebok in other geographical areas, but these were left out of this analysis because they were not thought to be relevant to the conditions of the present study. These parameters and the reasons for their exclusion are listed below.

The density of edible forbs is a direct measure of the amount of food available for grey rhebok within a given area, but was not included in the analysis because a two-way ANOVA (Table 11) found no evidence of a difference in densities between steep and flat areas. There was, therefore, no point in considering forb density as a predictor of home range size.

Veld age, measured as the time elapsed since the last fire, has been shown to influence habitat selection in grey rhebok (Beukes, 1984), but was not included in the analysis because it was the same throughout the study area. Rainfall was not included because variation in the study area was negligible, while distance to water was excluded because the home ranges of all grey rhebok herds adjoined sections of the dam and all had access. Aspect was not included because most steep slopes faced west over the dam.

An important factor in grey rhebok ecology is the concealment of lambs for about one month after birth. Observations indicated that grass over 40 cm in length was sufficient to conceal lambs (pers. obs.), and in December/January when lambs were born, almost all parts of the study area had a grass cover that was as long or longer than this. Because most areas were similar in this trait, this variable was excluded.

For mountain reedbuck the variables selected were the following:

1) The average number of attending females, estimated from counts of females either with territorial males or within their home ranges. This was included because the sign of a good territory for a mountain reedbuck male has been shown to be one which females regularly use (Dunbar & Roberts, 1992). Also, a good territory is often subject to more intensive competition and tends to be compressed (Dunbar & Roberts, 1992);
2) The amount of steep slope available, found to be important for females in Kenya (Dunbar & Roberts, 1992);
3) The area of cover for shelter and hiding, calculated using aerial maps and knowledge of the terrain. Mountain reedbuck tend to hide when threatened and use shelter more than grey rhebok. Cover in this sense indicates long grass (> 80 cm) or very rocky areas.

For mountain reedbuck, grass density can be considered a direct measure of the amount of food available, but was not included for the same reasons as given for forbs and grey rhebok. Veld age, rainfall, distance to water and aspect were also not included for the same reasons given for grey rhebok.

Statistical methods

Analyses of home range areas were carried out using the software package CALHOME. Differences between summer and winter home range areas were investigated using paired t-tests. Grass and forb densities on different slope gradients were compared using a two-way ANOVA. In an attempt to find factors that influence the use of home range area, Backward Stepwise Regression analyses were conducted using variables thought most likely to affect use of space.

Results

Accumulative home range area graphs

The approximate number of locations required for reliable home range analysis in grey rhebok herds varied between 80 and 180 positions (Appendix I). Group 5's home range reached an asymptote at 80 positions, but later the harem male died and was replaced by its neighbour. The home range subsequently increased again but did not level out. The number of locations required for mountain reedbuck varied between 50 and 120 positions (Appendix I). The graphs for Males 8 and 10 did not reach asymptotes.

Home ranges areas

The positions of the home ranges of grey rhebok herds did not perceptively change over the entire study period, so their geographic positions invariably indicated which herd they belonged to.

Ninety-five percent MCP home ranges of grey rhebok herds varied between 23.3 ha and 104.1 ha (Table 7), with an average of 57.9 ha, while 95 % AK home ranges varied between 30.7 ha and 113.5 ha. In all cases, the 95 % AK values were larger than their corresponding MCP values. Fifty percent AK areas varied between 7.5 ha and 29.1 ha, corresponding to 24 % and 29 % of their respective 95 % AK home ranges. The smallest ratio of 50 % to 95 % AK was 9 % for Group 1. Groups 4 and 5 were only located for 17 months (143 and 147 positions respectively) because Group 4 ceased to exist in September 2001, while the dynamics of Group 5 changed at the same time.

Table 7. Home ranges of six grey rhebok harem herds between February 2000 and April 2002. During analyses, the number of grid cells was set at 30 cells x 30 cells. MCP = minimum convex polygon, AK = adaptive kernel.

Group	Period observed (months)	Number of positions	Asymp- totic number	Band- width (m)	MCP 95 % (ha)	AK 95 % (ha)	AK 50 % (ha)
1	24	287	150	244	73.7	108.5	9.7
2	24	327	180	185	76.8	100.1	29.1
3	24	395	150	219	104.1	113.5	22.4
4	17	143	100	172	39.7	63.3	7.8
5	17	147	80	131	23.3	30.7	7.5
6	24	205	80	140	29.9	37.8	9.4

Differences between summer and winter home range areas were investigated for Groups 1, 2, 3 and 6 (Table 8). Groups 4 and 5 were omitted because they had insufficient positional fixes for comparison. Summer months were October to March, while winter months were April to September. A paired t-test found no evidence of a seasonal difference in home range sizes (t = -0.055, df = 3, p = 0.960).

Table 8. Seasonal variation in home range areas of four grey rhebok herds.

Group	95 % MCP Summer	95 % MCP Winter
1	82.4	62.2
2	72.1	77.7
3	88.4	102.3
6	28.3	27.4

Male mountain reedbuck home ranges were smaller than grey rhebok herd home ranges (Table 9). Ninety-five percent MCP values for male mountain reedbuck varied between 7.1 ha and 21.4 ha, with an average of 14.8 ha, while 95 % AK values varied between 8.5 ha and 29.4 ha. Fifty percent AK home ranges varied between 1.8 ha and

4.1 ha, corresponding to 21 % and 14 % of their respective 95 % AK home ranges. The smallest ratio of 50 % to 95 % AK was 8 % for Male 1. Home ranges of Males 8 and 10 were probably underestimated because sufficient positions were not collected for accumulative area graphs to reach asymptotes (Appendix I).

Table 9. Home ranges of 10 territorial male mountain reedbuck between February 2000 and April 2002. During analyses, the number of grid cells was set at 30 cells x 30 cells. MCP = minimum convex polygon, AK = adaptive kernel, * = asymptote not achieved.

Male	Period observed (months)	Number of positions	Asymptotic number	Bandwidth (m)	MCP 95 % (ha)	AK 95 % (ha)	AK 50 % (ha)
1	17	101	70	98	16.3	23.2	1.9
2	24	127	90	108	21.4	29.4	4.1
3	17	143	50	76	9.3	13.8	2.1
4	16	135	120	114	17.0	26.0	3.0
5	19	157	90	92	14.7	22.5	3.9
6	22	118	50	102	17.9	27.8	3.7
7	18	120	80	80	7.1	8.5	1.8
8	15	99	*	90	16.8	21.3	3.1
9	20	114	80	86	14.5	21.9	3.3
10	12	74	*	94	13.3	17.5	3.7

Figure 10 shows the overall home range distributions and core areas of six grey rhebok herds in the main study area. The outermost boundaries used are from the 95 % MCP values because it was felt that they gave the best visual representation of the true extent of the home ranges, while the 95 % AK values projected a statistically estimated boundary that often exceeded the known borders of those same home ranges (pers. obs.). Core areas are, however, represented by 75 % and 50 % AK values because this method estimates utilisation distributions statistically, while the MCP method (50 %) can only determine the geographic centre of the range, which may have no bearing on the actual utilisation of space.

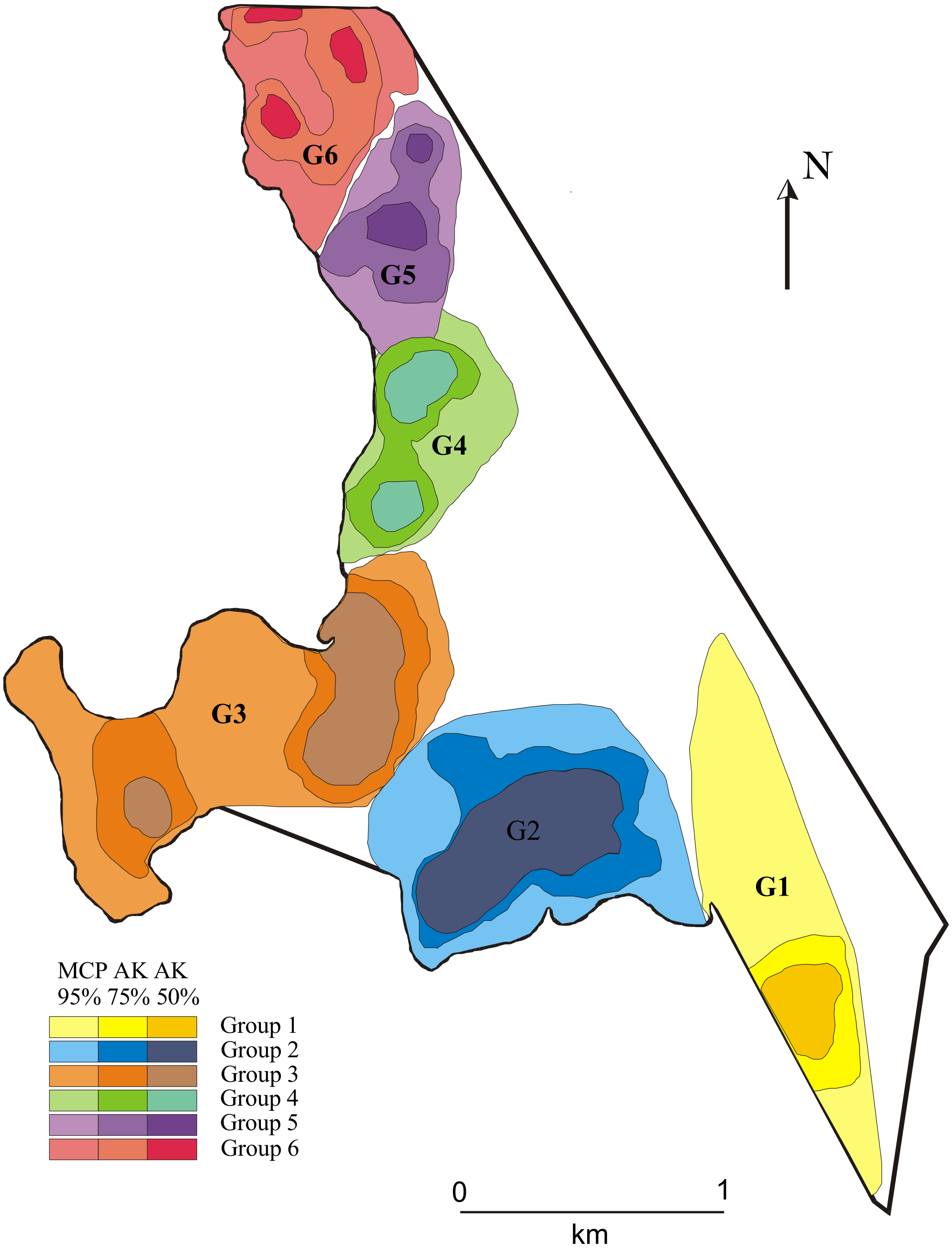


Figure 10. Home ranges of six harem herds of grey rhebok in the main study area of Sterkfontein between February 2000 and April 2002. External boundaries of ranges are taken from 95 % MCP results, while core areas are taken from 75 % and 50 % AK results.

All the herds occasionally strayed slightly into the home ranges of their neighbours, but these movements were temporary and usually only occurred after the initial position of the herd had been fixed for the day. Such positions were, therefore, not often recorded and this meant that there was very little overlap between neighbouring herds. The core areas of Groups 1 and 2 each comprised only one continuous area, while those of the remaining herds were split into two or three separate areas.

The home ranges of Groups 5 and 6 were predominantly within areas of steep slopes with gradients over 10° (Figure 11), while the home ranges of Groups 1, 2 and 3 were predominantly in flat or gently sloping areas with gradients of less than 10°. One third of the home range of Group 4 was on steep slopes.

Ninety five percent MCP home ranges of territorial male mountain reedbuck showed little overlap between individuals (Figure 12), while the core areas of most of these animals were single continuous patches. The home ranges of Males 7, 8, 9 and 10 were predominantly within areas of steep slopes while the home ranges of the other males were not. These remaining animals did, however, all have steep slopes within their home ranges and their cores areas overlapped to some extent with these steep slopes. No territorial males within the main study area had home ranges without any steep slopes. Most of the males had territories adjacent to or close to the dam, and all had access to permanent water without having to cross through another male's territory.

The home ranges used by three female mountain reedbuck are shown in Figure 13. These areas should not be compared statistically to the home ranges of males because they only comprised about 50 positional fixes for each animal. They are shown here to demonstrate the relatively large areas used by females in comparison to males and that the space use by the females overlaps with more than one territorial male. The red collar female appeared to have a larger home range than most other females, many of which spent the majority of their time on the steep slopes in the northern part of the study area. There was a very high degree of overlap between the home ranges of grey rhebok herds and male mountain reedbuck within the main study area (Figure 14).

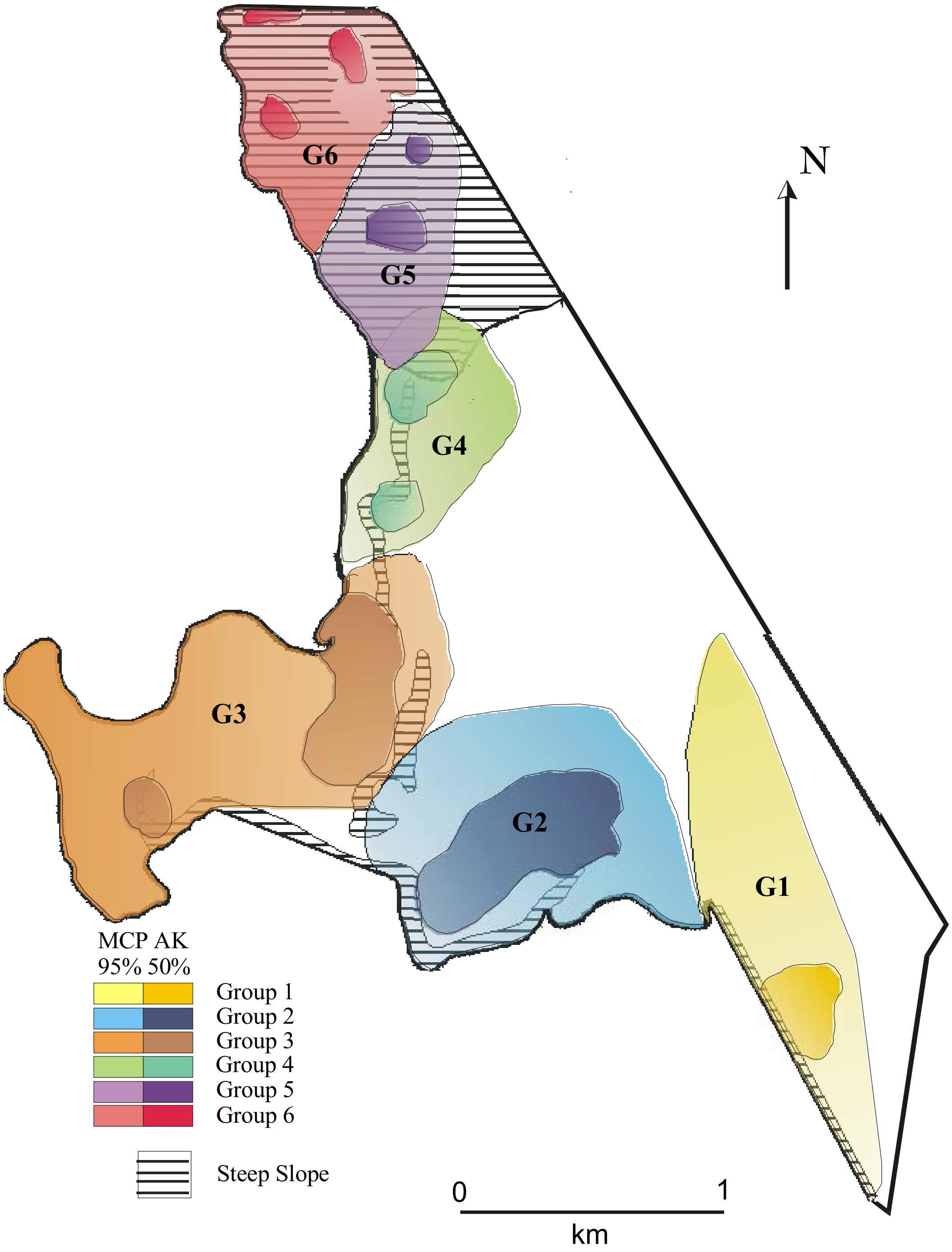


Figure 11. Grey rhebok home ranges and steep slopes (>10°) in the main study area at Sterkfontein. External boundaries of ranges are taken from 95 % MCP results, while core areas are taken from 50 % AK results.

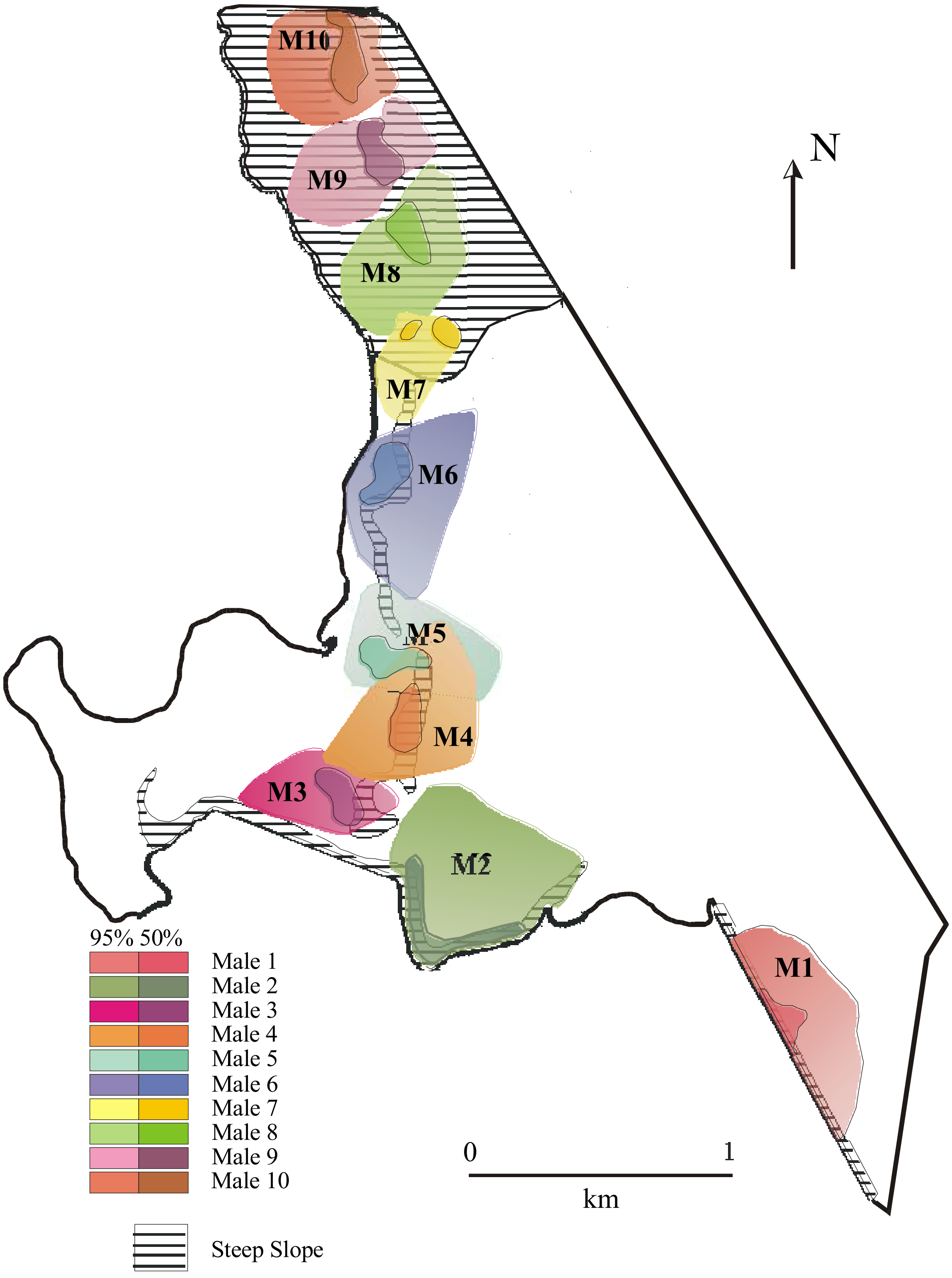


Figure 12. Home ranges of 10 territorial male mountain reedbuck in the main study area between February 2000 and April 2002, superimposed over steep slope (>10°). External boundaries of ranges are taken from 95 % MCP results, while core areas are taken from 50 % AK results.

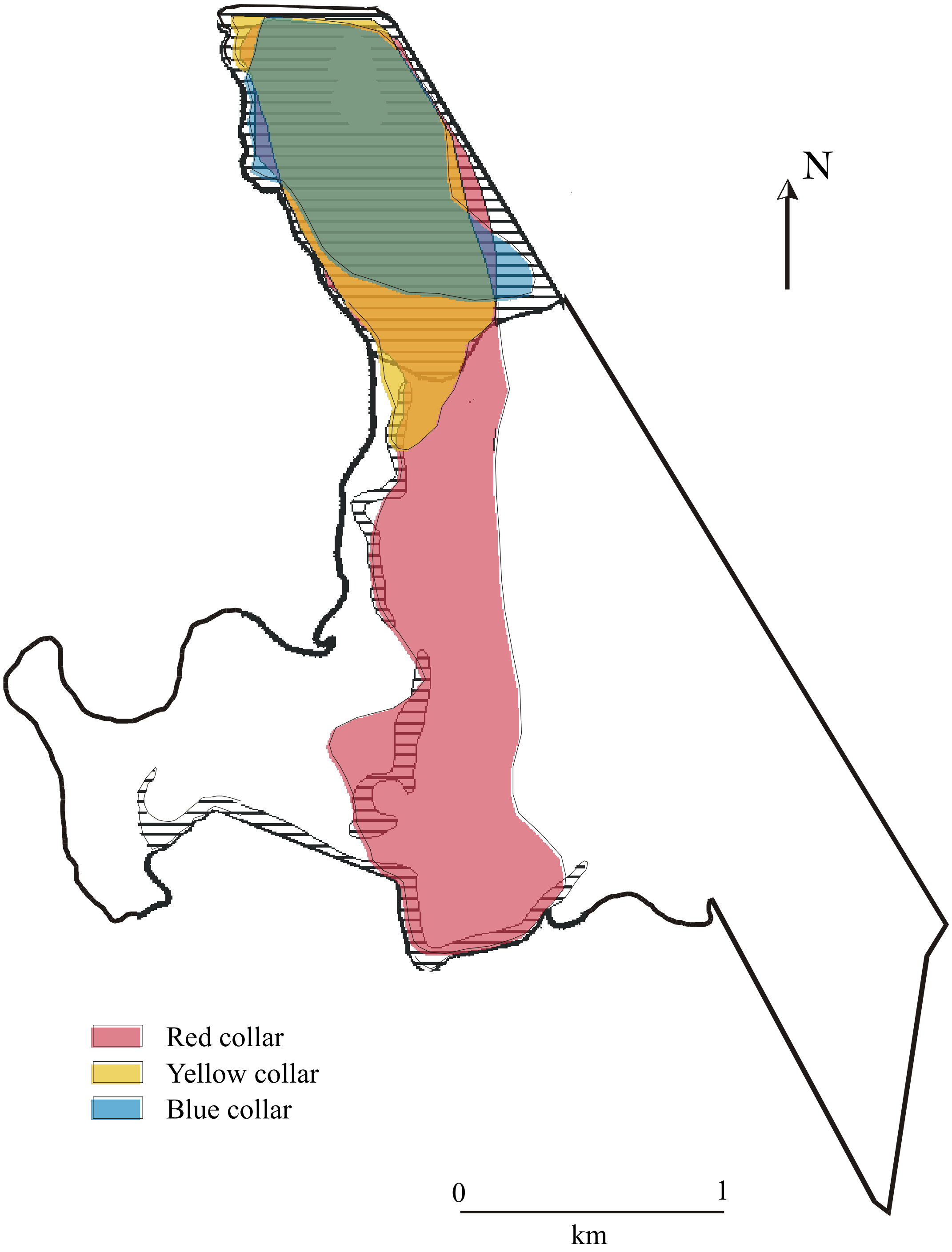


Figure 13. The space use of three mountain reedbuck females within the main study area.

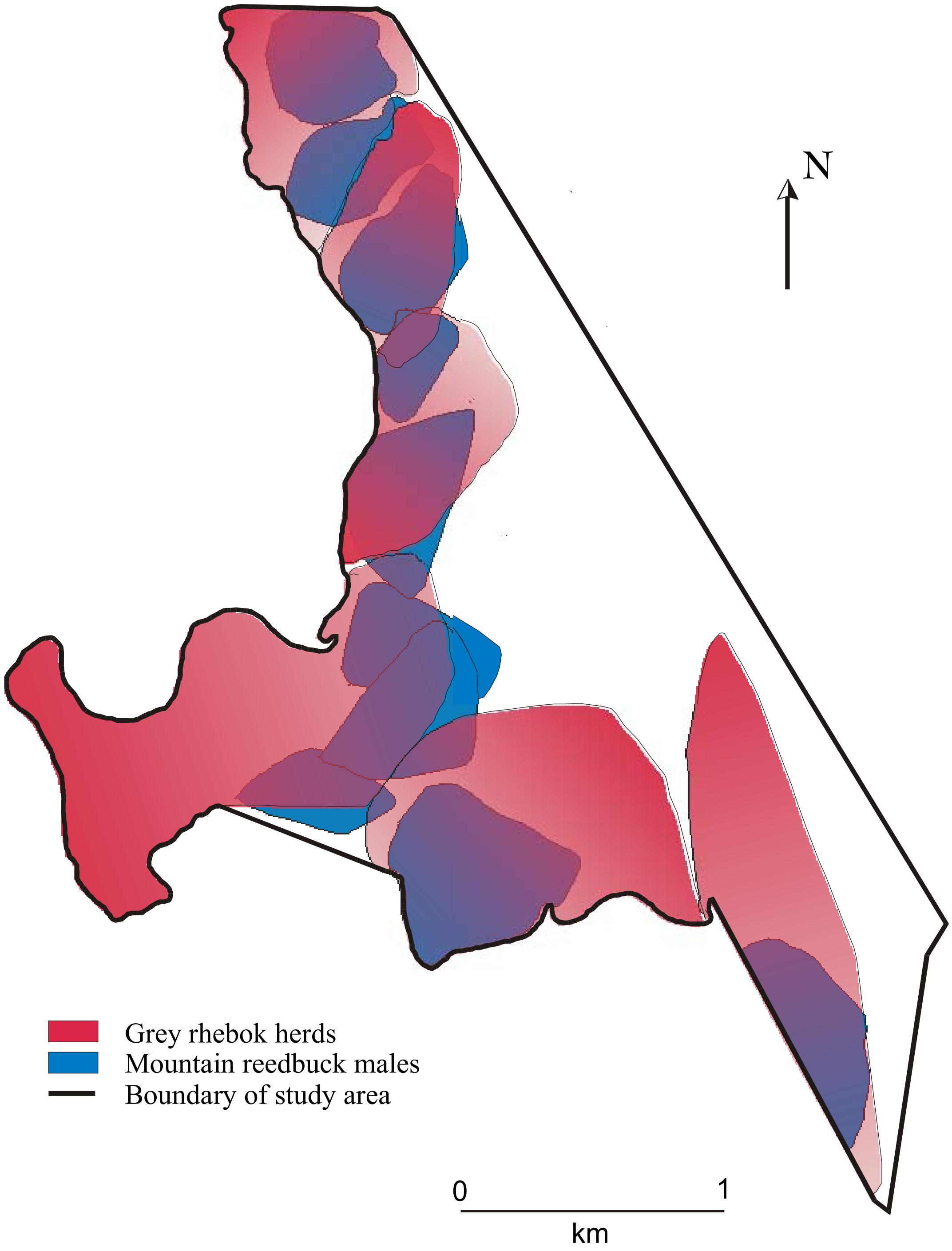


Figure 14. Home range overlap between grey rhebok herds and territorial male mountain reedbuck in the main study area between February 2000 and April 2002.

Ecological densities

The ecological density of grey rhebok in the main study area was 1/15.7 ha (taken from an average of 35 animals in 550 ha), while for mountain reedbuck before the snow it was 1/8.7 ha (at an average of 63 animals in 550 ha).

Vegetation surveys

Grass and forb densities are shown in Table 10. Overall, the average distance to the nearest grass was 29.5 mm, while the average distance to the nearest forb was 89.5 mm. A two-way ANOVA indicated a significant difference between plant types but no difference between flat and steep slopes, and no interaction (Table 11). All data points within a single transect were averaged and treated as one sample. Grass densities were higher than forb densities.

Table 10. Grass and forb densities on steep slopes and flat ground in five survey areas, given as the average distances to the nearest grasses and forbs. Standard deviations are in parentheses.

Gradient	Survey area	Average distance to nearest grass (mm).	Average distance to nearest forb (mm)
Flat	1	29 (31)	107 (78)
	2	20 (17)	64 (51)
	3	22 (19)	86 (59)
	4	31 (26)	86 (67)
	5	35 (26)	77 (60)
Steep	1	26 (26)	81 (63)
	2	30 (31)	89 (72)
	3	43 (32)	111 (72)
	4	29 (18)	77 (61)
	5	30 (21)	117 (121)

Table 11. Two-way ANOVA comparing grass and forb densities within steep and flat areas.

Source of variation	Df	SS	MS	F	P
Grass/forb	1	18000	18000	110.2	< 0.001
Slope	1	289	289	1.8	0.202
Grass/forb x slope	1	58	58	0.4	0.560
Residual	16	2612	163		
Total	19	20959	1103		

Causes of variation in home range size

The parameters included in the Backward Stepwise Regression of grey rhebok variables were the numbers of animals, area of steep slope and escape distance (Table 12). The dependent variable home range area can be predicted from a linear combination of the independent variables: area of steep slope (p = 0.015) and number of animals (p = 0.098). Using a Spearman Rank Correlation Coefficient there was a negative correlation (non-significant) between home range size and area of steep slope (r = -0.714, p = 0.136), but no correlation between home range size and number of animals per group (r = 0.314, p = 0.564). There was, however, a strong negative correlation between area of steep slope and escape distance (r = -0.943, p = 0.017). Groups with larger areas of steep slope available tended to have smaller home ranges, while in areas of steep slopes, the escape distance tended to be less.

The parameters included in the Backward Stepwise Regression of mountain reedbuck variables were the numbers of accompanying females, area of steep slope and area of cover (Table 13). All the variables were eliminated from the model so none were good predictors of home range size in mountain reedbuck. A Spearman Rank Correlation Coefficient found no evidence of correlations between home range size and average number of attending females (r = 0.055, p = 0.865), home range size and area of steep slope (r = 0.006, p = 0.973), or home range size and area of cover (r = -

0.188, p = 0.583). There was, however, a very strong positive correlation between the average number of attending females and area of steep slope (r = 0.818, p = 0.002).

Table 12. Parameters selected to test for predictor variables for home range areas for grey rhebok herds.

Group	MCP home range area (ha)	Average number of animals	Area of steep slope >10° (ha)	Average escape distance (m)
1	73.7	4.57	1.6	397
2	76.8	6.74	3.7	114
3	104.1	7.54	5.6	70
4	39.7	3.81	13.3	100
5	23.3	4.23	22.3	59
6	29.9	7.89	25.2	51

Table 13. Parameters selected to test for predictor variables for home range areas for territorial male mountain reedbuck.

Male	Home range (ha)	Average number of attending females	Area of steep slope >10° (ha)	Area of cover (ha)
1	16.3	0.67	1.6	0.5
2	21.4	0.68	3.5	2.0
3	9.3	0.27	0.9	4.1
4	17.0	0.22	2.6	5.5
5	14.7	0.08	1.1	4.4
6	17.9	0.78	4.5	1.9
7	7.10	0.57	6.0	1.4
8	16.8	2.96	14.0	2.6
9	14.5	8.44	13.1	7.8
10	13.3	8.18	9.0	9.2

Discussion

Home range areas

The geographic positions of the home ranges of the grey rhebok herds went virtually unchanged for the entire study period and there were no apparent seasonal variations. This was because the harem males retained their territories and harems for most of the period and this maintained the status quo (see Chapter 3). Their home range areas were similar to those found in Highmoor State Forest in Natal (Oliver *et al.*, 1978), where they varied between 31 and 135 ha (average 76.7) for eight males, and 43 ha and 117 ha for two females. Males and females were treated separately in that study, but the results should have been the same if herds had been used as the sampling unit instead of individuals. In the Free State, home ranges of herds averaged 61 ha with a range of 46 to 187 ha (Ferreira, 1983). Judging by the low average, the 187 ha value was probably a high outlier in the data set.

