The role of the ram in the impala (*Aepyceros melampus*) mating system

by

Colin Malcolm Oliver

Submitted in partial fulfilment of the requirements for the

degree of

MSc. (Veterinary Science)

in the Faculty of Veterinary Science, University of Pretoria,

Pretoria

July 2002

The role of the ram in the impala (*Aepyceros melampus*) mating system

by Colin Malcolm Oliver

Project Supervisor: Professor J.D. Skinner
Veterinary Wildlife Unit
Faculty of Veterinary Science
Onderstepoort
0110
South Africa.

ABSTRACT

The role of territoriality was investigated using 25 impala rams in a site in South Africa. Field data were used to determine known rams as territorial and bachelors, as well as aspirant and indeterminate. The mean territorial tenure was 67.25 days, with a mean territory size of 21.0 ± 11.27 ha, compared to the home ranges of 34.1 ha ± 9.03 ha for territorial and 58.8 ha ± 33.35 ha for bachelor males. Territory boundaries seemed to remain constant through the season, and are smaller when bordering important features such as water holes, which appear to be neutral in terms of territoriality. Mating was observed on three separate dates between 16 May - 4 June 2001, three times by territorial males, the exception being an aspirant ram.

The most important diurnal behaviour was feeding, followed by watching, walking, ruminating, resting and licking salt. It was found that bachelors browse more than territorial males, and all males browse and lick salt more in the non-rut. All rams were also more vigilant after lions were released. Only bachelors spar and allogroom, and they also orally groom themselves more than territorial males. Territorial males chase and roar more, and perform longer object aggression acts during the non-rut than bachelors. Other behaviours were rare or performed by all rams during the year.

KEYWORDS:

Impala, *Aepyceros melampus*, territory, home range, rut, behaviour, reproduction, seasonality, grooming, vigilance.

ACKNOWLEDGEMENTS

<u>CONTENTS</u>

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

The impala (*Aepyceros melampus*) is a medium-sized antelope and the only representative of the subfamily *Aepycerotinae* (Skinner & Smithers, 1990). They are abundant in Africa, being distributed widely in the eastern mosaic woodland biomes, from Kenya south to northern Natal, and westwards along the Kunene river. They have been widely introduced in southern Africa, and are thus found throughout private land, game reserves and ranches.

Much research has been done on the social organisation of impala. Behaviour has been extensively studied by Jarman (1979) in the Serengeti, and by Murray (1982b) in northern Zimbabwe; with minor studies in Hluhluwe Game Reserve (Anderson, 1972a). Impala have been investigated in many other ways, partly as a result of their abundance, and therefore convenience as a study animal. This is discussed in the relevant chapters.

Anderson (1972a) described impala in Hluhluwe Game Reserve, Zululand as existing in five distinct social groupings: that of lamb herds (nurseries), yearling herds (young males), female herds (with young and sometimes one adult male), male herds and lone males. Jarman & Jarman (1973b) observed that weaned juvenile males are driven out of the female herd by territorial males at which point, after repeated evictions, they join an all male bachelor society in which they must establish an individual hierarchical rank, roughly based on age. On the other hand, females generally remain in their natal clan, which Murray (1982a) describes as a stable discontinuous dispersion of female and juvenile impala as a result of selection for small home range size and large group size. It is therefore clear that with males dispersing (even simply to a neighbouring clan) and with females largely remaining in the flexible groups in which they were born, incest is avoided. This is dependent on large herd sizes and areas in which to disperse.

Research done on territoriality in impala can be split into two main sites, southern Africa and east Africa. These are separated because the environmental conditions differ. Southern Africa has a short, seasonal rainy season from approximately December till the end of February, and a dry season from May through to July, with a significant variation in daylength between the seasons. On the other hand, eastern Africa has a longer rainy season and being closer to the equator, more constant daylength (Skinner & Skinner, 2001), which therefore results in differences in the response by impala to climatic variables. For example in Kenya, Schenkel (1966), in the first detailed study of impala, stated that there is no rutting season, with dominant males permanently herding a group of females and defending their possession. He therefore implied that aggressiveness and competition between males is a permanent element in the social life of impala and that 'female defence' is the main mating adaptation shown. On the other hand, Dasmann & Mossman (1962) observed impala in Zimbabwe, and noticed rutting behaviour was evident in the latter part of March, being widespread and general by May. Murray (1982b) noted the earliest fight between rams in Zimbabwe six weeks before the start of mating, and fighting carried on to approximately six weeks after mating. This, combined with conspicuous piles of dung, increased aggressive behaviour and greater spacing between males, illustrated male territoriality during the rut.

Leuthold (1970) confirmed that impala rams are territorial. Criteria included repeated observations of a known male in the same location with and without females, observations of the same male in the same area with different females, and observation of a new male in an area where a known male had been seen repeatedly but is at that point somewhere else. Leuthold (1970) noted however that, unlike the seasonal climate in Zimbabwe, seasonal changes in Kenya are less pronounced, and so impala breed throughout the year, showing peaks correlated with rainfall patterns. Therefore, territorial behaviour exists throughout the impala's range, but is far more apparent in the contracted rutting period of impala in southern Africa, than in eastern Africa where a more consistent daylength confounds the issue. In her extensive study, Jarman (1979) made similar conclusions, whilst suggesting that more work needed to be done in southern Africa as most long-term behavioural studies had taken place in east Africa, where daylength conditions were different.

The daily behaviour of impala is highly routine and consistent. Jarman & Jarman (1973a) discuss the daily activity of impala over different time periods and at different times of the year. Looking at the different activities carried out by females, feeding takes 38-55% of the diurnal period, ruminating takes 14-35% of the time, moving takes 9 –13%, standing takes 7-14%, grooming takes 3-4% and lying down takes 1-4% of the overall day. Whilst ruminating and standing time did not seem to differ when looking at territorial males, all aspects of territorial defence and herding and attention to females increased dramatically, with a resultant drop in feeding, and in feeding and ruminating combined. Reproductive behaviour such as flehmen, mounting and laufschlag are all behaviours noticed by Jackson (1995) in springbok (*Antidorcas marsupialis*), and in most cases would be more likely in males involved with mating, which in springbok was the territorial males. Jarman (1979) noted however that laufschlag was only infrequently reported in territorial impala males and was not an integral part of pre-mating behaviour as reported in other antelope. Whether these all differ between impala rams holding territories or not is important to examine in the impala mating system, as are the daily activities such as feeding, ruminating and resting, time for which has been recorded as declining as a result of these other reproductive activities. The rut involves an increase in aggressive behaviours, but how that differs between rams of different social status is a matter to be determined.

   The main objectives of this study were therefore to investigate:

1) Whether only territorial males mate.

2) The length of time territories are set up before the rut, the relative sizes and nature of the territories and how long they are held for.

3) The nature of territorial rams, how they lose their territories and what happens to them afterwards.

4) The differential usage of habitat by territorial and non-territorial rams.

5) Whether the impala rut is related to the lunar cycle.

6) The variation in time and occurrence of various daily behaviours, between territorial and non-territorial rams.

7) The effect of lion introduction on the vigilance of territorial and non-territorial rams.

4

CHAPTER 2

STUDY SITE

The study was conducted at Touchstone Game Ranch, situated in the Waterberg mountain region, Limpopo Province, South Africa (23°45'S, 28°23'E). Touchstone is situated on the north-eastern periphery of the Waterberg plateau (van Rooyen & Skinner, 1989) and covers approximately 9500 ha. Van Rooyen & Bredenkamp (1996) describe Touchstone as containing Waterberg Moist Mountain Bushveld habitat, as part of the savannah biome of South Africa. It has an acidic, sandy, loamy to gravely soil derived from sandstone, quartzite or shale, and is rugged and rocky. The Waterberg area as a whole used to be an important cattle-farming region, but now is increasingly used for game ranching, the grazing from which along with fire and aspect are important influences on the vegetation types found on the rocky slopes and summits. The site itself consists of a valley containing past arable land, which is therefore relatively flat and open, surrounded by steep rocky slopes of shrubs and bush as described above.

Dunham (1980), Monro (1980), and Skinner, Monro & Zimmermann (1984) all describe how impala are mixed feeders, being able to graze and browse throughout the year. Young (1972) also noted that at night, impala usually spend their time in open country, and they are very dependent on water. Therefore, a small waterhole present in the study valley, along with open and bush habitats made the area ideal for impala.
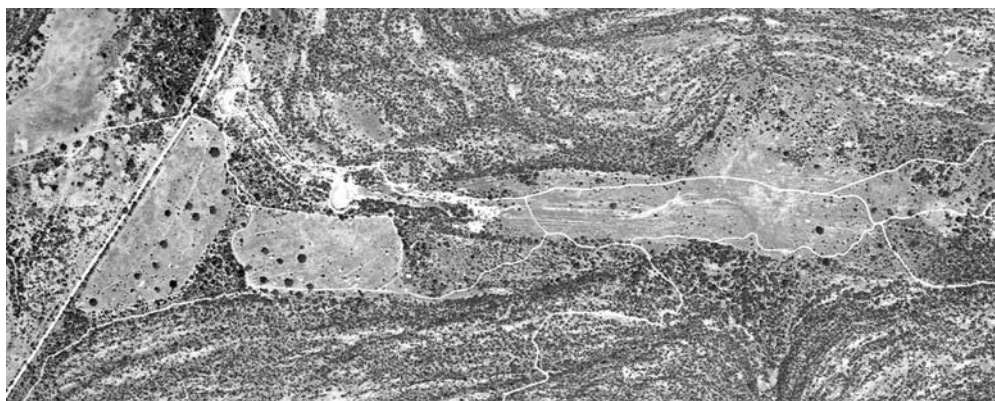
Figure 1 - A 1:10,000 aerial photo (1983) of study site within Touchstone Game Ranch.

A map of the study site was produced using the Geographical Information System ArcView®, as described in Chapter 3. This is displayed in Figure 2, and can be compared to the 1983 aerial photo shown in Figure 1. Using the scale provided, it is evident the area of the study site is approximately 200 ha (2 km^2).
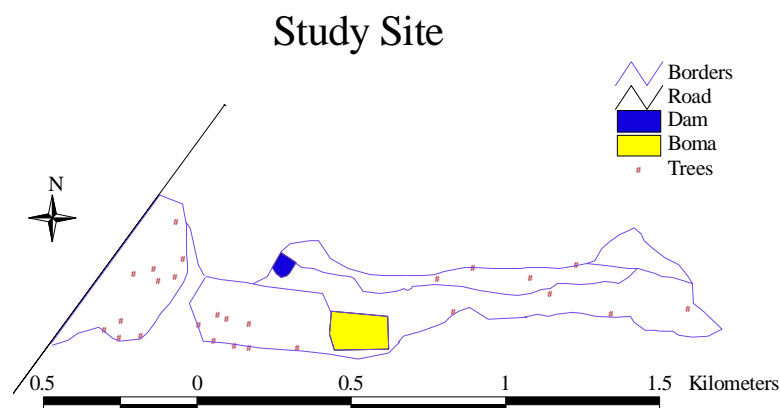
Study Site

Figure 2 - Study site drawn by the GIS package ArcView®.

Climate

Van Rooyen & Bredenkamp (1996) state that the annual rainfall is 650 to 900 mm, with temperatures ranging from -6°C to 39°C with an average of 18°C. Data provided by the South African Weather Service illustrates the monthly trends and are displayed in Figures 3 and 4.
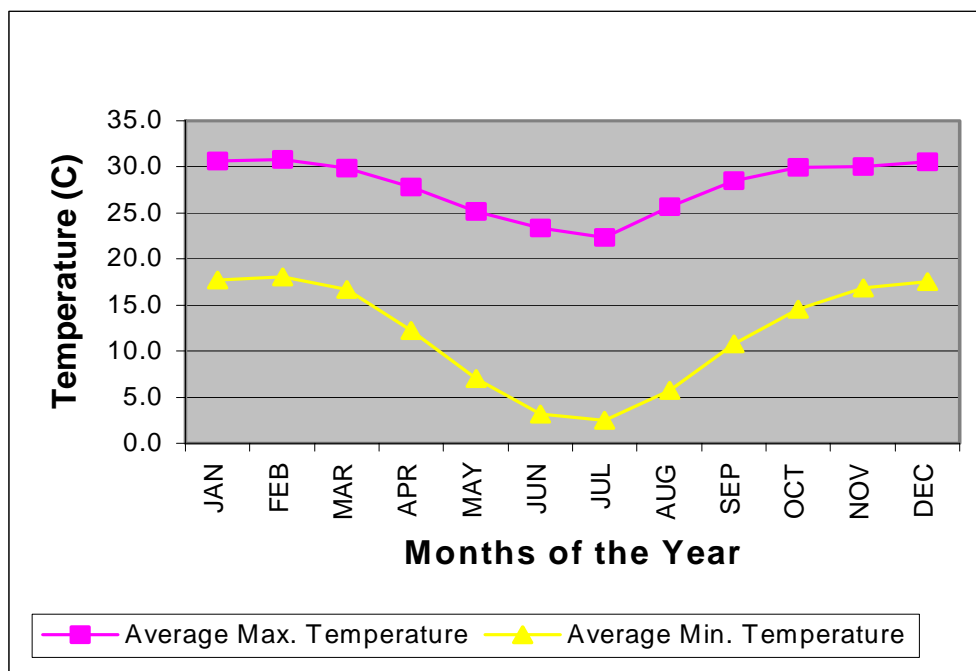
Figure 3 - The variation in mean monthly maximum and minimum temperatures at Marken (20km north of the study site) from 1994 – 2001 (South African Weather Service).
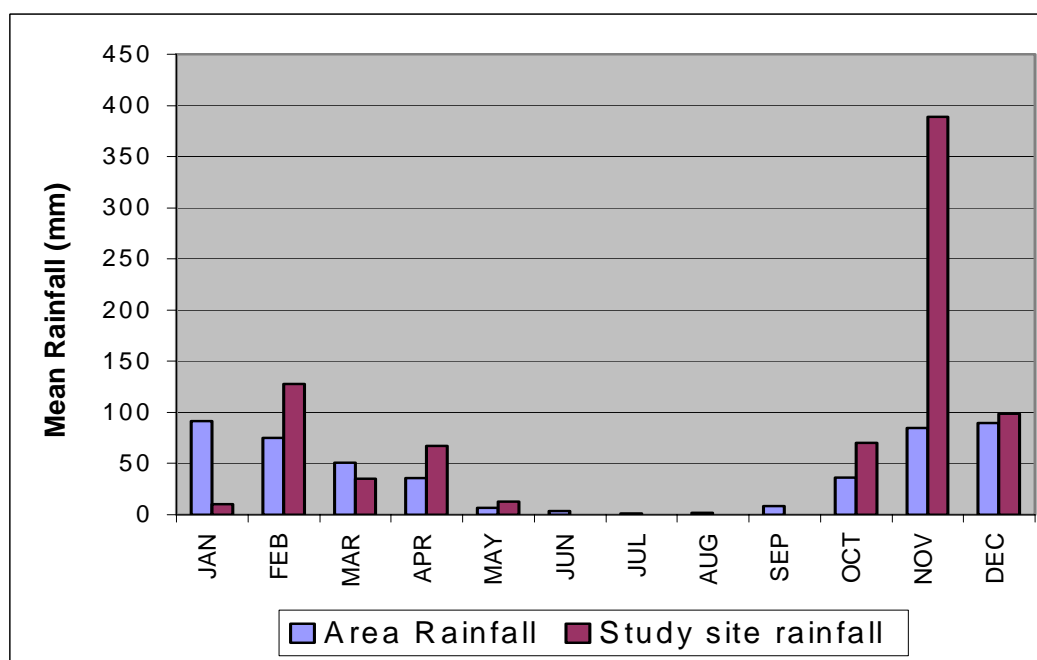
Figure 4 - The variation in mean rainfall recorded at the study site in 2001, and at nearby Daggakraal from 1960 – 2002. (South African Weather Service).

Flora

Van Rooyen & Bredenkamp (1996) document the tree layer as characterised by species such as *Faurea saligna* (African beechwood), *Acacia caffra* (common hookthorn), *Burkea africana* (red seringa)*, Terminalia sericea* (silver clusterleaf) and *Peltophorum africanum* (weeping wattle) on the deep sandy areas; *Kirkia acuminata* (white seringa), *Englerophytum magalismontanum* (stemfruit)*, Protea caffra* (common sugarbush)*, Croton gratissimus* (lavenda croton), *Combretum apiculatum* (red bushwillow), *Diplorrhynchus condylocarpon* (horn-pod tree), *Pseudolachnostylis maprouneifolia* (kudu berry), *Albizia tanganyicensis* (paperbark albizia), and *Combretum molle* (velvet bushwillow) are characteristic of the rocky slopes. The shrub layer is moderately developed and includes *Euclea crispa* (blue guarri), *Ochna pulchra* (peeling plane), *Rhus lancea* (karee), *Rhoicissus revoilii* (bushveld grape), *Tapiphyllum parvifollium* (small velvet leaf), and *Grewia flavescens* (sandpaper raisin). W. Erasmus (pers. comm.) notes that other notable tree species found in the study site are *Schotia brachypetala* (weeping boer-bean), *Sclerocarya caffra* (marula), *Dichrostachys cinerea* (sicklebush), *Acacia robusta* (splendid acacia), *Acacia karoo* (sweet thorn), *Acacia nilotica* (scented thorn), and *Acacia nigressins* (knob thorn), the latter of which show evidence of sweeter veld in the area.

The grass layer is moderately to well developed, and grasses such as *Elionurus muticus* (wire grass), *Loudetia simplex* (common russet grass), *Diheteropogon amplectens* (broad-leaved bluestem), *Panicum maximum* (guinea grass), *Trachypogon spicatus* (giant spear grass), *Digitaria eriantha* (finger grass), *Setaria lindenbergiana* (mountain bristle grass), *Pogonarthria squarrosa* (herringbone grass) and *Urelytrum agropyroides* (quinine grass) are all conspicuous. Other grasses mentioned are *Aristida congesta* (tassel three-awn), *Melinis repens* (Natal red top), *Setaria sphacelata* (common bristle grass) and *Themeda triandra* (rooigrass). W. Erasmus (pers. comm.) states that the study site also contains *Panicum natalense* (Natal panicum), *Cynodon dactylon* (couch grass), *Perotis patens* (cat's tail), *Heteropogon contortus* (spear grass), and *Eragrostis gummiflua* (gum grass). The study area was recently assessed as having a grazing value of 12.63 ha / Large Stock Unit.

