# 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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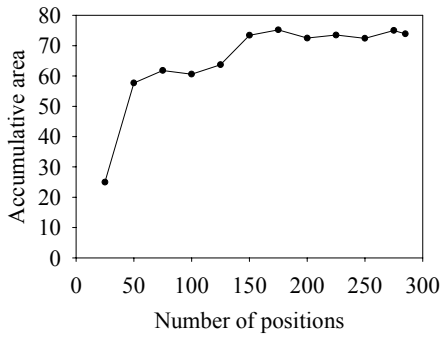
# APPENDIX I

## *Accumulative home range areas for grey rhebok herds*

Group 1

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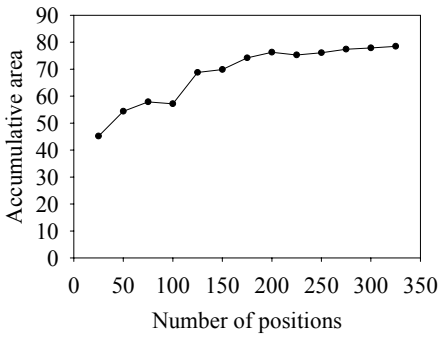


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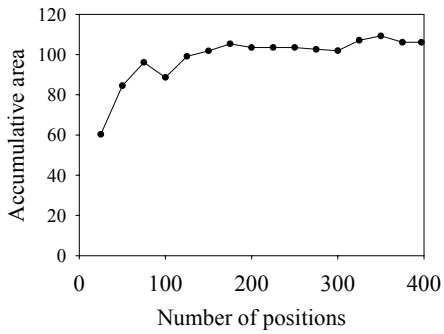


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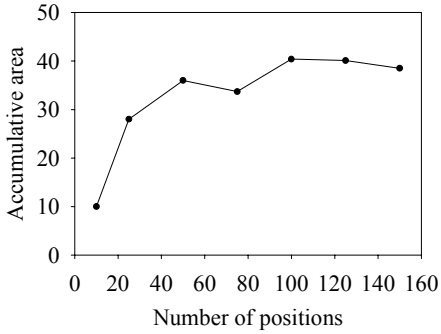


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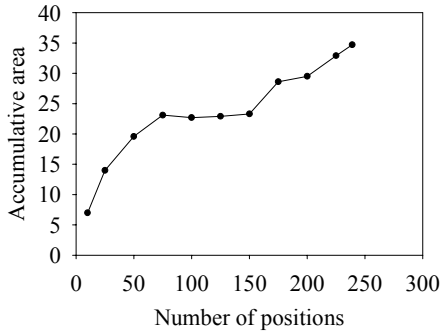


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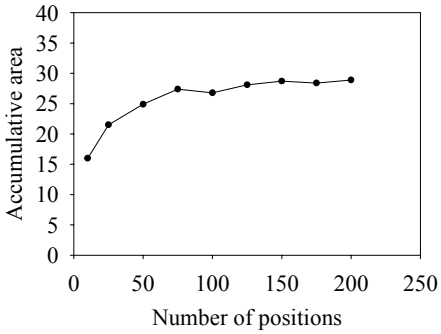
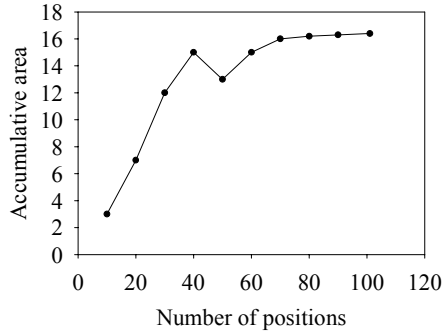


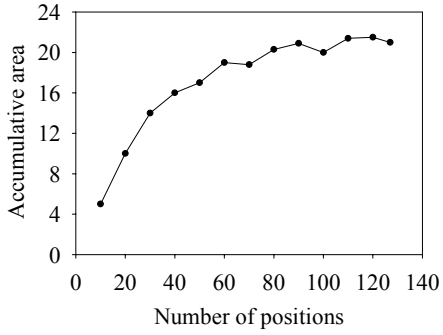
# APPENDIX I (continued)