Fifty percent AK areas were small relative to their corresponding 95 % AK home ranges. In all six herds, these core areas comprised much less than 50 % of their territories, and in the case of Group 1 it was as low as 9 %. Also, all core areas either incorporated or were adjacent to steep slopes (Figure 11), even though for Group 1 the steep slope of the dam wall was not used very much. Grey rhebok, therefore, used some areas of their home ranges preferentially over others and they appeared to stay close to steep slopes on most occasions.

Ecological densities of grey rhebok at Sterkfontein were high compared to other areas. In Highmoor State Forest, ecological densities were 1/42 ha (Oliver *et al.*, 1978), while in the Drakensburg they ranged between 1/23 ha and 1/57 ha (Rowe-Rowe, 1994). Densities of 1/15 ha in the Bontebok National Park (Beukes, 1984) were very similar to those found in the present study, and in the former it was suggested that these values were high (Beukes, 1984). Although it was not proven in the present study, this must indicate a superior habitat for grey rhebok than other sites, which might result from the high number of forbs available at Sterkfontein compared to many other sites (pers. obs.).

There was very little overlap in home ranges between grey rhebok herds, and this fits with the highly territorial nature of the harem males (Ferreira, 1983; pers. obs.). Five antagonistic interactions were observed whereby one male strayed into another's territory when the resident male was present. In all cases, the intruding male was aggressively chased back to his territory. There was no toleration of trespasses and territories were almost entirely exclusive.

Grey rhebok herds used approximately 2/3 of the study area (estimated from 95 % MCP results), leaving only one gap large enough to incorporate an extra home range. That gap was between the straight north-eastern fence line and the home ranges of Groups 1, 2, 3 and 4 (Figure 10). At no time did any of the resident herds use this space, nor did any animals from within or outside the study area try to establish a new herd there. The reason for this was not established, but two plausible explanations were the lack of access to water and the lack of steep slopes. The only permanent free standing water was the Dam, but for an extra herd to get to this it would have had to pass through the home range of another group, running the gauntlet of interactions with other herds. Although grey rhebok previously have been considered independent of water (Skinner & Smithers, 1990), at Sterkfontein they were regularly observed drinking from the dam during the winter months between May and August (pers. obs.). They needed to do this because many of their food plants died during winter and must have provided very little moisture (pers. obs.). The animals were sometimes observed eating dead plant material that turned out, on examination, to be dry (pers. obs.). Within the gap there were also no steep slopes, and this may have been important. However, a near absence of steep slopes did not stop Group 1 from maintaining a long-term home range in an almost entirely flat area.

The fact that the number of territories and their positions within the study area hardly changed, and that no new herds were established for over two years, even with a large number of yearling males requiring territories at the end of every year, indicated that the area was probably saturated with herds. Introducing males into this area with the aim of increasing genetic variability would have been mostly unsuccessful because there was no space for an extra herd. It would have resulted in a territorial fight, with the most likely victor being the resident male.

Compared to mountain reedbuck at other sites, Sterkfontein males used smaller areas than males at Loskop Dam Nature Reserve (Loskop), where home ranges averaged 28 ha (Irby, 1976), but used larger areas than males in Kenya, where home ranges varied between 3.1 and 5.5 ha (Dunbar & Roberts, 1992). As found by Irby (1976) at Loskop, males at Sterkfontein occupied their territories throughout the year regardless of the presence of females.

Fifty percent AK home range core areas were small relative to their corresponding 95 % AK home ranges, indicating that mountain reedbuck males used certain areas within their home ranges preferentially over others. Core areas of all ten males included steep slopes (Figure 12). Ecological densities at Sterkfontein (1/9.2 ha) were higher than found previously in other areas. Loskop had densities of 1/15 ha to 1/21 ha (Irby, 1976), while in the Drakensburg densities varied from 1/11 ha to 1/32 ha (Rowe-Rowe, 1994). As expected from their territorial behaviour (Irby, 1976; pers. obs.), there was very little overlap in the home ranges of territorial males. There was, however, almost complete overlap between male mountain reedbuck and grey rhebok herds, indicating that they did not exclude each other.

Territorial male mountain reedbuck only used 27 % of the study area (estimated from 95 % MCP results), leaving areas large enough to incorporate many territories of similar size to those found during the present study. However, all male mountain reedbuck home ranges incorporated some steep areas and there were only two unused sites where steep slopes were available. These were on the west side of Male 3, and in the northern section near Males 7 and 8 (Figure 12). Also, all ten males had access to water from the dam. If males had held territories on the east side towards the fence, not only would they have had no access to steep slopes, but they would have had to pass through the territory of another male to get to the water. Mountain reedbuck are recorded as a water dependent species (Skinner & Smithers, 1990).

Vegetation surveys

Grass densities were higher than forb densities in all areas, but within in each plant type there were no differences between steep and flat areas and there was, therefore, no general pattern in relation to slope gradient. As a result, it is unlikely that grass and forb densities had any effect on home range size in mountain reedbuck or grey rhebok within the study area.

Although not tested statistically, there was further evidence for this. Within the home range of grey rhebok Group 3, between the two 75 % core areas (Figure 10), there was a site that had visibly high, although not quantified, densities of edible forbs available (pers. obs.). The herd was, however, rarely located in the area, and when they passed through it they generally did not remain for long. This high availability of food did not appear to influence their use of the site, and it may have been that some other factor affected the time they spent there. The position was very open and quite far from steep slopes.

Causes of variation in home range size

For grey rhebok, the best predictors of home range size were the area of steep slope available and the number of animals within each herd. As there was a negative correlation between home range size and area of steep slope, greater amounts of the latter apparently conveyed some advantage to herds. It either provided more of a certain resource that in turn made it possible for herds to survive in smaller areas, or caused increased competition between herds resulting in compression of territories (Dunbar & Roberts, 1992). There was, however, no correlation at all between numbers of animals in a herd and home range area when these were compared on their own but, when the amount of steep slope available was taken into account, the number of animals became a good predictor of home range size. This makes sense logically because more animals require more food, and because no pattern was found between forb densities and slope gradient, a higher food requirement translates to a larger area requirement.

The average escape distance was not found to be a good predictor of home range area, but it was strongly negatively correlated with area of steep slope. This is not surprising as the steep slopes provided lots of small hills and rocky outcrops that animals could run around to get out of sight. It is possible that escape distance was important to grey rhebok, but was not found to be a good predictor because the steep slope parameter was better.

For territorial male mountain reedbuck, none of the variables proved to be good predictors of home range size. This either indicates that there was no pattern to home range size, or that it was influenced by an untested parameter such as the strength of the dominance of the individual males. In this case, however, it is more likely that stronger males would have held territories with better access to females (Dunbar & Roberts, 1992), and this was not correlated to home range area.

There was a strong positive correlation between the average number of attending females and the area of steep slope. Females showed a strong preference for steep slopes, concurring with Dunbar & Roberts (1992), who found that there was a strong positive correlation between the female/male index and cliff height. It was hence suggested that female mountain reedbuck traded access to food resources against safety from predators and steeper terrain provided this safety. In the present study there were no apparent patterns to grass densities between the different sites tested, so females were not selecting steep slopes for greater food availability.

Interspecific comparison of home range size

The home ranges of territorial male mountain reedbuck in the present study were nearly four times smaller than the home ranges of the grey rhebok herds. The reason for this is most likely the different mating strategies of the two species. Female mountain reedbuck often concentrate on steep slopes for defensive purposes (Dunbar & Roberts, 1992), and the amount of food available within a male’s territory is not a deciding factor for them. The mating system is resource defence polygyny but, rather than defending food resources, territorial males defend areas that offer protection to females, and successful males will hold territories where females congregate regularly. In such places males have regular, although not constant, access to females and the potential for mating is high. However, although territories do not have to contain enough food to satisfy a herd of females, they may have to have enough to sustain one territorial male. This is because territories/home ranges of different animals do not overlap and males rarely move out of their own areas into those of other males. They must, therefore, acquire most, if not all, of their food from within their own territory and this sets a lower limit for territory size.

Territorial male grey rhebok defend a harem of females all year, staying with them almost constantly and herding them around if necessary. This is female defence polygyny. The area defended by the male must, therefore, contain everything that female's need for survival and reproduction. This includes adequate food resources, adequate areas to evade predators, access to hiding places for newborn lambs and access to water. The fact that home range size was negatively correlated to the amount of steep slope available, but that there were no differences in forb density between steep areas and flat areas (i.e. smaller areas contain less food regardless of slope gradient), implies that the larger home ranges may have had food resources that exceeded requirements. This is corroborated by the observation that some areas within home ranges that were known to have a plentiful food supply were under-utilised (see above).

The higher overall densities of mountain reedbuck compared to grey rhebok suggests a larger food supply for the former. Grasses are certainly more abundant than forbs at Sterkfontein (Table 10), so the standing crop (biomass) is most likely bigger. This in itself, however, does not imply that there is more food available for mountain reedbuck because they are selective grazers, and large amounts of the standing crop of grass is unavailable to them. Moreover, the nutritional values of the grasses and forbs for the two antelope species were not known and greater quantities of grass may not equate to greater nutritional quality for feeding. Generally browse plants have higher levels of nitrogen than do grasses, but these can be bound to secondary compounds during mastication, making them less available for digestion (Robbins *et al.*, 1987a,b; Gordon, 2003).

Chapter 5

ACTIVITY PATTERNS, FORAGING BEHAVIOUR AND SOCIAL BEHAVIOUR

Introduction

Although grey rhebok and mountain reedbuck share similar habitat, they differ significantly in their feeding and social behaviour. As described in earlier chapters, grey rhebok are browsers (Ferreira, 1983; Beukes, 1984) and live in harems where a single adult male defends a small group of females and young on a permanent basis (Esser, 1973; Beukes, 1984). Mountain reedbuck are grazers (Irby, 1976), and although males are territorial, they only defend an area that female herds move in and out of temporarily (Irby, 1976). Female herds are transitory, with animals breaking up into small groups and reforming larger groups on a regular basis (Irby, 1976).

Foraging behaviour should differ between the two species as a result of the differences in growth habit of the food they eat. Grass plants grew at higher densities than forbs at Sterkfontein (see Chapter 4) indicating that the food supply of mountain reedbuck was generally closer together than that of grey rhebok. Although small, these differences in densities should influence the average distances that the two species need to move between food sources, thus affecting foraging behaviour with a knock-on effect to other behaviours. Additionally, nutritional differences between forbs and grasses might influence the quantities of food required which would influence the time spent feeding.

Klein & Fairall (1986) compared foraging behaviour and associated energetics of two antelope species with different feeding requirements (impala and blesbok) and found that the grazer (blesbok) had a shorter daily feeding time than the mixed feeder (impala). This was thought to be associated with the blesboks' efficiency as a bulk feeder and the longer time required for digestion of its coarser diet. In the present study, due to the similarity in size of grey rhebok and mountain reedbuck, and similar use of marginal habitat, a comparative behavioural study of the two species, similar to that of Klein & Fairall (1986), was expected to find that grey rhebok fed for longer but spent less time digesting food than mountain reedbuck due to their contrasting feeding requirements.

The differing group structures should result in contrasting male reproductive behaviour due to the disparate access to females. Harem male grey rhebok have access to their females at all times with no competition from other males (apart from rare challenges from intruding males: see Chapter 3), and are, therefore, always aware of the reproductive status of these females. In contrast, male mountain reedbuck are often solitary and have sporadic access to females. To increase their chances of detecting oestrus in females and thus mating, they might be expected to test females whenever they get the opportunity. Moreover, mountain reedbuck are relatively aseasonal when compared with grey rhebok (Irby, 1979; Esser, 1973; Skinner & Smithers, 1990), and should test females over longer periods of the year. There were two aims to this component of the study:

1) To quantify behaviour and estimate activity budgets and patterns for both species;
2) To compare differences in behaviour between the two species in relation to ecological differences such as foraging and social behaviour.

To accomplish these aims, the following questions were considered:

a. How much time overall is spent performing different behaviours during the day and how do the two species compare? (i.e. what are the activity budgets)?
b. How do the two species spread these different behaviours throughout the day (activity patterns)?
c. Are they more active or inactive at certain times of day?
d. Is there any seasonal variation in activity (resting and feeding behaviour)?
e. How active are the two species at night?
f. When, and how often, does reproductive behaviour take place?
g. How do males demarcate their territories?

Methods

Study site and animals

This component of the study was conducted within the main study site at Sterkfontein in an area of approximately 550 ha (see Chapter 2). Behavioural observations were made over a one-year period between May 2001 and April 2002. These were carried out primarily in daylight between 06h00 and 18h00, and at varying times of the day in an attempt to represent different periods equally. Three harem herds of grey rhebok were monitored (Groups 2, 3 and 4), while the remaining herds were difficult to observe either because of rough terrain (Group 6) or because of skittish behaviour (Group 1). Group 5 ceased to exist in September 2001 and was excluded from the study. Six adult male mountain reedbuck were monitored and observations were made whether or not females accompanied them. Due to female movement patterns, three of these males were predominantly solitary. Female mountain reedbuck were observed in differing group sizes without differentiating between individuals.

Behaviour

Behaviour was measured predominantly by scan observations (Martin & Bateson, 1993). Normally only one herd was observed at a time, but when grey rhebok and mountain reedbuck were close together behaviour of both species was recorded simultaneously, so long as all animals could be observed clearly. Solitary animals were also observed. Observations were carried out either from a vehicle, or on foot from a hidden position, so that the subjects' behaviour was not affected by the presence of the observer. If the animals were disturbed, behavioural recording was delayed until they appeared to pay no attention to the observer. Animals were watched with binoculars from distances varying between 50 and 300 m.

Observation periods lasted a minimum of 1 hour, unless the subjects moved out of sight or were disturbed, while 2- and 3-hour periods were also regularly monitored. These longer observations often allowed an entire period of behaviour to be recorded. For example, if the animals were feeding when observations started, but then became inactive, data collection sometimes continued into the next active period. For purposes of estimating activity budgets and patterns, these longer observation periods were split into separate hourly periods. In total, 295 one-hour observation periods were conducted on grey rhebok herds. Of these, harem males were observed for only 247 hours because on 48 occasions they were either not present or were only present for a short period. For mountain reedbuck, 141 one-hour observation periods were conducted on males and 109 on female herds.

Every 2 minutes the whole group of subjects were rapidly scanned and the behaviour of each animal recorded at that instant. Within grey rhebok herds, male behaviour was differentiated from that of females and young over the age of five months, while the behaviour of lambs under five months old was also differentiated. After five months they were considered fully weaned and males between the ages of five- and eleven months were grouped with the females because they remained sub-ordinate to the harem male and showed no signs of sexual maturity. It was also difficult to differentiate between them from a long distance in a short space of time. Females within the same herd, as well as young over five months age were treated as one “individual”, with their data being pooled. At about the age of eleven months, young males were evicted from their natal groups by the harem males and disappeared.

In mountain reedbuck, male behaviour was also differentiated from that of females, but the behaviour of lambs younger than six months age was not recorded due to the difficulty of observing them. Again, female behaviour was recorded without differentiating between individuals and their data were pooled.

Although Jarman & Jarman (1973) found that a 4 minute recording interval was adequate when studying the activity of impala in the Serengeti, and that compared with a 1- or 2 minute interval, 4 minutes did not substantially increase the error in recording major activities, it was decided in the present study that a 2 minute interval was manageable. Apart from increasing the data set, it reduced the time wasted between recordings.

During observations, behaviour was split into the following categories:

Feeding (grazing/browsing)
Standing head up (not feeding)
Standing alert (vigilant)
Standing grooming
Walking/running
Defecating/urinating
Territorial marking (adult males only)
Ruminating
Lying inactive
Lying grooming
Sexual behaviour (adult males only): Urine sniffing, vulva sniffing, flehmen, licking lips, laufschlag, & mounting.

When observations were made from distances greater than 100 m, and on animals that were either lying inactive or standing but not feeding, it was difficult to determine whether they were ruminating. At these times ruminating was excluded and behaviour was only recorded as lying inactive or standing head up (not feeding). Quantification of ruminating behaviour was, therefore, restricted to observations from less than 100 m.

Scan sampling allowed the recording of behaviour from more than one individual at the same time, so it was unnecessary to watch individuals continuously. However, certain uncommon or short duration behaviours were watched for continuously and recorded whenever they occurred, regardless of whether they occurred at the 2-minute interval. These behaviours were territorial marking by males (grey rhebok: see below), sexual behaviour (normally initiated by males), submissive behaviour (young males submitting to adult males), and drinking. Alert behaviour was recorded but was unusual because there were virtually no natural predators and the only threat came from humans.

In addition to diurnal observations, nocturnal behaviour was recorded for both species over a number of separate six-hour periods. Grey rhebok were observed at night on eight occasions, while mountain reedbuck were observed on four occasions. Due to the difficulties of viewing at night, behavioural categories were restricted to active or inactive (lying), and the scanning frequency was reduced to five-minute intervals. Due to the low number of observation periods, only averages were determined and no statistical analyses were attempted.

Activity budgets and activity patterns

Activity budgets are used here to indicate the overall average percentage of time spent engaged in various behavioural activities during the day. Behaviours were placed in the following categories: feeding, standing (not feeding but sometimes ruminating), walking (including running), grooming (both standing grooming and lying grooming), resting (including lying inactive and lying ruminating) and other (including defecating, marking, standing alert and sexual behaviour). Ruminating was excluded as an independent activity. Budgets were estimated for males and females of both antelope species, using overall averages calculated from hourly averages (i.e. all times of the day were equally represented). No seasonal patterns were considered.

Activity patterns indicate the percentage of time spent engaged in various behaviours at different times of the day and in two seasons, summer and winter. Behaviours were categorised as for budgets, but for each gender of each species, summer (November to February) and winter (May to August) were differentiated, and days were split into periods of two-hours (06h00 - 07h59, 08h00 - 09h59, 10h00 - 11h59, etc.).

Territorial marking

Male grey rhebok performed territorial marking by frequently defecating small amounts of faeces within their home ranges. Whereas females and young males defecated once every 1 – 2 hours, harem males defecated much more often, sometimes more than 20 times per hour. This was often done at visible markers such as grass tufts, bushes, termite mounds or telephone poles, while females appeared to defecate randomly.

The frequency of territorial marking was investigated in three harem male grey rhebok from groups 2, 3 & 4 between May 2001 and April 2002. During scan observations for general behaviour (see above), the males could be individually monitored for marking behaviour because it was easy to detect when they lifted their white tails to defecate. To standardise the results, the number of marks made during the males' active periods were divided by the time of observation, and the number of marks per hour derived from this (periods of inactivity were excluded).

Although male mountain reedbuck were territorial, they did not perform the same marking behaviour and were, therefore, not monitored for it.

Statistical methods

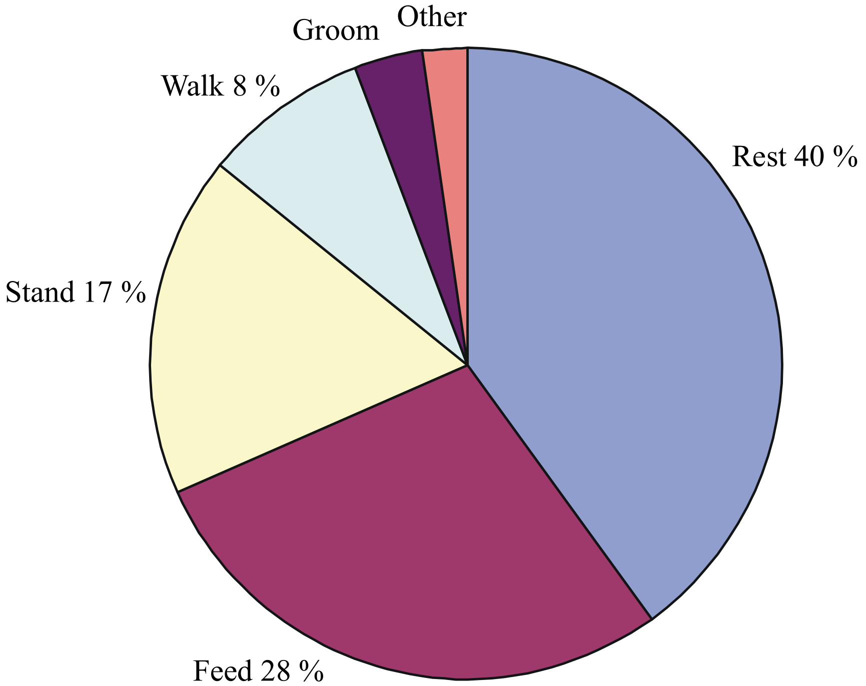
Seasonal differences in time spent resting and feeding were investigated using paired t-tests, and then analyses of variance were used to make comparisons between genders, species, and times of day. Times of day were split into 1-hour periods (unlike the activity pattern graphs below which were split into 2-hour periods) starting at 07h00 and finishing at 18h00. Seasonal differences in marking frequencies between three territorial male grey rhebok were tested for using a two-way ANOVA, as were submissive behaviour of young male grey rhebok from three herds.

Results

Diurnal activity budgets

Male grey rhebok rested for 40 % of daylight hours, compared to 44 % by female grey rhebok (Figure 15). Male mountain reedbuck rested for 57 % of daylight hours, compared to 54 % by females (Figure 16). In contrast, the percentage of time spent feeding was more similar between the two species, with male and female grey rhebok feeding for 28 % and 33 % of daylight hours respectively, and male and female mountain reedbuck feeding for 28 % and 31 % respectively.

(a) Males



(b) Females

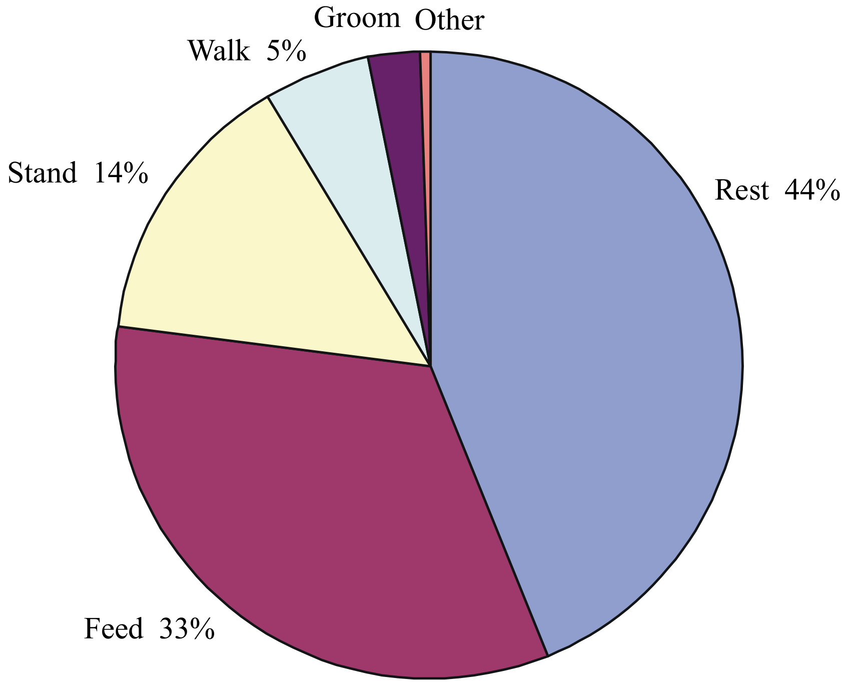
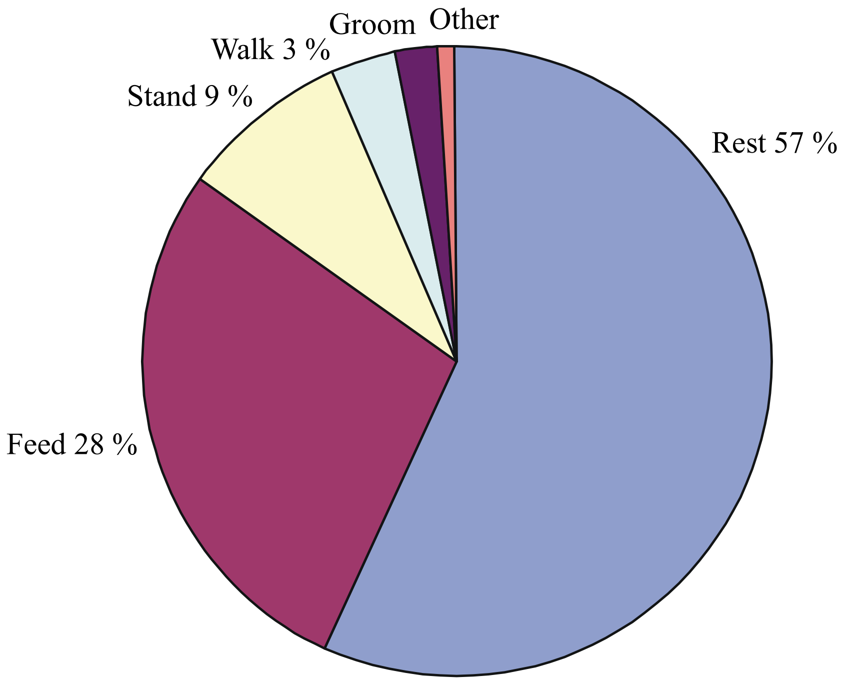


Figure 15. Activity budgets of grey rhebok at Sterkfontein: (a) males; (b) females.

(a) Males



(b) Females

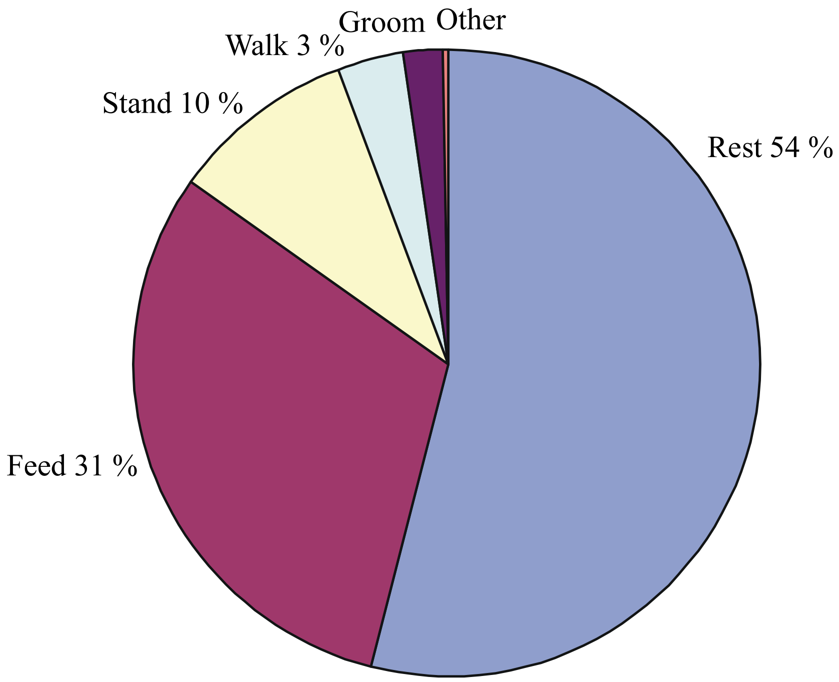
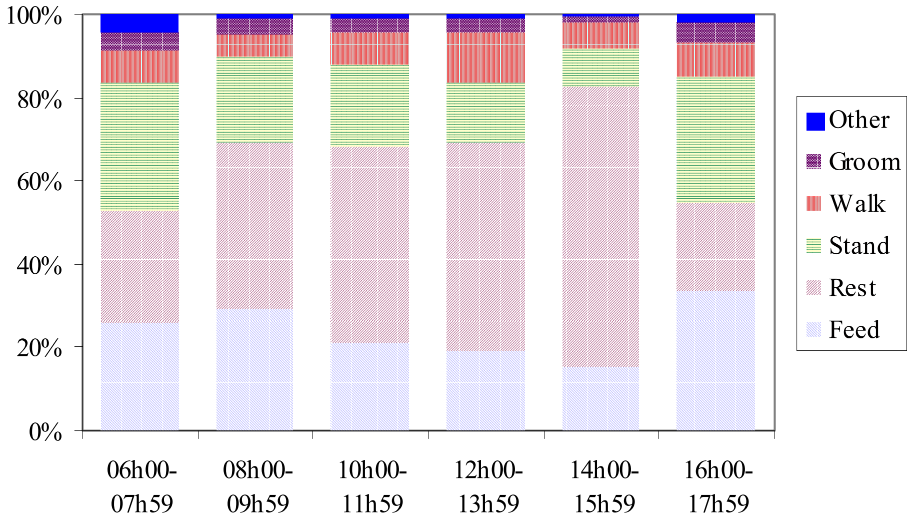


Figure 16. Activity budgets of mountain reedbuck at Sterkfontein: (a) males; (b) females.

Diurnal activity patterns

Male grey rhebok had similar feeding patterns in both summer and winter, whereby they fed most during the periods 08h00-09h59 and 16h00-17h59, and least during the periods 12h00-13h59 and 14h00-15h59 (Figure 17). In both seasons they were most active (i.e. they rested the least) during the periods 06h00-07h59 and 16h00-17h59.

(a)



(b)

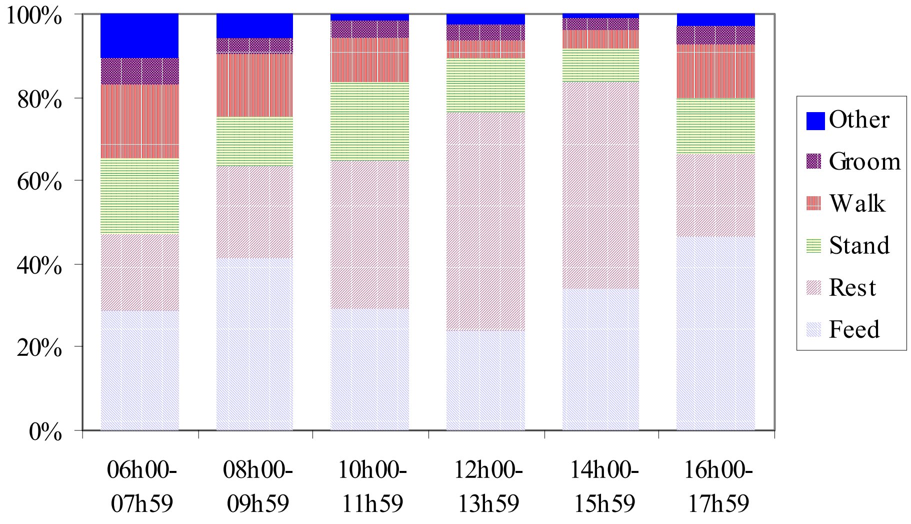
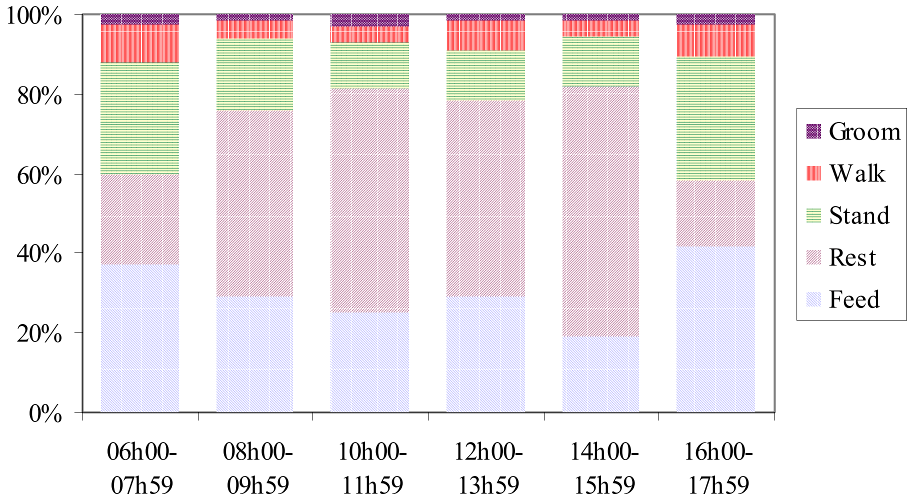


Figure 17. The diurnal activity patterns of male grey rhebok: (a) November to February; (b) May to August.