Fauna

Many animal species are present on the reserve, including nearly all species of antelope, of which there are 607 impala and 389 *Tragelaphus strepsiceros* (kudu) according to the 2002 game count figures (W. Erasmus, pers. comm). *T. angasii* (nyala), *T. oryx* (eland), *Kobus ellipsiprymnus* (waterbuck), *Connochaetes taurinus* (blue wildebeest), *Equus burchelli* (zebra) and *Phacochoerus aethiopicus* (warthog) are also present. The reserve is also home to *Loxodonta africana* (elephant), *Ceratotherium simum* (rhino) and *Giraffa camelopardalis* (giraffe) that were seen on occasions. Several species of carnivore are present, including *Canis mesomelas* (black-backed jackal) which were seen regularly, and *Felis caracal* (caracal), *Hyaena brunnea* (brown hyaena), *Acinonyx jubatus* (cheetah) and *Panthera pardus* (leopard) which were seen rarely. The three free-ranging lions (*Panthera leo*) present were introduced during the course of the study, and are discussed in further detail in Chapter 4.

As earlier described, variation in daylength as displayed below between east and southern Africa, is responsible for a number of differences in impala reproductive behaviour observed in animals at different latitudes in the impala range. Figure 5 shows this variation. Touchstone Game Ranch is found at 23°45'S *cf* Kenya found on the Equator.
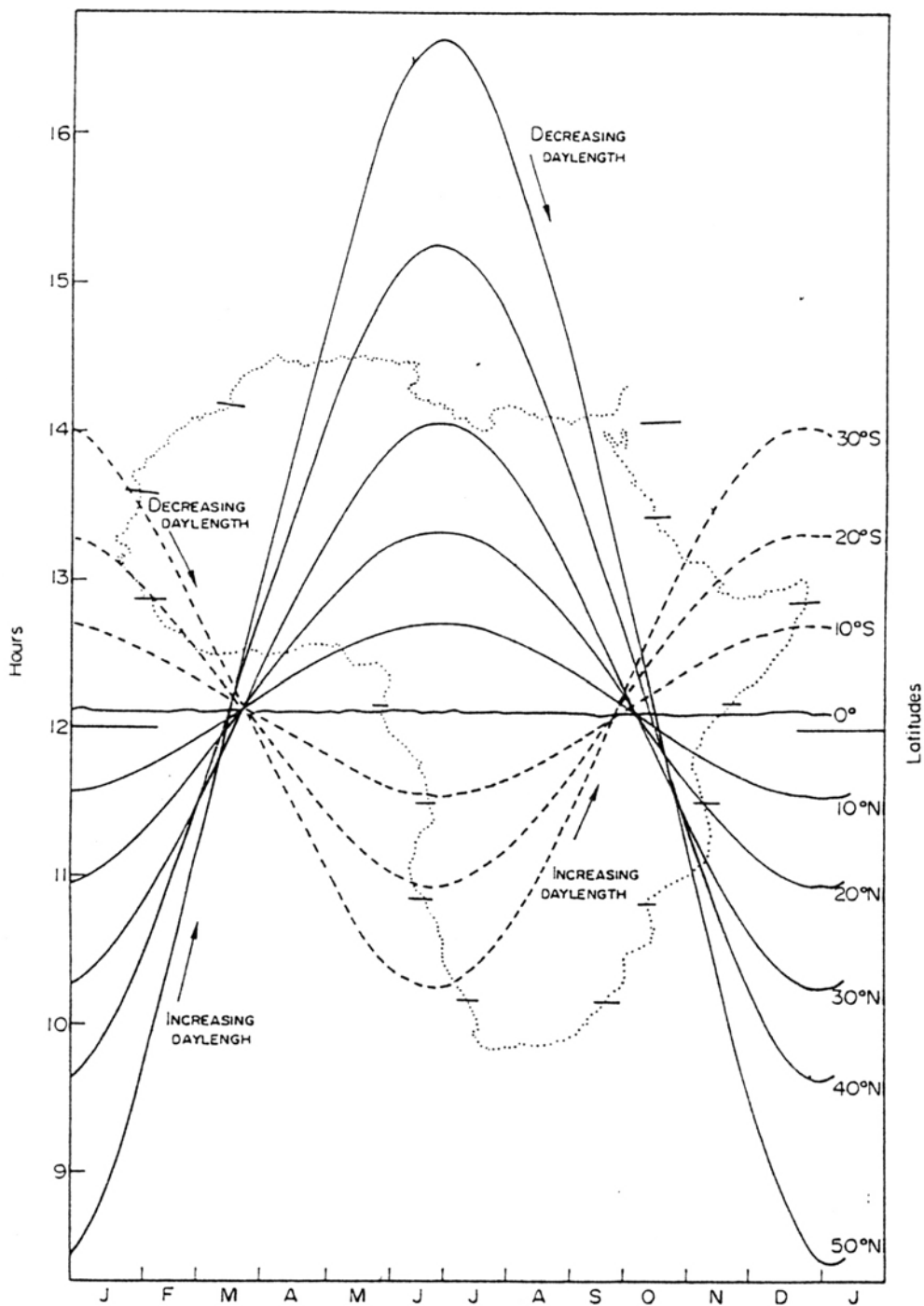
Figure 5 - Hours of daylight and darkness throughout the year for 0° to 50°N and 0° to 30°S (Spinage, 1973), using daylight as the hours between sunrise and sunset.

It is evident therefore, that the study site is a reliable representative of the southern African range of the impala, and thus can be used to compare the resulting behavioural differences with impala elsewhere.

10

CHAPTER 3

TERRITORIALITY

Introduction

Anderson (1972b) stated that impala rams in Zimbabwe hold territories in the best areas, thus adopting 'resource defence' by defending areas most likely to be favoured by females, an adaptation used throughout the impala's range. This also has the effect of enabling females to choose the strongest male, who will be the territory holder. What a 'best area' in a habitat would consist of has not really been determined. Access to important resources such as food and water, which in turn attract females, should all be important. Young (1972) noted that young grass shoots serve as special sources of attraction to impala, whilst more than 50% of herds observed in the Kruger Park occurred less than 1.6 km (1 mile) from the nearest water (Young, 1970). Young (1972) also noted that at night, impala prefer open country mostly away from water, perhaps to increase predator detection. Dasmann & Mossman (1962) note that areas containing vital resources such as water holes, may become neutral territories. This would enable all the rams to visit as is necessary for their survival, without aggressive behaviour of incumbent territorial rams around water holes preventing this.

Various estimates have been made for the home ranges and territory sizes of impalas in different sites. Using the Minimum Convex Polygon (MCP) method, non-territorial (bachelor) males, females and juveniles in the Serengeti National Park occupied a home range of approximately 5 km^2 (Jarman, 1970); female home range size in Zimbabwe was between 0.92 and 1.7 km^2 (Murray, 1982a); two female impala in the Kruger National Park occupied home ranges of 5.81km^2 (du Toit, 1990); whilst the average impala home range estimated using a simpler, rectangular area in Kruger was 0.98 km^2 (Young, 1972); in Botswana, the mean home range size for impala was 3.3 km^2 using a Harmonic Mean Contour (HMC) method (Ritter, 1993). Using MCP's, Jarman (1970) stated adult males in the Serengeti occupied territories of 74 ha (0.74 km^2), and averaged 45 ha (0.45 km^2) from February to April, and 42 ha (0.42

km^2) in June (Jarman, 1979). Lone males (presumably territorial) in Zimbabwe had an average territory size of 50 ha (0.5 km^2) (Murray, 1982a). Jarman (1979) noted that territory physiognomy varied as well as the different proportions of vegetation type and facets, river frontages, ridges and so on. She stated that the impala preferred open woodland ecotone, with the larger territories containing a relatively high proportion of open grassland and very open woodland.   Analyses were unable to show the importance of relative land facet contents of territory, but supported the theory that the territory contents rather than the territorial males per se were attractive. It was suggested that the more attractive territories were those containing the greatest diversity of vegetation, as well as other important assets such as drinking places, salt licks and shade trees. Novellie (1975) found that blesbok (*Damaliscus pygargus phillipsi*) maintained territories with rigid boundaries between neighbours, and it is likely that impala do the same. It is apparent that more work can be done on the nature and size of impala ram territories, whilst also comparing these with non-territorial and female home ranges.

Unlike arid adapted antelope which are opportunistic breeders (Skinner & Skinner, 2001) or impala in east Africa which can breed throughout the year (Leuthold, 1970), southern African impala populations have a definite mating season from approximately the beginning of May through until approximately mid-June (Dasmann & Mossman, 1962; Mason, 1976; Fairall, 1983;), depending on latitude. Thus breeding occurs whilst the males are in peak body condition just after the wet summer season, and when ewes have weaned their lambs. The relatively short breeding season covers the two oestrous cycles shown by female impala (Fairall, 1983), and imposes a high price on territorial rams. Indeed, Jarman & Jarman (1973a) note that the territorial behaviour of impala rams such as herding, chasing and marking, impinges on feeding and ruminating time and territorial rams lose condition rapidly during this period (Skinner, Jackson & Marais, 1992). Anderson (1965) noted that the kidney fat of impala rams, as well as the mass of both testes, which had increased to a peak prior to the rut, declined sharply as mating commenced. Similarly Skinner (1971) observed that epididymal sperm numbers, sperm motility and androgen production all decreased after the rut, and remained at low levels until they built up again to peak at the beginning of the next rut. The territorial system collapses when these stresses cannot be contained, resulting in a decline in libido, and

explaining the short impala breeding season in southern Africa (Jarman & Jarman, 1973b). Unfortunately, the only situation in which the length of territory tenure has been calculated is in east Africa, where mean length of territoriality by males was 82.5 days, ranging from 5 to 267 days (Jarman, 1979). Despite the wide range, the majority (94%) of territorial periods were under four months, and 70% were under three months.

Jarman (1979) showed that the territorial behaviour of the impala was highly complex. Rams advertised their presence in many ways; using static stances; urinating and defecating in concentrated dung patches; bush horning and frontal rubbing of the head on bushes, marking the area with a strong smelling oily secretion. Roaring is the loudest and most frequently used vocalisation of territorial impala males, which Jarman (1979) stated was mainly used by territorial males (86% of records). Warren (1974), in northern Zimbabwe found a low incidence of roaring up until May when in the second week, there was a marked increase in vocal displays which continued until the end of the month, after which there was a sharp decline. Roaring continued at low levels throughout June and July, and was rarely heard from August onwards. However, in east Africa with continuous breeding, Leuthold (1970) observed far less roaring displays. Murray (1982b) also observed that the impala rut in north-west Zimbabwe was distinguished by a high frequency of rutting calls which coincided with a peak in matings. It was concluded that roaring and matings were probably influenced by the lunar cycle, as the first observed mating was within six days of a full moon in the six years investigated. Warren (1974) observed that the highest levels of roaring activity were observed at night when the moon was brightest, and declined towards the new moon.

Roaring performances are seen in many situations, and were described by Schenkel (1966) as an "expression of activated male dominance". Skinner *et al.* (1992) suggested that the roaring of impala rams could fulfil a role in advancing the onset of oestrus in females. This 'ram effect' has been shown to occur in a number of species, including cattle *Bos indicus* (Skinner & Bonsma, 1964), and goats *Capra hircus* (Skinner & Hofmeyr, 1969), while McComb (1987) found that both the presence of a red deer (*Cervus elaphus*) stag, and roaring presented as an isolated stimulus, can advance conception dates in red deer hinds. The effect is even greater

13

when a vasectomized male is present, as pheromone secretions, roaring, chasing and other reproductive behaviour clearly have an important stimulatory role. Skinner, Cilliers & Skinner (in press) also found that introducing a springbok ram into a herd of aseasonally breeding cycling ewes caused an increase in the duration and amplitude of the luteal phase, which lead to synchronised ovulation within two cycles. In the same way, Marais & Skinner (1993) showed that introducing a male blesbok to a herd of females (seasonal breeders), led to a sharp increase in progesterone concentrations within a week, resulting in a synchronisation in cycling ewes and a close date of conception. They concluded that the seasonal reproductive behaviour of sexually active territorial rams acts as a fine tuner, synchronising female ovulation. As du Plessis (1972) observed, this resulted in 75% of blesbok lambs being born within a 16-day period. It seems likely that this behaviour in impala rams, with roaring playing an important part, would therefore have the added advantage of enabling the territorial male to mate with as many females as possible. Skinner & van Jaarsveld (1987) also state that synchronised matings have the effect of synchronised births, which can be an advantage to young as they are born to coincide with a flush of new plant growth, whilst at the same time swamping predators so that a smaller percentage are taken at their most vulnerable age. An exception that proves the rule is the highly aseasonal impala birth in the Nxai Pan, Botswana, recorded by Ritter & Bednekoff (1996). The lamb was first observed in May even though the normal lambing period occurs in late December to early January.

Murray (1982b) observed that when aggressive behaviour between rams was shown, it was often highly ritualised with displays such as parallel walking and the lowering of heads. On the occasions that the confrontation resulted in a fight, it was found that generally only superficial head wounds were suffered, and it was rare to suffer serious injury. This may be in part due to a dermal shield of thickened skin, which Jarman (1972) showed exists in the impala ram, covering the head, shoulder and upper neck regions, and extending along the back to the level of the scapulae. This would protect them in the majority of fights during which the opponents meet head on. It is important to note that females do not have this dermal shield, emphasising its role in protection during inter-male conflict. However, J.D. Skinner (pers. comm.) observed two dead rams in Botswana and another in Kwazulu-Natal, South Africa, with punctured abdomens resulting from fights with other rams, and one

younger black impala ram at Touchstone Game Ranch was killed in 2000 by the older, territorial ram in the same way. This suggests that in some cases deaths may be more prevalent, but are not always noticed due to the removal of the carcass by scavengers. Mooring (1999) noted that although territorial males defend against challenging rivals and attempt to eject bachelor males, they will tolerate nearby bachelor herds provided they stay away from the females. Murray (1982b) observed an increase in aggression between rams from six weeks before the start of mating, increasing in frequency until they reached a peak just prior to the first mating. Most aggression involved high-ranking rams, but less dominant rams also showed increased aggression, as well as 'contagious' chasing and roaring in bachelor groups (termed 'mass roaring', by Jarman, 1979). Murray (1982b) observed that coincident with the start of mating, relations between territorial rams stabilised whilst remaining dynamic amongst the rest. However, all territorial take-overs are not necessarily as a result of fighting. As already mentioned, rams lose condition dramatically whilst holding territories. This combined with other factors such as the decrease in territorial habitat value through the dry season can stimulate rams to give up territories. Jackson (1995) observed that springbok rams passively abandoned 78% of territories, especially as the dry season progressed. Moreover, predators killed 10% of territorial springbok rams.

Jarman & Jarman (1973b) observed that males had a lower survival rate than females between weaning and three years old, leading to the sex ratio favouring females as ages increase. This reflects the males being evicted from the female herd at a younger age, integrating with a bachelor society and establishing themselves in the hierarchy, before taking over and holding a territory, which then leaves them open to increased predation and increased nutritional stress. This is similar to what happens to the territorial rams after they become non-territorial. Murray (1982b) observed that they interacted frequently in bachelor groups, and often fought with these other males, suggesting that relative dominance amongst males is important, and may even carry over to subsequent breeding seasons. Jarman (1979) observed that most ex-territorial rams joined bachelor herds sooner or later, although an inverse relationship was shown to occur between length of territory tenure, and number of days it took for the ram to join up with other males. It was also found that 24% of

defeated territorial males never became fully integrated with a bachelor herd, and would remain largely on their own until taking over a territory the following year.

Murray (1982b) observed that in Zimbabwe, almost all matings in peak periods were limited to territorial males, with four males accounting for 78% of matings in one year, and 66% of matings in another. Leuthold (1970) also stated that territorial males mate most females. In springbok only territorial males mated, whilst non-territorial males never showed interest in oestrus females, being for all intents and purposes, emasculated (Skinner & Skinner, 2001). Jackson, Skinner, & Richardson (1993) also noted that springbok rams are perennially territorial, in order to be established on territories during rutting, whilst also holding a territory when receptive females intrude at other times of the year. This is especially true for the springbok that are capable of producing lambs twice in one year (Skinner, Von La Chevalliere & van Zyl, 1971), compared to impala that are seasonal breeders in southern Africa (Skinner & van Jaarsveld, 1987). It is unclear however whether only territorial impala males mate, as in springbok, or whether the concentrated breeding seasons enable more bachelor males to mate, as individual territorial males cannot serve all the receptive females at the same time.

It is apparent from the conclusions of Jarman (1979) mentioned in Chapter 1, that there is a gap in the knowledge of ram behaviour in southern Africa, as opposed to the more optimal, continuous breeding areas of east Africa. Hence the present study was proposed to investigate these apparent anomalies.

Methods

Capture and identification

In May 2000, seven male impalas were immobilised using combinations of etorphine hydrochloride (M99® - Virbac, Centurion, RSA.), xylazine hydrochloride (Rompun® - Kyron, Johannesburg, RSA.) and fentanyl (Kyron, Johannesburg, RSA.) in varying dosages (D.G. Meltzer, pers. comm.) as shown in Table 1. Two more rams were immobilised in March 2001.

Table 1 - Drugs and dosages used to immobilise nine impala rams.

Animal Number	M99 (mg)	Fentanyl (mg)	Xylazine (mg)
1	2.5	*	5
2-3	1.5	*	15
4-9	*	20	15

Once the animals had been immobilised, a number of parameters were measured, including: shoulder height; girth which can predict the body mass using methods following Fairall & Braack (1976) in the Kruger National Park, and Talbot & McCulloch (1965) in the Serengeti; neck diameter just above the shoulder, as Jarman (1979) observed that at any one time of the year, territorial males have significantly thicker necks than non-territorial males, an observation also reported in red deer (Lincoln, 1971) and springbok (Skinner, van Aarde, Knight & Dott, 1996). Skinner (1971) and Anderson (1965) noted that testis size varied throughout the year, peaking during the rut, so the left testis length and width was taken. The rams were also weighed as Skinner (1971) noted body weight declines in territorial rams during the rut, and remains fairly stable in non-territorial males (van Rooyen, 1990).

