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.

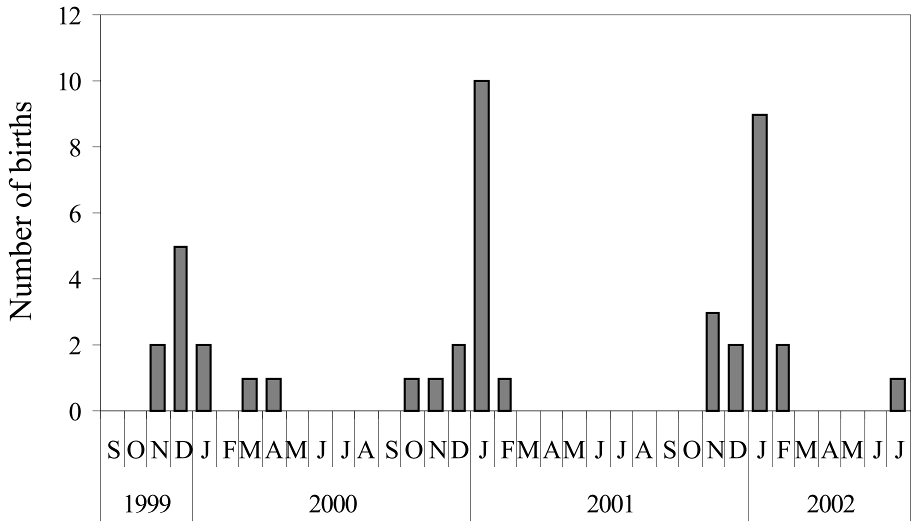

Figure 6. Grey rhebok births for three lambing seasons at Sterkfontein between September 1999 and July 2002. Data were from direct observations of live animals.

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.

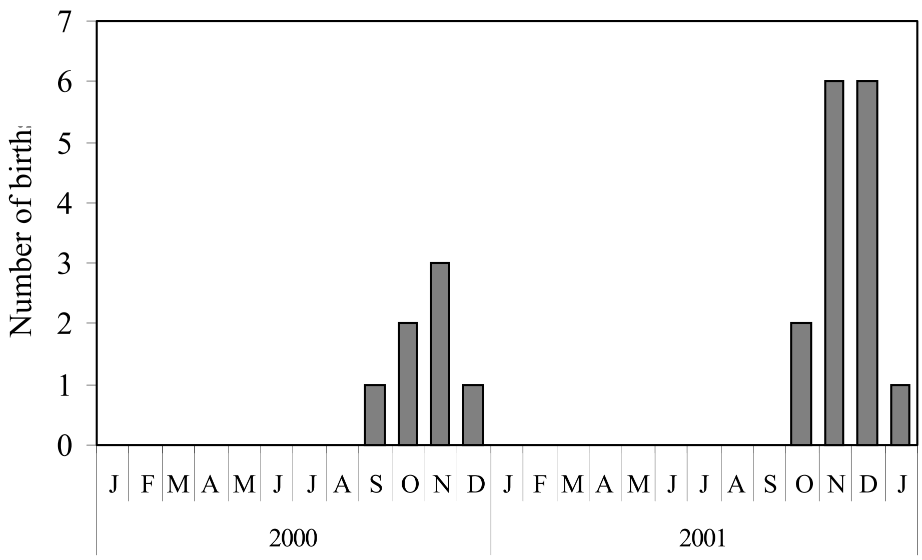

Figure 7. Mountain reedbuck birth months at Sterkfontein, obtained by extrapolation of foetus masses using the Hugget & Widdas (1951) formula, adapted for mountain reedbuck by Norton (1989).

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).