In summer, female grey rhebok fed most and were most active during the periods 06h00-07h59 and 16h00-17h59, while in winter they fed most and were most active during the periods 08h00-09h59 and 16h00-17h59 (Figure 18). In general, the activities of male and female grey rhebok overlapped so that they were normally active at the same times and inactive (resting) at the same times.

(a)



(b)

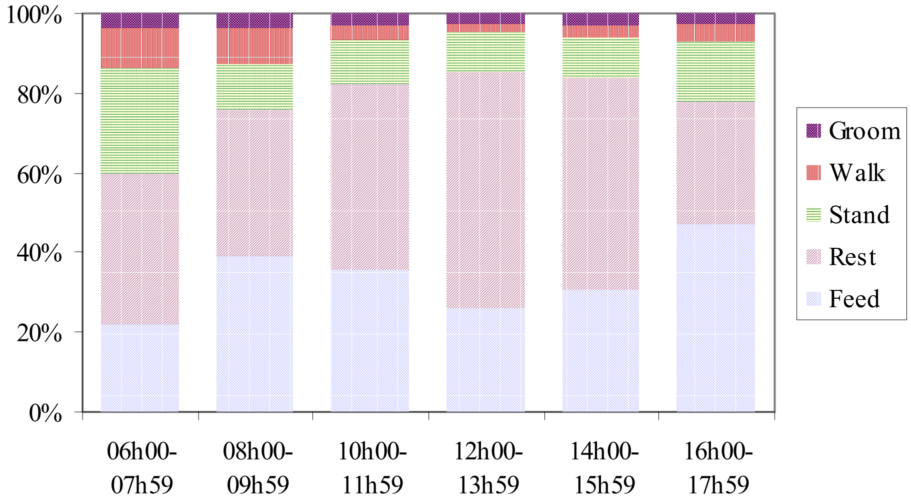
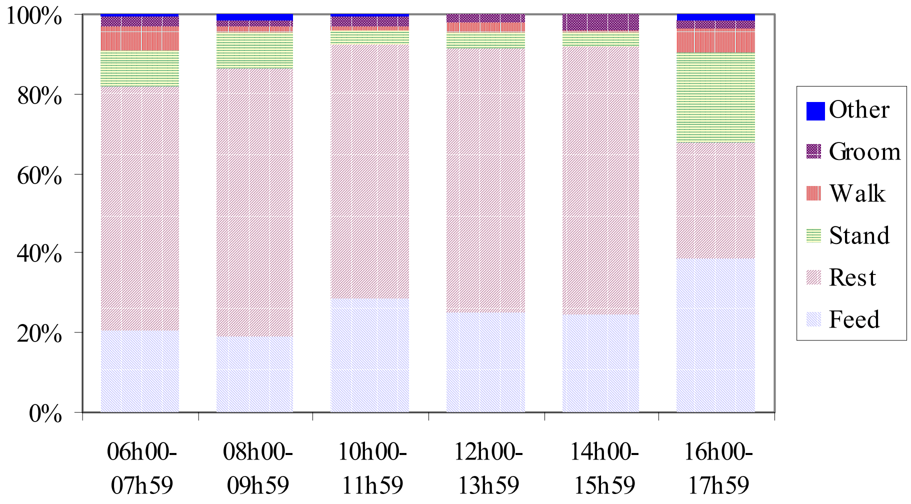


Figure 18. The diurnal activity patterns of female grey rhebok: (a) November to February; (b) May to August.

Male mountain reedbuck fed most during the period 16h00-17h59 in both seasons (Figure 19). In summer they rested to a similar degree in all time periods, except 16h00-17h59, when they rested much less, while in winter they rested more during the periods 12h00-13h59 and 14h00-15h59, and least during 16h00-17h59.

(a)



(b)

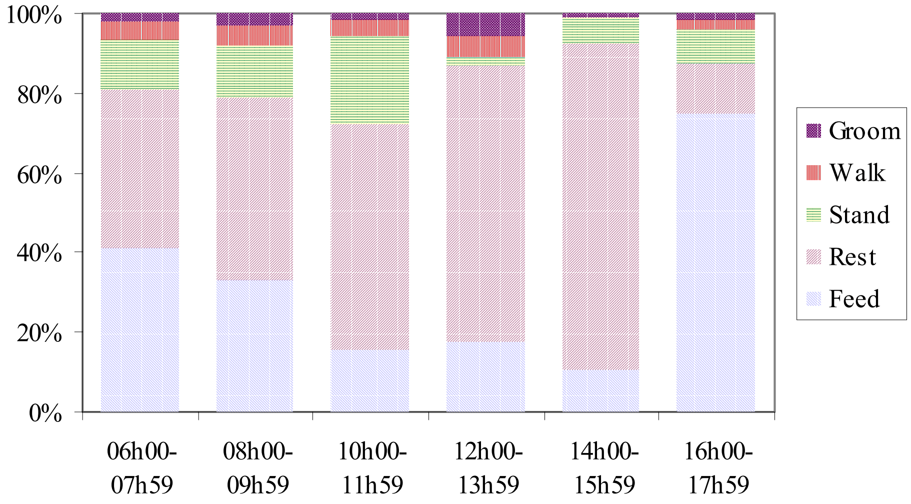
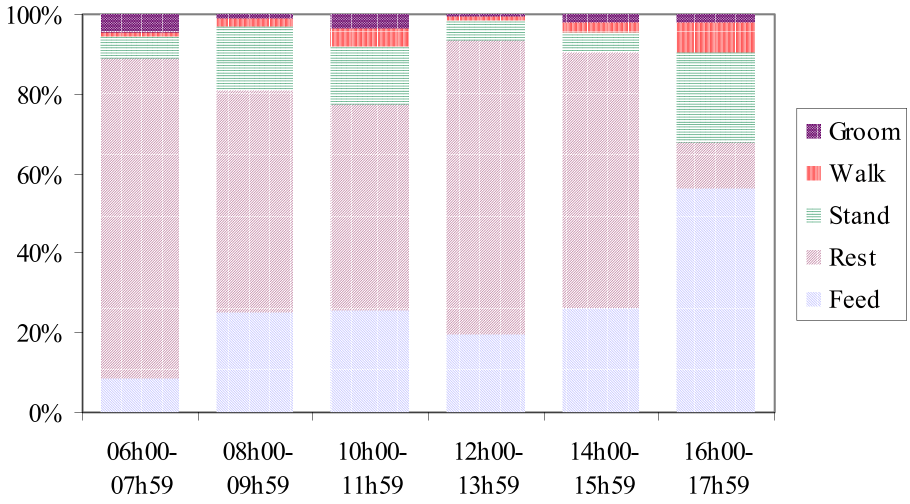


Figure 19. The diurnal activity patterns of male mountain reedbuck: (a) November to February; (b) May to August.

Female mountain reedbuck fed most during the time period 16h00-17h59 in both seasons (Figure 20). In summer they rested more during the periods 06h00-07h59 and 12h00-13h59, while in winter they rested by far the most during the period 10h00-11h59.

(a)



(b)

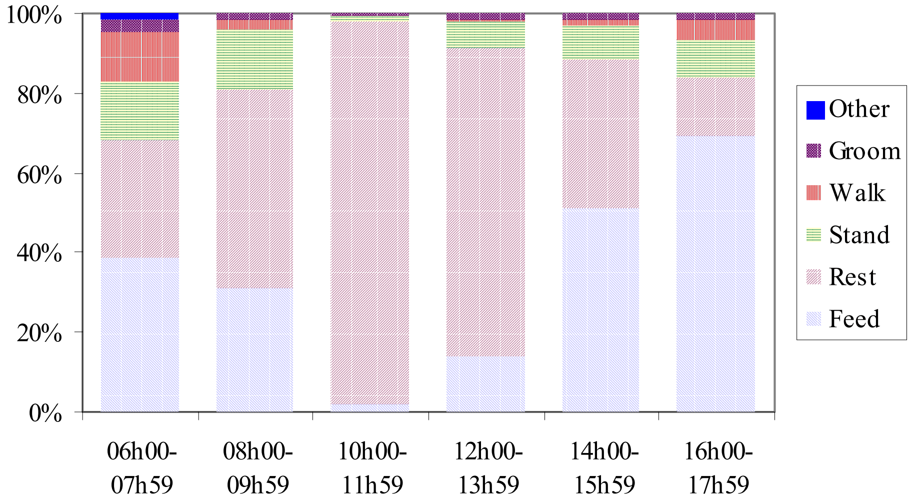


Figure 20. The diurnal activity patterns of female mountain reedbuck: (a) November to February; (b) May to August.

To investigate seasonal variation in resting behaviour of male and female grey rhebok, and male and female mountain reedbuck, four separate paired t-tests were conducted using summer (Nov – Jan) and winter (May - Jul) data. Overall averages from 11 one-hour time periods were included for each season within a species (e.g. 6h00-06h59, 07h00-07h59, etc.). There were no seasonal differences found (Male grey rhebok: $t = 1.404$, $df = 10$, $p = 0.191$; Female grey rhebok: $t = -0.154$, $df = 10$, $p = 0.881$; Male mountain reedbuck: $t = 0.523$, $df = 10$, $p = 0.612$; Female mountain reedbuck: $t = 0.295$, $df = 10$, $p = 0.774$). Seasonal data were, therefore, pooled for the rest of the analysis.

A two-way ANOVA was used to investigate variation in resting behaviour between different times of the day for both genders of both species (Table 14). Highly significant differences were found between species categories, between times of day, and there was also an interaction. Multiple pairwise comparisons using the Tukey test indicated that both male and female grey rhebok spent less time resting than male and female mountain reedbuck, but that male and female grey rhebok did not differ from each other, and male and female mountain reedbuck did not differ from each other. Between time periods, male grey rhebok were less active from 12h00-14h59 than from 06h00-08-59 and 17h00-17h59, while female grey rhebok were less active during the period 12h00-12h59 than 17h00-17h59. Both male and female mountain reedbuck were more active during the period 16h00-17h59 than at any other time of day. The interaction term indicated that the differences found in activity levels between different times of the day depended on which species or gender was considered (i.e. it differed between grey rhebok and mountain reedbuck).

Table 14. Two-way ANOVA comparing the differences between grey rhebok and mountain reedbuck (of both genders) and between periods of the day in the time spent resting. Species category refers to male grey rhebok, female grey rhebok, male mountain reedbuck, and female mountain reedbuck.

Source of variation	DF	SS	MS	F	P
Species category	3	11961	3987	16.4	< 0.001
Time	10	32327	3233	13.3	< 0.001
Species x time	30	12243	408	1.7	0.033
Residual	88	21395	243		
Total	131	77925	595		

Although time spent resting was used as an indication of levels of activity (because lying/resting was defined as inactive), periods of activity (defined as not lying down) did not necessarily mean feeding. As a result, variation in feeding behaviour was also tested using a two-way ANOVA (Table 15). No differences were found between species categories (although the result was marginal), but there was a strong difference between times of day. There was no interaction, although again this was marginal. Multiple pairwise comparisons using the Tukey test indicated that all animals fed more during the period 16h00-17h59 than at any other time of day.

Table 15. Two-way ANOVA comparing the differences between grey rhebok and mountain reedbuck (of both genders) and between periods of the day in the time spent feeding. Species category refers to male grey rhebok, female grey rhebok, male mountain reedbuck, and female mountain reedbuck.

Source of variation	DF	SS	MS	F	P
Species category	3	0.080	0.027	2.249	0.088
Time	10	1.186	0.119	10.011	< 0.001
Species x time	30	0.520	0.017	1.462	0.088
Residual	88	1.043	0.012		
Total	131	0.022	0.022		

Because territorial male mountain reedbuck did not have full time access to females, it was thought that when they did have access, they might spend more time testing females for oestrus and less time feeding. Time spent feeding by solitary males was, therefore, compared with time spent feeding by males with attending females (using hourly averages). No differences were found ($t = 0.497$, $df = 20$, $p = 0.625$).

Patterns of activity and inactivity

A typical day for grey rhebok involved foraging for between one and two hours, followed by a rest period of similar length. This was then followed by more activity for one to two hours, and then more resting. Although grey rhebok were on average less active during the middle of the day than early morning and late afternoon (see above), the times when animals were active varied from day to day and were often determined by the timing of previous activities. For example, on one day a herd might have been active at 08h00 and inactive at 12h00, while on the next day the same herd could have been inactive at 08h00 but active at 12h00, even in hot weather.

Mountain reedbuck activity periods were generally more fixed, with early morning (06h00 – 09h00) being a period of activity, and midday being a period of inactivity. Following this, late afternoon was normally an active time, while the night included alternating periods of activity and inactivity. These patterns were not rigidly fixed, however, and animals were sometimes active at midday.

Nocturnal activity patterns

At night, grey rhebok were active for 57 % of the time, while mountain reedbuck were active for 72 % of the time (Figure 21). No comparative statistical analyses were attempted. Both species were active on and off throughout the night during both summer and winter.

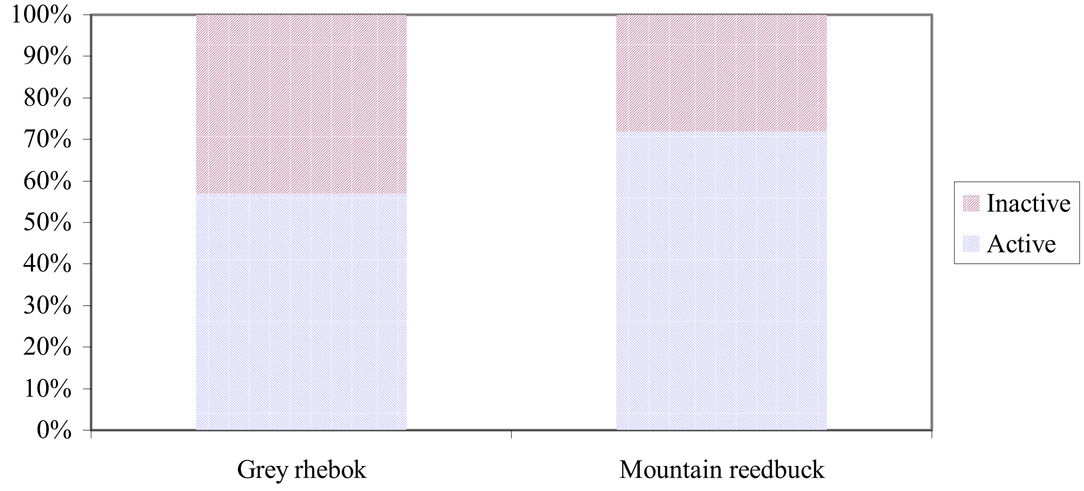


Figure 21. The nocturnal activity budgets of grey rhebok and mountain reedbuck at Sterkfontein.

Ruminating and drinking

Due to the difficulties in observing ruminating behaviour clearly, especially in mountain reedbuck, the number of observation periods in which it was quantified was small and unevenly spread between times of day. This meant that no statistical analysis was possible to compare differences between the two species. No attempt was made to quantify ruminating behaviour at night.

Grey rhebok generally ruminated while lying down, although they occasionally did so while standing. During periods of resting they spent an average of 33 % of the time ruminating, and this gave an overall time spent ruminating of 14 %. Similarly, mountain reedbuck ruminated mostly while lying down, and they spent an average of 40 % of the time ruminating during these periods. This gave an overall time spent ruminating of 22 %.

Grey rhebok groups were seen drinking on 58 separate occasions during diurnal observations in 2000 and 2001 (Figure 22). Most observations occurred between June and September, while none occurred between November and February. No drinking occurred during scan observations. Mountain reedbuck were never seen drinking during the study period, although there were occasions when they were found very close to the dam, and were thought to have been drinking before being found.

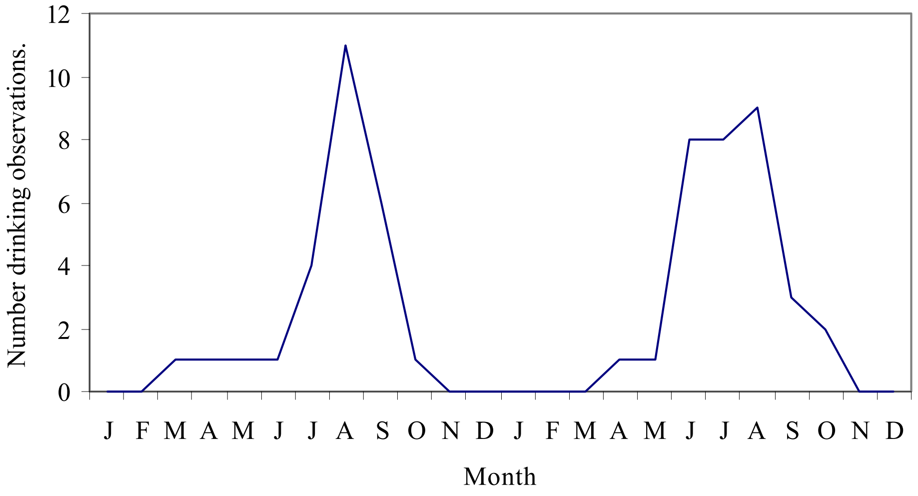


Figure 22. Number of drinking observations made on grey rhebok between January 2000 and December 2001.

Male reproductive behaviour

Harem male grey rhebok were often seen smelling female urine and faeces on the ground, apparently testing for signs of oestrus. This appeared to be opportunistic, however, and was only carried out when males noticed females urinating or defecating nearby. In most cases the males followed this up by marking with their own faeces at the same site. Unlike mountain reedbuck (see below), male grey rhebok did not often test female reproductive condition by sniffing at their rump areas.

Mating behaviour was only seen six times in grey rhebok during the entire study period, and harem males always initiated it. Mating occurred in January (once), March (twice), April (once), May (once), and November (once). The January and November observations were from the same male and female, both of which resulted in successful lambing, and both of which resulted in two of only three lambs born out of season during the study period (see Chapter 3).

A characteristic posture of a sexually aroused male from the beginning of a mating sequence was to stand with his neck at a vertical angle, ears pinned back horizontally, while at the same time licking his muzzle continuously (this was also seen in males responding to females returning to the group after being separated for a short time). The males' black penis was generally visible at these times as well. In all observed mating sequences the male followed the female around continuously, keeping his nose close to her rump, while repeatedly licking his muzzle and sniffing and licking around her tail and vaginal area. He often rested his head on the females' rump or back, and raised his front legs underneath her in a stiff gait (laufschlag). This sometimes continued for a few minutes while the female foraged and flicked her tail. Several mounting attempts then followed, generally with the behaviour described above taking place between consecutive mounts. Ejaculation was marked by a convulsive thrust, after which the male immediately stopped following the female, groomed, and then moved away to feed or lie down.

In all six mating observations, males mated (i.e. ejaculated) more than once with the same female, and often many times in one day. Males also stayed with females between mating episodes and, therefore, performed mate guarding. The time interval between first signs of sexual behaviour and the first mount varied between three and ten minutes, while time intervals between ejaculations of separate copulations varied between five and 45 minutes. On one occasion, the harem male from Group 3 mated with the same female 10 times in a five-hour period between 12h00 and 17h00, after which observations ceased. He was then seen mating with the same female the following morning, albeit for a shorter time period. The receptive period (oestrus) of female grey rhebok was, therefore, at least 24 hours.

Mountain reedbuck males were observed sniffing the rumps of females in all months of the year except August, but in most cases no further sexual behaviour occurred. The average number of tail sniffs recorded for males that were accompanied by more than one female (observations of solitary males and males with only one accompanying female were excluded) was 3.7 times per hour (n = 33). Males sometimes showed no interest in females during an observation period, even if females were present, while the most active male sniffed the rump of 28 females in one hour after a large group of females had entered his territory.

Occasionally males followed females for a short period after testing, but extended sexual and mating behaviour was only seen on two occasions (once in June 2001, and once in December 2001). This behaviour was well described by Irby (1976). Males initiated mating sequences by smelling the vaginal area of a female, and continued by following her closely, while smelling and licking around her vaginal area. At these times some females continued feeding, others assumed a tense head down posture, while others ran off. Males then performed the high, stiff legged gait (laufschlag). Multiple mounting attempts were then made, with the final one ending in a convulsive thrust signifying ejaculation. After this males stood quietly for a few seconds and then began grooming. The males were not seen to mate with the same female again the same day, implying that the female receptive period was very short and ended after the first mating. Males were not seen guarding females after mating.

Territorial marking and territory patrols

Harem male grey rhebok marked within their territories using faeces and urine in every month of the year. Marking could be clearly differentiated from the standard defecation behaviour of females and young animals because of the difference in frequency and volume of faeces produced. Whereas the average hourly frequency of defecation by harem males varied between five and sixteen deposits per hour (Table 16), females and young animals only defecated once every one or two hours (pers. obs.). The average wet mass of a single deposit of faeces produced by harem males was 4.9 g (S.D. = 2.4, 3 separate males, n = 54), compared to 36.8 g for females (S.D. = 8.2, 5 females, n = 47). Also, harem males generally defecated at visible markers, such as large tufts of grass, bushes, or termite mounds, while females and young animals often deposited faeces where there were no apparent markers. The markers used by the males often had old faeces around them, although these were not easily seen because they were normally underneath vegetation. It was known that these older faeces predominantly originated from the same males because they were often seen marking at the same places and because territories did not overlap (except to a very small degree at the edges; see Chapter 4). Occasionally, however, males patrolling the edges of their territories located middens that had been deposited by a neighbouring male (pers. obs.). When this occurred, the male being observed invariably sniffed at the site and then marked over the other male’s faeces. In addition to the standard marking behaviour, harem males also marked over the fresh urine and faeces of females if the male was close by when the females defecated.

Table 16 shows the average hourly frequency of territorial marking by three harem males over three different time periods. December to February represented summer, May to August represented winter, and October/November represented the period when yearling males were evicted from their natal groups. This latter period was included to test whether harem males marked more during this relatively "aggressive" time.

Table 16. Average hourly frequency of territorial marking by three harem male grey rhebok over three time periods.

	Male 2		Male 3		Male 4	
	mean	std.dev.	mean	std.dev.	mean	std.dev.
December-February	8.273	4.221	8.842	5.419	8.417	6.215
May-August	12.071	5.929	11.667	7.062	5.167	2.787
October-November	15.917	6.807	13.235	7.155	11.625	6.116

The variation in marking frequency was tested using a two-way ANOVA, comparing the three males and three time periods (Table 17). Data were $\log_{10}$ transformed. There was evidence of a difference between males and strong evidence of a difference between time periods, but no evidence of an interaction. The differences between seasons were not dependent on which males were considered. Multiple pairwise comparisons using the Tukey test indicated that the differences between the males occurred between males 2 & 4 in winter, at which time the marking frequency by male 4 was lower. At other times of the year there were no differences between males. All three males marked their territories more frequently during October/November (the "aggressive" period) than during other months.

Table 17. Two way ANOVA comparing the frequency of territorial marking by three harem male grey rhebok over three time periods. Data were $\log_{10}$ transformed.

Source of variation	Df	SS	MS	F	P
Male	2	0.468	0.234	4.003	0.021
Time period	2	1.138	0.569	9.731	<0.001
Male x time period	4	0.404	0.101	1.729	0.148
Residual	114	6.666	0.059		
Total	122	8.856	0.073		

Harem male grey rhebok were occasionally found away from their herds and appeared to be patrolling the boundaries of their territories and marking these with faeces. Patrolling was most common between November and January, and least common between March and August (Figure 23). Because territorial male mountain reedbuck were often solitary as a consequence of females moving in and out of their territories, and because they did not perform marking behaviour in the same way as grey rhebok, they were not monitored for territory patrols.

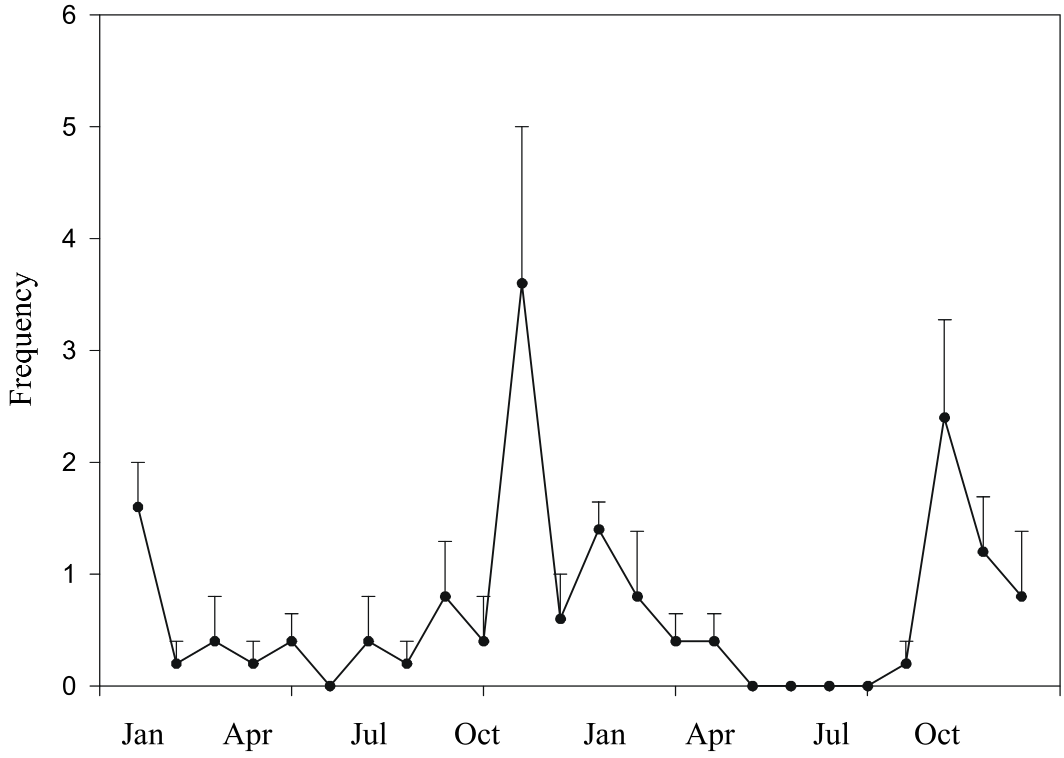


Figure 23. Average monthly frequency of territory patrols by harem male grey rhebok at Sterkfontein. N = 5 males. Error bars represent standard error.

Juvenile submission

In grey rhebok, submissive behaviour of young males reacting to the presence of harem males was first observed at the age of two months. At that stage it was not strongly pronounced, and was characterised by a slight lowering and shaking of the head so that the ears could be seen moving. As the lambs got older, the submissive behaviour became more exaggerated, with the head and body being lowered closer to the ground, and the head shaken more strongly. When they reached the age of nine months the submissive posturing sometimes became more extreme, particularly when the harem male was close, and they lowered their whole bodies to the ground. Between this age and the period of eviction, the young males often approached the harem male with the apparent intent to show submission. Such submissive posturing was not seen in female grey rhebok lambs, nor was it seen in mountain reedbuck lambs.

There was a significant increase in the frequency of submissive behaviour from the age of two months through to 11 months in male grey rhebok lambs (Figure 24 & Table 18). There was also a highly significant difference between Groups but no interaction. Multiple pairwise comparisons using the Tukey test indicated that young males from Group 3 submitted more frequently to their harem male than those from Groups 2 and 4, while in all Groups young males submitted to harem males more frequently during the period 8 – 11 months age than during the period 2 – 5 months age.

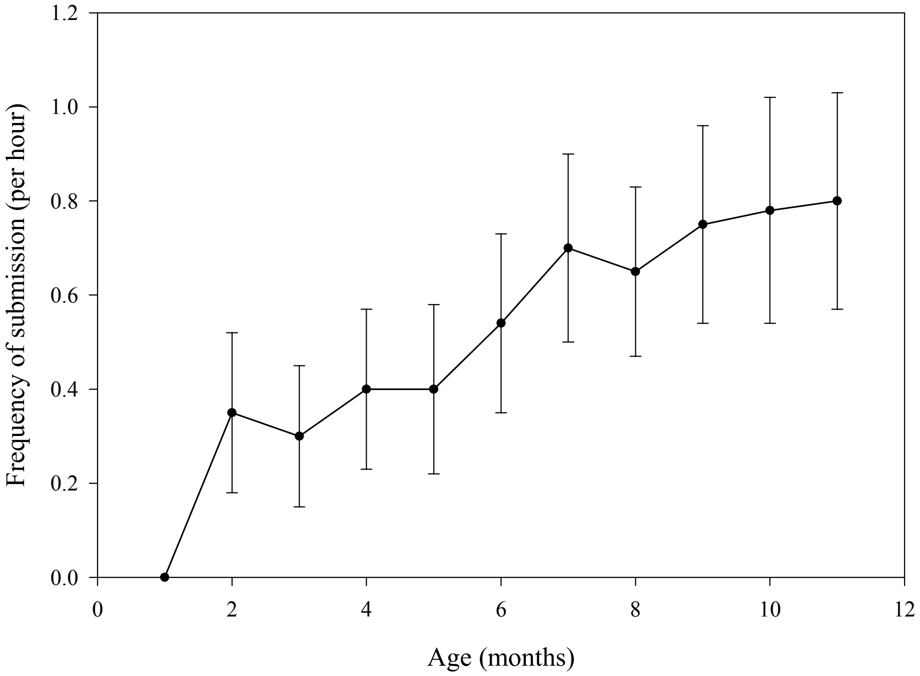


Figure 24. Variation in the frequency of submission in male grey rhebok lambs with increasing age. Error bars represent standard error.

Table 18. Two-way ANOVA comparing the differences in frequency of submissive behaviour between three groups and three age categories (2 – 5 months, 5 – 8 months, 8 – 11 months) of male grey rhebok lambs.

Source of variation	Df	SS	MS	F	P
Group	2	12.012	6.006	6.939	0.001
Age	2	5.485	2.743	3.169	0.045
Group x age	4	0.129	0.032	0.037	0.997
Residual	162	140.211	0.865		
Total	170	157.836	0.928		

Eviction of juveniles

All juvenile male grey rhebok were evicted from their natal groups at the age of about 11 months (Table 19). The actual eviction event was observed twice, while for those events not seen, the eviction date was estimated indirectly as the day after which they no longer mixed with the group.

Table 19. Eviction dates for 13 juvenile male grey rhebok.

Group	2000		2001	
	Eviction date	Eviction age	Eviction date	Eviction age
1	November 29	11 months	Died before	-
2	October 28 & 31	11 months	December 18	12 months
3	November 1 & 3	11 months	December 18	13 months
4	October 25 & 26	11 months	Died before	-
5	November 24	11 months	November 10	11 months
6	November 6	11 months	October 15	11 months

One such eviction event proceeded as follows. The harem male approached the juvenile male, who in turn submitted. Instead of moving away, as was the custom on previous occasions, the adult kept moving towards the juvenile in a threatening manor, with head lowered trying to butt him. The juvenile tried to move away, but the adult kept following, initially at a walking pace. The more the juvenile moved away, the more the adult followed with increasing pace. The whole herd became disrupted and eventually the juvenile tried to hide behind adult females. The young male eventually got separated and the adult chased him at full running speed in circles and then out of sight. The juvenile male could often be heard making bleating sounds. A few minutes later the adult male returned but the juvenile did not. The latter was never aloud to rejoin the herd again.

For about two months after juvenile males were evicted, the harem males were often found on their own in areas peripheral to their territories, where the young males were known to reside. The harem males appeared to search for the juveniles to reinforce their dominance and chase them away again. One young male was cornered by a harem male and was repeatedly butted and prodded by the latter, but the accidental interference of the observer probably prevented serious injury to the juvenile. Another young male was chased along a fence into the dam and had to swim around the fence, which protruded 25 m into the water, to escape. The adult remained at the water line to make sure the young animal did not return, so if the fence had not been there, the yearling would have drowned.

In addition to the juvenile males, the harem males evicted four young female grey rhebok between eight and 12 months age. One such event was seen, with the harem male aggressively chasing the female around until she moved away from the herd. Two of the females evicted were allowed to return to their herds after about two months, but before being allowed back they remained on the peripheries of their home ranges and avoided contact with their natal groups.