To assess age of impala is somewhat difficult, as techniques using eye lens mass (Fairall, 1969a), and tooth eruption (Child, 1964) or bone measurements are all impractical as they are only really possible in dead or young animals. Thus the age was mainly assessed using horn growth as described by Child (1964), Roettcher & Hofmann (1970) and Spinage (1971). The straight-line length of each horn from base to tip was taken, as well as the total length, the circumference of each horn and the width between the horn tips (Spinage, 1971). The number of ornamental rings on the horn was also counted. Shoulder height was measured as this reaches a maximum by 15 months of age (Lane, Kock, & Hill, 1994), and thus is a good indicator that the male has reached sexual maturity, as it is at approximately this age that spermatogenesis begins in rams (Hanks *et al.*, 1976). In the same way, Skinner *et al.* (1996) also found that shoulder height remains constant in adult springbok, and that this measurement can therefore be used as a criterion for the maturity of the animals. Horn and body sizes were far easier methods to assess age from a distance. For the

purpose of the present study, only adult (sexually mature) males were observed, as these at 2.5 years old or older generally have fully formed lyre shaped horns, which in the field is a relatively easy way of distinguishing the age of rams. Above 2.5 years, Roettcher & Hofmann (1970) state that differences in the shape and length of horns are influenced by locality, habitat, feeding and individual variation.

Dunham & Murray (1982) showed that the fat reserves of adult males increased during the wet season prior to the rut, and declined sharply during the rut, a fact they attributed to the reduced feeding time experienced when accompanying females. Jarman (1979) noted that as they lost weight, the bones of the pelvic and pectoral girdles, the ribs and vertebrae all began to protrude, and they developed dull, staring coats. As a result, four categories of 'good', 'fair', 'poor' and 'bad' were devised and used to classify the males' condition before and after the rut. Monro & Skinner (1979) noted that the kidney fat index and the percentage of dissectable fat in the buttock were the most reliable condition indicators, but clearly these are only possible on dead animals. Riney (1960) provided diagrams for categories of 'good', 'medium' and 'poor' condition of ungulates and these were used for the condition rating of 1 - 4, with 'bad' taken as an extremely thin looking animal in level 1, and good condition as level 4. Jarman (1979) also noted that territorial males develop black patches above and below the eyes. The patches were graded into four categories, ranging from Grade 1 'no black' to Grade 4 'very black', and were used in order to examine whether they were good predictors of territoriality. Both condition and eye colour scores were assessed visually in the pre-rut and post-rut periods. This was done on as many animals, as close to the same days (10th March and 10th August) as possible in order to have comparable scores and grades to assess.

When the rams were darted, they were each fitted with a collar made of web belting, with coloured shrink-wrap plastic to identify individuals. Two of the rams were fitted with radio collars, which also allowed visual identification. In addition, ear tags were attached to some rams. Loomis & Wright (1989) found that pinna infections associated with ear tagging are uncommon and, as far as it was possible to identify, none of these procedures caused any harm or change in behaviour to the animal. As time went on, it became easy to identify other rams using a combination of horn length and shape, facial markings, and distinctive scars and body marks. As a

result, 25 adult rams were identified during the course of the study, though six of these ended up with only ten observation days or less, and were therefore discounted from most of the analyses as data were too few to be accurate.

An important aspect of the study was being able to tell when an impala ram was territorial, and when he was non-territorial (bachelor). Dasmann & Mossman (1962) observed that territorial behaviour was shown by rams when they were observed making displays of aggressive behaviour whilst being spread out from other rams. Jackson (1995) used to define territoriality in springbok as a ram that has dominance over others in an area. In addition, he defined a male as territorial if showing sexual interest in females, and restricting movements to a small area in which he was alone or with females in greater than half of the sightings. The aggressive displays and signs described by Dasmann & Mossman (1962) determine the rut, and though these could be seen in the latter part of March, it was not until May that this behaviour was widespread and general. Anderson (1975) recorded the monthly percentage frequency occurrence of lone adult impala males in three sites in South Africa, showing a big peak between mid April and mid June, as well as a smaller one between September and November. Warren (1974) observed and quantified the rut by counting the number of roaring or snorting and grunting displays of the male (as did Murray, 1982b), by observing the percentage of lone males relative to other herd types, by recording changes in herd size, and by witnessing copulation.

Observations and status definition

Observations from a vehicle took place from the beginning of February to the end of September 2001. As a result of vehicle restrictions, as well as to limit any damage to the veld, all observations were restricted to that possible from the graded border roads, at a range from 20 to approximately 200 m. So as to avoid altering the behaviour of the impala, all observations were carried out from inside the vehicle using Nikon 10 by 25 binoculars and only commenced when it was apparent the rams were habituated to the vehicle.

To keep a record of which impala rams associate with which others in order to establish territoriality, it was noted with whom the known rams were found, at different periods of the day. In order to make this as accurate as possible, first thing on entering the study site, I drove round the whole area and recorded each ram present and with whom it was associated. In each case where there was more than one individual in that class (unknown ram, female, young male) present, the number was also recorded. It is also important to note that females and their current young were all counted as females. In a large female herd it was extremely difficult to accurately distinguish a juvenile from an adult female, as body sizes vary so much. In the same way, the horns developed by the young rams only started being visible after 3 or 4 months of age, and even then from a distance were hard to spot until the end of the study. However, in view of the fact they played little part in the ram dynamics and largely remained in the female herd, it was better to continually refer to all females and juveniles in a herd as 'females', so as to maintain a consistent approach throughout the study. The only distinction made was when the young, juvenile rams specifically acted differently from the females, such as during mating events. These observations proceeded in as 'continuous' a form as possible, so that at the end of each one hour session the rams were found again where possible, and their associations re-noted. In the same way, during one-hour scan and focal observations, any changes in association were noted. Although there is a danger of autocorrelation between rams, it is hoped that this method would make the overall interactions and associations more accurate, whilst at the same time providing as near to continuous observations as possible. This process was applied as equally as possible to all rams, as the aim was always to get as equal a number of hour-long sightings as possible for the different rams.

It can often be difficult to devise a 'rule of thumb' for which to determine when animals are associating with which others. Various individuals or herds can be within sight of each other, and yet not be interacting at all. In one area, there may be several adjacent territories, the boundaries of which the impala are extremely aware of, but to the human observer are totally invisible. As a result, animals were assessed as being 'together' if they were within approximately 20 m of another individual in the group, or were clearly interacting with an individual or members of a group. For example, a bachelor male herd may spread out quite a way, and yet clearly still be

'together'. This may involve a certain amount of subjectivity, but consistency in the method has meant that this should still be accurate.

The location of the rams was also recorded in the initial 'pass' through the study site. This was done having initially used a Garmin12® Global Positioning System (GPS) to map out the road network on the valley, as well as identifying features such as large trees, the boma, dam etc. The Waypoint+® (version 1.8.00) programme was used to convert the data from the GPS into computer format.   Taking this outline of the site, a grid was then drawn over, at a scale of 1 cm to 55 m. This was then blown up to double the size, so the grids covered 1 cm to 27.5 m. In order to place the animals into particular squares, recognisable landmarks such as trees were used to work out relative positions. If it was difficult to do this accurately by eye, compass bearings were taken from two different known objects to the ram, and these were then used to place the ram in a particular square. It was assumed that even if the impalas walked slowly whilst feeding, they could cover the whole site in approximately three or four hours. Thus, locations of the rams were noted at a minimum of five-hour intervals, so that each position was independent from the others. This meant that in most cases, there was a maximum of three locations per ram per day. The exceptions to this were the observations of young males and females. This is because there were sometimes large numbers of animals all classified under the same group. As a result many females for example, could be found throughout the study site at the same time. Where it was possible to identify these different groups, they were treated as individual groups for the day, and their locations plotted at a minimum of five-hour intervals. If it was not possible to re-identify the group, as was often the case, they were noted down on a five-hour interval pass through the site as a separate sighting. This meant that for these categories there were often more than the three locations per day, but it is accepted as reflecting the abundance of female and young male groups, as opposed to individual rams.

All these data were then analysed with respect to whether rams were territorial or non-territorial. This was done by working out the proportion of sightings a ram spent alone, with females, or with males on a particular day. He was then graded as being territorial when the proportion of sightings spent with males was less than with females, and a bachelor when with males more than with females. If the proportions

21

of time spent with males and females were equal, then an undecided grading was set. If the ram was neither with males or females, but was alone, he was classified as alone. This is different from other authors such as Jackson (1995) who classified rams alone as territorial. The reason for doing it this way was that from my behavioural observations, it was apparent that some non-territorial rams frequently remained alone, either because they were aspiring to take over territories, or after they had lost territories. Classifying 'alone' rams as territorial confuses the issue in many cases and, as a result, they were given a separate classification. The distribution of ram sightings on different dates was used to back up or otherwise, dates set for territories that have been shown through the data.

Another factor that was involved in assessing whether a ram was territorial or not, was in its aggressive encounters with other males. This fits with authors such as Jarman (1979) who defined territorial rams as those dominant over all others. This was done using data of all interactions observed between known rams. These data were incorporated into the behaviour data that are analysed in Chapter 4. However, for the purpose of determining dominance, two categories were important: chasing, where a ram chases another animal, and walk out, when one ram follows another at walking pace, out of a territory or area of conflict. For the purpose of determining territoriality, interactions involving females, young males or unknown adult rams were removed. What is important is which ram was 'dominant' over which other. Status' of the rams then resulted because they were 'dominant' when the subject of a chase or walkout encounter more than a target on a particular day, and were 'submissive' when they were a target more than a subject for these interactions. Where these were the same, he was classified as 'unknown', as it was difficult to make a judgement. Again this is not perfect, as bachelor rams may be 'dominant' over other bachelor rams and thus rated as such, even though they are submissive whenever they come into contact with a territorial ram. However, it does help to further fine tune a switch for rams changing from one status to another, especially in the cases of territorial rams that lose their territories, and as a result eventually become submissive. Using these interactions, associations and areas inhabited on different days, all combine together to give clear definitions of territoriality or non-territoriality, for individual rams at different times. These were then combined with what was seen in the field to give as accurate a status as possible. However, it is

apparent that it is always going to be difficult to be inflexible about dates and definitions regarding natural events that are often, far more fluid.

Using the methods described, territoriality was described for each ram. Of the 19 rams for which data were collected and analysed, eight were determined to be 'pure' bachelors, eight showed definite territoriality, and three showed mixed behaviour that, for reasons to be explained, were less easy to categorise. In the analysis, it became clear that there were some data that didn't always fit the field observations, and thus needed categories other than territorial or bachelor. In one case, a non-territorial ram who was alone but testing the territorial rams to see if he could force them off and therefore showed some territorial behaviour, was termed 'aspirant'. In the same way, an 'indeterminate' was a ram who had recently lost his territory and was yet to join a bachelor herd, thus showing a lag in the data changing from territorial to bachelor status. The other situation needing its own category was for rams that held territories after the rut. Territoriality slowly relaxed as the year progressed after the rut and, as a result, territorial rams began to show the behaviour of non-territorial rams, becoming more tolerant again to other rams in the area. This was determined as 'relaxed'.

Home range analysis

The location data, as already described, was determined using grids, placed onto a map of the study site. These were then converted as points on a map using the ArcView$^®$ GIS software (version 3.2). With several data points per ram per day in some cases, all data points were labelled by date for each animal, and it was then possible to select any combination of dates on which to carry out analyses. The importance of these maps was to analyse the home range of each individual, and compare these ranges for periods when rams were territorial, versus when they were not. This should show the relative sizes and areas of the territories occupied at different times by different rams. This was done using an animal movements and ranges extension (Hooge & Eichenlaub, 1998) in conjunction with the Spatial Analyst extension (version 1.1) of ArcView$^®$. To analyse this a large number of methods are available and all have varying uses. Ritter (1993) used the HMC method that Boulanger & White (1990) found performed the best of the methods they examined,

yet they found it was imprecise in some situations. Worton (1987) found that estimates of approximately zero or even infinity can occur and bias can increase with sample size. Worton (1995) extended the Monte Carlo simulation but included 95% contour kernel density-based estimators, finding that they out-performed the other methods, whilst being less biased than the HMC method. The most commonly used method in the past has been the MCP method. Many of the authors who estimated impala home ranges used this method, yet Worton (1987) and Boulanger & White (1990) are two who observe that MCP frequently overestimates home range size, with the bias increasing with sample size. This is because it draws a polygon using the outermost points, without accounting or providing information on internal space usage. Even if you select 95% or 90% MCP that remove 5% or 10% of the outliers, it will overestimate on many occasions. However, as part of the purpose of carrying out the present study is in order to compare the home range and territory sizes found in other studies, the MCP method is used to provide a comparable value. It is also relatively simple, both to use and to interpret, explaining why it has been used so much in the past (Bowen, 1982). The Kernel density-based methods on the other hand, provide a method of smoothing locational data to make more efficient use of them, using a least-squares cross-validation (LSCV) method to calculate the global smoothing parameter (Worton, 1989). This means that they are far more influenced by where the points are placed and therefore show core areas (areas of concentrated activity) and boundaries based on various percentage contours, making them more accurate for estimating the utilisation density (UD) (home range) of a ram (Worton, 1987). Tufto, Andersen & Linnell (1996) used the adaptive kernel method of Worton (1989) to measure the home range size of female roe deer (*Capreolus capreolus* L.), calculating the 90% contour so as remove the 10% of points that would represent outliers. Seaman & Powell (1996) suggested that the adaptive kernel method also overestimated the area of the distribution under certain circumstances, and that the fixed kernel gave more accurate areas. This latter method has been infrequently used in the past as it was not often provided on computer analysis programmes. However, due to its availability on the animal movement extension of ArcView[®] and its increased accuracy, a 95% fixed kernel method was used along with the 95% MCP method, to give two estimates of home ranges and territory sizes.

Most authors still use Burt's (1943) definition of a home range. This is "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young". Thus, for the purpose of the present study, the home range included all the points where the ram was observed in the study site, 5% of which were later removed as outliers. It is important to note that I was unable to leave the roads, and was restricted to where I could get in a car and observe with binoculars. Thus, the movement of rams in the dense bush on the hills either side of the open valley areas was often unseen, especially in the wet season when the foliage reduced visibility. As a result any overestimation of the home range analysis methods used may in fact make the estimate more accurate, even if the boundaries could be debated. All home range analysis methods assume the data are independent, something which has hopefully been established by separating any observations by a minimum of three hours. As Boulanger & White (1990) reviewed these various methods, they also made the very relevant point that these estimates of home ranges can never be totally accurate, but instead provide a 'best guess', general measure of the areas used. Worton (1987) states that there is little that can be done if the animal changes its range during the study, unless the change is large enough to be detected in the locational data. It is hoped that by knowing when the switch of rams from territorial to non-territorial or vice versa took place, a change in the ranges used can be shown, and the resulting significance of this investigated.

Home range and territory size data were compared using a paired t-test, as was a comparison between the two methods. In one case, the test for normality failed, and therefore a Wilcoxon Signed Rank test was used. To compare home range size obtained using territorial and bachelor rams, the assumptions of normality and equal variance were not met, and therefore a Mann-Whitney Rank Sum test was applied to the data. The same tests were applied to the body condition and eye colour data as appropriate.

Results

Dates were determined for when each ram fitted the different territorial categories. These data are displayed in Appendix 1. Using the eight rams that were territorial with reliable dates for the beginning and end of their territorial tenure, the

25

duration was an average 67.25 days, which works out as just over two months. The longest observed territory tenure was 99 days, and the shortest reliable tenure was 23 days. Of these rams, three set up territories before the rut and lost them during the rut, one (the shortest) held his territory within the rut, and four took over territories during the rut and held them until territoriality relaxed. Of the other three rams that showed brief territoriality, two showed territoriality lasting an average of 7.5 days, but were only observed for less than ten observation days, and one was territorial but the field data and calculated data differed making it hard to determine reliably. Eight of the remaining rams that were observed on more than ten days were non-territorial (bachelors) the whole time they were observed, and are from hereon described simply as bachelors. Others that had a good enough sample size showed some aspirant behaviour. Mean aspirant behaviour shown by seven rams (one showed aspirant behaviour twice) was 6.13 days (n=8). Four of these rams followed up aspirant behaviour by becoming territorial, the other three did not achieve this and became bachelors. Mean indeterminate behaviour shown by five rams was 6 days.