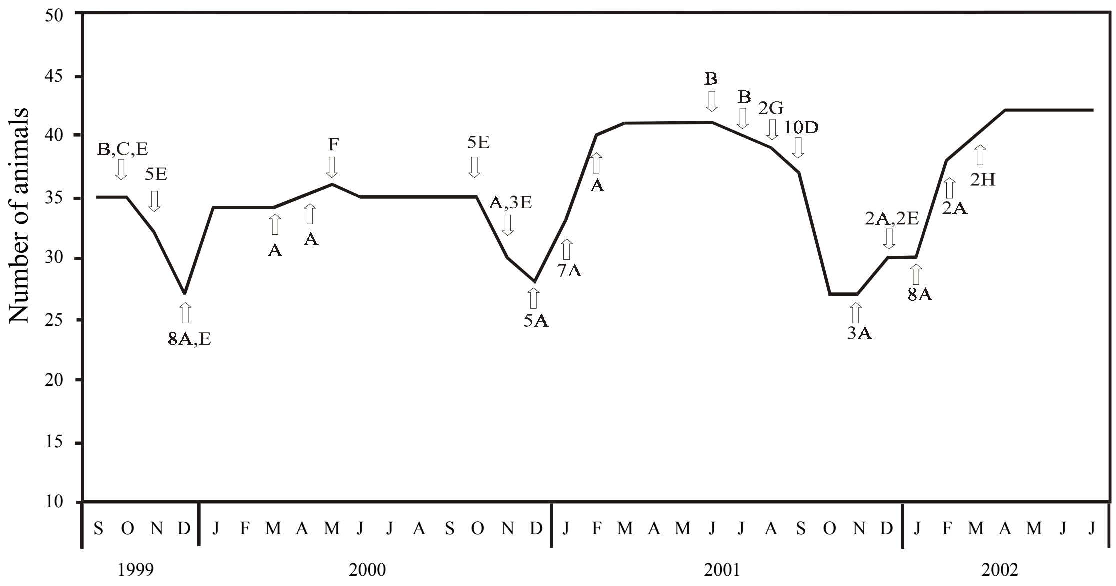

Figure 8. The population dynamics of all grey rhebok within the main study area at Sterkfontein between September 1999 and July 2002. Up arrows indicate increases in population; down arrows indicate decreases. Letters indicate reasons for change: A = birth, B = natural death, C = accidental death, D = 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).

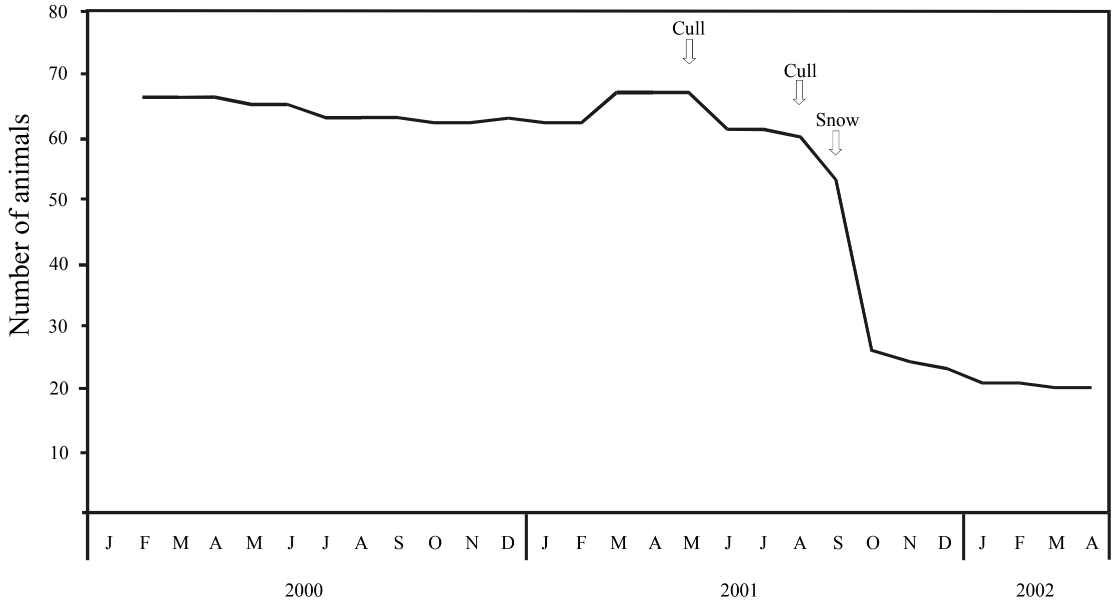

Figure 9. Population dynamics of mountain reedbuck within the main study area at Sterkfontein between February 2000 and April 2002. The numbers are approximations from counts taken every two weeks.

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.