Eviction was not so well defined in mountain reedbuck because juvenile males did not live in harems. Rather, when they reached the stage of being a potential threat to territorial males, they were chased away from their mothers into another male's territory, from where they would be chased again. Territorial male mountain reedbuck were seen chasing juveniles of 6 to 12 months age on five occasions. These chases occurred in April (x 3), September and November, and generally continued for 2-300 m with the young males being forced out of the adult's territory. However, because the females and young animals were not identifiable, it was not possible to tell whether these young males were able to return to their mothers.

Discussion

Activity budgets

Activity budgets of grey rhebok are not well described by other authors. Beukes (1984) found that foraging was the dominant activity during the day, taking up an average of 56 % of daylight hours. Assuming foraging in this case meant being active, this was very similar to the results of the present study, where grey rhebok males were active for 60 % and females for 56 % of daylight hours.

According to Beukes (1984), this percentage time foraging was higher than expected, because of a positive correlation found by Owen-Smith & Novellie (1982) between body mass and the proportion of time spent foraging in different ungulate species. According to this theory, an antelope the size of grey rhebok (22 kg) should spend only 35 % of the day feeding. Beukes (1984) suggested that grey rhebok might have spent less time feeding at night, which would have compensated for the excess in the day, and that the amount of leaf and branch material that they made use of was relatively small in proportion to the total vegetation available, and this would have increased the time necessary for foraging. However, Beukes' (1984) value of 56 % was for foraging, not feeding, and in the present study grey rhebok spent 28 % (males) and 33 % (females) of daylight hours feeding. This was closer to the predicted value determined using the correlation found by Owen-Smith & Novellie (1982). Moreover, grey rhebok were found to be active at night to the same degree as during the day at Sterkfontein, so this could not have compensated for any excess feeding during the day.

Activity budgets of mountain reedbuck are also not previously well described, with Irby (1981, 1982) only giving a break down of periods of activity and inactivity. Southern mountain reedbuck at Loskop showed an average diurnal activity frequency of 47 % (Irby, 1981). Of this, feeding comprised 62 % and, therefore, made up an average of 29 % of the daily activity budget. Results from Chanler's mountain reedbuck in Kenya were very similar (Irby, 1982). This compares favourably with the present study, although in the previous examples, standing was considered "inactive". Roberts & Dunbar (1991) provide the only break down of activity budgets into other behaviours including feeding, resting, standing, moving and other infrequent behaviour. Chanler's mountain reedbuck at Eburru Cliffs, Kenya, spent 39 % of diurnal observations feeding (males and females were similar) (Roberts & Dunbar, 1991). There were no inter-sexual differences in time budgets across months for feeding, moving and standing, although females lay down more than males.

Klein & Fairall (1986) compared the foraging behaviour of a grazing antelope, the blesbok, with that of a mixed feeder, the impala. They found that the grazer spent less time feeding and more time resting than the mixed feeder, and the reasons for this were thought to be associated with the formers efficiency as a bulk feeder, as well as the longer time required for digestion of its coarser diet. In a similar way during the present study, the grazing mountain reedbuck spent more time resting during the day than the browsing grey rhebok.

Unlike with the blesbok and impala (Klein & Fairall, 1986), however, the present study did not find a difference in the time spent feeding between grey rhebok and mountain reedbuck. This may be partially because mountain reedbuck were selective grazers (Irby, 1976), unlike blesbok, and would have taken longer to select food items than bulk grazers. In addition, although grey rhebok probably required lower quantities of food than mountain reedbuck (an assumption made because they have a slightly lower body mass, and are browsers), their food was more spread out and smaller in size per item (pers. obs.). It is possible, therefore, that the differences in food quantities required (greater for mountain reedbuck) and gathering times (less for mountain reedbuck) of the two species cancelled each other out, but this remains to be tested.

Diurnal activity patterns

There was a common trend to the diurnal activity patterns of both grey rhebok and mountain reedbuck at Sterkfontein, and this was that animals generally rested more in the middle of the day, and fed more in the early morning and late afternoon. The pattern was more accentuated in mountain reedbuck, which were especially active in late afternoon. Moreover, mountain reedbuck tended to rest more than grey rhebok in all periods. Additionally, there were no obvious seasonal differences, with both species following similar patterns in both summer and winter.

There was, however, a difference in the general sequential pattern of behaviour through the course of a day. Grey rhebok tended to be active for up to two hours, then inactive for a similar period, then active again. They showed no periods of extended activity or inactivity, and continued the pattern throughout the day and night. Mountain reedbuck had more fixed periods of activity and inactivity whereby they were generally active in the early morning and late afternoon, and inactive during midday.

Esser (1973) found a pattern of increased foraging activity in the late afternoon in grey rhebok, which was similar to the present study with the addition that grey rhebok were more active in the morning as well as late afternoon relative to the middle of the day. Beukes (1984) indicated that the activity patterns of the male and females within a harem herd alternated, so that when the male was active, the females were not, and vice versa. This was suggested to result from the advantage conveyed by always having some animals vigilant. In contrast, the present study found that during most observation periods males and females were generally active or inactive at the same time, although there were short periods during which some animals were active while others were inactive. It was a common occurrence that once one animal within a herd lay down, the rest followed suit within a few minutes.

Beukes (1984) found that grey rhebok spent more time feeding in winter (June) than summer (December), although there was no seasonal influence on the overall activity budget. The feeding differences were thought to result from changes in the availability of young plant material (leaves and branches) and protein content caused by changes in rainfall. There were no seasonal differences in the feeding behaviour of grey rhebok at Sterkfontein, which was perhaps surprising considering the degree to which forbs dried up or died at Sterkfontein towards the end of winter (pers. obs.).

The activity patterns of mountain reedbuck in the present study were similar to those found by Irby (1981, 1982) at Loskop, and in the Rift Valley, Kenya, as well as by Roberts & Dunbar (1991) at Eburru Cliffs. The two Kenyan studies were conducted on Chanler's mountain reedbuck, a subspecies of the southern mountain reedbuck found in South Africa. These studies found that mountain reedbuck had well defined diurnal cycles of activity, with distinct resting periods around midday. The activity cycles of males and females were closely correlated, with temperature being an important determinant of activity. In dry months, animals were more active between 06h00 and 09h00 than in wet months, but less active between 14h00 and 16h00. In the present study no statistical seasonal differences were found in activity levels, although descriptively mountain reedbuck were more active between 06h00 and 09h00 in the dry months relative to the wet months. The diurnal cycles found by Irby (1981, 1982) and Roberts & Dunbar (1991) were more extreme than was the case at Sterkfontein, with the earlier studies finding that mountain reedbuck became almost totally inactive in the middle of the day. One factor that could have been responsible for this difference was the temperature at midday. Maximum diurnal temperatures at Eburru Cliffs were 35° C in summer (Roberts & Dunbar, 1991), while at Loskop they were 32° C (Irby, 1981). Maximum diurnal temperatures at Sterkfontein were only 25° C in summer, and this may have allowed animals to remain active occasionally at the warmest time of day.

Roberts & Dunbar (1991) also found that activity and feeding levels of mountain reedbuck, as well as the proportion of time spent ruminating, were lower in the wet season when forage quality and availability were higher. No such seasonal differences were found in activity habits of mountain reedbuck during the present study where activity levels were compared between summer and winter. Patterns of rumination were not compared between seasons.

All previous studies found that mountain reedbuck exhibited a consistent diurnal movement pattern, wherein animals habitually descended slowly in the morning from the upper slopes of the hills they inhabited, remained on low ground during the early afternoon, and returned up slope in the late afternoon. Temperature was considered the most likely proximate factor regulating this movement pattern. Similar diurnal movement patterns in mountain reedbuck at Sterkfontein did not occur. This was probably because the hillsides on which they were observed were not as high as occurred in the previous studies, and the subsequent temperature differences between different heights on slopes were not as extreme. Mountain reedbuck did often descend to lower slopes or to the water at night, but the reasons for this were not tested. Temperatures at night, especially in winter, would be coldest at the bottom of the slopes near the dam, so it is unlikely that the movement down slope at night was temperature driven. It may have been related to human activities.

Nocturnal activity patterns

Grey rhebok were active at night to a similar degree (57 % mixed gender) as they were during the day (60 % males, 56 % females). No previous studies have monitored activity at night, although Beukes (1984) suggested that they might be less active at night. Clearly this is not the case, with grey rhebok conducting the same activities at night as they do during the day.

Mountain reedbuck were more active at night (72 % mixed sex) compared with the day (43 % males, 46 % females). This agreed with Roberts & Dunbar (1991), who found that Chanler's mountain reedbuck in Kenya were also active throughout the night, with periodic peaks and troughs in feeding and resting. Activity levels tended to be higher at night than during daylight, with less pronounced resting periods.

In contrast, some other antelope species including impala (Jarman & Jarman, 1973) and blesbok (Du Plessis, 1968) are reported to be less active at night.

Ruminating and drinking

Both species in the present study ruminated primarily while lying down. This was similar to blesbok (Klein & Fairall, 1986), but different from impala (Klein & Fairall, 1986; Oliver, 2002), with the latter ruminating while standing. Grey rhebok ruminated for 14 % of daylight hours compared to 22 % by mountain reedbuck. This fairly small difference was probably the result of differing digestibility of their food plants.

Grey rhebok at Sterkfontein regularly drank during the dry period at the end of winter when their food plants were low in moisture (pers. obs.). On some occasions animals were seen eating dead plant material that was almost completely lacking any water content (pers. obs.). Grey rhebok were previously recorded as being water independent (Skinner & Smithers, 1990) but it is possible that at the end of winter there was not enough moisture in their food to provide for all their needs. It was not tested whether drinking was obligatory during the present study, but the regularity of this behaviour at the relevant time during both 2000 and 2001 indicates that it might have been. Also, all six herds of grey rhebok that lived within the study area (see Chapter 4) had access to water (the dam), and although there was sufficient space left within the study site to hold another herd, this did not happen. The potential site would have had no access to the dam, and it is possible that the lack of water access excluded the possibility of another herd being founded. This was not tested, however.

Mountain reedbuck were never seen drinking during the study period, although they are recorded as water dependent (Skinner & Smithers, 1990). It was unusual for them to be on the lower slopes during the day, hence the lack of drinking observations, but they were sometimes found very close to the dam at night, and this was probably the time when they did most of their drinking. Additionally, there was a small area on the main hillside that almost always had a small amount of freestanding water that originated from a spring. Mountain reedbuck were often seen in the vicinity of this area, although they could never be observed closely enough to determine whether they were drinking.

Irby (1976) observed mountain reedbuck drinking during daylight hours in all seasons at Loskop, but at such low frequencies that no seasonal comparisons could be made. No drinking observations occurred at other sites (Irby, 1976), although as occurred during the present study, animals were seen near water in Ohrigstad, Giant's Castle, and the Cole Ranch (Kenya).

Male reproductive behaviour

An important difference in the reproductive behaviour of grey rhebok and mountain reedbuck was that grey rhebok harem males rarely sniffed the vulva region of their herd females (although they did sometimes test urine on the ground), while mountain reedbuck did this in almost every month of the year, apparently at every chance they had. There were two probable reasons for this difference. The first, and most important, was that grey rhebok males defended females, and had access to them at any time they wanted, and at all times of the year. They were only separated from these females for short periods when they patrolled their territories, and they very rarely had competition from other males. In contrast, territorial male mountain reedbuck only had temporary access to females because they defended resources that females selected preferentially (steep slopes). Males, therefore, needed to test the females every time they roamed into their territories to check for signs of oestrus. They had regular competition from other males because every time the females moved out of one territory, they consequently moved into another one, whereupon a different male investigated them. The second reason was that grey rhebok are seasonal in their breeding behaviour (with the exception of rare out of season births, see Chapter 3; also Skinner & Smithers, 1990), while mountain reedbuck are generally more aseasonal (although in the present study, material obtained from culled animals showed that mountain reedbuck were fairly seasonal, see Chapter 3; also Irby, 1979). Breeding males from aseasonal species should test females for signs of oestrus for more extended periods of the year relative to seasonal species.

A second difference between grey rhebok and mountain reedbuck occurred in the mating behaviour. Although both species showed similar behaviour leading up to and including ejaculation (including multiple mounting attempts before ejaculation), they differed in the number of times males mated with the same female (i.e. number of ejaculations), the time period over which mating took place (i.e. the length of oestrus), and mate guarding. Harem male grey rhebok mated with a specific female in oestrus many times in one day, and over the period of several hours. Sometimes it continued into a second day. After the final mount and ejaculation of one mating, there was a transitory period when normal activities resumed before the male started showing interest in the female again. Mate guarding, and the virtual permanent defence of females, meant that harem males were almost guaranteed to be the fathers of all the offspring in their herd.

Territorial male mountain reedbuck, however, only mated once with a certain female, and after ejaculation there were no more attempts. Irby (1979) did not establish the duration of female receptivity. As with the present study, males normally only mated once with females, but one observation was recorded where a male copulated with a female at least three times during one 12-hour period. This is in contrast to the findings of the present study, but implies that oestrus lasts a short time in mountain reedbuck, which is more in line with mating behaviour of other antelope species. Males did not perform mate guarding, and this may have been partly because females can move between the territories of different males whenever they chose. As a result, a male that does guard a female during her receptive period would be wasting his time if that female moves into a separate territory while still in oestrus and mates with another male.

Mating events were not seen very often, so cannot be used as a measure of seasonality. The observations of grey rhebok lambs and foetuses of culled mountain reedbuck are a better guide for seasonality (see Chapter 3).

Territorial marking and territory patrols

Harem male grey rhebok performed distinct marking behaviour within their territories during all months of the year using faeces and urine, while territorial male mountain reedbuck did not. Although both species were territorial and prohibited other males from using their areas, the differences in social structure of the two may be the reason for the difference in marking. Grey rhebok males maintained a harem of females year-round, while mountain reedbuck males did not; they only maintained a territory from which females came and went. Also, grey rhebok home ranges, which were the same areas as the territories (see Chapter 4), were larger than those of male mountain reedbuck, and it was uncommon for two grey rhebok herds to be in sight of each other, so visual cues between harem males, such as posturing, were not often used. In contrast, territorial male mountain reedbuck were more often within view of each other, so visual cues between them were used regularly (pers. obs.), possibly reducing the need for odour cues.

Many species demarcate their territories using faeces, because faeces are a good substrate for glandular secretions, can be used as visual signposts, and have a low energetic cost to produce (Gosling, 1985). Marking is most commonly carried out by males that have established dominance over their peers in contests and is almost universally linked to agonistic behaviour, forming a central part of many ritualised contests between males (Gosling, 1990). However, marking does not often repel intruders, and in some species non-territorial males carry it out as well. At Sterkfontein, juvenile male grey rhebok that still belonged to their natal harem herds never performed marking behaviour, but one intruding male (from outside the study area) did mark within another male's territory before being chased out.

Other southern African antelope species that use faeces include, amongst others, black wildebeest, springbok, klipspringer, oribi, and steenbok (Skinner & Smithers, 1990). These species have differing social structures, and none have the same harem structure of grey rhebok. There seems, therefore, to be no specific type of social structure that results in territorial marking using faeces. Unlike some of the abovementioned species, such as the oribi, the middens produced by grey rhebok are small in scale and cannot be used as a visual signpost because they are generally hidden under vegetation. They may, however, be used as olfactory cues, and indeed males were occasionally seen sniffing middens on the edges of their territories that had been deposited by a neighbouring male (pers. obs.). When this occurred, the male being observed invariably marked over the other male's faeces.

Harem male grey rhebok marked their territories in all months of the year, but the frequency of marking was highest at the time when juvenile males were evicted from their natal groups. For most of the year, harem males had few competitors to contend with, and during the present study only three intruding males were seen within the study site (only one of these challenged for a territory) (see Chapter 3). During the period when juvenile males were evicted, however, there were many young males roaming around searching for new areas to live in and territories to start. This would have resulted in an increase in the number of interactions between intruding males and harem males, and this may have caused the increase in frequency of territorial marking by harem males to strengthen the odour signals that indicate their presence (Gosling, 1990). It was at this time as well that harem males moved away from their herds more frequently to patrol their territories, and this fits with the increased marking rate.

The use of faeces in marking is constrained by production, and their availability may limit the marking rate in species that use them to advertise territorial boundaries (Komers, 1996), or mark over the faeces and urine of females (Moodie & Byers, 1989). Animals should then regulate the volume of each mark and prioritise the placement of marks to areas where their value as an advertisement is greatest (Brashares & Arcese, 1999). Harem male grey rhebok marked more frequently and with smaller volumes of faeces than juvenile males and females, so they were apparently constrained by production. However, they did regularly mark well within their boundaries, not just on the edges (pers. obs.).

In contrast, territorial male mountain reedbuck did not clearly mark areas with faeces or urine, even though they were territorial and defended their areas from other males. Irby (1976) also found that mountain reedbuck males did not utilise obvious advertisement devices such as prominent glandular secretions or defecation along territorial boundaries. Instead they used optic marking displays comprising a head up, alert posture with stiff legged jumping gait in conjunction with short whistles. The use of whistles as a territorial marker could not be differentiated from their use as warning signals.

Juvenile submission

As juvenile male grey rhebok got older they became more submissive to harem males, and were most submissive in the last three months before being evicted. This makes sense because the harem males would have been expected to become more aggressive towards these young males as they approached sexual maturity and become more of a threat to the dominance of the adults.

Submissive behaviour was not observed in juvenile male mountain reedbuck during the present study, and the only related behaviour was territorial males chasing young males around occasionally. Irby (1976) did not record any submissive behaviour amongst mountain reedbuck either.

Eviction of juveniles

All juvenile male grey rhebok were evicted from their natal herds at the similar age of 11 months. This generally occurred between October and November, shortly before new lambs were born (see Chapter 3). The main reason for the evictions was probably that the young males were approaching sexual maturity and would have become a threat to the mating rights of the harem males. Additional benefits arising from their expulsion would have been incest avoidance and reduction in intra-specific competition for feeding resources just before group sizes increased with new lambs.
The reason for eviction of juvenile female grey rhebok was less clear when it is considered that some of these females were allowed back into their natal herds. Incest avoidance would be a likely cause of their removal, but one such female was mated by her father after returning to the herd and successfully produced a lamb.

Juvenile male mountain reedbuck were expelled from the territories of adult males sometime after the age of nine months. Irby (1979) found that most males left or were forced from their groups with which their mothers were associated between the ages of nine and 15 months. Separation was described as a slow process characterised by aggressive behaviour initiated by the adult male followed by long periods when the immature male was ignored. Tolerance of immature males within groups varied between individual adult males and between populations.

Chapter 6

BODY CONDITION

Introduction

Yousef (1982), Spinage (1986) and Payne (1990) list a number of potential advantages that African antelope have over domestic livestock for meat production when they live under similar conditions in marginal areas. First, when they form multi-species assemblages, antelope make use of a wider spectrum of plant parts and species. Murray & Illius (1996) state that in parts of East Africa, ten or more species of grazing ungulate may be found in close proximity. Such species-rich communities are found in southern Africa as well. Within grazing antelope, different species show variation in diet selection according to grass height and variation in the selection of different parts of the grass plants (Jarman, 1974; Murray & Illius, 1996). Additionally, alongside grazing species there are also browsing antelope that select non-grass plants and feed from different heights within the vegetation. In contrast, cattle are bulk roughage grazers and are not very selective due to their wide flat muzzles (Wright & Connolly, 1995). Accordingly, the biomass of a multi-species assemblage of antelope is generally greater in a given area of habitat than is possible with domesticated cattle alone, with herbivore biomass being positively related to the number of species present (Murray & Illius, 1996).

Estimates of the biomass of game animals should, however, be accepted with caution as there are many variable assumptions in the calculations (Payne, 1990). The fact that a specific environment supports a high biomass of wild ungulates does not necessarily mean that productivity per unit area of land will be high. If the animals grow slowly, then most of the available feed would have to be used for maintenance purposes and annual off-take would be low.

A second advantage of antelope in marginal areas is that some species have evolved specialised physiological and behavioural adaptations to survive in their hot and dry climate (Yousef, 1982). An example is the ability of gemsbok (*Oryx gazella*) to reduce water loss via evaporative cooling (sweating) by undergoing hyperthermia without adverse health risks. Additionally, indigenous antelope tend to have a greater resistance to endemic diseases and can, therefore, be cropped in regions where domestic livestock cannot be utilised or are only marginally economic. However, it should not be assumed that the disease factor might be totally ignored in wild game (Payne, 1990).

Yousef (1982) states that wild ungulates produce a given quantity of meat more quickly than domestic livestock because they breed and grow more quickly on their preferred diet. Some studies have shown that indigenous wild ungulates are more efficient in converting the flora into animal protein than might be expected from the use of domestic livestock (Yousef, 1982). However, this is only the case in areas where domestic livestock are not well adapted to the environmental conditions, and Payne (1990) indicates that there is little evidence to suggest that indigenous wild ungulates are able to make better use of the food they consume than do domestic animals. It has been shown that in the same environment, the productivity of eland is inferior to that of Hereford cattle, with higher food consumption and more protein being required for each unit of meat produced (Taylor & Lyman, 1967). Watson, Graham & Parker (1969) estimated that the off-take of game animals under favourable conditions could be of the order of 10 % per annum on a sustained yield basis. This is similar to that achieved by an indigenous cattle herd, but much lower than what could be achieved with a well-managed modern integrated livestock unit.

Antelope have dressing percentages between 50 % and 65 % (Crawford, 1968; Payne, 1990), and these are comparable to dressing percentages of domestic cattle (Crawford, 1968; Payne, 1990). However, the percentage of lean meat is much higher in antelope than in domestic species (Ledger, 1963), with East African gazelles having a lean constant of 45 % compared to 32.5 % in Boran steers (the lean constant being the weight of carcass lean expressed as a percentage of the live animal). In well-fed adult Boran steers, the percentage of fat in the cold dressed carcass was 24 % (Ledger, 1990), compared to 2.5 % fat for wild ungulates (Crawford, 1968). The percentage fat on heifers is even higher because bulls and steers convert food into carcass gain more efficiently (age is also important, with young animals having less fat than adults). Allen and Kilkenny (1980) compared the carcass composition of 18 month-old

Friesian bulls and steers and showed that bulls had a fat percentage of 14 %, while steers had a fat percentage of 20 %. Ledger (1963) states that at dressing percentages of 60 %, domestic cattle may carry as much as 30 % fat content.

Not all of the above advantages apply when comparing mountain reedbuck or grey rhebok with domestic cattle at Sterkfontein. For example, domestic cattle are not often exposed to endemic diseases in this part of Africa, or are inoculated against them, so are not at a disadvantage in this regard, while the antelope in this region do not need to make use of physiological adaptations to conserve water loss. Moreover, there is generally plenty of freestanding water to suit the needs of cattle. Be that as it may, mountain reedbuck and grey rhebok often form part of multi-species assemblages in areas where they occur naturally, so information that improves utilisation is of value. Additionally, there are areas where these two species occur, especially the Karoo, where productivity of indigenous antelope such as mountain reedbuck will be higher than domestic cattle due to the unsuitability of the Karoo vegetation to hold large numbers of livestock.

Mountain reedbuck (*Redunca fulvorufula*) and grey rhebok (*Pelea capreolus*) utilise similar habitats in South Africa that are marginal for domestic livestock. In many areas they are sympatric. The favoured habitat of mountain reedbuck is grassland on steep slopes, up to 2200 m in the Drakensburg (Rowe-Rowe, 1994). They are selective grazers, feeding only on certain grass species and are water dependent (Irby, 1976). The living requirements of grey rhebok are grassland, where they occur on hills and mountains at high altitudes (up to 3300 m) (Rowe-Rowe, 1994). Grey rhebok feed selectively, almost entirely on forbs, and favour short, burnt veld for feeding (Beukes, 1984, 1988). They are independent of water for much of the year but will drink in winter when conditions are dry (see Chapter 5).

Mountain reedbuck are more abundant than grey rhebok and are regularly shot for their venison, which is palatable and normally free from parasites (Skinner, 1980). They have a high reproductive potential, may breed aseasonally and utilise marginal habitat without competing with livestock (Irby, 1975). They have the potential, therefore, to be harvested on a commercial basis (Skinner, 1980), although their dispersed social structure makes culling operations fairly inefficient.

Grey rhebok are less likely candidates for commercial meat production because they are less common and are not favoured for consumption. They form small social herds that stick to rigid territories (Beukes, 1984; see also Chapters 3 & 4) and are notoriously skittish. The high degree of difficulty involved in hunting them makes them unviable for cropping. For trophy hunting, however, they are highly marketable, although this is restricted to males with large horns. One advantage they have is that they eat forbs and, therefore, do not compete with many other ungulates, especially in marginal habitat.

Body condition can been defined in terms of levels of fat deposits in different parts of the body (Riney, 1955). In well-bred farm animals and northern hemisphere wild ungulates (deer) fat constitutes an important part of the overall carcass (see above), and the use of fat as an index of condition is implicit in growth rate principles. In African antelope, fat deposits are not consistently so well developed because of poorer nutrition, but it is still possible to distinguish three main centres of location of their fats: subcutaneous connective tissue, the abdominal cavity, and the inter-muscular connective tissue (Riney, 1955). These depots of fat serve as the principal fuel storage reserves of the body and can, therefore, be used as the main criterion for assessment of condition. Moreover, fat in wild ruminants is produced endogenously (Riney, 1955), making it a particularly useful index of the metabolic level and potential energy reserves of the animal. Fat could, therefore, be taken as a direct measure of condition, reflecting the goodness of physiologic adjustment of an animal with its environment.

There are a number of methods for measuring body condition. The kidney fat index, proposed by Riney (1955), is a quick and easy method of assessing body fat and is commonly used as an indicator of body condition in ungulates (Dauphine, 1975). It has been utilised by many authors, including Smith (1970) in East African ungulates, Sinclair & Duncan (1972) in tropical ruminants, Monro & Skinner (1979) in impala, Skinner (1980) in mountain reedbuck, and Dunham & Murray (1982) also in impala. Kidney weight is included in the index to allow comparison between animals of different sizes and, therefore, makes the assumption that kidney weight is proportional to body weight.

This assumption has been contested because there is evidence that kidney weight varies seasonally in some species (Batcheler & Clarke, 1970; Dauphine, 1975; Van Vuren & Coblentz, 1985). However, Spinage (1984) found in waterbuck (*Kobus ellipsiprymnus*) and Grant's gazelle (*Gazella granti*) that, although kidney weight did vary seasonally, it did not fluctuate sufficiently to bias a kidney fat index significantly. Van Vuren & Coblentz (1985) found that in feral sheep on Santa Cruz Island, California there was a linear relationship between kidney weight and body weight in adult sheep, but the kidneys of small sheep were larger in proportion to body weight than kidneys of larger sheep. They also found that kidney weights fluctuated seasonally and suggested that kidney fat index be adjusted for seasonal differences in kidney weight. In contrast, Shackleton & Granger (1989) found that kidney weights did not vary significantly seasonally in antelope species in the Transkei.

A second method of assessing body condition is the measurement of fat in one hind leg (buttock). Leg fat has been shown to correlate highly with total body fat in cattle (Butterfield, 1962) and eight East African antelope species (Smith, 1970). It can thus be used to estimate total body fat without dissecting a whole carcass.

A third and fairly commonly used method is the extraction of fat from the bone marrow of leg bones. Although it is a poor method for measuring changes in upper parts of condition scale, i.e. when animals have lots of fat (Riney, 1955), it has the advantage of allowing the assessment of animals that died weeks prior to collection. As material was available immediately after death, it was not necessary to make use of this factor. Also, it is a more complicated method that requires chemical extraction and was not considered for this study.

During the present study mountain reedbuck were being culled for management purposes and biological material was used to investigate body condition. Grey rhebok were not culled and because they were considered less common than mountain reedbuck and less desirable as a food product, no decision was taken to do so. There were two aims to this component of the study:

1) To determine levels of body fat in mountain reedbuck at Sterkfontein;
2) To investigate seasonal and sexual variation in body fat of mountain reedbuck.

The expected outcome of the second aim was that body fat and, therefore, body condition would vary seasonally, and that it would be lowest when environmental conditions were worst for the animals in terms of food supply. Additionally, reproductive status might also influence body condition.

To accomplish the above aims, the following questions were considered:

1. What are the dressing percentages of mountain reedbuck at Sterkfontein and are there any differences between the sexes?
2. Are there any seasonal differences in dressing percentages?
3. What are the kidney fat indices and leg fat percentages of mountain reedbuck at Sterkfontein?
4. Are there any differences between the sexes, between seasons, or between animals in different reproductive condition?
5. How do the two indices of body condition compare with each other?

The intended benefits to management were twofold. First, results should indicate whether animal numbers were kept at levels allowing high productivity, i.e. not too high or low. The presence of animals with excess fat during poor veld conditions would imply that more animals could be carried, while the presence of animals with very little body fat might indicate that there were too many animals. Second, knowing the condition of animals at different times of year allows culling to be carried out at appropriate times, depending on management requirements.

Methods

Study site and animals

This component of the study was primarily carried out at Sterkfontein but some material was also collected from Tussen die Riviere (TdR). Forty-one mountain reedbuck were culled at Sterkfontein between March 2000 and February 2002. Culling periods were divided into eight separate months under the following schedule: five animals were culled in March 2000, five in June 2000, five in September 2000, five in December 2000, six in May 2001, six in August 2001, five in November 2001, and four in February 2002. Numbers culled in the final two periods were reduced because a large number of mountain reedbuck died in heavy snowfalls in September 2001. In a typical culling period, two adult males, two adult females, and one juvenile of either sex were selected. The age and condition of adult mountain reedbuck were not known before they were shot, and because animals were located randomly, the selection was not considered biased.

The spacing of the culls, spanning eight different months over a two year period, meant that body condition of mountain reedbuck could be compared in both warm and cold periods as well as wet and dry periods. They hence covered times when animals had abundant food supplies available and times when food resources were limited. They also covered periods of differing reproduction condition. The months were categorised into seasons in the following way: autumn = February and March; winter = May and June; spring = August and September; and summer = November and December.

Forty-four mountain reedbuck were also culled at TdR over three separate culling periods, spanning one summer (December 1999) and two winters (June 2000 and 2001).

Body condition indices

At Sterkfontein, a maximum of two animals were shot in one day. Carcasses were bled where they were shot and transported to the slaughtering area within two hours. This time varied depending on whether another animal was to be shot in the same hunt. Biometric measurements (chest girth, neck girth and shoulder height) were recorded at the slaughter area and the carcasses weighed to the nearest 0.5 kg. After slaughter, dressed carcasses were left to hang for approximately one hour while other biological sampling was carried out, and then weighed. This was done for 16 males and 17 females. Due to the lack of cold storage facilities, carcasses could not be left to hang for 24 hours, as is often the procedure. Dressing percentages were, therefore, based on fresh weights. The dressed carcass in this case was the whole animal minus skin, head, legs below the knees and hocks (severed between the carpal and metacarpal bones or between the tarsal and metatarsal bones), and all internal organs and reproductive tracts.

As a means of assessing body condition, two indices of fat content were determined in addition to the dressing percentages. These were the kidney fat index (hereafter KFI) and leg fat percentage (LFP). To determine the KFI, both kidneys were extracted from the carcass along with all the perirenal fat. This included fat directly around the kidneys as well as fat lying on the inside surface of the abdominal wall, from the level of the kidneys to the pelvis. The kidneys were then separated from the fat and the two weighed independently. The KFI was calculated using the following equation:

$$\text{KFI} = (\text{kidney fat weight} / \text{kidney weight}) \times 100$$

The LFP was determined using the right hind leg (buttock) from the hock up to and including one half of the pelvis. The buttock was stored in a fridge for a minimum of 24 hours before being dissected. To assess fat content, the leg was completely separated into meat, bone, fat and sinew, by dissection. During the procedure, all processed parts were kept in closed plastic bags to avoid moisture loss. On completion of dissection, all parts were weighed separately.

At TdR animals were shot in larger numbers, twice during culls and once by hunters, so it was not possible to collect all the material as at Sterkfontein. During culls animals were selected randomly. The KFI was the only condition index measured because the hunters were paying for their carcasses.