Home range size varied between individual rams. These are described in Appendix 2 and displayed in figures 6 to 21. It was then possible to calculate the mean home range and territorial sizes of both territorial and non-territorial males.

a)

BLUE 4

Home range size = 21.2 ha
Territory size = 7.3 ha

Territory-MCP
Home range-MCP
Borders

N

0.5   0   0.5   1   1.5 Kilometers

b)

BLUE 4

Home range size = 19.0 ha
Territory size = 10.7 ha

Territory - fixed kernel
Home range - fixed kernel
Borders

N

0.5   0   0.5   1   1.5 Kilometers
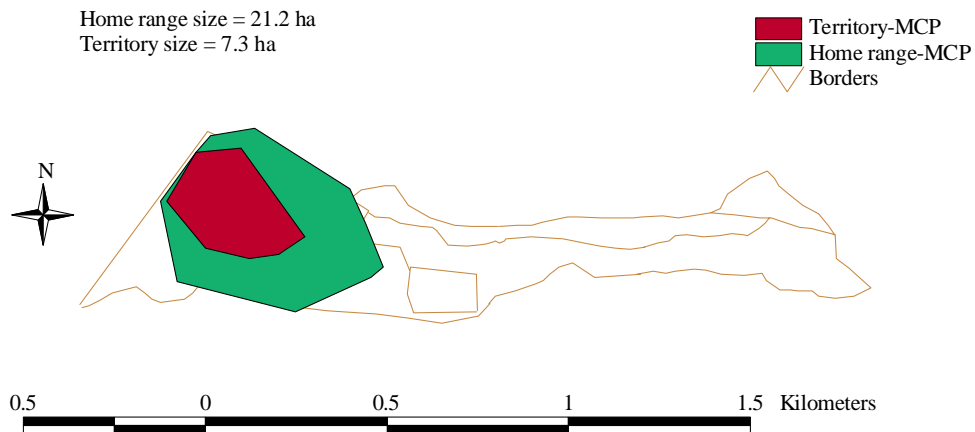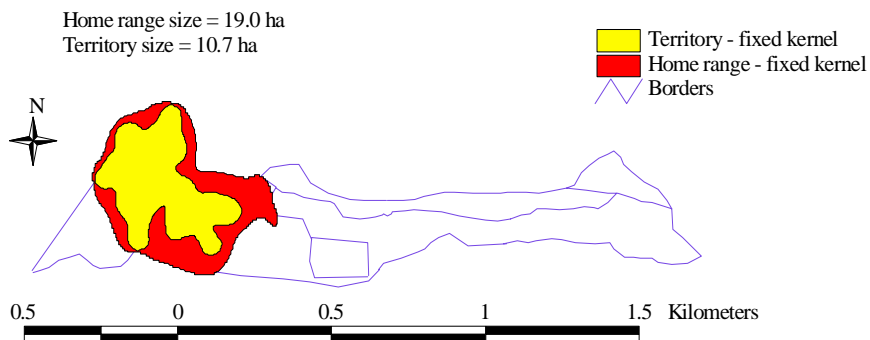
Figure 6 - Blue4 home range and territory sizes using; a) 95% Minimum Convex Polygon, b) 95% fixed kernel method.

a)

PATCH

Home range size = 24.2 ha
Territory size = 11.0 ha

N

	Territory - MCP
	Home range - MCP
	Borders

0.5   0   0.5   1   1.5   Kilometers

b)

PATCH

Home range size = 29.3 ha
Territory size = 16.2 ha

N

Territory - fixed kernel

Home range - fixed kernel

Borders

0.5   0   0.5   1   1.5   Kilometers
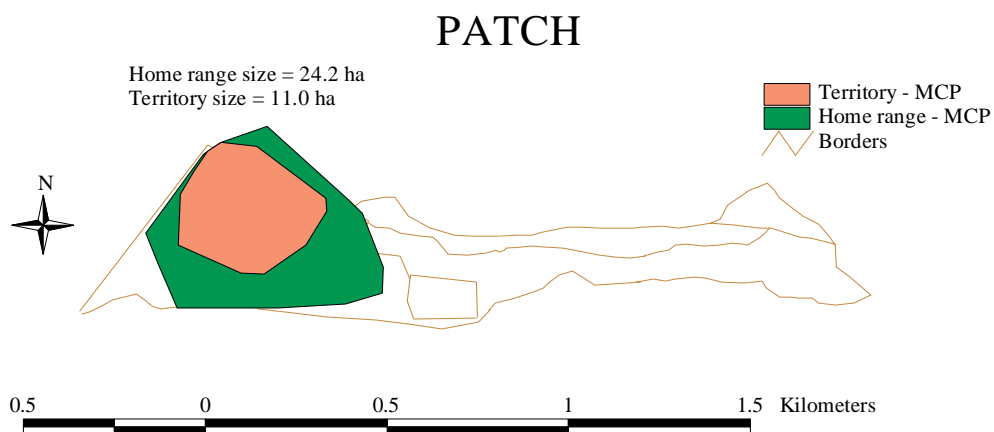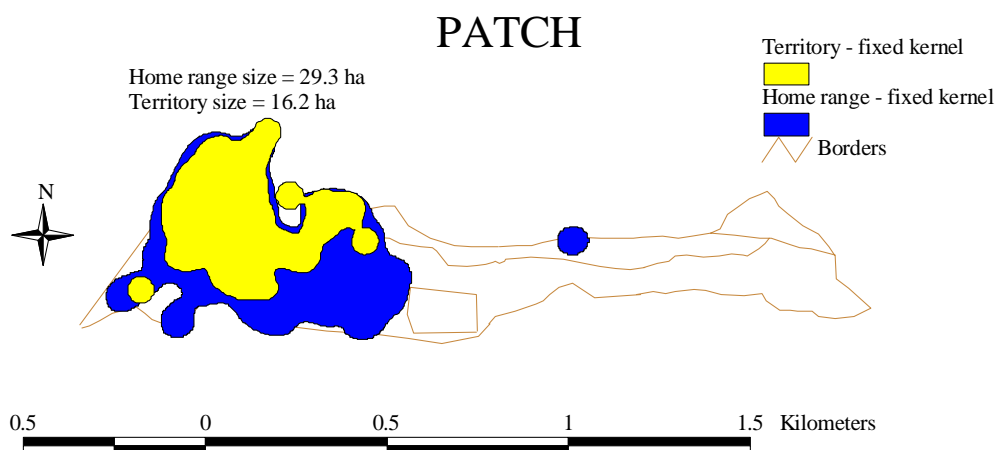
Figure 7 - Patch home range and territory sizes using; a) 95% Minimum Convex Polygon, b) 95% fixed kernel method.

28

a)

BLACK 5

Home range size = 25.5 ha
Territory size = 4.3 ha

Territory - MCP
Home range - MCP
Borders

N

0.5   0   0.5   1   1.5   Kilometers

b)

BLACK 5

Home range size = 30.4 ha
Territory size = 8.6 ha

Territory - fixed kernel

Home range - fixed kernel

Borders

N

0.5   0   0.5   1   1.5   Kilometers
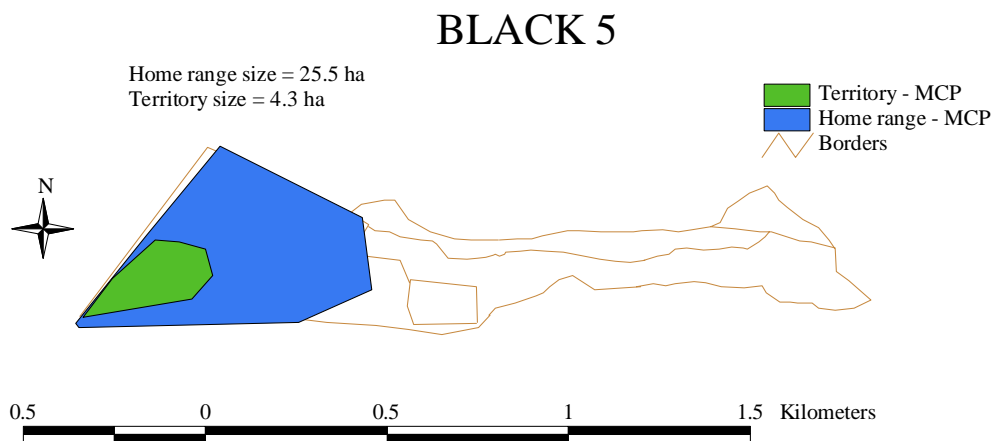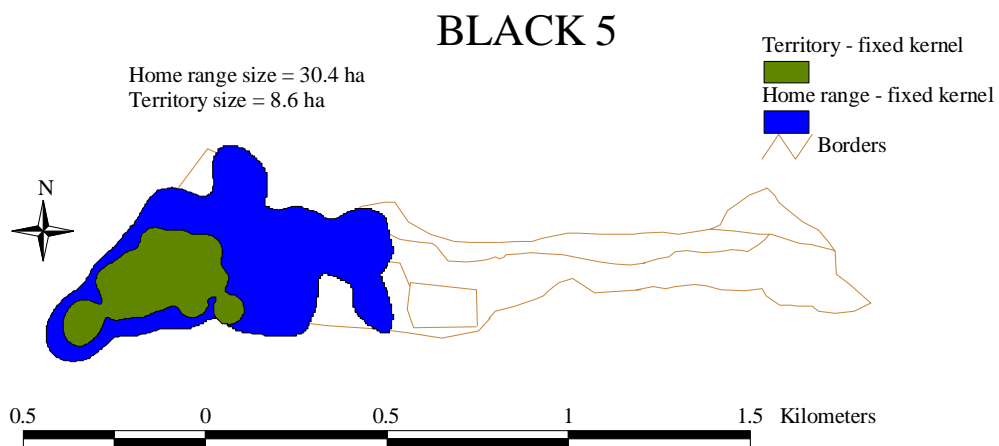
Figure 8 - Black5 home range and territory sizes using; a) 95% Minimum Convex Polygon, b) 95% fixed kernel method.

29

a)
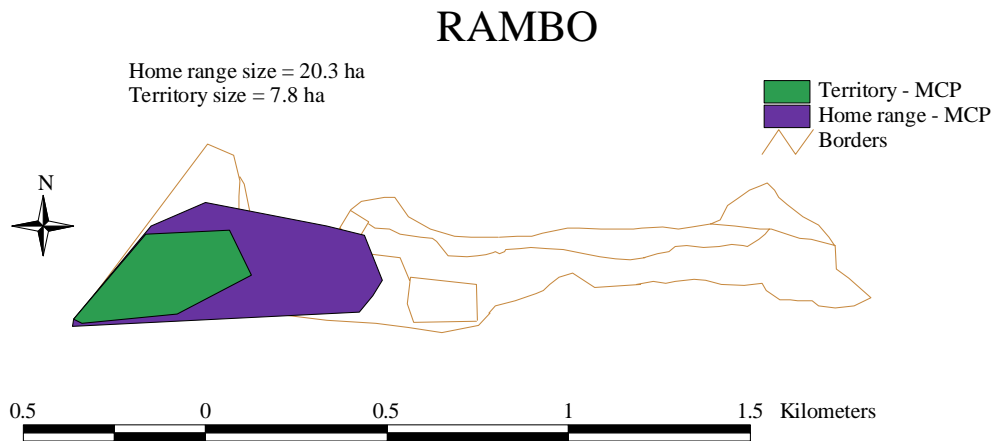
b)
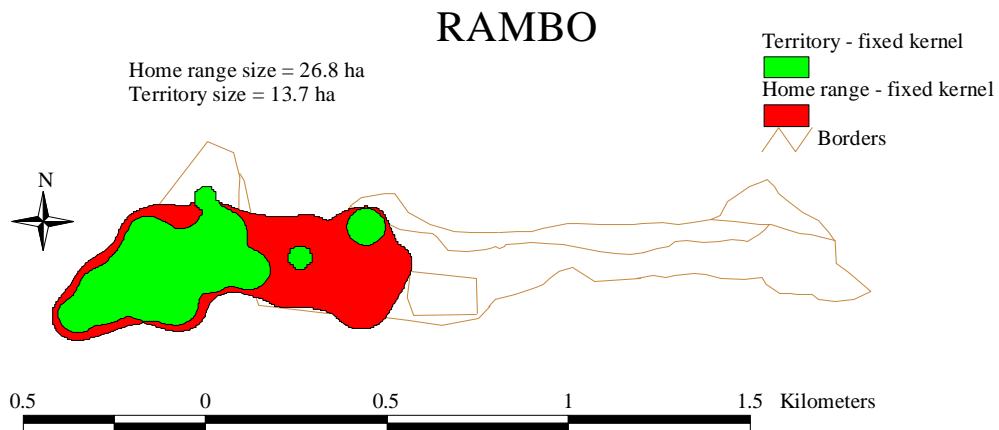
Figure 9 - Rambo home range and territory sizes using; a) 95% Minimum Convex Polygon, b) 95% fixed kernel method.

a)

BLACK

Home range size = 44.1 ha
Territory size = 7.8 ha

Territory - MCP
Home range - MCP
Borders

N

0.5   0   0.5   1   1.5   Kilometers

b)

BLACK

Home range size = 44.9 ha
Territory size = 17.4 ha

Territory - fixed kernel

Home range - fixed kernel

Borders

N

0.5   0   0.5   1   1.5   Kilometers
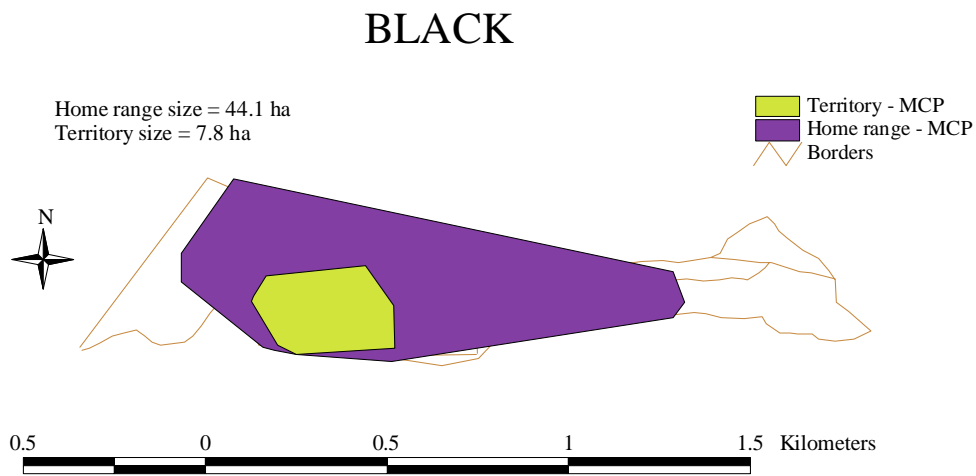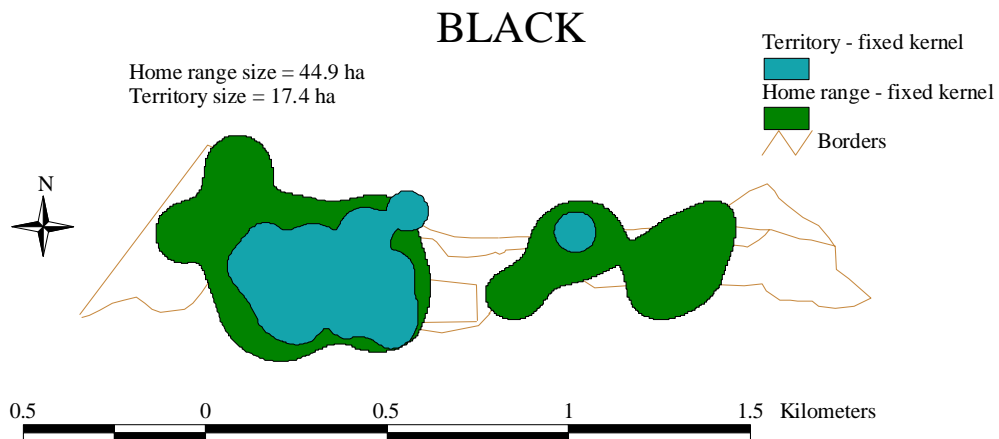
Figure 10 - Black home range and territory sizes using; a) 95% Minimum Convex Polygon, b) 95% fixed kernel method.

31

a)

Y6

Home range size = 38.6 ha
Territory size = 19.3 ha

Territory - MCP
Home range - MCP
Borders

N

0.5   0   0.5   1   1.5   Kilometers

b)

Y6

Territory - fixed kernel

Home Range - fixed kernel

Borders

Home range size = 40.2 ha
Territory size = 28.7 ha

N

0.5   0   0.5   1   1.5   Kilometers
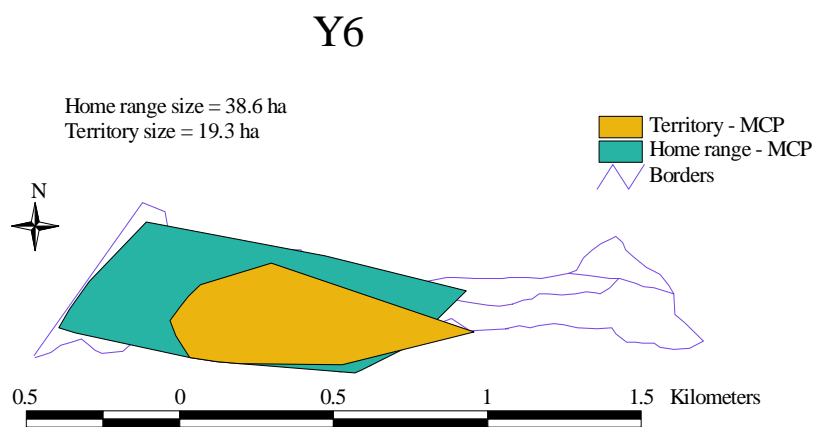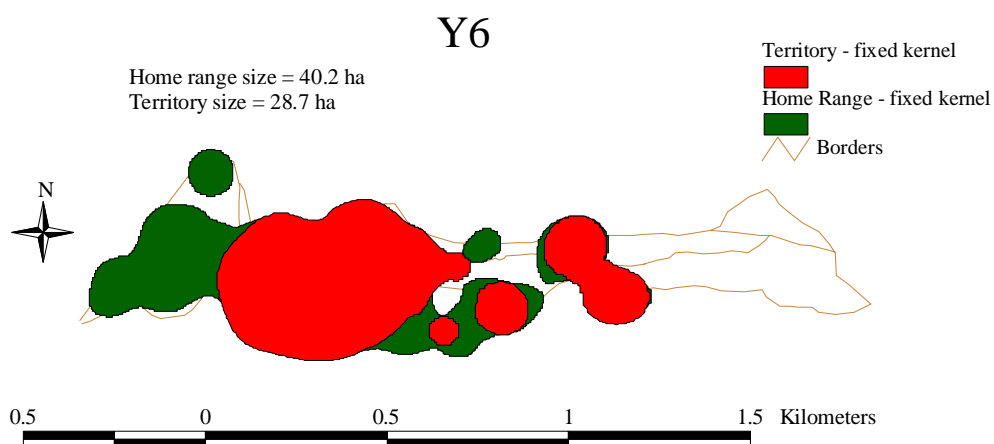
Figure 11 - Y6 home range and territory sizes using; a) 95% Minimum Convex Polygon, b) 95% fixed kernel method.