## *Accumulative home range areas for mountain reedbuck males*

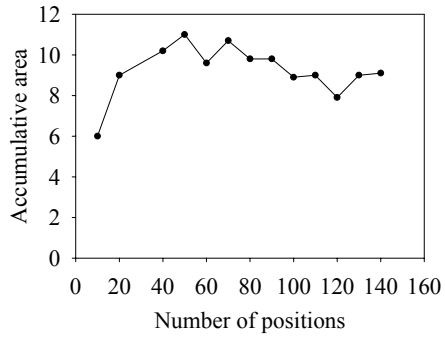
Male 1



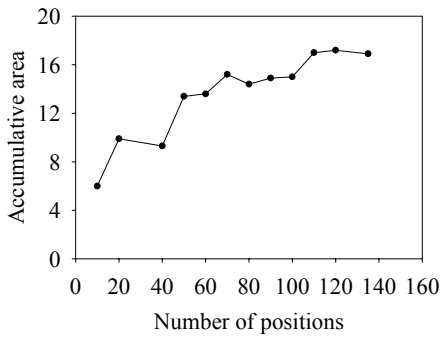

Male 2



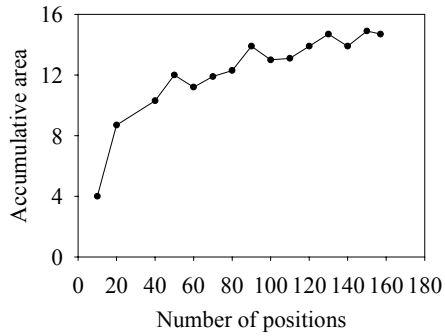

Male 3



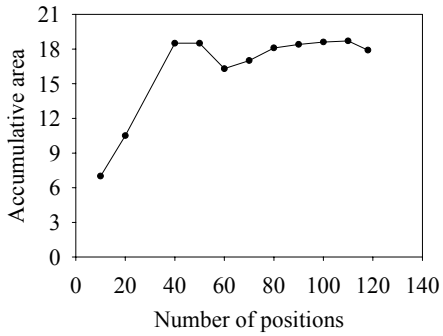

Male 4




Male 5



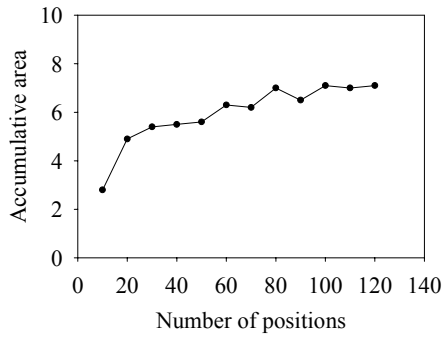

Male 6



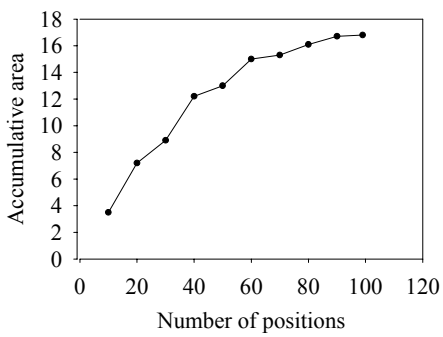
# APPENDIX I (continued)

## *Accumulative home range areas for mountain reedbuck males*

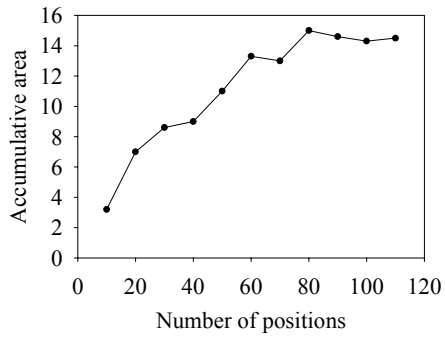
Male 7



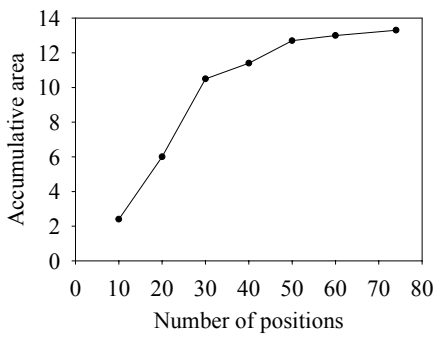

Male 8




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 * | Males 29.9 kg (sd ± 2.97, n = 18) |
| | Females 20 kg * | 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 | Territorial |
| | Same area as home range | Same area as home range |
| Social structure | Territorial herd (1 male, 2 – 9 females plus young) | Territorial male (solitary) |
| | Non-territorial male (solitary) | Non-territorial male (solitary) |
| | Young males evicted at 11 months age | 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 % |