Statistical methods

In view of the potential problem of kidney weight not being proportional to body weight, these two parameters were compared using log-log linear regression. The ratio of kidney weight to body weight was also analysed between seasons to determine whether the KFI should be adjusted to allow for any differences. Further analyses using KFI were then conducted in light of these findings. For the fat indices of Sterkfontein, simple linear regression was used to compare KFI and LFP. To investigate the seasonal variation in fat indices, as well as any differences between males and females, two-way ANOVAs were used. To investigate the possibility that KFI was related to body weight, linear regression analyses were carried out for males and females at both Sterkfontein and TdR. If necessary, the data were transformed, and the methods used described in the relevant sections.

Results

Sterkfontein Dam Nature Reserve

Carcass weights and dressing percentages

Adult rams averaged 29.9 kg (range 23.0 – 35.0 kg, n = 18) and adult ewes 28.0 kg (range 23.5 – 34.5 kg, n = 19) at Sterkfontein. In dressing percentages, there was little apparent difference between males and females within seasons, but there were small seasonal differences (Figure 25).

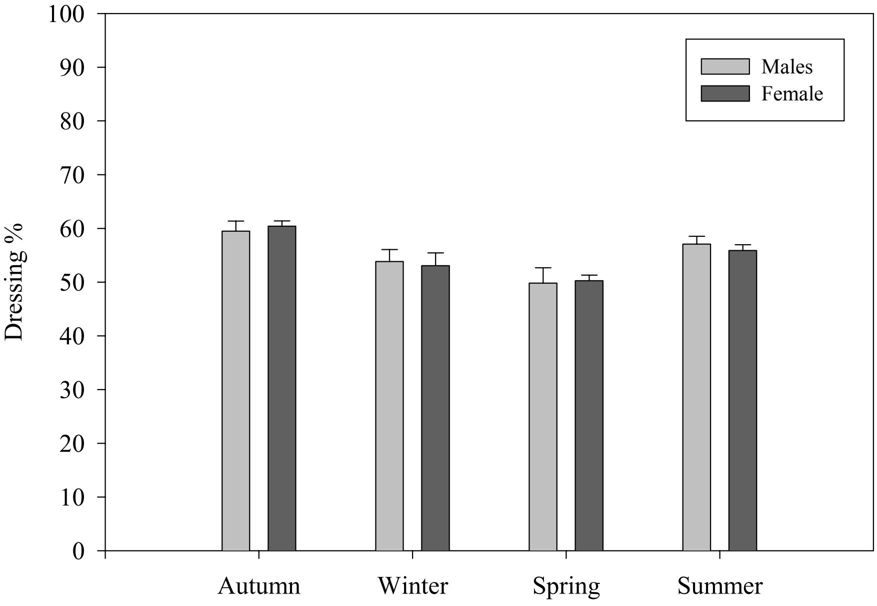


Figure 25. Seasonal variation in dressing percentages of male (n = 16) and female (n = 17) mountain reedbuck at Sterkfontein. Autumn = February/March, winter = May/June, spring = August/September, summer = November/December. Error bars represent standard error.

These differences were tested using a two-way ANOVA (Table 20). There was strong evidence of a difference between seasons but no evidence of a difference between genders and no interaction. Multiple pairwise comparisons using the Tukey test indicated that dressing percentages were lower in spring compared to autumn and summer, and lower in winter compared to autumn.

Table 20. Two-way ANOVA comparing dressing percentages of 33 mountain reedbuck between gender (16M: 17F) and between seasons at Sterkfontein.

Source of Variation	df	SS	MS	F	P
Gender	1	0.200	0.200	0.013	0.910
Season	3	376.335	125.445	8.194	< 0.001
Gender x season	3	5.448	1.816	0.119	0.948
Residual	25	382.734	15.309		
Total	32	774.010	24.188		

Regression analysis of kidney weight and body weight

To determine whether the effect of body weight (BW) on kidney weight (KW) was allometric, log-log linear regression analyses were carried out using data from all the animals (Figure 26a) and then with animals less than 20 kg excluded (Figure 26b). Male and female data were pooled because their scatter plots of BW against KW were very similar. When animals under 20 kg were included, the slope of the regression curve was less than 1, so the relationship was allometric (i.e. smaller animals had relatively larger kidneys). However, when the animals under 20 kg were excluded, the regression did not differ significantly from 1, so kidney weights varied proportionally relative to body weight. As a result, further analyses using the KFI were carried out with the data for animals under 20 kg removed.

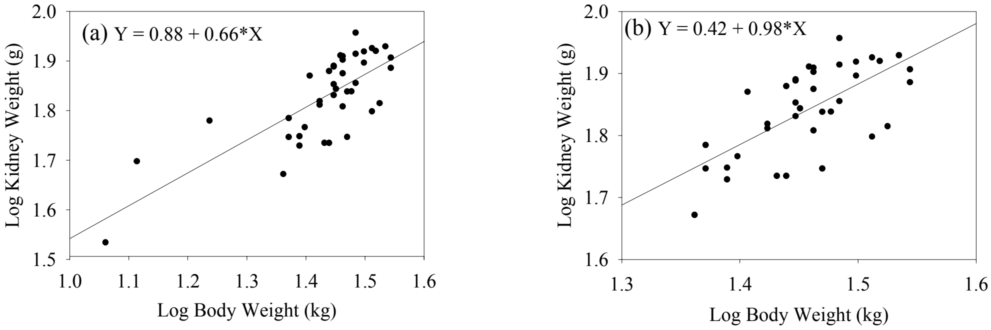


Figure 26. Log-log linear regression of mountain reedbuck body weight against kidney weight at Sterkfontein. (a) All animals (b) animals less than 20 kg excluded.

Females had more seasonal variation in KW than males (Figure 27), and spring (August/September) was the period when it was lowest. However, a two-way ANOVA comparing KW between genders and seasons (with animals under 20 kg excluded) found no differences between males and females or between seasons (Table 21). It was, therefore, not necessary to adjust the KFI according to seasonal variation in KW for animals over 20 kg.

Table 21. Two-way ANOVA comparing KW of 38 mountain reedbuck between gender (M18: F20) and seasons at Sterkfontein.

Source of Variation	DF	SS	MS	F	P
Gender	1	6.479	6.479	0.057	0.813
Season	3	644.418	214.806	1.893	0.152
Gender x season	3	254.135	84.712	0.747	0.533
Residual	30	3403.458	113.449		
Total	37	4393.101	118.732		

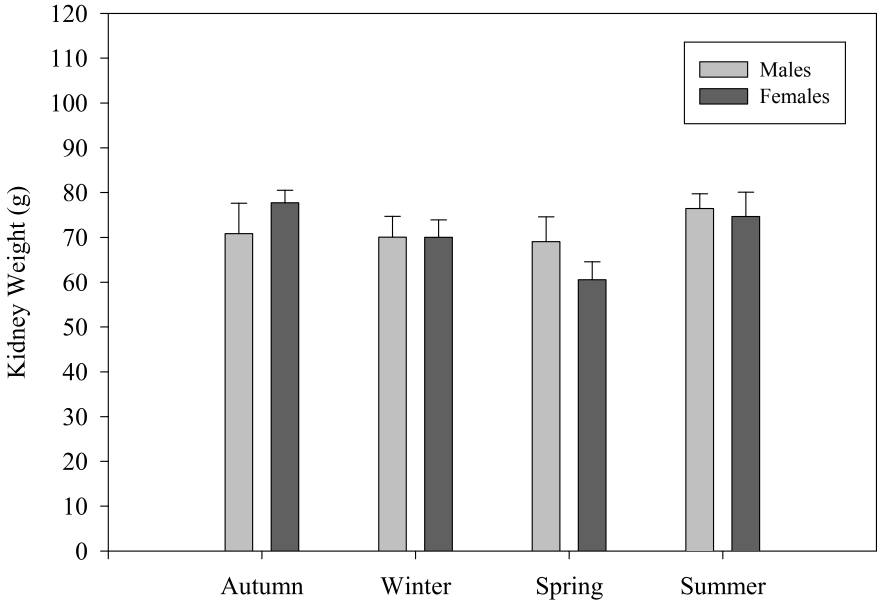


Figure 27. Seasonal variation in KW of mountain reedbuck at Sterkfontein. Autumn = February/March, winter = May/June, spring = August/September, summer = November/December. Error bars represent standard error.

Regression of LFP on KFI

The KFI and LFP were tested against each other using linear regression (Figure 28). There was a highly significant positive correlation between them (t = 13.1, df = 37, p < 0.001).

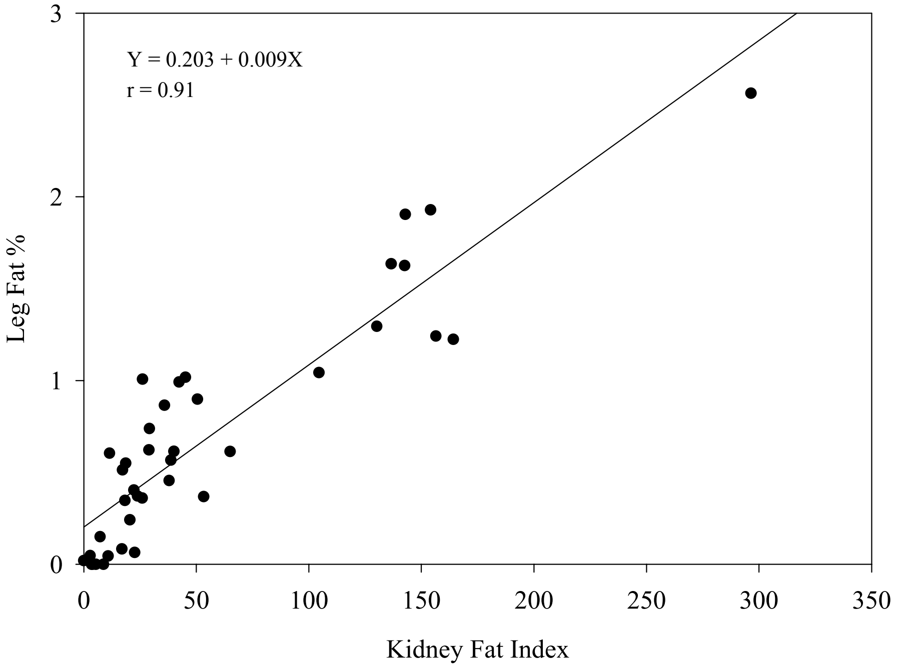
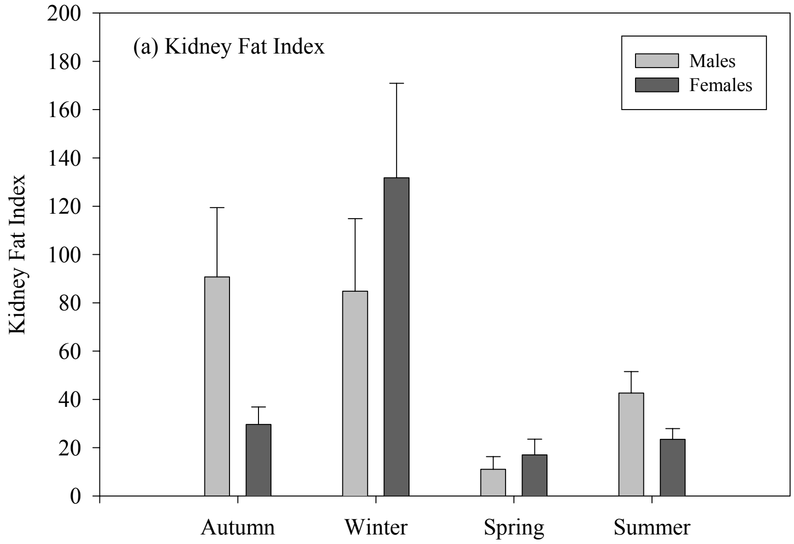


Figure 28. Linear regression comparing KFI with LFP in mountain reedbuck at Sterkfontein (n = 39).

Variation in body condition from KFI and LFP

Males had higher KFI than females in November/December and February/March (summer and autumn), while females had higher KFI than males in May/June and August/September (winter and spring) (Figure 29a). The same pattern was demonstrated by LFP (Figure 29b). Overall, fat indices were highest in winter (especially in females) and lowest in spring.

Differences in KFI between genders and between seasons were tested using a two-way ANOVA (Table 22). Data were $\log_{10}$ transformed. There was strong evidence of a difference between seasons but no evidence of a difference between genders, and no interaction. Multiple pairwise comparisons using the Tukey test indicated that the KFI were lower in spring than in autumn or winter.



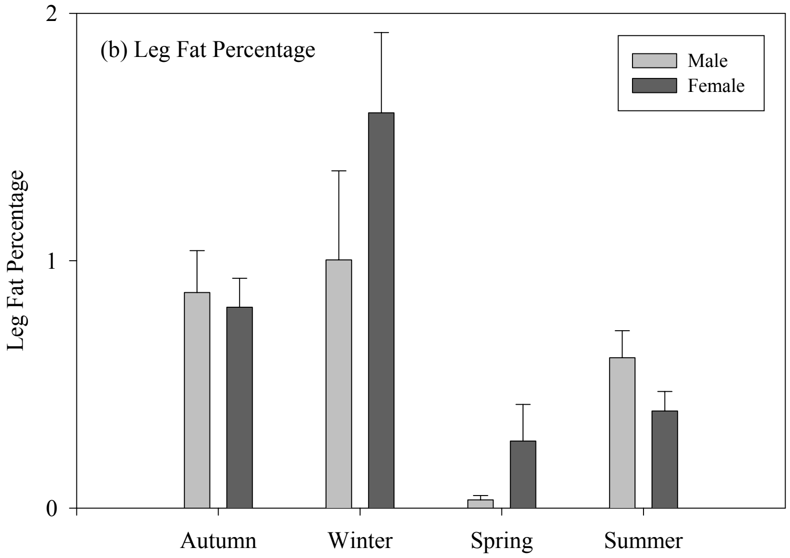


Figure 29. Seasonal variation in (a) KFI and (b) LFP for male and female mountain reedbuck at Sterkfontein. Autumn = February/March, winter = May/June, spring = August/September, summer = November/December. Error bars represent standard error.

Table 22. Two-way ANOVA comparing KFI of 38 mountain reedbuck between gender (18M: 20F) and between seasons at Sterkfontein. Data was Log_{10} transformed.

Source of variation	DF	SS	MS	F	P
Gender	1	0.003	0.003	0.015	0.903
Season	3	4.335	1.445	7.016	0.001
Gender x season	3	0.933	0.311	1.511	0.232
Residual	30	6.179	0.206		
Total	37	11.586	0.313		

Differences in LFP between genders and between seasons were also tested using a two-way ANOVA (Table 23). Data were arcsine transformed (percentage data). The reason a second two-way ANOVA was used rather than a three-way ANOVA, incorporating both KFI and LFP, was that these indices were measured using two independent methods. KFI was calculated as a ratio of fat to kidney weight, while leg fat was measured as a percentage of total leg weight. They were, therefore, incompatible and required different types of transformation. There was strong evidence of a difference between seasons but no evidence of a difference between genders and no interaction. Multiple pairwise comparisons using the Tukey test indicated that the LFP were lower in spring than winter, autumn and summer, and lower in summer than winter.

Table 23. Two-way ANOVA comparing LFP of 39 mountain reedbuck between gender (20M: 19F) and between seasons at Sterkfontein. Data were arcsine transformed.

Source of variation	DF	SS	MS	F	P
Gender	1	0.001	0.001	1.219	0.278
Season	3	0.039	0.013	15.616	< 0.001
Gender x season	3	0.004	0.001	1.470	0.242
Residual	31	0.026	0.001		
Total	38	0.068	0.002		

The arcsine transformation did not completely stabilise the variances of the LFP data, so a two-way ANOVA randomisation test was carried out to test the validity of the parametric test. Using mean squares as the test statistic and 5000 randomisations: p = 0.323 for differences between gender, and p = 0.0004 for differences between seasons.

To investigate the possibility that body condition was related to body weight, linear regression analyses were carried out for males and females at both Sterkfontein and TdR using the KFI (Figure 30). Animals under 20 kg were excluded. There were no linear relationships between body weight and KFI in any of the groups, although males at TdR were marginal (Males Sterkfontein: r = 0.22, p = 0.391; Males TdR: r = 0.45, p = 0.052; Females Sterkfontein: r = 0.03, p = 0.91; Female TdR: r = 0.34, p = 0.11).

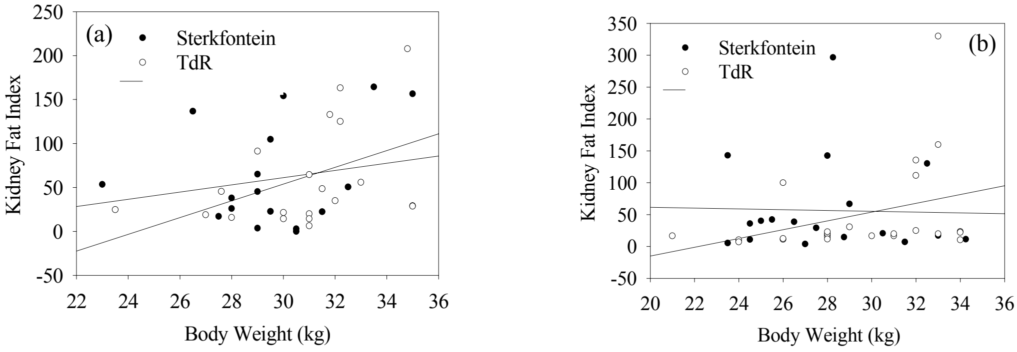


Figure 30. Linear regression comparing mountain reedbuck body weight with KFI for (a) males at Sterkfontein and TdR (b) females ate Sterkfontein and TdR. Animals under 20 kg were excluded.

The possibility exists that female reproductive condition affects body condition. However, a comparison of pregnant versus non-pregnant females using the KFI could only be done by pooling data from all seasons. Considering the seasonal differences shown in Figure 29, this was not attempted.

In September 2001, Sterkfontein experienced heavy snowfalls of 20 cm depth. Below freezing temperatures and strong winds occurred for one day, and there was considerable drifting of snow in places. The snow started melting on the second day, at which time mountain reedbuck and grey rhebok were counted and searches made for missing animals. It was determined that 51 % of mountain reedbuck and 27 % of grey rhebok died of hypothermia as a result of the snow (see Chapter 3). Fifteen mountain reedbuck and three grey rhebok carcasses were found before decomposition started, and KFI were measured in each. None of the animals examined had any perirenal fat at all.

Tussen die Riviere Nature Reserve

Adult rams averaged 31 kg (range 23.5 - 35 kg, n = 20) and adult ewes 30.2 kg (range 24.0 - 34 kg, n = 20) at TdR. Animals had more kidney fat in June than December, and in winter females appeared to have more kidney fat than males (Figure 31). These differences were tested using a two-way ANOVA, with data Log_{10} transformed (Table 24). There was strong evidence for a difference between summer and winter, but no evidence of differences between males and females. There was also no interaction.

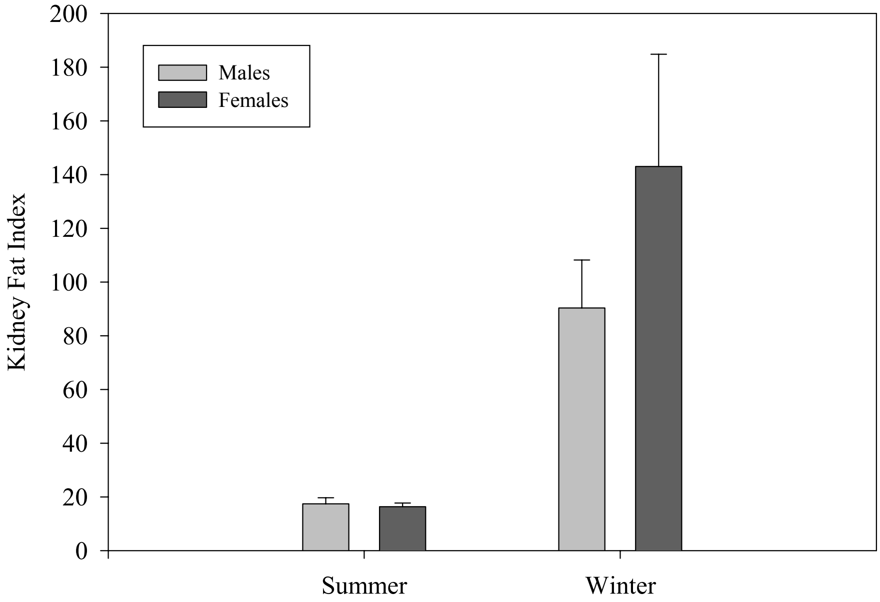


Figure 31. Seasonal variation in KFI for male and female mountain reedbuck at TdR. Error bars represent standard error.

Table 24. Two-way ANOVA comparing KFI of mountain reedbuck between gender and between seasons at TdR. Data were Log_{10} transformed.

Source of Variation	DF	SS	MS	F	P
Gender	1	0.055	0.055	0.946	0.336
Season	1	5.327	5.327	92.428	< 0.001
Gender x season	1	0.092	0.092	1.596	0.214
Residual	41	2.363	0.058		
Total	44	8.247	0.187		

To investigate whether the reproductive condition of females affected body condition at TdR, KFI were compared between pregnant and non-pregnant females in summer. There were no differences between pregnant and non-pregnant females ($t = -1.371$, $df = 18$, $p = 0.187$)

KFI and endoparasitic nematodes

A part of the present study involved the collection, quantification and identification of nematodes from the gastro-intestinal tract (GIT) of mountain reedbuck (see Chapter 7). To investigate whether there was any correlation between numbers of nematodes harboured and body condition, numbers of parasites from the abomasums, small intestines (SI) and large intestines (LI) were plotted separately against KFI (Figure 32). A Spearman Rank Correlation Coefficient found no evidence of a correlation between the numbers of parasites in either the abomasum or SI with KFI (Abomasum: $r = -0.13$, $p = 0.435$; S.I.: $r = 0.03$, $p = 0.843$). LI was not tested because Figure 32c indicated no correlation.

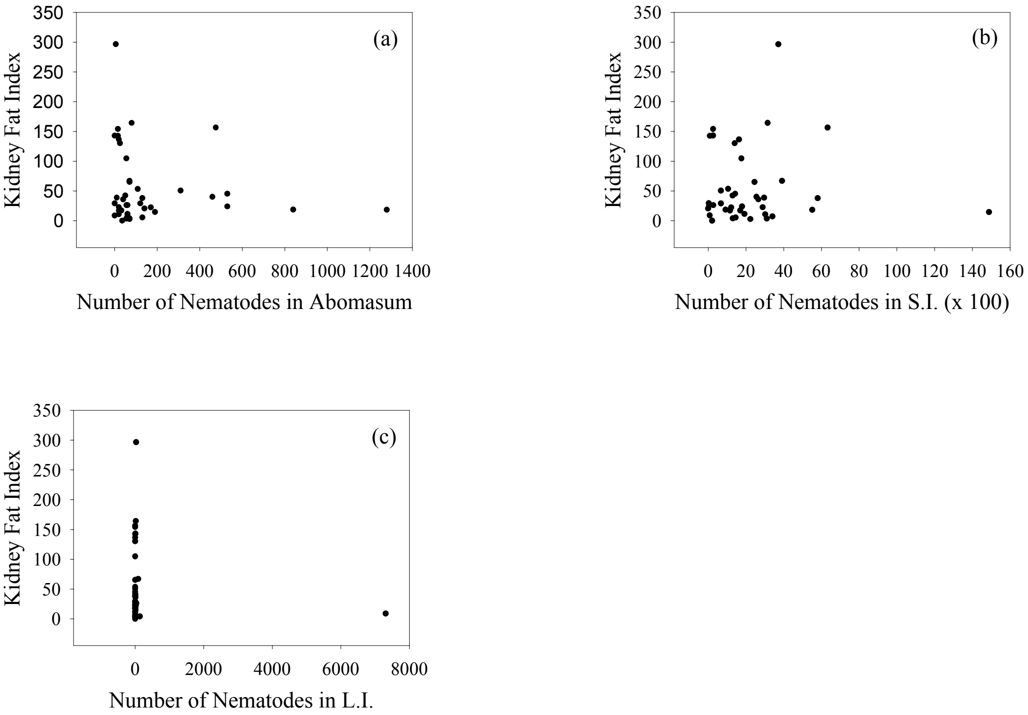


Figure 32. Scatter plots of KFI against (a) number of nematodes in the abomasum, (b) number of nematodes in the SI, (c) number of nematodes in the LI.

Discussion

Carcass weights

Body condition of mountain reedbuck was investigated at Loskop Dam Nature Reserve (Loskop) (Irby, 1975), and Mountain Zebra National Park (MZNP) (Skinner, 1980), using culled animals. Body weights of adult rams and ewes averaged 30.9 kg (range 21.8 - 37.6 kg) and 29.5 kg (range 23.0 – 35.2 kg) respectively at Loskop, while at MZNP they averaged 30.2 kg (range 24.0 – 35.5 kg) and 28.6 kg (range 24.5 – 33.8 kg) respectively. These values are very similar to those of mountain reedbuck at both Sterkfontein and TdR.

Seasonal differences in adult body weight were not tested for in the present study because the sample size per gender per season was low (n = 5). Unless the population is very well sampled, overall body mass is unlikely to be a very good estimate of body condition. An animal might be lighter simply because it is younger, rather than being undernourished, and if the population is not sampled randomly the results might over-represent a certain age group. In contrast to this, dressing percentages and fat indices take into account the size of the animals and will better reflect the condition of individuals. In this case, even with fairly small sample sizes, as long as only adults over 20 kg were used, the effect of body size was negated.

Dressing percentages

As found by Irby (1975) and Skinner (1980), dressing percentages of mountain reedbuck at Sterkfontein were consistent with those of other species of antelope (von La Chevallerie, 1970). Dressing percentages of males at Loskop averaged 60.6 % from March to June, 47.5 % from July to October, and 59.4 % from November to February (overall average 55.8 %) (Irby, 1975). In females they averaged 56.3 % from March to June, 51.7 % from July to October, and 58.6 % from November to February (overall average 55.5 %). These seasonal differences were significant, with the lowest values occurring between July and October. At MZNP dressing percentages in males were 54.2 % in March, 54.2 % in June, 55.5 % in September, and 57.5 % in December (overall average 55.3 %) (Skinner, 1980). In females averages were 52.4 % in March, 50.6 % in June, 50.6 % in September, and 52.2 % in December (overall average 51.5 %). Seasonal differences were not significant although males were found to dress out consistently heavier than females.

In the present study, dressing percentages of males were significantly higher in February/March (59.5 %) than August/September (49.8 %). The same pattern occurred in females (60.4 % in February/March; cf. 50.2 % in August/September). This differed from the pattern at MZNP, where the highest percentages occurred in December and lowest in June. At Loskop only three seasons were used, but dressing percentages were similar to those of Sterkfontein whereby they were lowest in the period July to October, which corresponds to late winter and spring.

The difference between Sterkfontein and MZNP may result from differences in vegetation types and weather patterns. MZNP falls within the South-Eastern

Mountain Grassland and Eastern Mixed Nama Karoo biome. The lesser differences between Sterkfontein and Loskop probably result from the slightly different choice of sampling periods. Rainfall patterns at Loskop are very similar to those of Sterkfontein, except that the summer rains at Loskop start in September (Irby, 1976), approximately one month later than at Sterkfontein. Annual rainfall averages 720 mm at Loskop compared to 680 mm at Sterkfontein.

In red deer stags and hinds on the Isle of Rhum, dressed carcass masses cycled annually as a result of a combination of environmental feeding conditions and reproductive condition (Mitchell *et al.*, 1976). In stags, dressed carcass mass was highest in autumn after a summer of good feeding conditions, but declined rapidly during the rut (autumn/early winter) when they were very active trying to acquire mates, while at the same time not feeding and undergoing acute starvation. After the rut their carcass masses continued to drop through the winter until better feeding conditions arrived in spring. Red deer hinds also showed well-defined annual cycles in dressed carcass mass, but these were asynchronous with stags. Lowest values occurred in spring and highest values in early winter, about two months after the rut when stags lost condition. Because females continued feeding through the rut, they did not lose condition at this time. In addition, there was a difference in the pattern of carcass mass change between milk hinds (females that are pregnant or lactating) and yeld hinds (females that are not pregnant or lactating during a specific year). Milk hinds had lower carcass masses throughout the year and also showed less variation in carcass mass. Yeld hinds had significantly higher carcass masses through the winter because they did not have the same energy costs of gestation and lactation that milk hinds faced.

Hewison *et al.* (1996) found that the dressed carcass mass of male roe deer in France varied seasonally, with a decrease in summer during the rut, and a continued fall through autumn. Male body mass was lowest in early winter before increasing in late winter to be maximal in spring. The dressed carcass mass of females also varied seasonally, being maximal in spring and lowest in summer. In contrast to males, there was no significant mass loss over winter. The asynchronous cycles in body mass of roe deer in France were attributed to differences in reproductive cycles. Males had lower carcass masses in early winter, at the end of the rut, while females had lower carcass masses in summer during the period of maximal maternal investment in reproduction. This period coincided with the last stages of gestation and the first two months of lactation. The increase in carcass mass of roe deer over winter in France (Hewison *et al.*, 1996) was in contrast to other studies on Cervidae that have shown decreases in body mass over winter (Anderson *et al.*, 1972; Mitchell *et al.*, 1976; Holand, 1992). This difference was thought to be partly a result of better environmental and feeding conditions over winter in France than in the other study sites.

Regression analysis of kidney weight and body weight

As with previous studies (Batcheler & Clarke, 1970; Dauphine, 1975; Spinage, 1984; and Van Vuren & Coblentz, 1985), although KW demonstrated a linear relationship with BW in mountain reedbuck at Sterkfontein, it was not directly proportional to BW. This appeared to be a result of smaller animals having relatively heavier kidneys. When animals under 20 kg were removed from the data sets, KW became more proportional to BW, with the slope of a log-log linear regression not differing from one. The KFI was thus found to be a reliable method of assessing body condition in mountain reedbuck when animals under 20 kg were excluded. Seasonal variation in KW, as found by Dauphine (1975) and Van Vuren & Coblentz (1985), that might influence the outcome of KFI results, were not found to be significant in mountain reedbuck at Sterkfontein. This concurred with a study by Spinage (1984) on waterbuck and Grant's gazelle, and a study on several antelope species in the Transkei (Shackleton & Granger, 1989).

Variation in body condition from KFI and LFP

Skinner (1980) found that there was some seasonal variation in KFI of mountain reedbuck at MZNP. Although no statistical analyses were conducted, males had a considerably higher KFI in June (KFI = 60.5) compared to March (9.6), September (26.1) and December (9.9). In females KFI was also highest in June (21.3), but there was not such a big difference compared with March (14.2), September (17.3) and December (19.4). Hanks (1981) suggested that a KFI value of > 80 indicates good condition, 40-80 medium condition, and < 40 poor condition. On average, therefore, at MZNP only males in June were in medium condition, while the rest were in poor condition. In contrast, at Sterkfontein, males were in good condition between February and June, medium condition in November/December, and poor condition in August/September. Females were in very good condition in May/June but poor condition for the rest of the year.

Comparisons of KFI at MZNP and Sterkfontein show some similarities and some differences. The main point of agreement is that both males and females had relatively high values in winter, (June at MZNP and May/June at Sterkfontein). KFI was highest for males in winter at MZNP, whereas at Sterkfontein it was second highest at this time. Nevertheless, values were still higher in winter at Sterkfontein than at MZNP. The highest values at Sterkfontein occurred in February/March (autumn), which was the time when KFI was lowest at MZNP.

In agreement with males, female KFI at Sterkfontein was lowest in August/September, but in contrast was not high in February/March. KFI in females at MZNP was lowest in March and highest in June, but values were very similar in all seasons. Comparing the two study sites, females at Sterkfontein had much higher values in winter than females at MZNP. Moreover, winter values at Sterkfontein were significantly higher than in other seasons within the same reserve.

At TdR mountain reedbuck were in good condition in June and poor condition in December, following the pattern at both MZNP (Skinner, 1980) and Sterkfontein. There were no differences between males and females.

At Sterkfontein LFP and KFI were highly correlated in both males and females, and both followed virtually an identical pattern of highs (winter) and lows (spring). LFP was significantly lower in August/September (spring) than in other months. In addition, it was significantly lower in November/December (summer) than May/June (winter).