a)
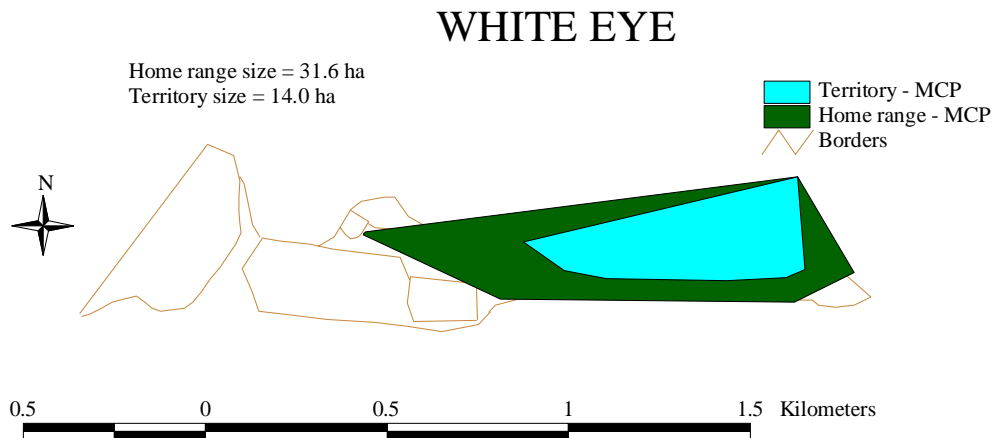
b)
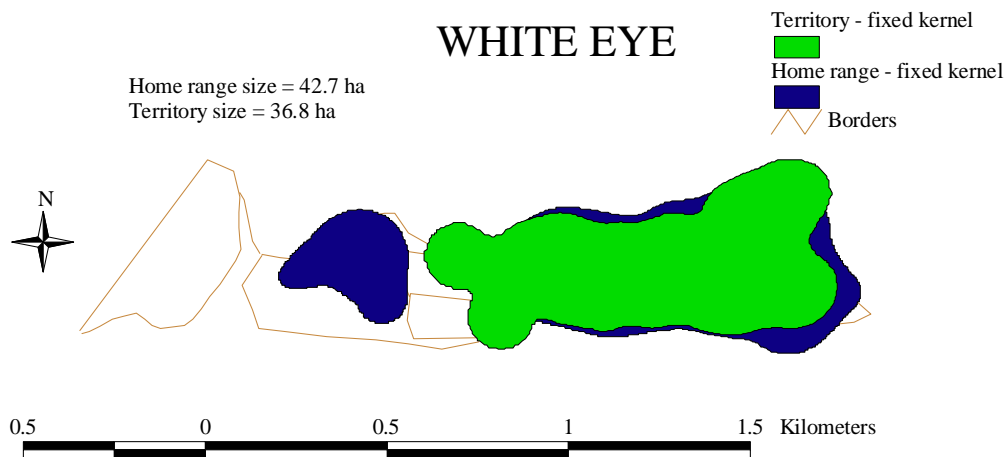
Figure 12 - White Eye home range and territory sizes using a) 95% Minimum Convex Polygon, b) 95% fixed kernel method.

a)

STRIPE

Home range size = 20.2 ha
Territory size = 12.8 ha

Territory - MCP
Home range - MCP
Borders

N

0.5   0   0.5   1   1.5   Kilometers

b)

STRIPE

Home range size = 39.1 ha
Territory size = 36.2 ha

Territory - fixed kernel

Home range - fixed kernel

Borders

N

0.5   0   0.5   1   1.5   Kilometers
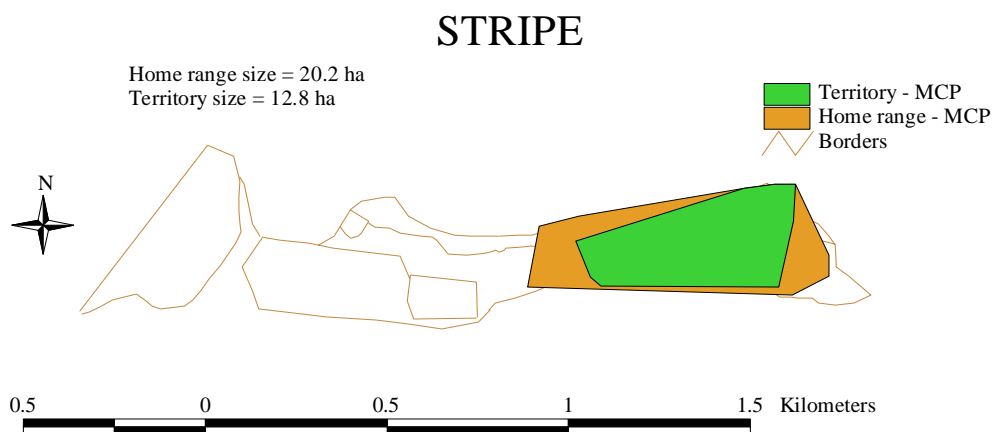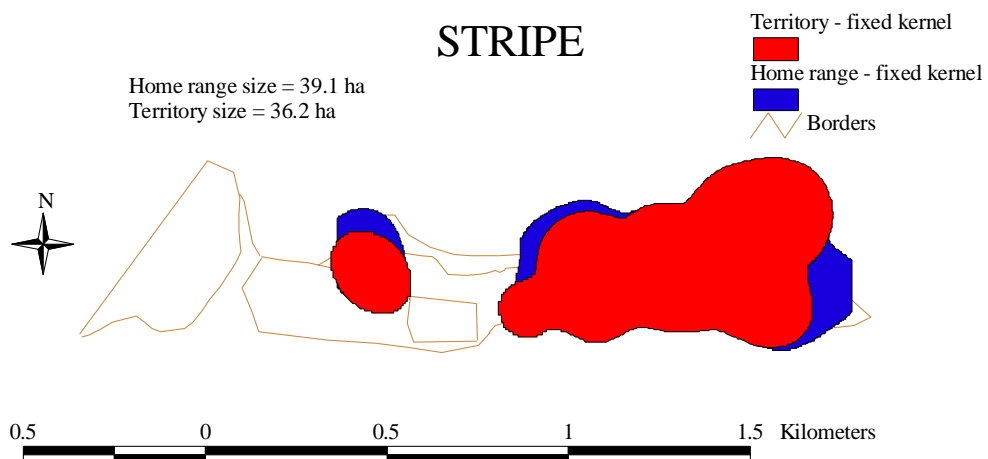
Figure 13 - Stripe home range and territory sizes using a) 95% Minimum Convex Polygon, b) 95% fixed kernel method.

a)

DUNNY

Home range size = 29.5 ha

N

0.5 0 0.5 1 1.5 Kilometers

■ Home range - MCP
⋀ Borders

b)

DUNNY

Home range size = 34.1 ha

N

0.5 0 0.5 1 1.5 Kilometers

■ Home range - fixed kernel
⋀ Borders
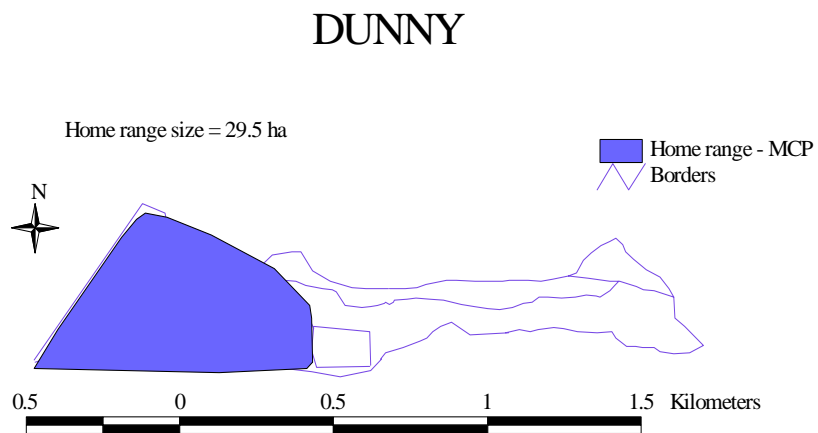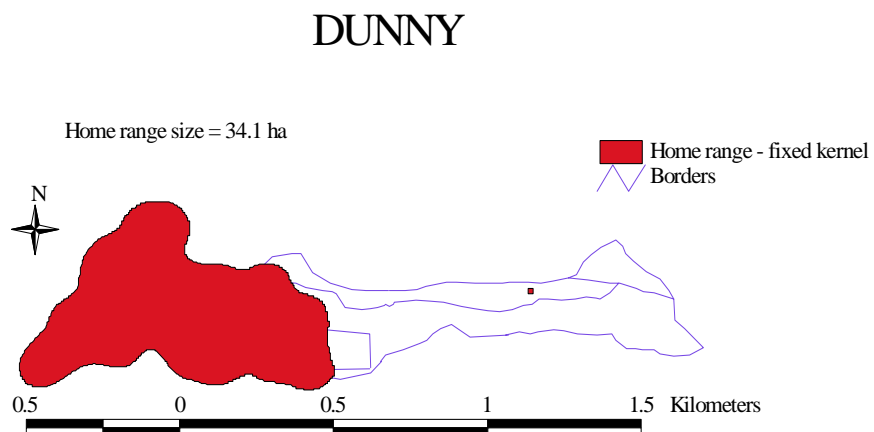
Figure 14 - Dunny home range sizes using; a) 95% Minimum Convex Polygon, b) 95% fixed kernel method.

a)

CIRCLE

Home range size = 59.3 ha

Home range - MCP
Borders

N

0.5   0   0.5   1   1.5   Kilometers

b)

CIRCLE

Home range size = 115.9 ha

Home range - fixed kernel
Borders

N

0.5   0   0.5   1   1.5   Kilometers
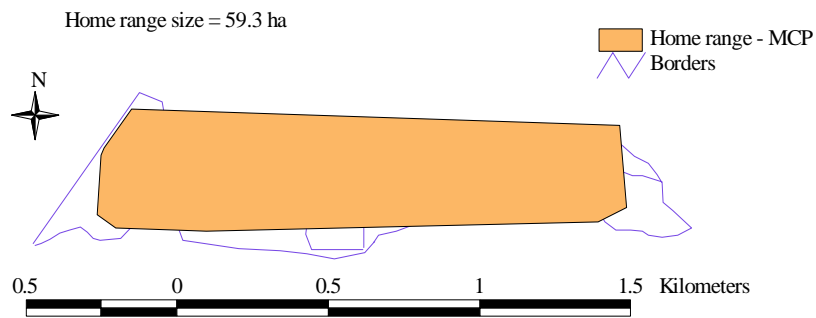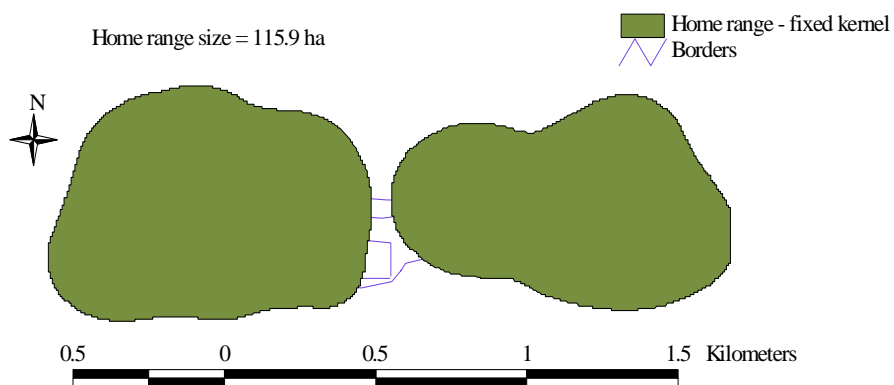
Figure 15 - Circle home range sizes using; a) 95% Minimum Convex Polygon, b) 95% fixed kernel method.

36

a)

EARY

Home range size = 22.5 ha

Home range - MCP
Borders

N

0.5   0   0.5   1   1.5   Kilometers

b)

EARY

Home range size = 64.5 ha

Home range - fixed kernel
Borders

N

0.5   0   0.5   1   1.5   Kilometers
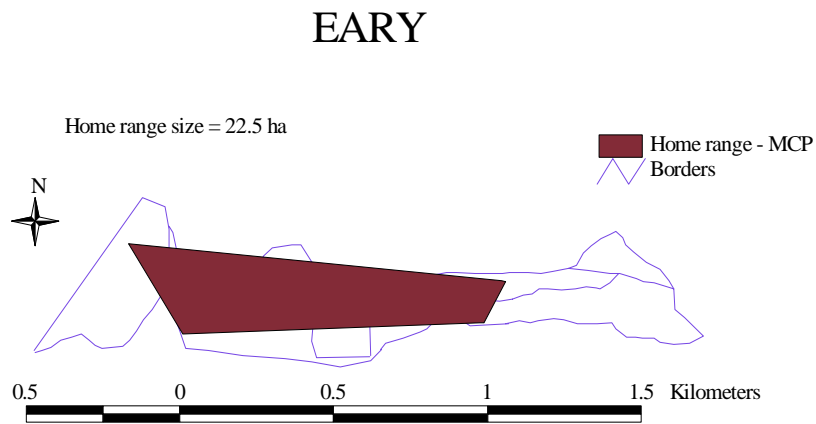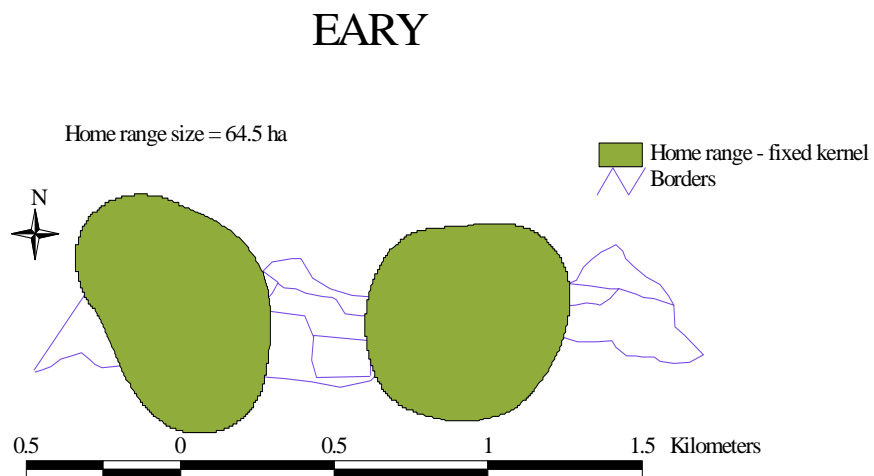
Figure 16 - Eary home range sizes using; a) 95% Minimum Convex Polygon, b) 95% fixed kernel method.

37

a)

FACE

Home range size = 19.0 ha

N

| Home range - MCP |
| Borders |

0.5   0   0.5   1   1.5   Kilometers

b)

FACE

Home range size = 64.4 ha

N

| Home range - fixed kernel |
| Borders |

0.5   0   0.5   1   1.5   Kilometers
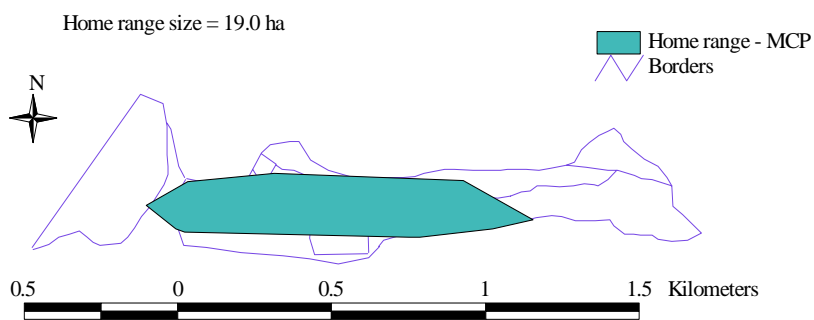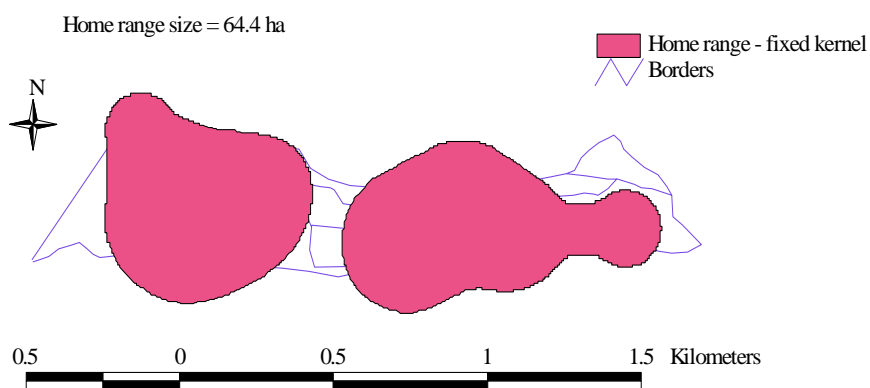
Figure 17 - Face home range sizes using; a) 95% Minimum Convex Polygon, b) 95% fixed kernel method.

a)

HORNEY

Home range size = 29.6 ha

b)

HORNEY

Home range size = 29.1 ha
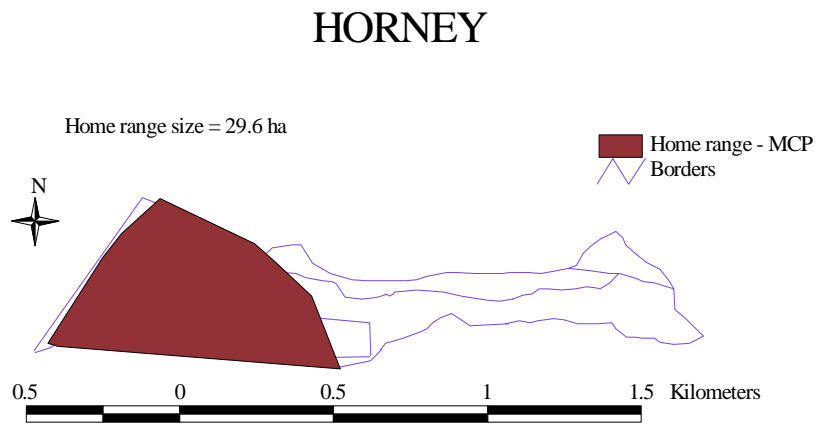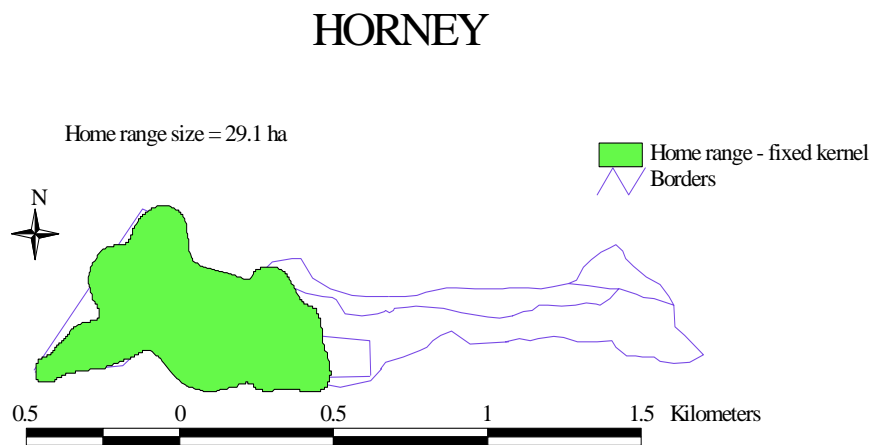
Figure 18 - Horney home range sizes using; a) 95% Minimum Convex Polygon, b) 95% fixed kernel method.

a)