In general, therefore, the seasonal patterns in dressing percentages and fat indices at Sterkfontein agreed that condition was lowest in spring, but differed in which season the animals were in best condition. KFI and LFP were highest in winter, while dressing percentages were highest in autumn at Sterkfontein. By the time winter arrived, dressing percentages were dropping. There was effectively a lag period, and body fat started being used up before kidney fat. This is probably related to predetermined physiological timing of fat deposition. However, as leg fat has been shown to directly correlate with total body fat (Butterfield, 1962; Smith, 1970), any decrease in dressing percentages should correspond with a simultaneous decrease in LFP. This did not occur at Sterkfontein. Instead LFP lagged behind dressing percentage in the same way as KFI.

Riney (1955) found that in red deer in New Zealand, fat was first deposited in bone marrow, followed by fat around the kidneys, intestines and stomach, and finally by subcutaneous fat on the back. Mobilisation of these fat deposits was then in the reverse order. This explains why decreases in kidney fat lags behind carcass fat in the dressed animals, but not why leg fat decreases at the same time as kidney fat. In red deer on Rhum, carcass mass, kidney fat and rump fat were all highest during the same periods (Mitchell *et al.*, 1976).

The poor condition of animals in spring can be explained by rainfall patterns. Winter in most parts of South Africa, including all four sites mentioned here, is characterised by very low rainfall. Rains only start in August or September, at which time the grazing is in its worst condition. At Sterkfontein, summer rainfall had barely started at the time of the spring culls (September 2000 and August 2001) so the veld would not have recovered from winter. Animals would, therefore, be expected to be in poor condition at this time. The vegetation types of Sterkfontein and Loskop also help explain the poor grazing conditions. Both reserves can be classified as falling within sour grassveld (Acocks, 1988), where the protein content of the grasses decreases markedly in winter. This leads to a decrease in nutritional quality of grazing for mountain reedbuck and a loss of condition.

Although there were no statistical differences between males and females in body condition, there was an asynchronous pattern demonstrated at Sterkfontein by both indices. Males were in better condition than females in November/December (summer) and February/March (autumn), while females were in better condition than males in May/June (winter) and August/September (spring).

A possible explanation for these differences might be as follows: Both genders were in their worst condition in spring, coinciding with the poorest feeding conditions. Between spring and summer the condition of the veld improved due to higher temperatures and rainfall, but the condition of females did not improve as much as that of males. This may have been because the period coincided with late stages of pregnancy, which would have led to increased energy requirements while males were free of such demands. Females then gave birth mainly in November and December (summer). Between summer and autumn, the condition of males increased markedly at a time when feeding conditions would have been at their best. The females at the same time only showed a slight improvement in body condition and this may have been due to the peak period of lactation (Skinner, 1980). So although feeding conditions were good, the energy demands of producing milk counteracted fat deposition to a certain extent.

Between autumn and winter, male condition dropped slightly, while that of females increased dramatically. Although mountain reedbuck can potentially breed aseasonally (Irby, 1979), they have a peak in breeding in April. Males do not have a defined rut (Irby, 1976; pers. obs.) as do impala and springbok (Skinner & Smithers, 1990) but they still have an increase in reproductive behaviour during this breeding season. Increased energy demands and decreased time for feeding might be expected to reduce their body condition. The significant improvement in female body condition was probably due to being released from the burden of lactation while feeding conditions were still good. Finally, between winter and spring, body condition dropped considerably in both sexes and this would have been due to the declining condition of the veld for grazing.

Similar reasons are given for asynchronous cycles in body condition for some cervid species, including red deer on Rhum (Mitchell *et al*., 1976), caribou (reindeer) in Canada (Adamczewski *et al*., 1987), and roe deer in France (Hewison *et al*., 1996). Annual cycles in body condition in these species have been found to occur partly as a result of seasonal weather changes that affect feeding conditions, and partly as a result of differences in reproductive timing between males and females.

Norton (1989) found significant differences in KFI between males and females at Rolfontein and Doornkloof Nature Reserves in the Karoo, with males having lower values. The indices were very variable, especially for the females, with some individuals having almost no perinephric fat and several having indices of more than 150. The mean KFI for immatures was similar in the two sexes up to the age of 20 months, but after that the males' condition dropped to just over half that of the females. It was suggested that males were subject to greater stress than females. No seasonal differences were tested for because the culls were carried out within a single month at both sites (August at Rolfontein and June at Doornkloof). At Sterkfontein males had lower KFI values than females in June and August as well, but higher values at other times. It is possible, therefore, that had separate culls been carried out at Rolfontein and Doornkloof between November and March, males would have had higher KFI values than females. In this case, rather than males being subjected to more stress than females overall, differential physiological requirements of the sexes may have driven seasonal variation in body condition.

Actual KFI values could not be compared with those of the present study because the KFI were calculated in slightly different ways. Norton (1989) suggested that the high variability in condition showed that all individuals were not affected equally during dry periods. Juveniles had relatively low condition up the age of one year, after which fat deposits increased quickly. This was probably because in that first year most energy goes into growing rather than fat deposition (Norton, 1989).

Shackleton & Granger (1989) investigated variation in body condition of six antelope species (four grazers and two mixed feeders) in the Transkei using KFI and bone marrow fat index (BMI) in conjunction with phytomass and crude protein content of grasses and forbs. It was found that peak condition was attained during spring and summer, coinciding with the period when phytomass and crude protein levels were highest. Levels of crude protein, BMI and KFI increased in sequence with a lag of approximately one month between each factor. Crude protein increased in September, followed by BMI in October and finally KFI in November. It was also found that the peak in KFI was short lived, indicating the absence of storage of perinephric fat. Females appeared to maintain better condition than males throughout winter (Shackleton & Granger, 1989), and it was suggested that this might have been a result of males experiencing reduced vigour upon entering the winter period because of the rut in the months immediately preceding winter. At Sterkfontein and TdR, males were also in poorer condition than females in winter, although the difference was not significant. This lack of significance might be explained by the lack of a well-defined rut in mountain reedbuck.

Variation in condition between antelope species was found to occur within the same game reserve in the Transkei (Shackleton & Granger, 1989). Gemsbok and red hartebeest (both grazers) were in poor condition throughout, blue wildebeest (grazers) were intermediate, and eland and blesbok (mixed feeder and grazer respectively) were in good condition. The latter two species were consequently considered to be well suited to the reserve. The poor adaptability of gemsbok and red hartebeest to this region was also manifested in their poor reproductive rate. Using the same argument of good body condition and high reproductive rate, Skinner (1980) found that mountain reedbuck at MZNP were particularly well suited to the terrain they inhabited. It was also suggested that the lack of seasonal change in carcass characteristics could have indicated that MZNP was under stocked.

The total lack of kidney fat in mountain reedbuck found dead in the snow at Sterkfontein in September 2001 indicates that they did not have sufficient energy reserves to survive the cold spell. It also reinforces the fact that they would have been in their poorest condition at this time, as found during the culling operations. Animals were on the threshold of survival and their immediate food intake was keeping them alive. When unable to feed because of the snow, they would have used up the last of their body fat, exhausted their glycogen stores, and then finally have had to utilise protein for an energy source. This process is too slow over the short term and the result was death for many individuals. Although temperatures were cold at the time of the snowfalls, they were not as cold as temperatures that regularly occur at Sterkfontein in winter, and at these times very few mountain reedbuck died as a result of hypothermia (Chapter 3). If the snow had fallen in June when they had greater supplies of body fat, the animals would not have died in comparable numbers, if at all.

KFI and endoparasitic nematodes

High parasitic loads can cause morbidity, reduced production, and even death (Wilson *et al.*, 2002), so it might be expected that animals with high loads would generally be in poorer condition. There was, however, no correlation between numbers of nematodes and condition. Nematodes at Sterkfontein did not appear to adversely affect body condition in mountain reedbuck.

Nematodes in the abomasum comprised two species that occurred in approximately equal numbers. The more important species, *Haemonchus contortus* is a bloodsucker, and may remove significant amounts of circulating erythrocytes if they occur in sufficient numbers (Georgi & Georgi, 1990). Pathogenic effects result from the inability of the host to compensate for blood loss. Infections of up to 500 worms have been found to have little effect on growth production of sheep under conditions of satisfactory nutrition (Georgi & Georgi, 1990). During the present study numbers of *H. contortus* did not go above 500 worms per animal (if one takes into account that about half the worms were *L. schrenki*) thus, possibly explaining the lack of influence of these nematodes on body condition. Less is known about the debilitating effects of *Longistrongylus schrenki*, but they appeared to be insignificant in these numbers in this case.

The main nematode of the small intestine, *Cooperia yoshidai* may penetrate the epithelial surface of the small intestine and cause disruption that leads to villous atrophy and a reduction in the area available for absorption (Georgi & Georgi, 1990). It appeared that infections of these nematodes in mountain reedbuck at Sterkfontein were not high enough to cause a decrease in condition either.

Chapter 7

PARASITES

Introduction

This was a study on factors influencing productivity of two sympatric antelope species of South Africa, the mountain reedbuck (*Redunca fulvorufula*) and grey rhebok (*Pelea capreolus*). The mountain reedbuck has the potential to be cropped for meat production because it is fecund (Irby, 1979; Skinner, 1980), has the potential to breed aseasonally (Irby, 1979), and produces good quality, edible meat that is generally free from parasites (Irby, 1975; Skinner, 1980). Additionally, it does not compete with other grazers because it utilises steep rocky habitat that is marginal for animal husbandry. Reproduction and body condition are the subjects of other chapters, but a potentially important aspect of antelope ecology that can play a significant role in productivity is parasitology. Parasites can negatively affect numerous fitness traits of their hosts, potentially causing a loss of condition, reduced productivity, disease and even death. The degree to which parasite effects translate into changes to host populations will likely depend on many factors including dispersion of parasites among hosts, magnitude of parasite effects, and degree to which ages and sexes differ in parasitism (Schalk & Forbes, 1997).

The parasites of mountain reedbuck are not well known despite these antelopes' relative abundance in South Africa (Boomker *et al.*, 2000). Baker & Boomker (1973) found 17 helminth species (14 nematodes, two cestodes and one trematode) in mountain reedbuck at Loskop Dam Nature Reserve and four species at Mountain Zebra National Park. Genera found included *Cooperia, Gongylonema, Haemonchus, Impalaia, Moniezia, Nematodirus, Oesophagostomum, Paramphistomum, Setaria, Skrjabinema* and *Taenia*. Boomker *et al.* (2000) additionally found *Ostertagia* type females and a *Trichostrongylus* sp. in mountain reedbuck at Mountain Zebra National Park. Mean adult nematode burdens were found to be negligible (283 worms).

The parasites of grey rhebok are even less well known (Boomker *et al.*, 2000) and have only been studied at Bontebok National Park. Work by Boomker, Horak & de Vos (1981), Horak, de Vos & De Klerk (1982), Boomker (1990) and Boomker & Horak (1992) found 12 nematode and one trematode species. Genera included *Fasciola, Haemonchus, Longistrongylus, Nematodirus, Ostertagia, Paracooperioides,* and *Trichostrongylus*. As with mountain reedbuck, nematode burdens were found to be negligible.

The aim of this component of the study was to identify and quantify helminths of mountain reedbuck and grey rhebok and to investigate effects of host gender and season on the occurrence and numbers of parasites. Mountain reedbuck occur at both Sterkfontein and Tussen die Riviere, while grey rhebok occur at the former but not the latter. As helminths from both of these antelopes were poorly known, and neither of the two areas had been surveyed quantitatively previously, this study provides new helminthological data for both the antelope species and the geographic localities.

Mountain reedbuck were regularly culled in the Free State, including Sterkfontein and TdR. Considerable parasite material was made available from animals culled during the study period from both reserves, and management assistance permitted seasonal and gender comparisons between host-parasite populations. Grey rhebok were not culled for meat production because they are less common and not favoured for consumption. Although they are occasionally utilised for trophy hunting, no systematic removal of grey rhebok occurred during the study. Parasite collection from the gastro-intestinal tracts (GIT) of these antelope could, therefore, only be carried out from animals that died naturally or accidentally, and as a result was only useful for limited helminth species identification. In an attempt to set a baseline of intestinal parasites in grey rhebok for comparison with mountain reedbuck at Sterkfontein, a limited amount of nematode egg quantification as well as faecal culture of nematode larvae was carried out. However, the relationship between these indirect measures and actual worm burden is very complex (Shaw & Dobson, 1995) and egg counts are not considered a reliable method for estimating the numbers of parasites within the GIT (Reinecke, 1983).

To accomplish the aims, the following questions were considered:

1. What are the helminth species of mountain reedbuck at Sterkfontein and TdR?
2. What are the prevalence's and abundance's, and how do these vary seasonally?
3. Are there any differences between the sexes, between animals in different reproductive condition, or animals of different ages?
4. Do animals with higher parasite burdens have poorer body condition?
5. Can faecal egg counts from mountain reedbuck be used as a means of estimating true worm counts from the GIT?
6. What are the helminth species of grey rhebok at Sterkfontein?

Methods

Study sites and animals

Alimentary helminths were recovered from mountain reedbuck culled at two Free State Provincial Nature Reserves, Sterkfontein and TdR. Culling schedules differed between the two sites as a result of differing management programmes. At Sterkfontein a total of 41 animals were culled over a two-year period. Eight separate culls were carried out at three-month intervals, and during each cull five or six animals were shot within a week. The culling schedule was as follows: five animals were shot in March 2000, five in June 2000, five in September 2000, five in December 2000, six in May 2001, six in August 2001, six in November 2001, and four in February 2002. Numbers culled in the final two periods were reduced because a large number of mountain reedbuck died in heavy snowfalls in September 2001. In a typical culling period, two adult males, two adult females, and one juvenile of either sex were selected. The age and condition of adult mountain reedbuck were not known before they were shot, and because animals were located randomly, the selection was not considered biased.

The spacing of the culls, spanning eight different months over a two year period, meant that parasitic loads could be compared in both warm and cold periods as well as wet and dry periods. They hence covered times when animals had abundant food supplies available and times when food resources were limited. For some analytical purposes these months were divided into four seasons: autumn = February/March, winter = May/June, spring = August/September, and summer = November/December.

At TdR mountain reedbuck were culled on three separate occasions, covering one summer and two winters. Seven animals were culled in December 1999 (summer), 10 in June 2000 (winter), and eight in June 2001 (winter). Most of the animals were culled at night using spotlights to locate them and were, therefore, selected randomly.

Grey rhebok were not culled at Sterkfontein during the study period, so no systematic investigation of their endoparasites could be made. However, three animals died naturally and one was shot for necropsy because it was visibly sick, and these animals were sampled for helminths.

Recovery of alimentary helminths

Alimentary tracts were removed as soon as possible after animals were shot, and the abomasal/duodenal and small-intestine/large-intestine junctions ligated to prevent transfer of parasites from one site to the other (Urquhart *et al.*, 1994). They were then stored in a cool sheltered place until they could be processed, usually within three hours.

The rumen and reticulum were opened and their walls and contents examined for paramphistomes. Any found were collected and preserved in 10 % formalin. The abomasum was then opened along the side of greater curvature and the ingesta poured into a large plastic bowl (50 cm diameter x 20 cm depth). The inside of the abomasum wall was thoroughly rinsed with approximately 1 L of water to remove the rest of the contents, and this was added to the rest of the ingesta. Once the inside lining appeared clean of any remaining contents, the abomasum was discarded. The ingesta and water were then thoroughly mixed in the bowl using a small beaker, and a one-fifth aliquot removed using a measuring jug. This one-fifth aliquot was then rinsed using a 15 µm sieve and stored in 10% formalin or 70% ethanol.

Similarly, the ingesta of the small intestine were emptied into a clean plastic bowl (see above). To achieve this, the intestine was cut into manageable segments and the contents of all segments squeezed out into the bowl. Each segment was then cut along its entire length and rinsed thoroughly in 1 L of water. Again, the water plus ingesta was thoroughly mixed in the bowl, a one-fifth aliquot removed and rinsed using a 15 µm sieve before being stored in 10% formalin or 70% ethanol. Finally, the contents of the large intestine and caecum were collected in the same way as the small intestine and stored in 10% formalin or 70% ethanol.

Helminths of the heart, lungs and liver

In addition to the alimentary canal, the heart, lungs and liver were examined for the presence of helminths at both Sterkfontein and TdR. The heart chambers were opened and examined macroscopically for visible parasites, then the walls of the heart muscle were cut into 10 mm slices and placed into a jar with normal saline, and incubated in a warm water bath at approximately 40° C for 2 h. The trachea and bronchi were opened, examined macroscopically for parasites and then rinsed with water over a sieve with 15 µm apertures. The right lung was also rinsed over the sieve then cut into 20 mm cubes and put into a separate jar of normal saline for incubation in a warm water bath for 2 h. Finally, the liver was cut into 10 mm strips, palpated to express any visible parasites and again placed into a separate jar of normal saline and incubated in a warm water bath for 2 h. The solutions were then sieved separately (15 µm apertures) and the residues stored in 10 % formalin. At a later stage, these solutions were examined under a dissection microscope for helminths. Nothing was found in any of the mountain reedbuck from either Sterkfontein or TdR, so no results are presented.

Worm identification and quantification

To extract the worms from storage, the samples were again rinsed over a 15 µm sieve to remove the formalin or ethanol preservative, and the ingesta then remixed with water to make a volume of about 200 ml. Approximately 2 ml red dye (Eosin) was then mixed with the sample and left for an hour to stain the worms. A small amount of the mixture was poured into a Perspex counting dish and all the helminths, including the fourth larval stages (L_4 larvae), extracted using a dissection microscope. Once completed, the remaining material was discarded, another small amount of mixture poured into the dish and the procedure repeated. The aliquot was thus worked through piecemeal until all the worms were extracted. All worms were stored in 70 % ethanol.

At a later stage nematodes were cleared in a drop of lactophenol on a microscope slide and examined under a compound microscope using magnifications between x 10 and x 40. Species were identified using species descriptions (Boomker, 1977, 1991; Boomker, Horak & de Vos, 1981; Gibbons, 1981; Boomker & Reinecke, 1989). Male nematodes were identified to the species level, and in most cases females could also be identified to species level by extrapolation. In cases where male nematodes were not present, or when two or more species of the same genus were found in the same animal, females were identified to the level of genus only. Trematodes and cestodes were identified to the generic level only.

Faecal egg counts

Faeces were only collected from animals at Sterkfontein. From mountain reedbuck they were collected from 18 culled animals with the aim of making comparisons between egg counts, larval counts (see below) and counts of adult worms from the GIT (as above). This was done to test whether egg or larval counts could be reliably used to estimate numbers of adult nematodes in grey rhebok. In grey rhebok, faeces were collected fresh off the ground while following live animals. Samples were taken twice a month from five animals within one habituated herd, between September 2001 and April 2002. Faeces were kept cool until microscopic analysis could be carried out, usually within 12 h.

Two grams of faeces were weighed and added to 58 ml saturated sugar solution (800 g sugar to 1 000 ml tap water). Nematode eggs float in this solution because they have a relatively lower specific gravity. A food blender was then used to break up the faeces and thoroughly mix it with the solution. One drop of amyl alcohol was added to the mixture to reduce surface tension and remove bubbles. The solution was then stirred well, a small amount extracted with a pipette and this placed into a McMaster slide ("Eggs-Acto" McMaster egg counting chamber, Focal Point, South Africa, www.mcmaster.co.za). This was left to stand for two minutes to allow any eggs to float to the top, placed under a compound microscope under low magnification (x 10) and the eggs counted in all three chambers. No attempt was made to identify the nematode species from the eggs.

Coproculture

After carrying out egg counts, the remaining faeces were used to culture larval nematodes. Faeces were weighed, crushed and thoroughly mixed with vermiculite at a ratio of 1:1 to aerate the faeces and allow movement of larval worms. A small amount of water was added if necessary so that mixture held together like clay. The faeces/vermiculite mix was then lightly compressed in the bottom of a 1 l fruit jar, leaving a circular space of about 2 cm diameter at the bottom. Using a pipette, a few millilitres of water were added to the mix and to the inside surface of the jars to increase humidity. Lids were then loosely screwed onto the jars to allow a small amount of air circulation, and the jars placed near a small heater to maintain warmth (approximately 20° C). After 10 days, cultured larvae were extracted from the inside walls of the console jars where they migrated to after hatching. This was achieved by splashing water onto the walls using a pipette and tipping the water into a petri dish without letting it come into contact with the faeces. The walls were rinsed twice using the same amount of water each time to make sure that all possible larvae were taken out. The jars were then placed back near the heater for another four days to collect a second set of larvae. After day 14, the faeces were discarded. Larval numbers were estimated in a Perspex counting dish using a dissection microscope. If very large numbers were present a sample was counted using a McMaster slide under a compound microscope and the numbers multiplied according to the total volume used. Species identification was not attempted.

Statistical methods

Two-way ANOVA were used to test for differences between genders and months. As with most parasite population data, the nematodes were strongly aggregated, so the data had to be Log_{10} transformed. Because the occurrence of one species of nematode in the GIT was not dependent on or affected by the occurrence of another species, it was not of interest to test for differences between nematode species. Therefore, three separate two-way ANOVA's were carried out for the three main nematode species. One-way ANOVA's and Kruskal Wallis ANOVA on ranks were used to test for differences in parasitic loads of animals of different ages and females in varying degrees of pregnancy. Spearman Rank Correlation Coefficients were used to compare faecal egg counts with cultured larvae counts and adult worm counts. They were also used to determine whether there was a correlation between the number of nematodes extracted and the kidney fat index of each animal (Chapter 6).

Results

Helminth species prevalence and abundance

Seventeen species of helminths, including fifteen nematodes, one trematode, and one cestode were recovered from mountain reedbuck at Sterkfontein and TdR (Tables 25 & 26). The most prevalent species at Sterkfontein were *Cooperia yoshidai*, *Longistrongylus schrenki* and *Haemonchus contortus*, found in 98 %, 80 % and 66 % of animals respectively (Table 25). *C. yoshidai* followed by *H. contortus* and *L. schrenki* were the most abundant species. The other ten species demonstrated low prevalence and abundance. There was one new species of *Cooperia*, as well as six new host records for mountain reedbuck at Sterkfontein. These were *L. schrenki, L. namaquensis, Ostertagia* sp., *Trichostrongylus deflexus, Impalaia nudicollis* and *Paracooperioides peleae*.

Eleven species were recorded at TdR (Table 26), including seven that were also found at Sterkfontein. The most prevalent was *Nematodirus spathiger*, found in 58 % of animals, while the most abundant species was *T. falculatus*. Overall, nematodes were considerably less prevalent and abundant in mountain reedbuck at TdR than at Sterkfontein. New parasite records were *C. rotundispiculum* and *I. nudicollis*.

Table 25. Prevalence and abundance of helminths recovered from 41 mountain reedbuck culled at Sterkfontein between March 2000 and February 2002. (Prev. = prevalence, Std. Dev. = standard deviation, T = trematode, N = nematode, C = cestode, L_4 = fourth larval stage, Rum = rumen, Abo = abomasum, SI = small intestine, LI = large intestine, * = new species).

Nematode genera and some species	Prev. %	Site in host	Mean	Std. Dev.	Range
Calicophoron sp. (T)	5	Rum	6.1	27.8	0 – 150
Haemonchus sp. L_4 (N)	32	Abo	21.4	61.9	0 – 350
Haemonchus contortus (N)	66	Abo	115.8	218.2	0 – 1050
Longistrongylus sp. L_4 (N)	44	Abo	72.9	135.0	0 – 470
Longistrongylus schrenki (N)	80	Abo	36.5	56.8	0 – 232
Longistrongylus namaquensis (N)	2	Abo	0.2	1.6	0 – 10
Ostertagia sp. (N)	2	Abo	0.2	1.6	0 – 10
Cooperia sp. L_4 (N)	66	SI	312.3	682.3	0 – 4050
Cooperia yoshidai (N)	98	SI	2037.5	2594.2	0 – 14880
Cooperia sp. (N) *	2	SI	3.7	23.4	0 – 150
Trichostrongylus falculatus (N)	12	SI	5.4	26.7	0 – 170
Trichostrongylus deflexus (N)	2	SI	0.2	1.6	0 – 10
Impalaia nudicollis (N)	2	SI	0.5	3.1	0 – 20
Paracooperioides peleae (N)	2	SI	0.2	1.6	0 – 10
Skrjabinema sp. (N)	39	LI	187.9	1140.4	0 – 7310
Moniezia sp. (C)	5	SI	0.1	0.2	0 – 1

Table 26. Prevalence and abundance of helminths recovered from mountain reedbuck at TdR between December 1999 and June 2001. (Prev = prevalence, Std. Dev. = standard deviation, T = trematode, N = nematode, C = cestode, Rum = rumen, Abo = abomasum, SI = small intestine, LI = large intestine, Vis = visceral cavity).

Nematode genera and some species	Prev %	Site in Host	Mean	Std. Dev.	Range
Calicophoron sp. (T)	4	Rum	2.0	12.5	0 – 80
Haemonchus contortus (N)	28	Abo	4.0	10.2	0 – 50
Longistrongylus albifrontis (N)	8	Abo	0.3	1.1	0 – 4
Nematodirus spathiger (N)	58	SI	15.1	22.5	0 – 100
Trichostrongylus falculatus (N)	31	SI	29.6	70.0	0 – 240
Cooperia rotundispiculum (N)	31	SI	19.3	64.2	0 – 320
Cooperia yoshidai (N)	4	SI	0.4	2.0	0 – 10
Impalaia nudicollis (N)	8	SI	1.7	6.0	0 – 24
Skrjabinema sp. (N)	4	LI	0.4	2.0	0 – 10
Setaria sp. (N)	4	Vis	0.1	0.2	0 – 1
Moniezia sp. (C)	4	SI	0.1	0.2	0 – 1

Frequency distributions of nematodes at Sterkfontein

Figure 33 shows the frequency distributions of the four most common nematode species found in mountain reedbuck at Sterkfontein. The degree of aggregation was tested using the corrected moment estimate of *k* (Wilson *et al.*, 2002):

$$k = (m^2 - s^2/n)/(s^2 - m)$$

where m = mean, s^2 = variance, n = sample size.

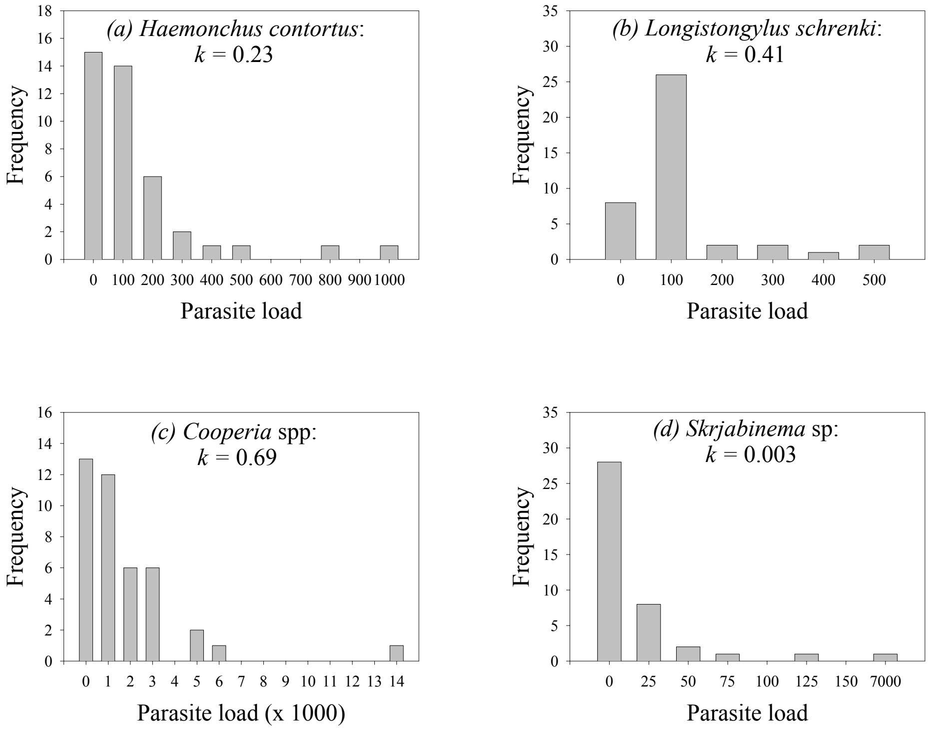


Figure 33. Observed frequency distributions of (a) *H. contortus*, (b) *L. schrenki*, (c) *Cooperia* spp. and (d) *Skrjabinema* sp. found in 41 mountain reedbuck culled at Sterkfontein between March 2000 and February 2002. *k* = the corrected moment estimate for aggregation.

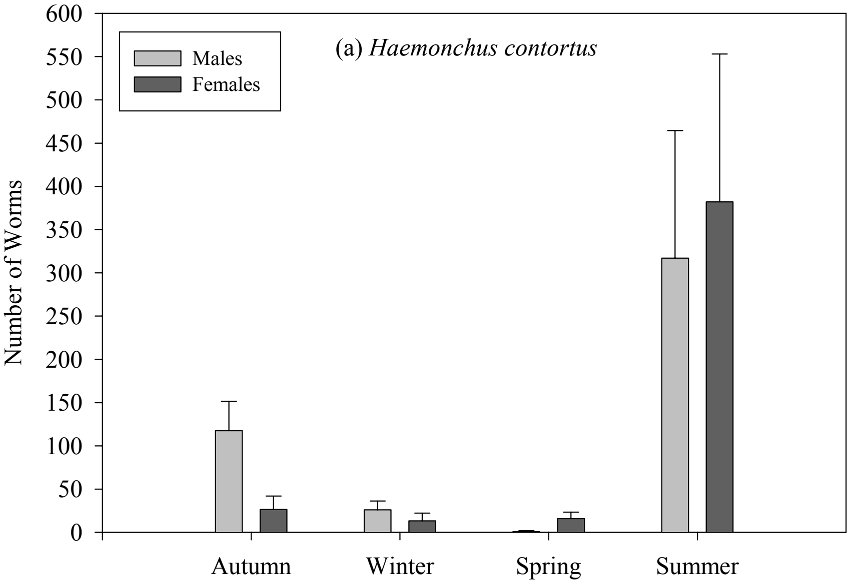
All four species were highly aggregated and their distributions could best be described by the negative binomial distribution. Out of a total of 4 499 adult *H. contortus* found, 78 % occurred in only 20 % of the animals. For *L. schrenki* (total 1 518 adult worms), 67 % occurred in 20 % of the animals, while in *Cooperia* spp. (total 89 759 adult worms), 52 % occurred in 20 % of the animals.

Abomasum nematodes at Sterkfontein

Numbers of *H. contortus* were highest in summer (November/December) for both males and females, and lowest in spring (August/September) for males and winter (May/June) for females (Figure 34a). Male mountain reedbuck had more worms than females between February and June, while females had more worms than males between August and December.

Similarly in *L. schrenki*, male mountain reedbuck had more worms than females between February and June, while females had more worms than males between August and December (Figure 34b). Males had most worms in February/March and least in May/June, while females had most worms in November/December and least in February/March.

Differences between genders and between months (not seasons) in the numbers of *H. contortus* were tested for using a two-way ANOVA (Table 27). The data were Log_{10} transformed. There was strong evidence of a difference in the number of parasites between months but no evidence of a difference between males and females. Although there was no evidence of an interaction at the 5 % level, the P value was quite close to being significant. This meant that the effect of different levels of gender was marginally dependent on the level of month present. Males had more *H. contortus* than females in autumn and winter, while females had more *H. contortus* than males in spring and summer (Figure 34). Multiple pairwise comparisons using the Tukey test indicated that numbers of *H. contortus* were higher in December than May, June, August and September.