NARROW HORN

Home range size = 27.2 ha

Home range - MCP
Borders

N

0.5   0   0.5   1   1.5   Kilometers

b)

NARROW HORN

Home range size = 29.5 ha

Home range - fixed kernel
Borders

N

0.5   0   0.5   1   1.5   Kilometers
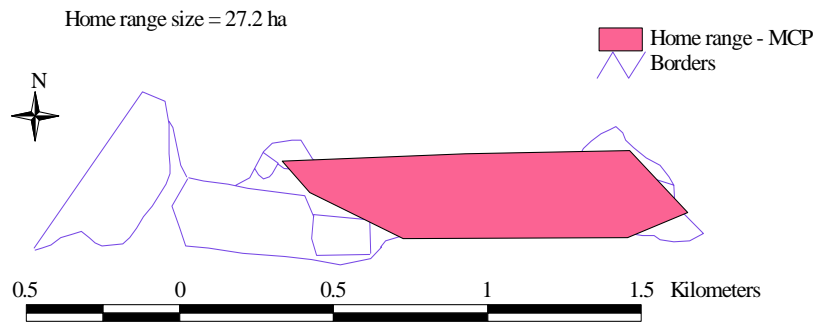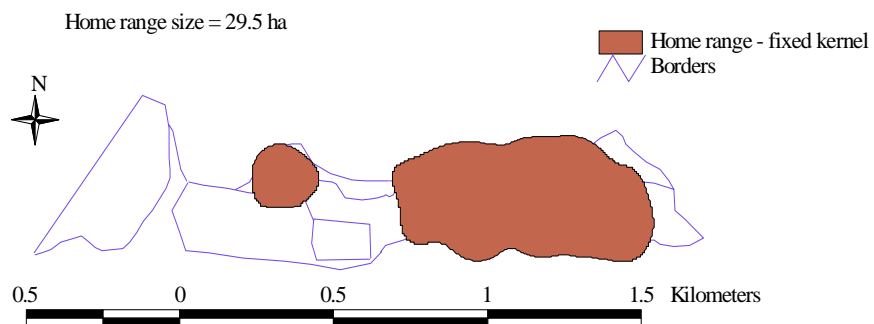
Figure 19 - Narrow Horn home range sizes using a) 95% Minimum Convex Polygon, b) 95% fixed kernel method.

a)

SCARRY

Home range size = 59.3 ha

Home range - MCP
Borders

N

0.5   0   0.5   1   1.5   Kilometers

b)

SCARRY

Home range - fixed kernel
Borders

Home range size = 98.1 ha

N

0.5   0   0.5   1   1.5   Kilometers
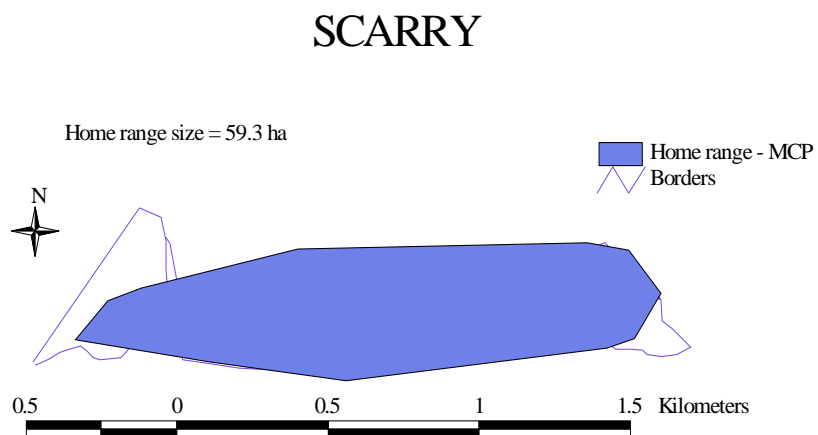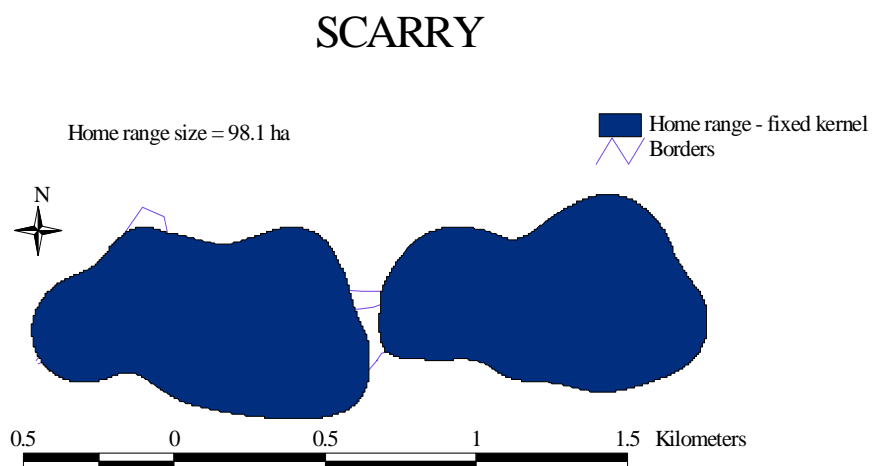
Figure 20 - Scarry home range sizes using; a) 95% Minimum Convex Polygon, b) 95% fixed kernel method.

41

a)

TEARY

Home range size = 32.5 ha

Home range - MCP
Borders

N

0.5   0   0.5   1   1.5   Kilometers

b)

TEARY

Home range size = 35.0 ha

Home range - fixed kernel
Borders

N

0.5   0   0.5   1   1.5   Kilometers
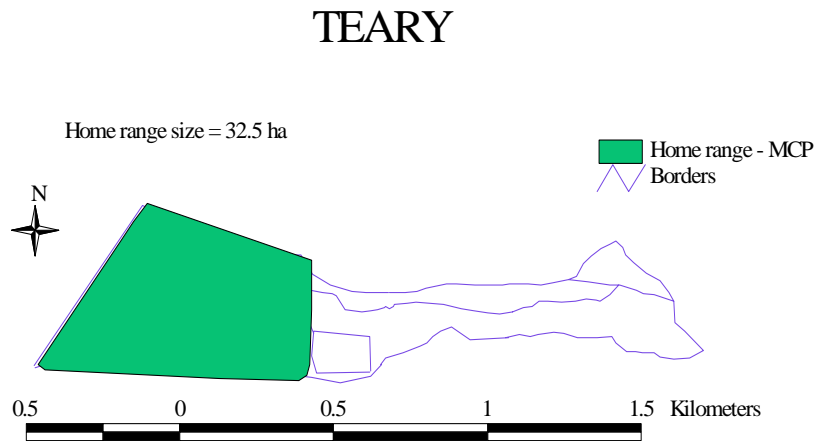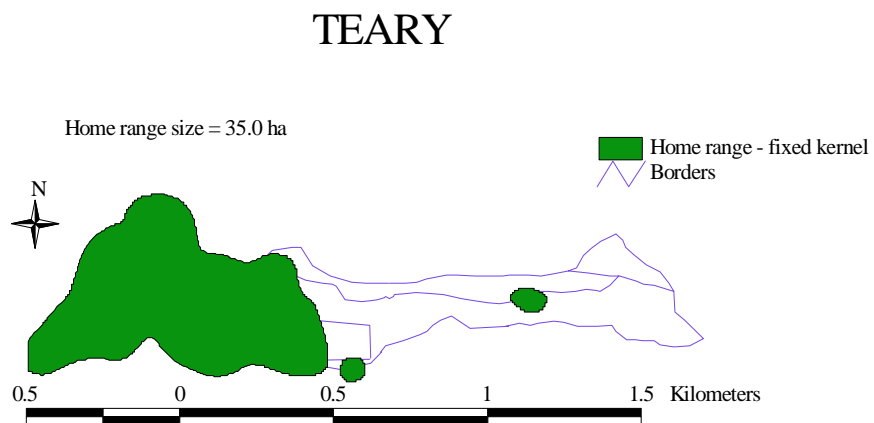
Figure 21 - Teary home range sizes using; a) 95% Minimum Convex Polygon, b) 95% fixed kernel method.

42

FEMALES

Home range size = 75.0 ha

N

Home range - MCP
Borders

0.5   0   0.5   1   1.5   Kilometers
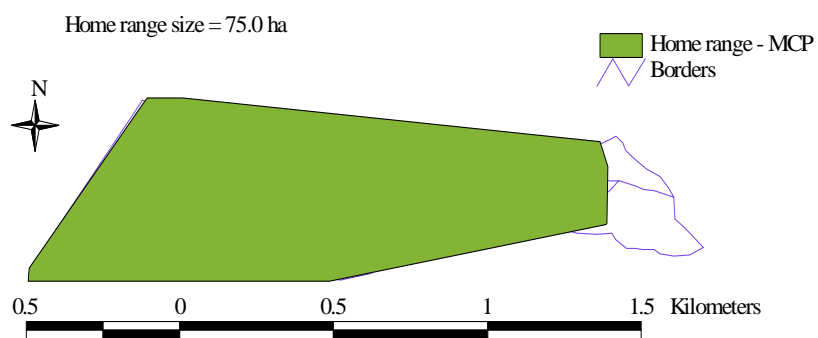
Figure 22 - Females home range size using 95% Minimum Convex Polygon.

YOUNG MALES

Home range size = 54.1 ha

N

Home range - MCP
Borders

0.5   0   0.5   1   1.5   Kilometers
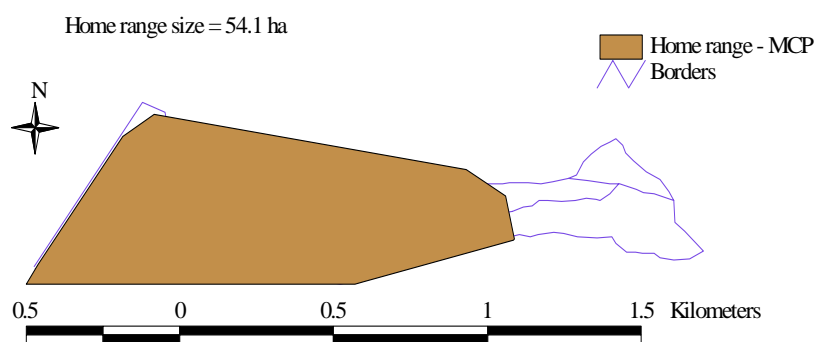
Figure 23 - Young males home range size using 95% Minimum Convex Polygon.

43

Mean home range and territory sizes of these rams are displayed in Table 2.

Table 2 - Mean size of home range and territory size for territorial and bachelor rams.

Territorial Rams	Home range – 95% fixed kernel (ha)	Home range – 95% MCP (ha)	Territory size – 95% fixed kernel (ha)	Territory size – 95% MCP (ha)
Mean	34.1	28.2	21.0	10.5
Standard Deviation	9.03	9.03	11.27	4.76

Bachelor Rams	Home range – 95% fixed kernel (ha)	Home range – 95% MCP (ha)
Mean	58.8	34.9
Standard Deviation	33.35	15.67

There is a significant difference between home range and territory sizes of territorial rams using both the fixed kernel (Paired t = 4.518, df = 7, P = 0.003) and MCP (Paired t = 5.753, df = 7, P < 0.001). Note that there is also a significant difference in home range size estimated by the different fixed kernel and MCP methods, both for territorial (Paired t = 2.489, df = 7, P = 0.042) and bachelor (Wilcoxon W = -34.0, n = 8, P = 0.016) rams. There is also a significant difference between the territory sizes estimated using both methods (Wilcoxon W = -36.0, n = 8, P = 0.008). However, there is no significant difference using fixed kernel (Mann-Whitney T = 55, n = 8, P = 0.20) or MCP (Mann-Whitney T = 60, n = 8, p = 0.44) between territorial and bachelor ram home ranges. In comparison, young male home range size was estimated at 54 ha (0.54 km^2), and female home range was 75 ha (0.75 km^2), using a 95% MCP (Figures 22 and 23). It was estimated that approximately 40 females were present in the study site along with their young.

The area inhabited by territorial males is also different. Using the MCP and fixed kernel diagrams, it seems clear that there were four territories held within the study site. These were those held by:

1) Blue 4 and then Patch (Figures 6 & 7),

2) Black 5 and then Rambo (Figures 8 & 9),

3) Black and then Y6 (Figures 10 & 11),

4) White Eye and then Stripe (Figures 12 & 13).

As a result, at any one time there were four territorial and therefore approximately 15 non-territorial rams in the study site. The dates of territory take-overs are often hard to establish accurately as the event was not always seen. The dates when territorial rams ended their territoriality are shown in Table 3, along with the process in which it happened, where observed.

Table 3 - Last date of observed territoriality, with method of territory loss where observed.

* Full dates of territoriality are not certain, but loss, as shown here, was observed and therefore included.

Only ten observation days or less are available for this animal.

LAST DATE OF OBSERVED TERRITORIALITY	RAM	METHOD OF TERRITORY LOSS
11/05	Cheeky *	Chased by Black
12/05	White Eye	?
16/05	Black5	Chased by Blue4
16/05	Blue4	Lost fight with Nosey
21/05	Roman #	?
25/05	Angry #	?
07/06	Black	Chased by Y6
20/07	Rambo	Relaxed
25/07	Stripe	Relaxed
02/08	Y6	Relaxed
07/08	Patch	Relaxed

Matings were observed by three rams on four occasions, and mountings as well as genital licking of females was also observed. Using the data from Appendix 1, the territorial status of the rams showing reproductive behaviour was established and is displayed in Table 4.

Table 4 - Territorial status of rams performing mating and sexual behaviours towards females.
* Juvenile males were observed carrying out these behaviours, even though they are approximately 6 months of age and therefore presumed to be sexually immature.

RAM	DATE	BEHAVIOUR	TERRITORIAL STATUS
Nosey	09/04/2001	Mount	Aspirant
Black	16/05/2001	Mount	Territorial
	23/05/2001	Mount	Territorial
Dark	16/05/2001	Mount	Aspirant
	16/05/2001	**Copulation**	Aspirant
Roman	16/05/2001	Mount	Territorial
	16/05/2001	**Copulation**	Territorial
Stripe	21/05/2001	Mount	Territorial
	04/06/2001	Mount	Territorial
	04/06/2001	Lick Female	Territorial
	21/05/2001	**Copulation**	Territorial
	04/06/2001	**Copulation**	Territorial
Juvenile Male *	16/05/2001	Mount	Juvenile
	04/06/2001	Mount	Juvenile

The date of first observed mating was 16th May 2001, which was nine days after the full moon. First observed birth of impala lambs on the reserve was estimated from the observation of one-day-old lambs at 29th November 2001 which is 197 days after the first observed mating date. A herd of young impala in the study site were estimated to have been born around 12th December 2001. Using the gestation period of 195 – 200 days stated by Skinner & Smithers (1990), the conception date of these lambs is calculated as between 27th May and 1st June.

No significant differences were found between territorial and bachelor males in the various morphological measurements. When examining eye colour, a chi-squared test was applied to compare the number of rams with a rating of 1 and 2 (no black and slight black) with the number of rams with a rating of 3 and 4 (black and very black). Unfortunately, it was only possible to get pre- and post-rut data for seven territorial and 5 bachelor rams and, as a result the chi-squared fails, as 25% of the cells have expected counts less than five. A Fisher's Exact test was applied, but no significant differences were found (P = 0.14). In the same way, body condition was assessed using a similar method, but again a Fisher's Exact test found no significant differences between the number of territorial and bachelor rams with a condition rating of 1 and 2 (poor and bad) and those with a rating of 3 and 4 (fair and good) (P = 0.14).

Discussion

The observed territorial behaviour is extremely interesting in light of previous research. As discussed, Jarman (1979) found a mean territorial tenure of 82.5 days, which compares with the 67.25 found here. Not only is the mean territorial tenure shorter, but the variation in tenure length is also lower, with the maximum tenure of this study noted as 99 days, as opposed to 267 by Jarman (1979) in east Africa. The minimum observed by Jarman was 5 days, which is less than the 23 days observed in the present study, although fairly similar to the 7.5 days averaged by rams who held territories during the rut, but who were not observed for more than ten days. This fits with the theory that the seasonal habitat of southern Africa results in a shorter breeding season, which seems to be reflected in shorter territorial tenures.

The first observed mating occurred on 16th May, which is thought to be fairly reliable, as the first lambs were born on the reserve 197 days after this date on 29th November. This fits with the gestation period described by Skinner & Smithers (1990), and even more so with the 196 days suggested by Fairall (1969b). As a result, first conception on 16th May occurred nine days after full moon, which is more than the six days stated by Murray (1982b). Although this is a small difference, there is no evidence to support the role of the lunar cycle, and it is far more likely that daylength is the sole controlling factor, as noted by Skinner & van Jaarsveld (1987). It is also

47

extremely interesting that three rams set up their territories relatively early in the year, during February, and yet all lost them during the rut before or on the day of the first recorded mating. This is contrary to the observations of Murray (1982b) that relations between territorial rams stabilised with the start of mating. In two cases rams lost their territories on the first day of the mating season, and this started a high degree of instability for approximately a week in these areas before rams finally took over the territories and held them for a significant time. As a result, one can conclude that setting up territories early in the year did not guarantee mating opportunities. It is therefore possible that these rams are younger ones that have not yet developed the characteristics necessary to hold a territory during the most competitive period of the rut. This setting up of 'practice territories' has not been documented before. It is possible that the length or success of setting up early territories is also extremely dependent on factors such as rainfall and therefore nutrition.

Unlike the observations of Jackson (1995) in springbok, and Leuthold (1970) and Murray (1982b) in impala, it seems that mating is not exclusively carried out by territorial males. Although the sample size is extremely small as only three mating rams were observed, one (Dark) was rated as aspirant when carrying out the mating. It took place amongst bushes, a small distance away from the territorial male and the main female herd. Therefore, the ram certainly was not the territorial male, but instead benefited from a 'sneak' mating as the territorial male was busy protecting the main female herd which is likely to have contained several oestrous females due to the synchronisation of oestrus as described by du Plessis (1972) in blesbok. This kind of 'sneak' mating is fairly unusual because normally if a ram shows interest in a female, he has to chase her around a lot before she submits and allows him to mount her. This attracts the attention of the territorial male, who chases away the intruder. Mounting (but not copulation) was also seen by another aspirant male (Nosey) and also by juvenile males. The latter mounted females that had just been mounted or mated by the territorial male in the female herd in which they still resided. Interestingly, the territorial ram did nothing to try and stop them or to chase them out of the herd, something that would certainly have happened if they had been a year older. It is likely that this is because though they perform this innate mounting behaviour, they are not yet sexually mature (Hanks *et al.*, 1976), and therefore did not

show the sexual behaviour driven by hormones that would have resulted in their certain expulsion.

The size of home ranges and territories differed from those recorded in earlier studies. Certainly the female and young male home range sizes are considerably smaller than those estimated by du Toit (1990) and even Young (1972), but this is expected as no known individuals were monitored amongst female and young male herds. Unfortunately it was only possible to carry out MCP estimates on these data. The observations were also limited to the study site valley earlier described, and therefore any movement outside that site was not included in the data.   This contributes to what could be a significant underestimate in home range size. This is also likely to be true for adult male impala, whose home range size when non-territorial, is similar to the female size estimated by Murray (1982a) in Zimbabwe. Using the fixed kernel estimate of 34.1 ± 9.03 ha (0.34 km^2) for territorial rams, and 58.8 ± 33.35 ha (0.59 km^2) for bachelor rams, these home ranges are lower than those described, the nearest of which is the 92-170 ha (0.92-1.7 km^2) (Murray, 1982a). The MCP estimates in the present study are even lower. Once again, it is likely that some movement of the rams was not included due to restricted visibility or mobility by the observer. Importantly, there is no significant difference between the home range size of territorial and non-territorial males due to the large variance. As a result, it is possible to conclude that when not territorial, all rams have a similar range in the area they inhabit.

The territory sizes on the other hand seem more reasonable, with the mean of 21.0 ± 11.27 ha (0.21 km^2) estimated using the fixed kernel and 10.5 ± 4.76 ha (0.11 km^2) using the MCP, comparing with 0.5 km^2 calculated by Murray (1982a), and 0.42 – 0.45 km^2 estimated by Jarman (1979). As was noted in the Results, there is a significant difference between the home range and territory size of territorial males, the latter being less than half the size of the former. Clearly when a ram is territorial, he restricts his movement which, whilst enabling the ram to mate with any females that enter his territory, also means that he is restricted in the number of available feeding sites and vegetation choices. As a result, the condition of the ram will be expected to drop, until he either loses his territory, or the territorial system collapses as a result of the decline in testosterone (Skinner, 1971).

49

It is apparent from the G.I.S. maps, and also from the calculated home range and territory sizes, that there is a large discrepancy between the estimates provided by the 95% MCP and 95% fixed kernel home ranges. In most cases, the MCP estimate was lower than the fixed kernel, the fixed kernel estimate being approximately double that of the MCP in the case of territory sizes. This seems to contrast with observations by Worton (1987) and Boulanger & White (1990) who suggested that MCP overestimates home range size. Clearly using a 95% as opposed to 100% MCP will have removed much of the overestimation, but it is likely that the shape and nature of the study site has also acted to restrict overestimation in both methods, instead tending towards underestimation. This is due to the fact that the area worked in was a long thin valley with steep inaccessible sides on which few if any impala sightings were recorded. As a result, movements onto these slopes may have gone largely unrecorded, and therefore 'expansion' of the home range estimate did not occur into these areas, as no data points were obtained there. The fixed kernel method suggested by Seaman & Powell (1996) is also likely to be affected in this way, and yet is much more likely to give an accurate home range estimate because it does not simply use observation points in which to draw the probability boundaries, as MCP uses points to draw the polygon perimeters. Thus, the fixed kernel method may 'hypothesise' more, which in this case is likely to be a benefit rather than a negative characteristic leading to overestimation. It is important to note however that in some places, the boundaries of the 95% fixed kernel may be not possible in the real world scenario. If you examine some diagrams such as Figures 15b and 16b, it is clear that the kernel boundaries cross the road that runs down the western edge of the study site. This is impossible due to the fence marking the edge of the reserve along that road, so the boundaries must not be taken as entirely real in the actual situation, but instead allowed simply as part of the home range size estimation.

There were four main territorial areas, which the eight main territorial rams held, four earlier and four later in the year. Clearly there were other rams between those, but as explained at length, it is not possible to include them, largely because only partial data are available. It does seem evident though that the later territorial rams held largely the same territorial areas, as those who held them earlier in the year. For example, in figures 6 and 7 it is possible to see that Patch took over a very similar territorial area to that held by Blue4, and likewise in the other cases of Black5 and

Rambo (Figures 8 & 9), Black and Y6 (Figures 10 & 11), and White Eye and Stripe (Figures 12 & 13).   These data and field observations suggest that the boundaries between territories were rigid as noted by Novellie (1975) in blesbok. It is largely unclear what defines these boundaries, but it is suspected that some geographical features are used, such as the ditch and denser bush present on the eastern side of the Black 5 / Rambo territory separated it from the territory of Black / Y6 (see Figures 8 - 11, and study site photo in Chapter 2). Each territory was based around a large open area that therefore contained both abundant grazing, as well as ecotone, the preferred habitat of impalas (Young 1970). This reflects the easier ability for the ram to be spotted by the observer in open areas, but also the fact that impala prefer to be in the open, especially in the evenings, to facilitate vigilance. Although the steep slopes apparently were not frequented as much, it was not easy to observe impalas there. It is however interesting that three of the four rams holding territories in the later part of the year (Rambo, Patch, and Y6) all have larger territory sizes than their predecessors holding the same territory earlier in the year. This would seem to coincide with them also being seen more at the waterhole in the middle of the study site, and therefore is likely to reflect the need for rams to visit the waterhole (and salt lick present there) more often in the dry season. A salt lick further east is also likely to be responsible for observations of an isolated home range spot by Patch (Figure 7b), and in the territories of Black (Figure 10b) and Y6 (Figure 11b). Dasmann & Mossman (1962) infer that all territorial males have to visit water holes daily, and thus the surrounding area acts as a neutral territory. This would benefit both bachelor and territorial males who need water access and ideally a salt lick in the dry season and, for the resident territorial male who would find it extremely hard to challenge every ram that visited, especially as they would be determined to drink out of physiological necessity. Moreover, those areas that are nearer the waterhole are the areas of the study site in which females seem to be more common. As females moved through the study site to gain access to water, males would try and herd them as they came and went, to restrict them to their territories as they travelled to and from the waterhole. The territory size of the Blue4 / Patch, Black5 / Rambo, and Black / Y6 territories are all smaller than the other White Eye / Stripe territory. This may reflect the fact that where females were more common, due to the presence of the waterhole, the territories were smaller as a result of increased competition for female access. Non-territorial males seem to inhabit all parts of the study site, showing individual variation but not consistent

restriction from certain areas. The effect or otherwise of this on diet is discussed in Chapter 4, but it is clear from these diagrams and also from field observations that, although bachelor males maybe restricted in their access to females, over time they are not geographically restricted from visiting any areas of the study site.   In fact, bachelor rams seem to be tolerated wherever they are in whatever season, providing they do not show interest in females, a situation commented on by Mooring (1999). The same can be said for all rams going to the waterhole, a trip that must invariably take them through other territories. Providing they do not show interest in females, they are largely unchallenged.

The method of territory loss is also important. Four rams that took over territories towards the end of the rut simply relaxed their territoriality around the end of July to beginning of August. This is not to say that they stopped herding or chasing females, although this also decreased.   More importantly, they reduced their aggressiveness towards other rams, allowing them to intermingle with the females within the territory, without chasing them away. This compares to three territorial rams that were observed being chased off their territories. In the case of Cheeky, the chasing ram (Black) was an aspirant who had been in the area for several days and had continually tested the reign of the territorial ram, chasing and herding females at the edge of the territory. Clearly on the day of the take-over, the territorial ram assessed that he would not win a fight, and therefore chose to flee. A similar situation occurred in the case when Black lost his territory to Y6. Although Y6 was officially rated as a bachelor, it was apparent to the observer that he was also showing interest in the females, and thus eventually the territorial male also chose to flee when challenged on the date in question. The final ram Black5 was observed being chased by the neighbouring territorial ram Blue4. This was an extremely unusual event, not least because the chasing ram also lost his territory later in the day. It is possible that, as this day was when the first matings were observed, the presence of oestrous females may have caused increased excitement and aggressiveness in males which therefore challenged and chased other rams they would normally have left alone, causing those which were already weak or tired, to give up their territory.

In the case of Blue4, this ram lost his territory as a result of a fight with Nosey. The territorial ram Blue4 was maintaining a female herd of some 17 individuals in his

territory, whilst 4 adult and 4 young males chased and hassled females as much as possible. This resulted in the territorial male chasing an adult or young male 16 times within an hour, and chasing a female four times. When it came to a display and then fight against Nosey, Blue4 lost. It is highly likely that this was due to the exertions of the afternoons activities, and is supported by the fact that Nosey was officially categorised as only an aspirant rather than territorial once he took over. This was because he did not seem to defend the territory for any significant time scale, whilst being absent for portions of the day. Blue4 was indeterminate for almost a week after the territorial loss, but it is important that regardless of why he lost his territory, it was never regained and the ram eventually became a bachelor, joining other rams. No injuries were inflicted during fights amongst rams, as far as could be seen.

The question of aspirant and indeterminate categories is one that has not been addressed by other authors, but is an important aspect in the territorial behaviour of impala rams. As observed, in seven rams (one other, Cheeky has data that do not correlate closely with the field observations, and is therefore not included in the analyses), aspirant behaviour was observed for an average of 6.13 days. In four of these cases, territorial behaviour followed, but in the other three cases, the ram left the area, or returned to bachelor-hood. This coincides with the presence of a number of new rams in the study site during the rut, and with the increased interest of bachelors in the females. Aspirant behaviour defined this period of female interest, and testing of the territorial ram. Some aspirant rams were ultimately successful and then took over a territory, whilst others were not successful and gave up. In two of these rams, the aspirant behaviour took place in early February. This is a measure of the beginning of male reproductive activity in the build up to setting up territories and ultimately, the rut. One ram (Nosey) was recorded as being aspirant twice. This was because although he seemed to take over a territory, the data did not support full blown territoriality, and therefore it was decided that he would be classified as an aspirant ram who took the opportunity to take over a territory, without truly ever becoming territorial.

In the same way, indeterminate behaviour observed in five rams (again, Cheeky is unreliable and therefore not included) averaged six days. This described behaviour lasting just under a week in the period after a territorial male had lost his

territory. However, in general the data did not support the field observations that he was no longer territorial, showing the ram to continue in a dominant, territorial way over other animals, and largely remaining on his own or where possible, with females. The same was seen and recorded by Jarman (1979) who observed that re-integration with bachelors was usually gradual, and found that the longer the territorial tenure, the more likely the ram was to rejoin the bachelors quickly. It is difficult to show the same with such a small sample size, but there does seem to be some sort of inverse relationship, whereby Black has a territorial tenure of 23 days and an indeterminate period of 15, as opposed to Black5, Blue4 and White Eye who have territorial tenures of 80, 99 and 88 days respectively, with indeterminate periods of 6, 6, and 2 days. Clearly this can be affected by other factors such as presence of the ram in the study site (without which it is hard to define his social status), but there is no evidence to disprove Jarman's (1979) theory. This indeterminate behaviour is explained as a lag in the psychology (and possibly physiology) of the ram. Having lost his territory, it is unlikely that he can easily switch from being dominant and aggressive over all other males, to suddenly join up and act passively in a bachelor herd. It is unclear why rams that had held territories for longer, would then join up with a bachelor herd quicker, as it is thought that they may be more aggressive. Perhaps the longer tenure leads to a weaker condition so that when the territory is finally lost, the ram is no longer as aggressive or as dominant as others are. It is emphasised that the relatively simple way in which the social categories were determined using data and field observations can only act to emphasise this indeterminate category, where social status in the data is unclear and therefore hard to categorise.

The various morphological measurements taken unfortunately showed no differences between territorial and bachelors, unlike the observations of Skinner (1971), Spinage (1971), and Jarman (1979). This is more than likely due to the method that was used. It was extremely difficult to dart impala in the study site, and as a result only nine of the known rams were caught, measured and collared. The rest were simply identified by visual characteristics and as a result, were not caught and measured. There was also the problem that rams were caught in different periods of the year, so that no consistency in the age or social status of the rams was maintained.

On the other hand, assessing condition and eye colour (black eye patches) visually was possible, although at times difficult. Again, due to the difficulty in measuring these characteristics in rams at a similar time in order to compare them, only seven territorial and five bachelor rams were used. This compares to the 150 rams used by Jarman (1979). In contradiction to her findings, no significant difference was found in the presence of black patches around the eyes in territorial versus bachelor rams, nor were there differences in the condition of rams. It is extremely difficult to conclude anything from these data however, due to the small sample size. It was also difficult to assess these characteristics visually when the animal was moving around. It was far easier when they were darted, and once again the data would have been much more accurate should more animals have been immobilised. However, there certainly did not seem to be any differences between the black patch markings between territorial and bachelor rams, and as a result, no evidence was found to support this as a reliable indicator of territoriality. In the same way, all rams seemed to be in reasonable condition pre-rut, and although some certainly lost condition, there were no dramatic changes that would indicate clearly why a ram lost his territory. It is likely that kidney fat index, as described by Monro & Skinner (1979) is far more accurate, and thus only by culling animals at different times of the year and assessing them in this way, can you get a true idea of the change in condition that occurs.

This knowledge of impala reproductive behaviour is important for reserve management. Young (1992) notes that the hunting and game capture season coincides with the mating season of the impala, and that big rams with beautifully shaped, long horns are often shot first during culling or as trophies. In addition, they are commonly shot for fresh meat biltong and are therefore important in the game ranching industry. Young (1992) therefore recommends that it would be better to hunt from the bachelor herds, and that culling should start as early as possible, preferably before the mating season. The black impala colour variant found at Touchstone Game Ranch (see Chapter 2) are also extremely valuable, reaching up to R140,000 at game auctions, instead of a price of approximately R650 for a common impala. Any information that can be used to manage these animals is clearly extremely useful.

CHAPTER 4

DAILY BEHAVIOUR OF TERRITORIAL AND NON-TERRITORIAL RAMS

Introduction

Jarman & Jarman (1973a) examined impala diurnal behaviour at different times of the year. They found that the most important behaviour was feeding, followed by ruminating, standing, moving, grooming and lying down. Feeding behaviour of impala has been examined for a number of populations. Dunham (1982) found that feeding time per unit distance covered peaked during the wet season and was at a minimum in the dry season, increasing with the onset of rain as the new growth occurred. Hofmann & Stewart (1972) classified impala as mixed feeders, and Rodgers (1976) observed that they predominantly grazed during the wet season, but browsed on Acacia savannah much more during the dry season. This was confirmed by Meissner, Pieterse & Potgieter (1996) who found that whilst 90% of the impala diet was grass during the wet season, the amount of browse increased to 35% during the dry period. Monro (1980) concluded that impala selected food rich in crude protein and so preferred grazing to browsing when succulent grass was available. Anderson (1972a) noted that females remained in the best foraging areas all year round. However, during the rut, non-territorial males are often forced out into less suitable areas by territorial rams which try to hold territories with the best food resources, thus having access indirectly to more of the females. Van Rooyen & Skinner (1989) found that territorial males had a poorer quality diet than females, probably due to the less available time they had for plant selection. Females specifically selected dicotyledons with the highest nutritional value in order to provide them with energy for pregnancy and lactation, whilst bachelors had a high dicotyledon diet throughout the year, simply due to the fact that they were restricted to poor quality areas that contained little grass. Bourgarel *et al.* (2002) found that in a year of high annual rainfall, impala were heavier than in a poor year, and adult females seemed to be less affected than males by variation in primary production.   Adult males suffered from a seasonal decrease in body mass, supposedly linked to the rut, particularly in good habitat. Their results also suggested that males (juvenile and

adult) are more susceptible to changes in food resource abundance and quality than females.   Van Rooyen (1990) noted however that non-territorial males on poorer habitat generally did not show the weight loss of territorial rams, because they were able to compensate and spend more time feeding.   Thus, feeding and resulting condition could be affected on a number of levels, and whether a ram is territorial or non-territorial may have a large significance on it's resulting survival.

Impala spend a significant amount of their day grooming.   Jarman & Jarman (1973a) recorded that observed territorial males spent between 0.07 and 0.53 daylight hours grooming, compared to a mean of 0.46 hours by females.   Mutual grooming was also a common activity at dawn and dusk between females, or between bachelor males.   This is generally in response to the threat from ectoparasites, most notably ticks.   Lightfoot & Norval (1981) described the various deleterious effects of ticks on hosts, including tick-borne diseases, toxicoses, secondary infections, and tick worry. The latter describes the time and energy costs of a host as a result of the annoyance, and the grooming that is required to relieve them of this.   They found that impala seldom carry large numbers of adult ticks, but become heavily infested with the larval and nymphal stages during the dry season in Zimbabwe.   Horak (1982) found that impala in the Limpopo Province of South Africa were hosts to six species of ixodid ticks, of which only 2.7% were adults peaking around the December to February wet season, with larvae peaking around April to July, and nymphae from June to October. It is likely that animals in poor condition as a result of factors such as under-nutrition, often become extremely heavily infested, and as a result can become anaemic.   Turner & Short (1972) observed that tick-infested Shorthorn Hereford cattle gained 46% less body mass over 27 weeks than identical, dipped counterparts.   Seebuck, Springel & O'Kelly (1971) suggested that only 35% of reduction in mass gain during tick infestation was due to blood loss, and that the remaining 65% loss was due to reduced food intake, which may reflect a loss of appetite by cattle.   Time and energy costs in trying to relieve these tick burdens may also play a significant role in accounting for this 65%, especially in wild species who have no supplementary food.   Clearly ticks can cause a significant problem for impala.   Mooring (1999) stated that studies have shown that even a moderate tick load on a growing impala lamb can theoretically cause a weight loss of up to 44 kg a year.

It is not at all surprising that impala, faced with this type of threat, have evolved to counteract it. McKenzie (1990) suggested that browsers such as the impala are for at least part of the year, potentially exposed to a greater external parasite infestation than the grazers of the open plains, due to the close contact with vegetation that inevitably occurs during selective feeding. As a result he concluded that the teeth of the impala have evolved to be an effective dental grooming organ with vestigial lateral teeth ideally sited so as to rake evenly the selected part of the pelage with a vertical movement of the head. McKenzie & Weber (1993) further examined the dentition of the impala, and found that the front teeth were loosely embedded enabling the tips to move approximately 1.5 to 2mm. This they suggest allows the hair of the pelage to pass between the teeth, whilst removing parasites. Clearly impala are highly adapted to deal with this tick problem.