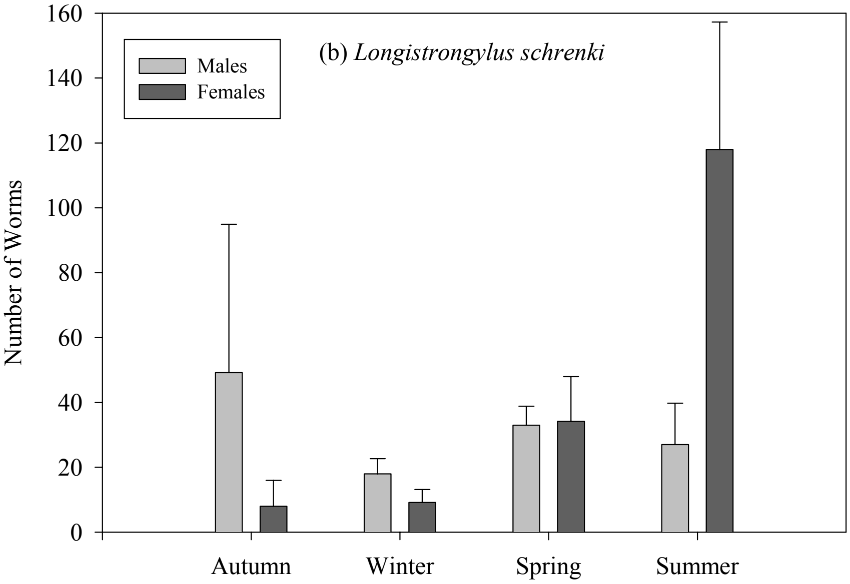


Figure 34. Seasonal variation in (a) *Haemonchus contortus* and (b) *Longistrongylus schrenki* in the abomasums of 20 male and 21 female mountain reedbuck at Sterkfontein. Numbers of animals per gender and per season varied between 4 and 6 (mean = 5). Autumn = February/March, winter = May/June, spring = August/September, summer = November/December. Error bars represent standard error.

Table 27. Two-way ANOVA comparing the differences between genders and between months in the numbers of *H. contortus* in 41 mountain reedbuck at Sterkfontein. Data were Log_{10} transformed.

Source of Variation	df	SS	MS	F	P
Gender	1	0.190	0.190	0.365	0.551
Month	7	19.505	2.786	5.352	< 0.001
Gender x month	7	7.448	1.064	2.044	0.089
Residual	25	13.016	0.521		
Total	40	42.334	1.058		

Differences between genders and between months were also tested for *L. schrenki* using a two-way ANOVA (Table 28). There was some evidence of a difference between months, but no evidence of a difference between genders and no interaction. Multiple pairwise comparisons using the Tukey test indicated that numbers of *L. schrenki* were higher in females in December than February.

Table 28. Two-way ANOVA comparing the differences between genders and between months in the numbers of *L. schrenki* in 41 mountain reedbuck at Sterkfontein. Data were Log_{10} transformed.

Source of variation	df	SS	MS	F	P
Gender	1	0.009	0.009	0.025	0.875
Month	7	6.464	0.923	2.464	0.045
Gender x month	7	3.686	0.527	1.405	0.247
Residual	25	9.367	0.375		
Total	40	19.603	0.490		

Small intestine nematodes at Sterkfontein

Female mountain reedbuck harboured most *Cooperia* spp. in November/December (twice as many as the other seasons) and least in February/March (Figure 35). In both February/March and November/December males had a similarly high numbers of worms, while they had the least amount in May/June. A two-way ANOVA comparing variation in numbers of *Cooperia* spp. found no evidence of any differences between genders or between months (Table 29).

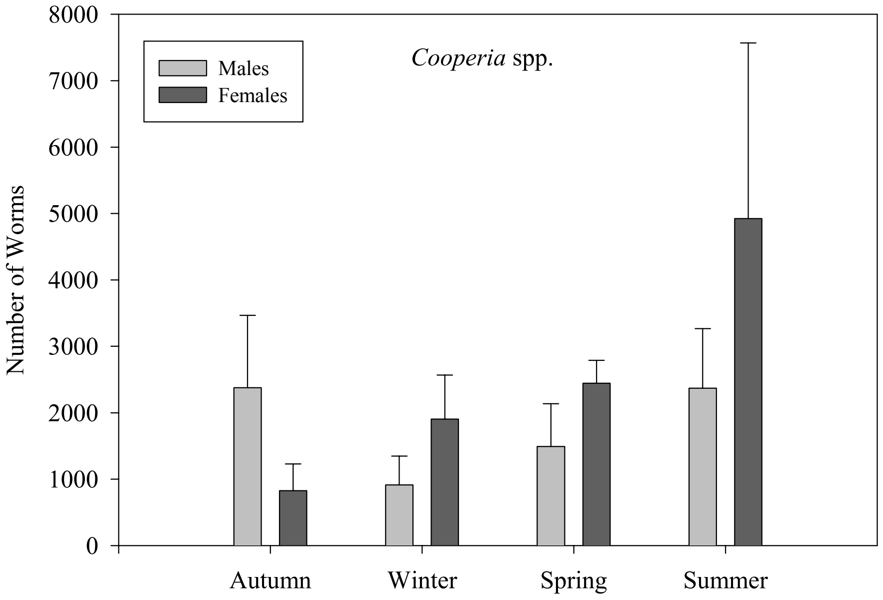


Figure 35. Seasonal variation in *Cooperia* spp. in the small intestines of 20 male and 21 female mountain reedbuck at Sterkfontein. Numbers of animals per gender per season varied between 4 and 6 (mean = 5). Autumn = February/March, winter = May/June, spring = August/September, summer = November/December. Error bars represent standard error.

Table 29. Two-way ANOVA comparing differences between genders and between months in the numbers of *Cooperia* spp. in 41 mountain reedbuck at Sterkfontein. Data were Log_{10} transformed.

Source of Variation	df	SS	MS	F	P
Gender	1	0.032	0.032	0.050	0.825
Month	7	1.946	0.278	0.435	0.871
Gender x month	7	4.835	0.691	1.081	0.404
Residual	25	15.972	0.639		
Total	40	22.753	0.569		

Large intestine nematodes at Sterkfontein

Skrjabinema sp. occurred in very low numbers in mountain reedbuck at Sterkfontein (Figure 36). The relatively very large numbers of worms found in males in spring compared to the other seasons, resulted from the occurrence of a large number of worms in only one animal. Due to low prevalence and very low abundance (except one animal) of this species, statistical analysis of differences between genders and between months was not carried out.

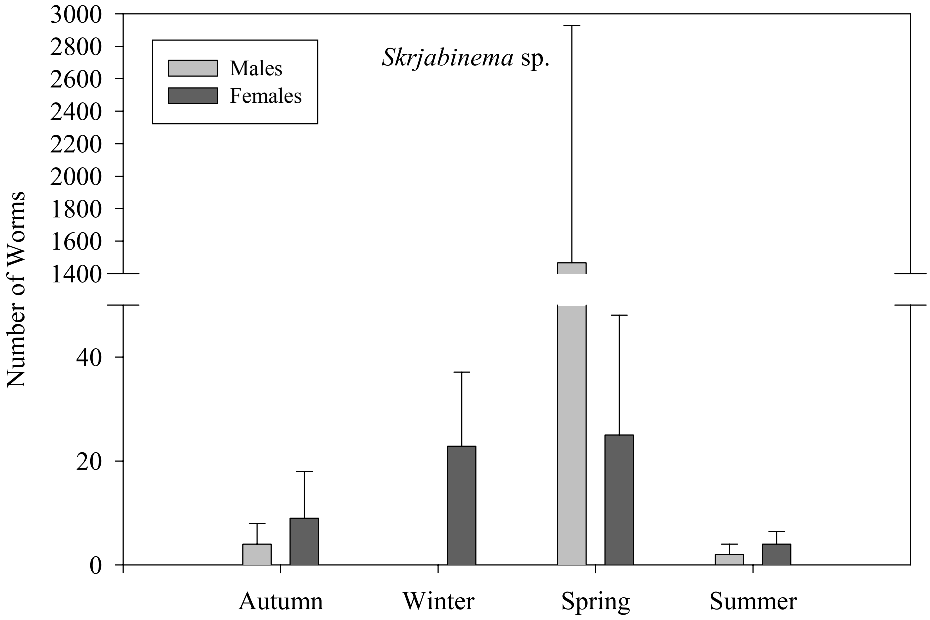


Figure 36. Seasonal variation in *Skrjabinema* sp. in the large intestines of 20 male and 21 female mountain reedbuck at Sterkfontein. Numbers of animals per gender per season varied between 4 and 6 (mean = 5). Autumn = February/March, winter = May/June, spring = August/September, summer = November/December. Error bars represent standard error.

Age differences

Analysis of the effect of age on parasite distributions in mountain reedbuck at Sterkfontein was limited because only a small number of young and old animals were sampled. The small sample size of the former was by design, where only one young animal was collected per cull. For old animals, sample sizes often decline with age due to mortality (Wilson *et al.*, 2002), and because sampling was random for adults, less old individuals were collected. Variation in abundance of *H. contortus* and *C. yoshidai* were tested for mountain reedbuck in three different ages classes. These included animals < 25 kg (juveniles), animals between 25 and 30 kg (young adults), and animals > 30 kg (adults over 2.5 years age). Old animals were included in the last group. Data for males and females were pooled because no statistical differences were found between them and because the sample size was too small to keep them separate.

Because the nematodes were considered independent, two separate Kruskal-Wallis tests were carried out. There was no evidence of any differences between the age groups for either *H. contortus* (H = 1.695, df = 2, p = 0.429) or *C. yoshidai* (H = 2.426, df = 2, p = 0.297).

Host body condition (kidney fat index)

Part of the present study involved the determination of body condition by means of a kidney fat index (KFI) (see Chapter 6). To investigate whether there was any correlation between the numbers of nematodes harboured and body condition of animals, numbers of parasites from the abomasums, small intestines and large intestines were plotted separately against KFI (Figure 37). A Spearman Rank Correlation Coefficient found no evidence of a correlation between the numbers of parasites in either the abomasum or small intestine with KFI (Abomasum: r = -0.13, p = 0.435; S.I.: r = 0.03, p = 0.843). The large intestine was not tested.

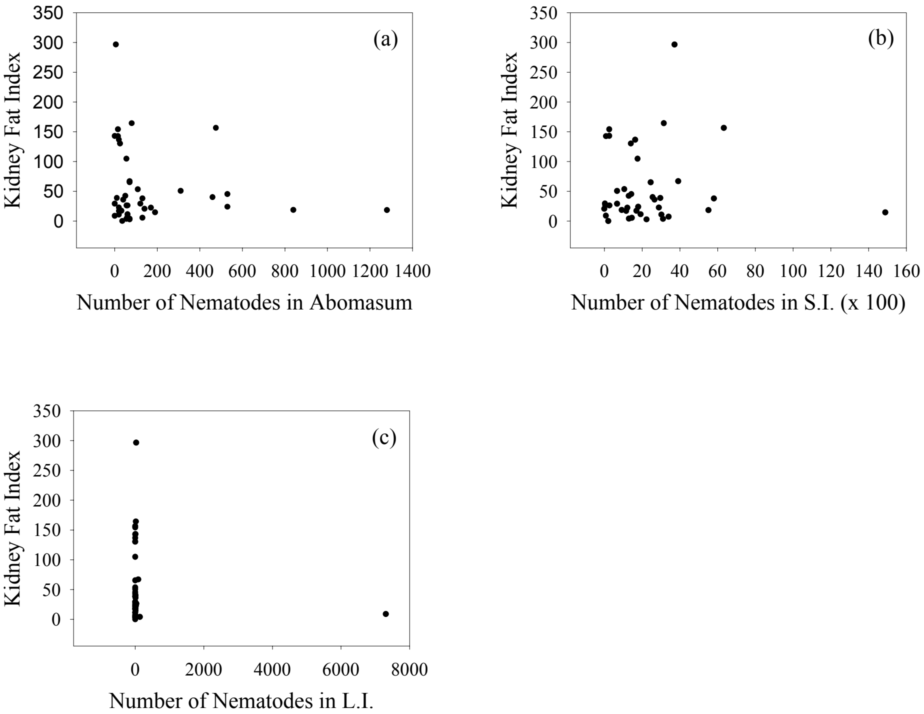


Figure 37. Scatter plots of kidney fat index against (a) number of nematodes in the abomasum, (b) number of nematodes in the small intestine, (c) number of nematodes in the small intestine.

Nematodes and pregnancy

Variation in the number of nematodes found in females at varying stages of pregnancy were tested for because of the possibility of an effect of hormones on the susceptibility of females to infection. Comparisons were made between non-pregnant females, pregnant females within the first half of gestation, pregnant females within the second half of gestation, and females that had recently given birth. Stage of pregnancy was determined by calculating foetal age using the Hugget & Widdas (1951) formula, adapted for mountain reedbuck by Norton (1989).

Although sample sizes were small using four groups, comparing all pregnant females with all non-pregnant females, regardless of the stage of pregnancy or whether they had recently given birth, was considered to have little biological meaning. Results should, however, be treated with caution. There was evidence of a difference in the number of *H. contortus* between females at different times of pregnancy and non-pregnancy (ANOVA: F = 5.11, df = 3, p = 0.011), but no evidence of a difference in the number of *C. yoshidai* (ANOVA: F = 0.780, df = 3, p = 0.522). For *H. contortus*, pairwise comparisons using the Tukey test indicated that females that had recently given birth had more worms than pregnant females within both the first and second halves of pregnancy.

Nematodes of Tussen die Riviere

Figure 38 shows the seasonal variation in numbers of the four most common species of nematode in mountain reedbuck at TdR between December 1999 and June 2001. Because of the low prevalence and abundance of the nematodes in the mountain reedbuck of TdR, and because of the lack of any apparent pattern in variation between genders and seasons, there was no reason to test the data statistically.

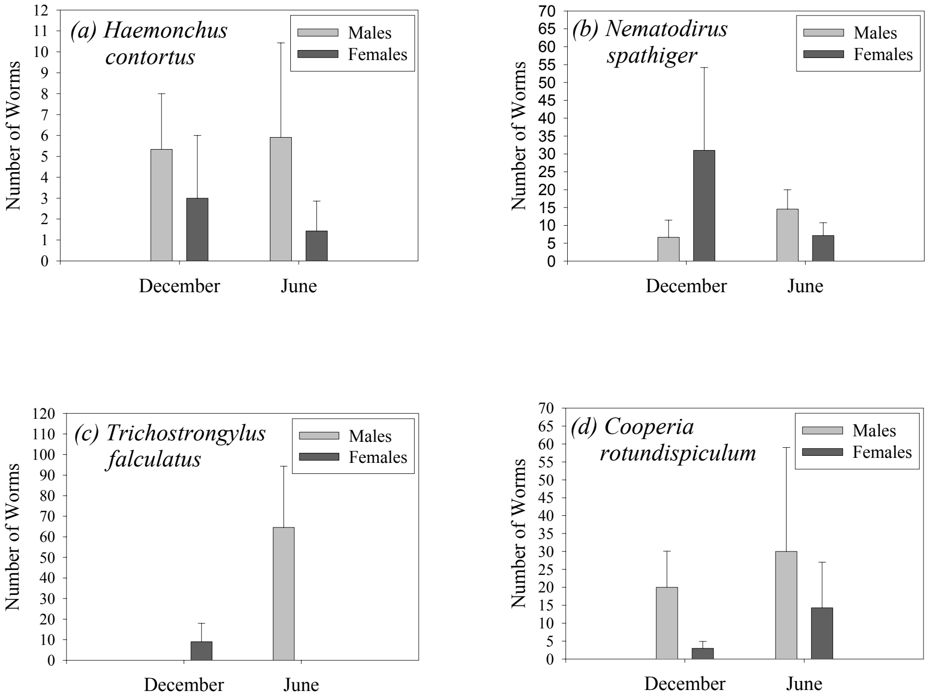


Figure 38. Seasonal variation in (a) *H. contortus*, (b) *T. falculatus*, (c) *N. spathiger*, and (d) *C. rotundispiculum* in 14 male and 11 female mountain reedbuck at TdR in one summer (December 1999) and two winter (June 2000, 2001) periods. Error bars represent standard error.

Nematodes of grey rhebok at Sterkfontein

Five nematode species were extracted from four grey rhebok that died at Sterkfontein during 2001 (Table 30). Four of these were also found in mountain reedbuck, while one, *Ostertagia* sp., was only found in grey rhebok. Due to the small sample size, not too much should be read into the details of the table. No gender or seasonal comparisons were attempted. *C. yoshidai* was a new parasite record.

Table 30. Prevalence and abundance of nematodes recovered from four grey rhebok at Sterkfontein in 2001 (Prev = prevalence, Std. Dev. = standard deviation, Abo = abomasum, SI = small intestine).

Nematode species	Prev %	Site in Host	Mean	Std. Dev.	Range
Haemonchus contortus	50	Abo	32.5	42.7	0 – 90
Longistrongylus schrenki	25	Abo	15.0	30.0	0 – 60
Ostertagia sp.	75	Abo	168.8	243.3	0 – 520
Cooperia yoshidai	100	SI	145.0	97.5	10 – 230
Paracooperioides peleae	50	SI	213.2	282.2	0 – 595

Faecal egg counts and coproculture in mountain reedbuck

Faecal egg counts, larval counts from coproculture and counts of adult worms in the GIT were carried out in 18 culled mountain reedbuck from Sterkfontein and compared using a Spearman Rank Correlation Coefficient (Table 31). Egg counts were very highly positively correlated with larval counts, but there was no correlation between egg counts and adult worms or between larval counts and adult worms. This means that neither egg counts nor larval counts were reliable methods for estimating numbers of adult nematodes in the GIT of mountain reedbuck.

Table 31. Spearman Rank Correlation Coefficient comparing faecal egg counts, number of larvae in faeces from coproculture, and the actual number of nematodes found in the GIT of 18 mountain reedbuck at Sterkfontein.

	Larvae from coproculture	Adult worms from GIT
Egg counts	$r_s = 0.952$ $P < 0.001$	$r_s = -0.173$ $P = 0.565$
Larvae from coproculture		$r_s = -0.211$ $P = 0.409$

Faecal egg counts and coproculture in grey rhebok

Faecal egg counts and larval counts from coproculture were carried out every two weeks from faeces of five live grey rhebok over a period of eight months between September 2001 and April 2002. A Spearman Rank Correlation Coefficient was carried out to test correlation between the two techniques. As occurred in mountain reedbuck, there was a strong positive correlation between the two sampling techniques ($r_s = 0.747$, $n = 57$, $p < 0.001$).

Figure 39 shows the monthly variation in nematode larval counts from the five grey rhebok between September 2001 and April 2002. Although larval counts were not found to correlate with the actual number of adult nematodes in the GIT of animals, there was a peak in average larval counts in December. The average number of larvae cultured from 100g of mountain reedbuck faeces was 223 187, compared to 7 702 in grey rhebok.

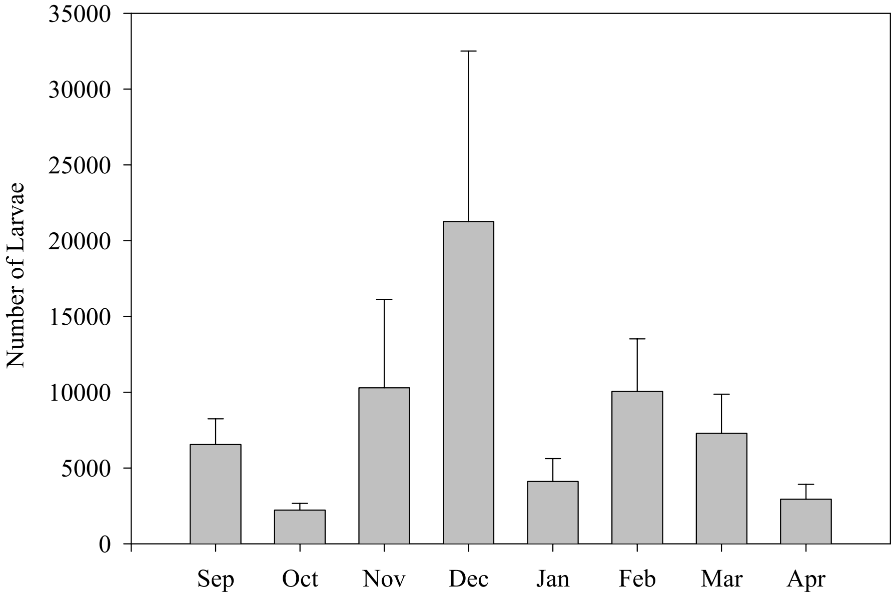


Figure 39. Monthly variation in nematode larval counts from coproculture of faeces from five grey rhebok at Sterkfontein between September 2001 and April 2002. Numbers of larvae were adjusted for 100 g faeces.

Discussion

Species prevalence and abundance

The 17 species of helminths found in mountain reedbuck at Sterkfontein and TdR compares favourably with the 17 species found at Loskop and Mountain Zebra National Park (hereafter MZNP) (Baker & Boomker, 1973). There were six new host records for nematodes at Sterkfontein (*L. schrenki, L. namaquensis, Ostertagia* sp., *T. deflexus, I. Nudicollis* and *P. peleae*) and one new host record at TdR (*C. rotundispiculum*). Half (7/14) the nematode species found were, therefore, new host records, emphasizing the fact that nematodes of mountain reedbuck in South Africa are poorly known. Genera of helminths found at Loskop and MZNP but not found in the present study were the nematodes *Gongylonema* and *Oesophagostomum*.

Four studies of grey rhebok at Bontebok National Park (Horak & De Vos, 1981; Horak, De Vos & De Klerk, 1982; Boomker, 1990; Boomker & Horak, 1992) recorded 12 nematode species, compared to five found at Sterkfontein. The species of the present study were, however, extracted from only four animals. Four of the species found at Sterkfontein were also found at Bontebok NP, while one (*C. yoshidai*) was a new host record. *P. peleae* has only ever been found in grey rhebok and, until the present study, only at Bontebok NP. At Sterkfontein it was again found in grey rhebok in two out of the four animals sampled. It was also found in one mountain reedbuck, but in very low numbers, so was probably an accidental parasite record.

Frequency distributions of nematodes

The nematode populations in mountain reedbuck at both Sterkfontein and TdR were highly aggregated. All of the animals at Sterkfontein had some worms, while at TdR there were four animals without any. In terms of overall numbers, the majority of the parasite population were concentrated into a minority of the host population. A relatively small number of individuals in the "tail" of the parasite distribution were then responsible for most parasite transmission and would have played an important role in the persistence of the parasite (Wilson *et al.*, 2002).

Heterogeneities in parasitic loads occur in most natural populations (Shaw & Dobson, 1995; Wilson *et al.*, 2002), and these could have a differential effect on host species fitness and ultimately population dynamics. However, it is difficult to tell whether parasite loads, as occurred in the most heavily infected individuals at Sterkfontein, were large enough to have a negative impact. Little information on the numbers of nematodes necessary to produce clinical disease in antelope is available (Boomker, 1990).

Pathogenesis caused by *H. contortus* is essentially an acute haemorrhagic anaemia due to the blood-sucking habits of the worms. Each worm removes about 0.05 ml of blood per day by ingestion and seepage from the lesions so that sheep with 5000 worms may lose about 250 ml daily (Georgi & Georgi, 1990). At peak infection, naturally acquired populations of *H. contortus* may remove one fifth of the circulating erythrocyte volume per day from lambs. The pathogenic effects of *H. contortus* result from the inability of the host to compensate for blood loss. Infections of up to 500 worms, however, have been found to have little effect on growth or wool production of sheep under conditions of satisfactory nutrition.

In mountain reedbuck the numbers of *H. contortus* needed for clinical signs of disease to be shown is unknown, but is probably in excess of 2000 worms (Boomker, pers. comm.). The highest count of *H. contortus* at Sterkfontein was 1050 worms. This number might have had some effect on the individual, especially if the animal was compromised in some way, but the mean of 116 worms per animal should certainly be considered negligible.

Cooperia spp. usually play a secondary role in the pathogenesis of parasitic gastroenteritis of ruminants although they may be the most numerous trichostrongyle present (Georgi & Georgi, 1990). However, in some tropical and subtropical areas, some species are responsible for severe enteritis in domestic calves. They may penetrate the epithelial surface of the small intestine and cause disruption, leading to villous atrophy and a reduction in the area available for absorption. In heavy infections diarrhoea has been reported. Approximately 300 000 larvae are needed to infect a cow within ten days for there to be any clinical effect (Boomker, pers. comm.). Although mountain reedbuck are about ten times smaller than domestic cattle, the average burden of 2 040 worms per animal would not have been enough to cause clinical signs. It is possible, however, that the 15 000 worms found in one animal might, in conjunction with other extenuating factors, result in some detrimental effects. This is speculative because such effects have never been tested in wild antelope. No information is available about the seasonal patterns in *L. schrenki* for comparison.

It is possible that the sample size of mountain reedbuck at Sterkfontein was not large enough to detect the animals with the largest parasitic loads (Wilson *et al.*, 2002), so there may have been individuals with loads large enough to cause clinical signs. However, Shaw & Dobson (1995) in their quantitative review of parasite abundance and aggregation used a minimal host sample size of 30 animals to reduce the effects of sampling error. By that standard, the 41 animals sampled at Sterkfontein should have been adequate.

Possible causes of aggregation

Aggregation, or variations in parasitism rates, may be associated with heterogeneities in the host population, including host age, gender, body condition, behaviour and genetics (Wilson *et al.,*, 2002). It may also be associated with heterogeneities in the parasite population genetics or extrinsic factors such as the spatial distribution of the parasites.

Host age could affect parasite distributions by a number of mechanisms. These include parasite-induced host mortality, acquired immunity, age related changes in predisposition to infection, and age dependent changes in exposure to parasites (e.g. changes in behaviour) (Wilson *et al.*, 2002). Although there was no evidence of a difference in parasitic loads between animals of different ages, a thorough evaluation of age-associated heterogeneities was not possible in this study because of the relatively small numbers of young and old animals sampled. Wilson *et al.,* (2002) stated that sample sizes often decline with host age due to mortality and, if sampling effort is not directed at obtaining equal numbers of hosts in all age classes, then it might appear that average parasite loads decline in old animals and that parasite aggregation declines with age, purely due to sampling biases. Collecting equal numbers of animals in all age classes was not an aim of this study, while investigating parasite-induced mortality, acquired immunity and predisposition to infection were not within its scope.

Schalk & Forbes (1997) found that in 12 out of 136 field studies on mammals, males exhibited higher rates of parasitism than females. In all 12, however, male biases were small (<5%). When meta-analyses were carried out using pooled data from these studies, including those that did not find male biases, males were still found to exhibit higher rates of parasitism. Poulin (1996) found that prevalence and intensity of nematode infection tended to be higher in male mammals, while Schalk & Forbes (1997) found that such male bias only occurred when arthropod data were also included. Moore & Wilson (2002) found that the mean prevalence of infection was male biased for helminths in mammals in general, but not for Artiodactyla alone. Even if sex biases exist, determining the relative importance of the different mechanisms capable of generating them may prove extremely difficult, due to the fact that many of the ecological and physiological factors covary (Wilson *et al.*, 2002). It has even been suggested that the small differences found between males and females will have little impact on parasite epidemiology, although Poulin (1996) argued that an increase in even a few parasites could be biologically meaningful.

Intrinsic biological differences between host sexes could lead to one sex being more prone to parasite infections than the other. Physiological, morphological and behavioural differences between sexes could operate to create a slight but consistent sexual bias in infection levels. The present study, however, found no evidence of differences between males and females in parasite abundance.

Moore & Wilson (2002) found that increases in sex-biased parasitism (SBP) were associated with increases in sexual size dimorphism (SSD), and that this resulted in an increase in adult male mortality when males were larger than females. Moreover, they also found that there was a significant positive relation between SBP and sex-biased mortality (SBM), even when SSD was controlled for. Thus sexual selection leads to an enhanced risk of parasitism and elevated mortality in males, and this is due in part to the negative impact of parasites. In mountain reedbuck, however, males are only slightly larger than females (approximately 6 % heavier) (Irby, 1975; Skinner, 1980; Anderson & Koen, 1993; see Chapter 6), so SBP and SBM should be less prominent.

Significant male biases may be found more often than expected by chance, but this does not mean that statistical significant male biases are a general rule. Sex biases in experimental studies, where hosts were artificially infected, were much stronger than those detected in field studies where hosts were naturally infected. This suggests that the main differences may lie in the host immune responses rather than the infection processes. Quantitative support for sex biases in parasite infection rates remains inconclusive (Wilson *et al.*, 2002).

Although no statistical differences were found between males and females in the present study, patterns of parasitic loads were slightly different. Males had more worms than females between February and June, while females had more worms than males between August and December. One physiological aspect implicated in male biased parasitism is that high testosterone levels can cause immuno-suppression (Grossman, 1985). The main breeding season for mountain reedbuck was April/May, but if testosterone levels were higher at this time, and males were immuno-suppressed, they should have had larger parasitic loads. This was not the case (see Figures 34 & 35). The only nematode species that showed significant seasonal variation was *H. contortus*, and at Sterkfontein males had their highest loads in December. Moreover, mountain reedbuck were considered aseasonal, so there were unlikely to be significant peaks in testosterone secretion.

In females, there is evidence suggesting that oestrogens stimulate humoral and cell-mediated immunity (Schuurs & Verheul, 1990). In contrast, energetic costs of pregnancy and maternal care, plus the immuno-suppressive effects of some hormones produced during parturition and lactation, may increase the susceptibility of females to parasites. Measuring immuno-competence is, however, fraught with difficulties (Wilson *et al.*, 2002) because it is not clear whether there is a simple relationship between immune function and disease susceptibility. Females at Sterkfontein had significantly more *H. contortus* in December than May, June, August and September, which is more consistent with the immuno-suppression theory during late pregnancy and parturition. Moreover, females that had recently given birth, and were therefore lactating, had significantly higher worm burdens than females that were still pregnant. Boomker (1990) found that the mean worm burden of lactating female kudu was more than double that of pregnant or quiescent females. The difference was ascribed to the stress associated with terminal pregnancy, parturition, lactation and anxiety during the first few weeks of the newborn calf's life.

High parasitic loads might decrease body condition and this will in turn reduce resistance to parasitic infection. Body condition is also likely to affect the hosts' ability to compensate for damage inflicted by parasites, such as repairing tissues or replacing critical nutrients. At Sterkfontein, however, there was no correlation between numbers of parasites and body condition.

Behavioural differences in feeding have been suggested as a possible cause of heterogeneities in parasitism, with host age or sex being potential factors. Feeding behaviour of mountain reedbuck was the subject of Chapter 5. The only change that is likely to occur with age would result from an older male being forced off a territory by a stronger one. Males so affected might be forced into peripheral areas where grazing is not so good, but such areas would not necessarily have greater densities of infective nematode larvae. In fact, they might have lower densities because there are less animals defecating in the area. Males defend resources (Irby, 1976; Dunbar & Roberts, 1992; pers. obs.) and territory selection is based on availability of females, which in turn is based on the availability of cover and feeding resources (Dunbar & Roberts, 1992; pers. obs.). Parasite avoidance is not a factor. Females don't hold territories so would not undergo changes in behaviour that might alter infection rate. Males of some antelope species feed less during their breeding periods because they spend more time guarding territories or females. In this case they should be less exposed to parasitic infection. In the case of mountain reedbuck, males do not have a defined rut, and do not feed any less during the breeding period than at other times (see Chapter 5).

There are very few good examples of genetic variation in disease resistance in natural host populations, particularly in vertebrates. There has been even less research conducted on the importance of parasite heterogeneities. The effect of host or parasite genetics on parasitic infection rates was not within the scope of the present study.

The most likely cause of heterogeneity in parasite loads, specifically in *H. contortus*, was temporal variation in distributions of the parasite populations. Horak (1978a, b, c, d, 1981) found that burdens of *H. contortus* in sheep, cattle, blesbok and impala peaked between October and March at a number of areas in South Africa, including the Hennops River (Bankenveld), Tonteldoos (North-Eastern Sandy Highveld), Lunsklip (Sour Bushveld) and Boekenhout (Mixed Bushveld). Reinecke (1964, 1983) found that the abundance of *H. contortus* was positively correlated with ambient temperatures and rainfall. In summer rainfall areas, infective larvae on pasture increased after rains in excess of 15 ml per month and temperatures of over 17° C. Sheep acquired infection in November and adult worms were dominant until February. At Sterkfontein monthly rainfall only exceeded 15 ml after August, and at the time of the September 2000 and August 2001 culls, the rains had barely started (Figure 3). Temperatures had also not yet exceeded 17° C. Under this scenario, peak infections would only have been expected in the next culling periods, i.e. December 2000 and November 2001 respectively, and this was indeed the case. *H. contortus* was more abundant in both male and female mountain reedbuck during December, after good rainfall, than during May, June, August and September.

Cross-transmission with domestic livestock

As this chapter was part of a larger study examining factors influencing productivity, it is worth adding a note here on the cross-transmission of nematode parasites between wild and domestic ruminants. Although it was not covered in the present research because these groups of animals did not mix in the areas surveyed, cross-transmission could be relevant in areas where they do mix because of the possible effect on productivity. There are conservation areas within South Africa where wild and domestic ruminants coexist, such as Qwaqwa National Park in the Free State, and there are many places where they mix on private land. In the case of the latter, wild ruminants such as mountain reedbuck can provide extra income from meat production and other by-products on top of that obtained from cattle and sheep husbandry. Cross-transmission would be of importance if either group was responsible for causing or even aggravating (by acting as a reservoir) increased parasitic burdens that might adversely affect productivity.

Boomker (1990) found that the majority of worms of domestic ruminants were found in wild browsers, but less of the worms found in wild browsers occurred in domestic ruminants. Both groups can act as reservoir hosts of each other's worms, but browsers may be better hosts for the worms of domestic stock than vice versa. As mountain reedbuck are grazers, they are more likely to have contact with nematode species of cattle and sheep. Horak (1979) stated that many of the helminths recovered from antelope (e.g. impala and blesbok) are those usually encountered in sheep and cattle (Horak 1978a, b, c, d).

Sheep were successfully infected with *H. contortus* larvae from blesbok (Horak, 1979), indicating that this nematode is well adapted to both host species and that cross-transmission can readily take place. Other nematode species, however, were not so easily cross-transmitted, e.g. *Cooperia hungi* from impala to sheep (Horak, 1979). In most nematode species, cross-transmission generally did not take place when the adult worm burden of a particular species in the donor antelope was less than 200 worms. This can probably be ascribed to the fecundity of the female worms and hence their contribution to the larval pool. *Haemonchus* spp. are particularly fecund and thus a few adult females would make a considerable contribution to the larval pool. Other species that are less fecund would contribute fewer larvae. Consequently, the chances of cross-transmission would be minimal from those donor animals in which only a few adult worms of the latter species were present. In impala and cattle utilising the same pasture in the Boekenhout area there was very little natural cross-transmission of nematodes (Horak, 1978c, d; 1979).

Horak (1978b) found that the main difference between the *H. contortus* burdens of sheep and blesbok was numerical. Whereas sheep generally harboured considerable burdens in the summer (Horak & Louw, 1977; Horak, 1978a), the worm counts in blesbok in the same season were relatively low. This may be one of the reasons why nematodes appear to be less pathogenic in wild antelope than in domestic animals (Boomker, 1990). However, the pathogenicity of nematodes in antelope is unknown.

Both Sterkfontein and TdR adjoin farmland where animal husbandry is practiced. The main study site at Sterkfontein was adjacent to an area of cattle farming, and cattle were seen almost every day. The only thing separating the wild and domestic ruminants in this case was a game fence so cross-transmission might have been possible, but only on the peripheries. At TdR the surrounding farmland was used primarily for sheep farming, but the mountain reedbuck culled on the reserve were separated from the farmland by the Gariep River (formerly the Orange River) and had no contact with it. They were generally not within sight of the domestic animals. Both reserves were previously used for domestic animal husbandry prior to their designation as Provincial Nature Reserves. Sterkfontein was used in this capacity as recently as 1980, while TdR was set aside for game farming in 1967. It may be that some of the helminth species found in the mountain reedbuck were there initially as a result of agriculture.

Nematodes of Tussen die Riviere

No statistical tests were conducted on the parasite data from TdR because prevalence and abundance of species were very low, so any patterns would have had no biological meaning. Nematode burdens at TdR were much lower than at Sterkfontein. This lower abundance may have resulted from lower densities of mountain reedbuck at TdR. Arneberg *et al.* (1998) showed that for strongylid nematodes of mammals, abundance may depend on host population density because as host densities increase, each parasite egg or larva enjoys an increased probability of contacting a host. Differences in habitat may also have played a role. At TdR grasses were clumped and numerous bare patches of earth occurred between tufts. In contrast, at Sterkfontein, percentage grass canopy cover was very high, allowing infective larval nematodes greater opportunity to attach themselves to grass clumps to be eaten by grazers such as mountain reedbuck.

Nematodes of grey rhebok at Sterkfontein

Only four species of helminth were found in grey rhebok at Sterkfontein, but this low number no doubt resulted from the very small sample size of four animals. Because the sample size was so small, no meaningful analyses were carried out. Faecal egg counts and larval counts from coproculture provided a more systematic data set for seasonal variation in grey rhebok nematodes. There was a peak in average larval counts in December, which was similar to the GIT results for mountain reedbuck, but because adult worm numbers did not correlate with egg counts, these faecal results should be treated with caution. One thing that does seem apparent, however, from both the limited GIT worm counts and faecal egg and larval counts, was that grey rhebok harboured considerably less helminths (on average) than mountain reedbuck. This might be explained in terms of feeding habits because, in contrast to mountain reedbuck which are grazers, grey rhebok are browsers. Wild ruminants that browse generally have lower parasitic burdens than those that graze (Boomker, 1990), and this probably results from differences in feeding habits. Grass cover is generally much higher than herbaceous cover, so more infective larvae should occur on grass and grazers, therefore, have a greater chance of acquiring worms. Grey rhebok at Sterkfontein do, however, feed on forbs that grow very close to the ground (pers. obs.), and to get to these plants the animals have to push through grass tufts. They hence feed from a very similar "microhabitat" to mountain reedbuck so, although forb cover is much lower than grass cover, grey rhebok should be exposed to the same nematode species as mountain reedbuck.

CONCLUSIONS

Grey rhebok and mountain reedbuck are similar sized, similar in appearance and use similar steep habitat that is marginal for most other antelope species. They occur sympatrically in many areas, including Sterkfontein, but are able to coexist because of striking social and ecological differences.

First, they have different breeding systems. Grey rhebok males maintain a harem of females with which they maintain constant contact, and from which they prevent contact with other males. This is female defence polygyny. At all times they know the breeding condition of the females and are able to ensure that they sire all lambs born within their herds. In contrast, male mountain reedbuck have little control over female movement patterns; rather they maintain year-round territories within which females come and go at will. This is resource defence polygyny. Male mountain reedbuck, therefore, tend to be quite opportunistic when it comes to mating (by testing for oestrus every chance they get).

Second, grey rhebok are browsers, eating mostly ground-hugging forbs, while mountain reedbuck are selective grazers, feeding on certain more palatable species of grass. Although grey rhebok will occasionally eat grass, this is generally only when forbs aren't readily available, such as just after a fire when fresh green grass is sprouting but forbs have not started emerging. Therefore, although the two species use the same areas at Sterkfontein, often intermingling with each other, and use similar habitat in other regions, there is very little competition for food resources between them.

Jarman (1974) discussed the social organisation of antelope in relation to their ecology, and suggested they could be divided into five broad social classes based on a relationship between group size and feeding style. According to this system, mountain reedbuck and grey rhebok fitted into Class B along with other reedbuck species, oribi, gerenuk, and lesser kudu. Accordingly, such species fed either entirely on a range of grass species or entirely on browse, and were very selective for plant parts. They remained in one or a few vegetation types and one home range throughout the year.

Their diets showed some seasonal variation, and food items were of high nutritional quality. These descriptions are accurate for both grey rhebok and mountain reedbuck, although the maintenance of home ranges in the two species is somewhat different.

Group sizes were thought to vary from one to 12, but were most commonly in the range three to six (Jarman, 1974). Adult females were generally accompanied by one or more other adult females, but female groups were considered unstable associations. The latter is true for mountain reedbuck, but not grey rhebok, where females within a herd form long lasting bonds and group sizes are constant. In terms of anti-predator behaviour, Jarman's (1974) classification indicated that species in this class either freeze and lie down, freeze then run for cover, or lie in a form until the predator is nearly on them, then erupt from it to escape using the element of surprise and an initial burst of speed. None were thought to depend on speed to escape over long distances. This, again is true for mountain reedbuck, but not so for grey rhebok. The latter do not freeze and hide when threatened by a predator, rather they run immediately and keep running until out of danger. Females of species in this class were not considered territorial (Jarman, 1974), while males were, defending territories only against other males. This is accurate for both grey rhebok and mountain reedbuck, although as described in this thesis, territoriality is conducted in different ways between the two species.

It has been suggested that grey rhebok males can be aggressive towards mountain reedbuck and sometimes attack them with their horns, but this seems unlikely as a result of their niche separation and resultant lack of competition. Moreover, such behaviour was never witnessed at Sterkfontein during 2.5 years of intensive observations, despite the close proximity of the species and frequent mixing (albeit incidental) in an area where the population densities were thought to be high (possibly maximal), and where competition, if it existed, would be most likely to occur.

The number of adult female grey rhebok within the study area fluctuated from 19 in 1999, through 18 in 2000, to 20 in 2001. Effectively the population did not increase, and this seemed to have been the case before the study started. This occurred despite the large number of lambs born, the high survival rate of these lambs, and the total lack of predation and disease. The direct (or proximate) causes of the static population levels during the study period were the loss of all yearling males and some yearling females through eviction, and the single “natural disaster” that resulted in a 27 % decrease in overall numbers. The underlying (or ultimate) reason, however, was probably that the population was saturated for the area available, so that there was not enough space to accommodate most of the sub-adult males and females within the population. Such a saturation might also have meant that the amount of food available was only enough to maintain a certain population size (that being approximately 20 adult females, their offspring, and harem males).

The numbers of harem males within the study area was saturated, so that nothing less than the removal of one of these animals would allow the immigration of a new animal (or a resident juvenile). The reason for the saturation was social, and harem males excluded all other males, except their own offspring up to the age of 11 months, from the area in which they moved with their females. The size of the territories varied, possibly as a result of factors including the area of steep slope encompassed by the territory and the number of animals within the herd. It is possible that the food availability was important as well, but there is no information about the nutritional values of the forbs eaten by grey rhebok, nor was this ascertained. Occasional removal of territorial males by hunting would be the best way to create space for new males and artificially increase the gene pool.

For mountain reedbuck, the population did not increase over the first 18 months of the study either, despite the large number of lambs born and lack of predation. The two culls reduced the population size slightly, and there must have been considerable loss of young males by aggressive interactions with territorial males, but the most significant limiting factor was the snow falls. Mountain reedbuck were more severely affected by the snow than the grey rhebok, suggesting that they were either more susceptible to extreme conditions, or had less access to food supplies prior to the event, resulting in them being in relatively poorer condition. The latter would have resulted either from overcrowding or from a poorer nutritional quality of grasses than forbs, or both.

Although mountain reedbuck have the potential to be aseasonal breeders, at Sterkfontein, in the sourveld, they were seasonal. The high percentage of snow caused deaths resulting from a lack of body fat reserves implies a possible reason for this. If females were to have lambs at the end of winter, even after a good rainfall year, their fat reserves would probably not be sufficient to sustain lactation.

Translocation of the two species between reserves, or even within reserves, should be carefully considered before being done, the pre-existing populations should be evaluated, and the amount of free space available for animals to form new territories or herds should be determined, as well as the suitability of that space to act as potential home ranges. Habitat factors that appear to be important for both species are access to steep slopes and possibly access to water. Obviously, the grazing and browsing capacities must be checked as well, and the supply of suitable food plant species ascertained.

To maximise meat yield for culling, mountain reedbuck at Sterkfontein and other such Reserves falling within the sourveld category should be harvested in early winter (assuming standard timing and quantities of rainfall) because this is when they are in their best condition. An added advantage of cropping at this time would be that densities of animals would be reduced, leaving more grazing for the remaining animals at a time when it is scarcest, thereby increasing their chances of survival. It would be advantageous to remove young males at this time as well (at 6 – 8 months age), because the majority of them will not remain much longer before being chased out by adult males.

In the case of grey rhebok, removing animals for meat is not really an option, but trophy hunting of harem males would bring in income, and at the same time allow the influx of a small number of new males to increase the genetic makeup of the population. Juvenile males should be removed in September (either for meat or translocation) before they are evicted so that they are not wasted.

Animals of both species are in their worst condition and at their most vulnerable after long dry winters (August and September at Sterkfontein), so any perturbations to their environment, especially ones that affect the amount of grazing available to them, should be avoided. This implicates burning programmes that could remove grazing at the wrong time, albeit for a short period.

The nematode populations in mountain reedbuck at both Sterkfontein and TdR were highly aggregated, and this is the normal situation. There was no correlation between high parasitic loads and poor body condition, and no evidence that parasites caused mortality, indicating that endoparasites at both sites were within acceptable limits. The lack of any signs of disease, the high reproductive rates, and the high population densities indicate that the populations of both grey rhebok and mountain reedbuck at Sterkfontein were healthy. The lack of an apparent increase in population size of either species, but in particular grey rhebok, was most likely the result of saturation of numbers and population self-regulation, rather than any underlying inherent problem. Due to the confined nature of both populations, however, it might be wise to introduce some new blood lines every three or four years (that is new males), but as mentioned above, this should only be done in conjunction with the removal of the same number of resident territorial males from the area in question.

SUMMARY

Population dynamics

Ninety-one percent of grey rhebok lambs were born between November and February, while only three out of 43 lambs were born between March and August. Over three breeding seasons an average of 74 % of adult females produced lambs at a ratio of 22M: 19F. Two female grey rhebok started breeding at the age of 16 months and gave birth for the first time at two years. The birthing interval for adult females was generally one year, although one female demonstrated an average birthing interval of nine months. Fecundity (lambs per female per year) was 74 % - 81 %. In all cases single lambs were born.

Extrapolated birth dates of mountain reedbuck foetuses were September to January, while field observations generally concurred, albeit with occasional births in other months. Sixty nine percent of culled and snow killed adult female mountain reedbuck were pregnant and 12 % were lactating, while most of the remainder were collected at a time when they were not expected to be pregnant anyway. Fecundity (lambs per female per year) was 92 %. In all cases single lambs were born and the sex ratios were 12 M: 8 F. See Appendix II for general reproductive comparisons between the two species.

Between October 1999 and April 2002, 16 grey rhebok died within the study area. Ten of these deaths were due to hypothermia during a single snowfall (representing 27 % of the population), and five were natural mortalities of unknown causes. There were no lamb mortalities outside of the snow incident, and there was no evidence of infectious disease or predation. All deaths occurred between June and November, corresponding mainly with winter and spring when conditions were cold and dry, and when food supplies were reduced.

Between February 2000 and April 2002, approximately 43 mountain reedbuck died in the study area. Thirty-two of these were caused by hypothermia during the snowfall incident (representing 51 % of the adult population), leaving 11 deaths from other natural causes. Again post mortems revealed no evidence of infectious disease or predation, and all mortalities occurred between June and November.

Grey rhebok formed very stable groups, and movement of animals between herds was rare. Immigration of new animals from outside the study area was also unusual (partly as a result of game proof fences), while emigration was thought to be common amongst yearling males in October and November when the harem males evicted them from their natal groups. Young females were also occasionally evicted at about eight months old, but they were sometimes allowed to return to their herds.

Only two changes in territorial 'ownership' occurred, and these were the result of the deaths of the resident males. A number of antagonistic interactions were observed between harem males, and every time the victor was the animal that was within his own territory at the time. No incidents of evictions of harem males by other males via aggressive interactions were observed.

Dispersal of female and young mountain reedbuck was not monitored, while occasional changes in ownership of male territories appeared to be the result of dynamics within the existing population. It appeared that the rate of turnover was low. However, an idea of the strength of competition for good territories was given by the speed (two days) at which an adult male extended its territory by moving into and taking over the territory of his neighbour after the latter was shot.

Attempted translocations of both grey rhebok and mountain reedbuck were relatively unsuccessful. Out of four grey rhebok introduced into the study area, only one young female remained, while two adult females and one young male disappeared. Out of seven mountain reedbuck introduced, three out of four females survived (one died), while all three males disappeared (with one confirmed death). The implication of this is that random translocations of animals to increase population sizes and gene pools do not necessarily work.

The population of grey rhebok increased only marginally during the study period, despite a high survival rate of lambs. The proximate reasons for this were a low recruitment rate, due to the eviction of all yearling males and some juvenile females before they reached maturity, and heavy snowfalls when they were in poor condition.

Adult mountain reedbuck mortality rates were also low. The principle reason for slow population increase was probably dispersal of yearling males, or unrecorded mortality, but neither could be confirmed. The fact that there were slightly more male foetuses than females, but twice as many adult females than males in the study area, suggests that young males disappeared from the study area at a greater rate than females.

Home ranges and habitat

Home ranges of grey rhebok herds varied between 23 ha and 104 ha (95 % MCP), with an average of 57.9 ha. There were no seasonal differences. There was very little overlap between neighbouring herds, which fits with the highly territorial nature of the harem males. The ecological density in the main study area was 1/15.7 ha. The best predictors of home range size were the area of steep slope available and the number of animals within each herd. Home ranges were smaller in steep areas.

Home ranges of territorial male mountain reedbuck were smaller than those of grey rhebok herds, varying between 7 ha and 21 ha (95 % MCP), with an average of 14.8 ha. There was little overlap between individuals, and all had steep slopes incorporated. Female home ranges were considerably larger than those of territorial males, and females showed a strong preference for steep slopes. The ecological density of mountain reedbuck was 1/8.7 ha. There was a very high degree of overlap between the home ranges of grey rhebok herds and male and female mountain reedbuck. See Appendix II for species comparisons.

Behaviour

Male and female grey rhebok rested for 40 % and 44 % of daylight hours respectively, while male and female mountain reedbuck rested for 57 % and 54 % of daylight hours respectively. The difference between the species was significant but the difference between the sexes within the same species was not. In the amount of time spent feeding there was no statistical difference between the two species. Male and female grey rhebok fed most in the early morning and late afternoon and their activities overlapped so that they were normally active at the same times. Male and female mountain reedbuck fed most during the late afternoon in both seasons. At night, grey rhebok were active for 57 % of the time, while mountain reedbuck were active for 72 % of the time.

Harem male grey rhebok often smelt female urine and faeces on the ground in an opportunistic manner, apparently testing for signs of oestrus, but did not often test female reproductive condition by sniffing at their rump areas. In contrast, male mountain reedbuck sniffed the rumps of females in all months of the year except August, although in most cases no further sexual behaviour occurred.

Male grey rhebok mated several times with a single female during one oestrus period, often over an entire day and into a second. They stayed with the females between mating episodes, thus performing mate guarding, and oestrus lasted approximately 24-36 hours. In contrast, mountain reedbuck males generally only mated once with any female in oestrus, and did not perform mate guarding. Oestrus was, therefore, shorter than in grey rhebok and lasted less than 24 hours.

Harem male grey rhebok marked their territories using faeces and urine in every month of the year, but marking was most frequent during October/November. This corresponded to an “aggressive” period when juvenile males were evicted from herds at the age of about 11 months. Eviction was not so well defined in mountain reedbuck because juvenile males did not live in harems. Rather, when they reached the stage of being a potential threat to territorial males, they were chased away from their mothers into another male’s territory, from where they would be chased again.

In grey rhebok, submissive behaviour of young males reacting to the presence of harem males was first observed at the age of two months. There was then a significant increase in the frequency of submissive behaviour leading up until the time when the young males were evicted. Young female grey rhebok and young mountain reedbuck did not show submissive behaviour to territorial males.

Body condition

Adult mountain reedbuck rams averaged 29.9 kg (range 23.0 – 35.0 kg) and adult ewes 28.0 kg (range 23.5 – 34.5 kg) at Sterkfontein. Dressing percentages were lower in winter and spring than in autumn and summer, but there were no differences between males and females. See Appendix II.

Body fat was measured in two ways: kidney fat index (KFI) and leg fat percentage (LFP). There was a highly significant positive correlation between KFI and LFP. Males had higher KFI and LFP than females in November/December and February/March, while females had higher KFI and LFP than males in May/June and August/September. Overall, fat indices were highest in winter and lowest in spring. All this variation could be explained by a combination of seasonal changes in vegetation, resulting in varying food quality, and differential timing of reproductive events between males (rutting) and females (pregnancy and lactation).

In September 2001, Sterkfontein experienced heavy snowfalls and below freezing temperatures. During this time, 51 % of mountain reedbuck and 27 % of grey rhebok died. All dead animals examined had no kidney fat and had, therefore, run out of energy stores.

At TdR, adult rams averaged 31 kg (range 23.5 - 35 kg) and adult ewes 30.2 kg (range 24.0 - 34 kg). Animals had higher KFI in June than December, but there was no difference between males and females.

There was no correlation between the KFI (body condition) of mountain reedbuck and the numbers of parasites in either the abomasum or small intestine.

Parasites

Seventeen species of helminths, including fifteen nematodes, one trematode, and one cestode were recovered from mountain reedbuck at Sterkfontein and TdR. The most prevalent and abundant species at Sterkfontein were *Cooperia yoshidai*, *Longistrongylus schrenki* and *Haemonchus contortus*, while the remaining ten species demonstrated low prevalence and abundance. There was one new species of *Cooperia*, as well as six new host records for mountain reedbuck at Sterkfontein. The most prevalent species at TdR was *Nematodirus spathiger*, while the most abundant species was *Trichostrongylus falculatus*. The four most common species of nematodes were highly aggregated and their distributions could best be described by the negative binomial distribution.

Numbers of *H. contortus* were highest in November/December for both males and females, and lowest in August/September for males and May/June for females. Males had more worms than females between February and June, while females had more worms than males between August and December. These differences were, however, not statistically significant. A similar pattern occurred for *L. schrenki*. Females harboured most *Cooperia* spp. in November/December and least in February/March. For the nematodes *H. contortus* and *C. yoshidai*, the age of their host made no difference to parasitic loads.

Five nematode species were recovered from four grey rhebok at Sterkfontein. Four of these were also found in the mountain reedbuck, while one, *Ostertagia* sp., was only found in grey rhebok.

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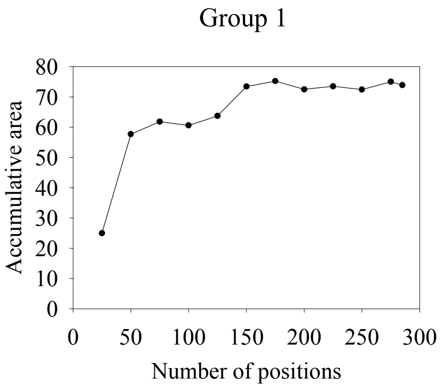
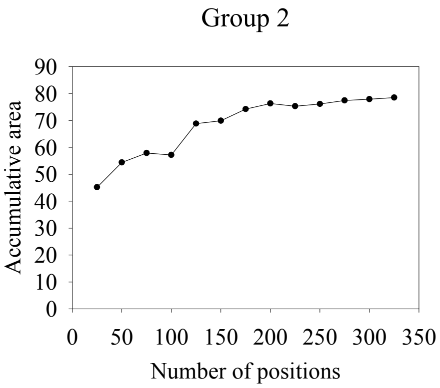
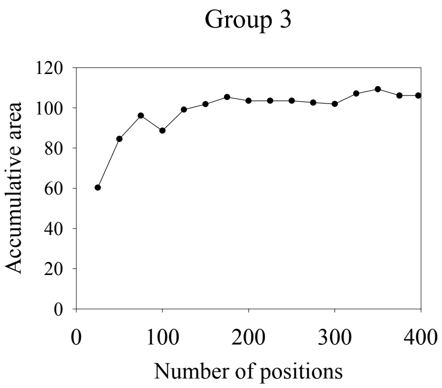
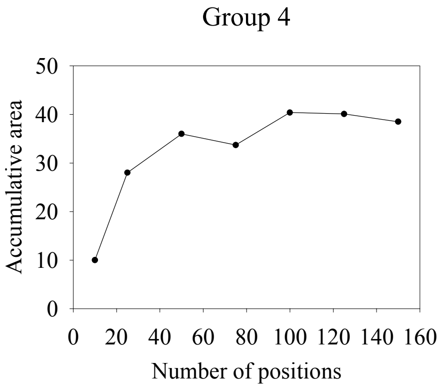
APPENDIX I

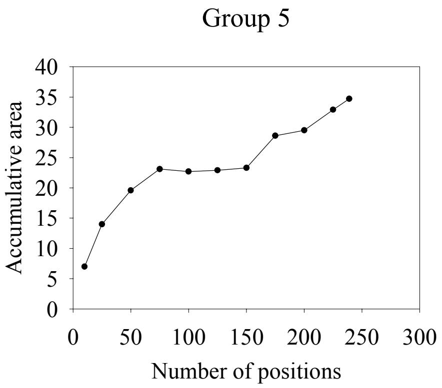
Accumulative home range areas for grey rhebok herds

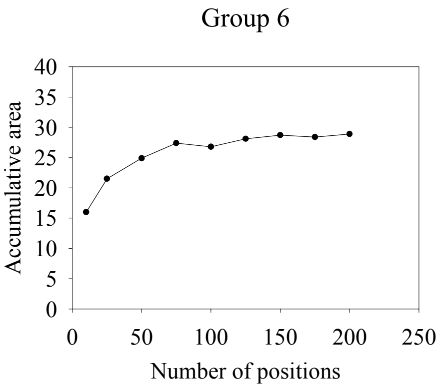








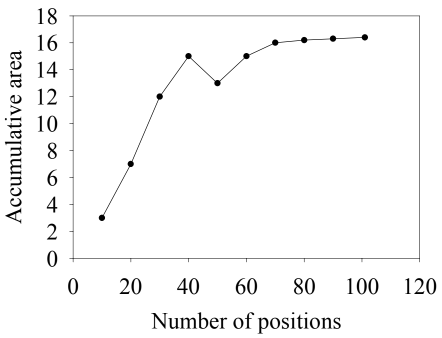




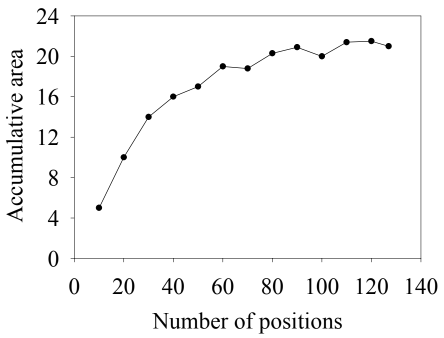
APPENDIX I (continued)

Accumulative home range areas for mountain reedbuck males

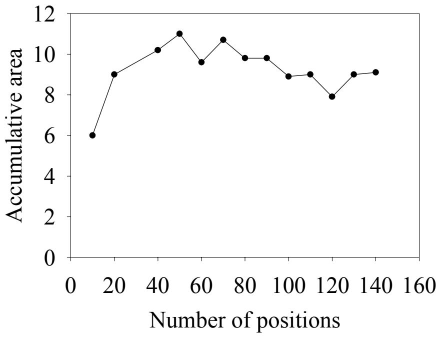
Male 1



Male 2



Male 3



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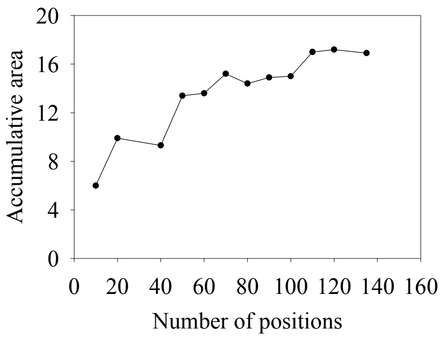
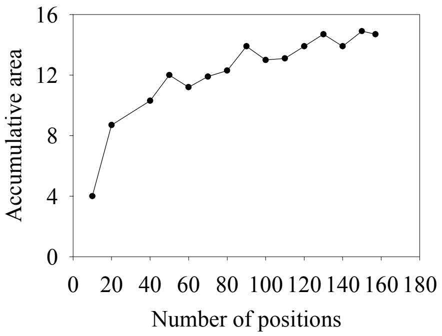
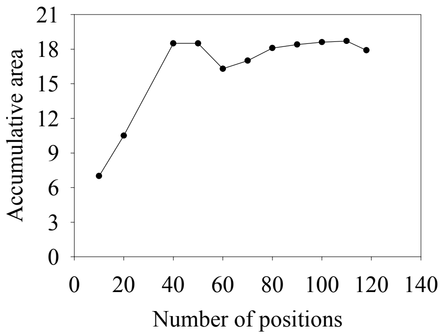


Male 5

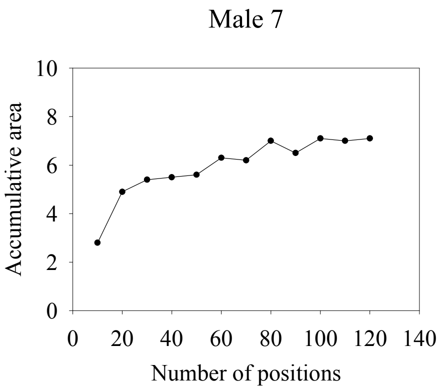


Male 6



APPENDIX I (continued)

Accumulative home range areas for mountain reedbuck males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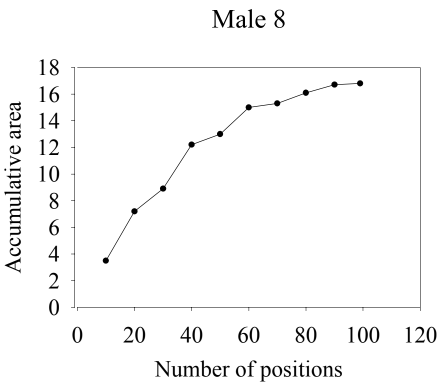
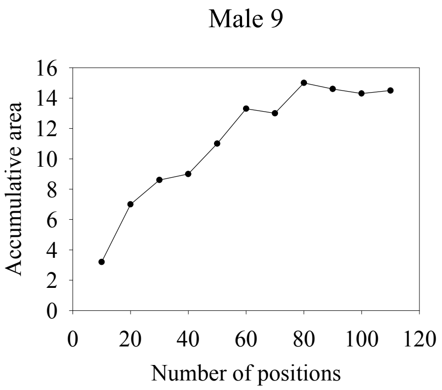
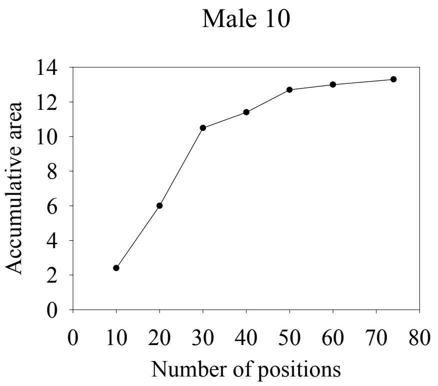

Male 8


Male 9


Male 10

APPENDIX II

Summary comparisons for grey rhebok and mountain reedbuck at Sterkfontein Dam Nature Reserve.

* = not measured during the present study (taken from Skinner & Smithers, 1990).

	Grey rhebok	Mountain reedbuck
Mass	Males 23 kg * Females 20 kg *	Males 29.9 kg (sd ± 2.97, n = 18) Females 28.0 kg (sd ± 3.23, n = 19)
Dressing %	Unknown	Males 54.9 % (sd ± 5.26, n = 16) Females 53.6 % (sd ± 4.64, n = 17)
Diet	Browser (forbs)	Selective grazer
Home range	Entire herd	Males only
95 % MCP	57.9 ha (range 23.3 - 104.1 ha, n = 6)	14.8 ha (range 7.1 – 21.4 ha, n = 10)
95 % AK	75.7 ha (range 30.7 – 113.5 ha, n = 6)	21.2 ha (range 8.5 – 29.4 ha, n = 10)
Territories	Highly territorial Same area as home range	Territorial Same area as home range
Social structure	Territorial herd (1 male, 2 – 9 females plus young) Non-territorial male (solitary) Young males evicted at 11 months age	Territorial male (solitary) Non-territorial male (solitary) Bachelor herd Female herd (3 – 8) with young

APPENDIX II (continued)

	Grey rhebok	Mountain reedbuck
Mating strategy	Female Defence Polygyny. Male defends females within territory	Resource Defence Polygyny. Male defends area within which females come and go
Lambing period	Seasonal (Oct – Jan)	Seasonal (Sep – Jan) Aseasonal in East Africa
Age at puberty	Males 12 – 24 months Females 13 months +	Males 15 months + (Irby 1979) Females 12 – 14 months (Irby 1979)
Age at first calving	20 months +	20 months + (Irby 1979)
Gestation	261 days (Skinner & Smithers 1990)	236 – 251 (Irby 1979)
Calving interval	1 year (or less)	1 year
Fecundity (lambs/female/year)	74 % - 81 %	92 %