Grooming behaviour is therefore extremely important for survival, but it also has a number of costs including loss of feeding time, reduced vigilance, water loss via evaporation from saliva, and vertical attrition of the lateral dental elements (Mooring, 1995). In confirmation of this, Mooring (1995) found a decline in grooming rate by 30-45% associated with the dramatic decrease in adult ticks from the warm/wet to hot/dry seasons, reducing the costly process of grooming when the tick burdens are lower. Self-grooming rates were significantly and positively correlated with adult tick challenge, whilst allogrooming was influenced by nymphal tick challenge, directed to the head, ears and neck. Allogrooming is clearly a strongly innate behaviour as hand-reared impala showed no alteration in occurrence of reciprocal grooming (allogrooming) compared to dam-reared control fawns (Mooring & Hart, 1992). Mooring & Hart (1993) found that allogrooming between captive impala was influenced by few social factors. However, Mooring, McKenzie & Hart (1996) found that territorial males never engaged in allogrooming, whilst they orally groomed themselves much less than females or bachelor males. As there were no differences found in grooming rates of territorial males with or without a breeding herd, they suggested that the higher testosterone levels reported for territorial males as a result of territorial activity (Bramley & Neaves, 1972) may cause a physiological suppression of oral grooming. The other reason maybe that vigilance and rutting behaviour is extremely demanding and thus grooming is reduced. Either way, it is not at all

surprising that Mooring *et al.* (1996) found territorial males support a higher density of ticks than either bachelor males or females.

A high tick load is clearly a significant cost, which must be traded off with the costs of grooming. Mooring & Hart (1995a) showed that territorial male impala oral groomed less and had six times more ticks than females during the breeding season, due to decreased grooming as a result of the need to remain vigilant for females and challenging males. In the same way, Mooring & Hart (1995b) showed that impala delivering allogrooming took longer to alert to a simulated predator than did the partner receiving allogrooming or not partaking before. FitzGibbon (1989) found that less vigilant Thomson's gazelles (*Gazella thomsoni*) were more likely to be preyed upon by cheetahs, and lower vigilance is likely to explain in part the fact that male impala have a higher mortality rate than females (Jarman & Jarman, 1973b). One adaptation to reduce these costs has been in forming a symbiotic relationship with oxpeckers (*Buphagus erythrorhynchus* and *Buphagus africanus*).   Hart, Hart & Mooring (1990) found impala were either accommodating or at least tolerant of oxpeckers, who foraged upon areas of the body the impala cannot reach with it's own mouth. Mooring & Mundy (1996) observed that two-thirds of adult ticks on female impala were present on the ears, with 75% of adult ticks found on the ear, head and neck areas. Oxpeckers were found to forage in these areas 71-74% of the time, showing that they forage for adult ticks which impala cannot reach themselves. They also found impala reduced their grooming rate when oxpeckers foraged upon them, to 11-36% of their grooming rate in the absence of oxpeckers. It is likely that oxpeckers may be even more important for territorial males who, as earlier reported, do not partake in allogrooming, and therefore would be expected to have a greater tick density on the head, neck and ear regions. This would reduce some of the costs of grooming, whilst decreasing the tick loads territorial males are subjected to due to their reduced grooming in the breeding season. A further comparison between the grooming behaviours of territorial and non-territorial males seems extremely important as a result of this work, especially as tick loads represent a potential reason for a territorial ram to lose condition and thereby his territory.

It is apparent that vigilance is an important behaviour that must often be traded off against the costs of performing another behaviour, such as grooming, instead.

Impala ram vigilance behaviour was investigated in order to try and analyse the effect that the introduction of three lions to the reserve would have on the rams' behaviour. This was especially interesting in its relationship with the trading off of reproductive behaviour during the rut, and a comparison between the importance given to vigilance by territorial and non-territorial males. A lot of research has been done on vigilance, notably by Underwood (1982) who stated that vigilance has roles in many situations, including scanning for predators, scanning as part of foraging and, in the case of impalas, scanning to maintain group cohesion. Pulliam (1973) used a mathematical model to predict a negative relationship between group size and vigilance rates. This has been confirmed in a number of studies, although Elgar (1989) notes that this is often confused as a result of other confounding variables. Dehn (1990) suggested that the increasing group size reduces vigilance for predators as a result of a trade off between increasing predator detection, and dilution of the risk of an individual being attacked. Berger *et al.* (1983) noted that whilst individual foraging efficiency increased with group size of pronghorn *Antilocapra americana*, they remained in large groups despite less profitable foraging when in a disturbed area, concluding that there is a trade off between foraging and predator detection. Vigilance is also determined by a number of other factors. Berger & Cunningham (1988) showed that small bodied species were more vigilant (per unit body mass) than larger ones. Burger & Gochfeld (1994) found that the location of the animal in the herd, sex and age all played contributing factors, as did whether the animals had young. Females with young were generally more vigilant than those without, and interestingly, herd size had no relationship on vigilance over a certain threshold, which in impala was estimated at about 50.

Dunham (1979) found that during the rut, impala show an increase in scanning time up until almost the end of the dry season, and attributed this to an increase in vulnerability to predators during this period. Hunter & Skinner (1998) noted that heightened social interaction occurs during the mating season, thus increasing vigilance behaviour. Alados (1985) showed this increased vigilance in Spanish ibex (*Capra pyrenaica*) during the rut, whilst the importance of peripheral animals in detecting predators, and therefore their vigilance, is diminished as social interactions based around reproductive behaviour take more interest. Berger & Cunningham (1988) found no differences in search times of bison (*Bison bison*) in areas with and

60

without predators. They concluded that this was either because bison have greater energy and nutrient requirements, and therefore anti-predator vigilance is less important, or that vigilance for predators is only affected by recent attacks. Hunter & Skinner (1998) stated that although their study showed the vigilance response of a naive prey population to the introduction of their historical felid predators, it took place between August and December, and therefore could not be used to account for variations in vigilance during the breeding season. Thus, by investigating the effects of releasing lions during the impala rut, a new area was been investigated to add to the extensive work done by Hunter (1998) on felid introduction.

<u>Methods</u>

After the initial pass through the study site first thing in the morning, as far as was possible, the ram that had been observed least was then selected. The ram was followed for a period of one hour. Several behaviours were observed, most of which were recorded using scan sampling. Starting with an initial observation (time 0), the behaviour of the ram was recorded every four minutes for one hour. As Jarman & Jarman (1973a) describe, four minute interval recording was reasonably accurate compared to the shorter one or two minute interval as used by Harker, Taylor & Rollinson (1954), who found that shorter intervals did not substantially reduce the error in recording major activities of cattle in Uganda. Spinage (1968) also used four-minute intervals when recording waterbuck (*Kobus ellipsiprymnus*) activity.   The activity recorded was on the 4-minute mark, and was classified under the following categories:

<u>Allogrooming</u> -   standing grooming or being groomed by another impala.

<u>Grooming</u> -   either oral grooming or scratching himself.

<u>Grazing</u> -   head down, eating grass.

<u>Browsing</u> -   eating bush, plant or tree material, other than grass.

<u>Sparring</u> -   clashing of heads between two rams (different, lower intensity to fight).

<u>Display</u> -   parallel walking or standing near another individual, yawning, eyeballing or lowering horns and 'air-fighting' with other ram.

<u>Fighting</u> -   intensive fighting between rams.

Chasing -   ram is chasing or is chased by another animal.

Object aggression -   thrashing objects such as bushes, or the ground, with horns.

Resting -   either relaxed lying down or standing still, not partaking in other activities.

Ruminating -   standing or lying down chewing continuously (normally following feeding).

Walking -   all movement, not standing still or chasing other individuals.

Watching -   standing still and alert, with head upright.

Salt lick -   licking salt block.

Lick female -   sexual activity whereby ram licks female genitalia.

Urinating/Defecating

Drinking

Not seen -   situation where, on the four-minute interval time, the observed animal is hidden from view.

Once one hour had been completed, the study site was then traversed again, checking on the positions of individuals. A new observation animal was then chosen, again where possible, the one that had been observed the least before. The animals were recorded at four-minute intervals for one hour, thus making 16 observations per period. As impala are often found in woodland, allowance was made for the fact that at some observation times, the animal in question would not always be visible. As a result, the 'not seen' category was incorporated. However, the data on the animal were only used if nine or more of the activities were observed (i.e. categories other than 'not seen'), that is, the animal was visible for at least half of the time. As well as always trying to choose the least studied animal to be the next observation focal animal, it was attempted to study focal animals as equally as possible over a particular time of the day, during each of the three periods of pre-rut, rut and post-rut. On any particular day, an animal was only followed for one hour, unless there were no others available. Observations were made from sunrise to sunset, and thus ranged between 10 and 14 hours a day, depending on the time of year, and therefore day length.

As well as scan data recording behaviour every four minutes, focal data were also collected whereby behaviours were recorded as they happened over the hour-long observations. The behaviours recorded were those that are generally short in their

nature, and thus are liable to be missed using scan sampling. Thus this method was used to put a frequency of incidences on these short behaviours, and not to repeat data for long lasting activities such as feeding which were measured in the scan sampling. Those behaviours that last a certain length of time, such as chasing or sparring, are recorded as times to the nearest five seconds, from when the behaviour starts to when it stops. Behaviours that involve definite discrete actions, such as roaring or rearing, are simply recorded as counts, as are behaviours such as grooming whereby the number of occurrences, rather than time was of interest. The behaviours and method of recording them include:

Allogrooming -   standing grooming or being groomed by another impala
                      (count and time).

Grooming -   either oral grooming or scratching himself (count).

Sparring -   clashing of heads between two rams (different, lower intensity
                      to fight). (count and time)

Display -   parallel walking or standing near another individual, yawning,
                      eyeballing or lowering horns and 'air-fighting' with other ram
                      (count and time).

Fight -   intensive fighting between males (count and time).

Flehmen -   act in which the upper lip is drawn up and the shape of the
                      nasal passages modified, in order to increase gaseous flow over
                      the vomeronasal organ to assess the state of a female's urine
                      (Jackson, 1995) (count).

Laufschlag -   the act in which a ram will approach a female with the front
                      legs held straight and moved in a stiff fashion. An animal may
                      also stand still whilst laufschlag is performed, in which case
                      the front legs are again held stiffly and raised in such a manner
                      (Jackson, 1995) (count).

Lick Female -   ram stands, or walks after a ewe licking her genitalia (count).

Rear -   ram stands on his back legs in front of females (count).

Mount -   ram attempts to climb on the back of the ewe in order to mate.
                      The ram fails to mate due to the ewe walking off (count).

Chasing -   ram chases or is chased by another animal (count and time).

Roaring -   vocal 'roar' produced by the ram, clearly distinguishable from
                              alarm snorts (count).

Object Aggression -   rubbing or thrashing horns against an object, such as tree, bush
                              or ground (count and time).

Vigilance -   the number of times a ram interrupts another behaviour to look
                              up (if feeding with head down) or around (if active with head
                              up) (count).

Defecate/Urinate -   (count).

All interactions between known rams were also recorded. These included events such as fights, and chases, and were recorded in detail as to whom was involved, how long the event continued for, and also which other known rams and how many unknown males, young males and females, were present. Some of these data were used in Chapter 3 to determine dominance between rams. It is also hoped they will show the relative number of aggressive encounters in which territorial and non-territorial rams were involved. For the vigilance behaviour, it is important to note that as the date of arrival of the lions was not known in advance, recording of the number of times rams looked up only began after the lions had been left in the holding facility on 2nd April 2001. They then remained there for two months, before being released on 5th June. As a result, the time after this date when the lions were free-ranging was compared to the time before when the lions were captive, to see the effect of the release of a predator on the impala.

The data processing was carried out using the SAS$^{®}$ statistical programme made available by SAS Institute Inc. (Carry, NC, USA.). The behaviour scan and focal data were analysed by fitting a General Linear Model (GLM) to the data containing predictor variables MTER (territorial / non-territorial) and RUT (rut / non-rut) where RUT is a repeated measures variable, as well as interactions between the two. We could assume normal distribution for these analyses, because each dependent variable was calculated from a minimum of approximately 80 records which therefore satisfies the conditions set by the Central Limit Theorem. The statistical procedure tests whether each of the predictors were significant predictors for each of the dependent variables (means). Least Square Means (LS Means) were also calculated for each of the territorial and non-territorial rams, as well as for rut and

non-rut, and for interactions between them.   These LS Means were corrected to prevent the predictors confounding each other.

Due to the relatively small number of rams that fitted the conditions necessary in the analysis, the significance of predictors should be interpreted with care. As a result, some P values that are slightly greater than the standard P = 0.05 are reported as significant.   It is noted that this increases the probability of getting false significance, but also decreases the probability of declaring a predictor non-significant when it is actually significant.

Results

For the analysis of the daily behaviour, as well as establishing whether a ram is territorial or not as described in Chapter 3, it is also important to determine when the rut took place. As has been described, a number of parameters have been involved in determining this in the past and all these were examined. It was found that the frequency of chases per day (by males chasing other males, females or young males) and the frequency of roars per day, both reflected the rut behaviour seen in the field most accurately.
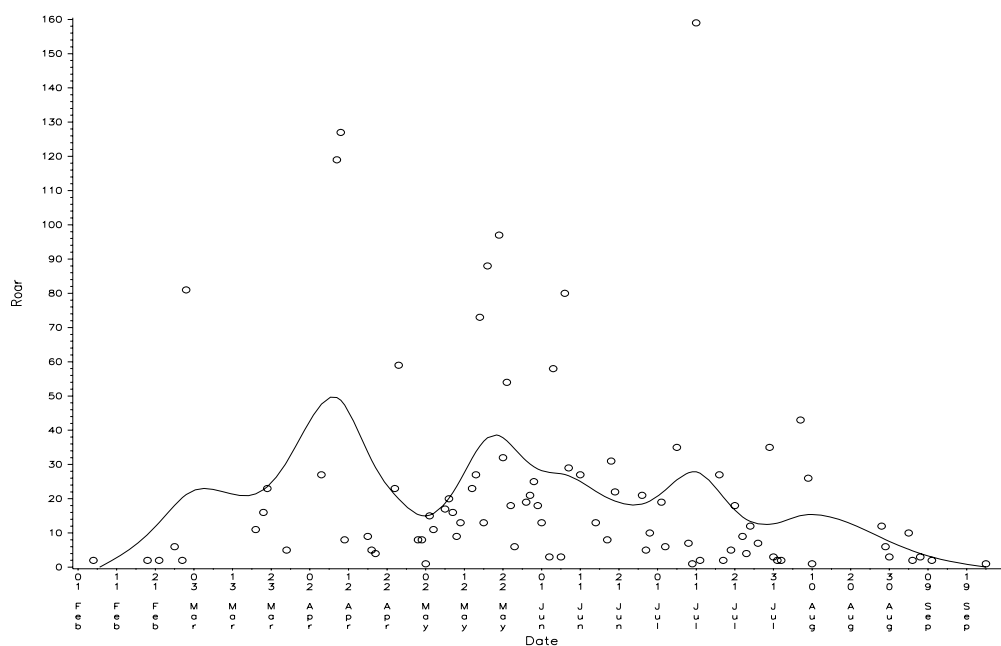
Figure 24 - The number of roars performed by rams throughout the project observation period.

As seen in Figure 24, roaring was seen to occur at at least a low level throughout the year, although much of this may have been down to individual, more-vocal rams. By March the incidence was starting to increase and, using a line smoothing function, a peak was seen around 10th April. However, it then seems to decline before re-peaking around the middle of May, then slowly decreasing until the middle of June where a smaller peak but some large roaring instances occur, and then declining slowly to the end of the year.
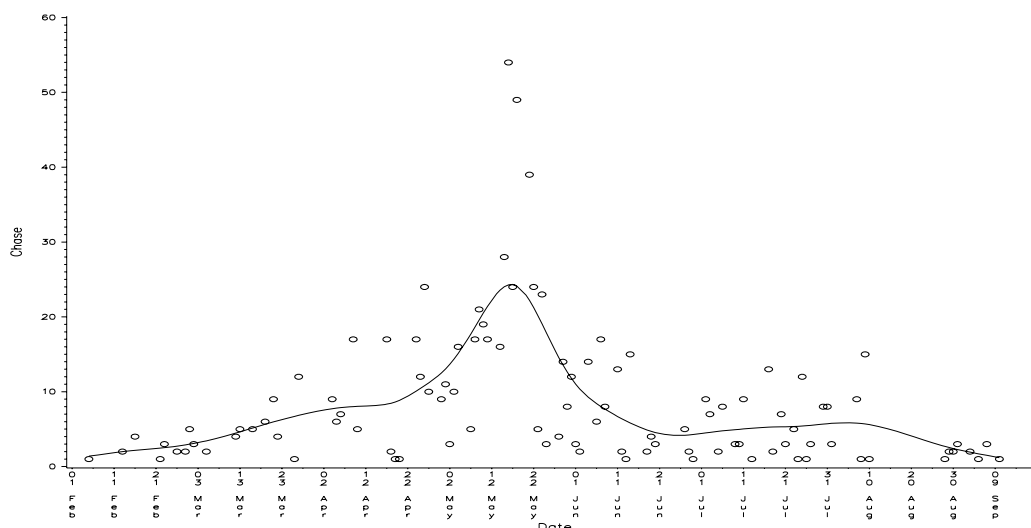
Figure 25 - The number of chases performed by rams against other impala throughout the project observation period.

In Figure 25, it can be seen that using a smoothed line of best fit, chasing shows a small increase around the middle of April, peaking in the middle of May, and then decreasing throughout June. In order to analyse the data, we need to take dates for the rut when it is definitely taking place. Therefore, using the two behaviours together, the rut was taken as occurring from 10th April through to 10th June. This roughly fits with the observations of Murray (1982b) who found that aggressive behaviour increased approximately six weeks before the first mating.

Although there were a number of identifiable rams, only a few fitted cleanly into the territorial or bachelor categories, and were present over most of the year. As a result, seven rams showing definitive territorial behaviour for part of the year and seven bachelors (non-territorial for the whole year), were observed over a number of hours and, using scan data, the percentage of time spent on daily activities was estimated. As shown in Figure 26, impala spent the greatest proportion of the day

feeding, with watching as the next most important. This was followed by walking, ruminating, resting and licking salt. On average the observer did not see the focal animals for 14.9% of the hour-long observations.
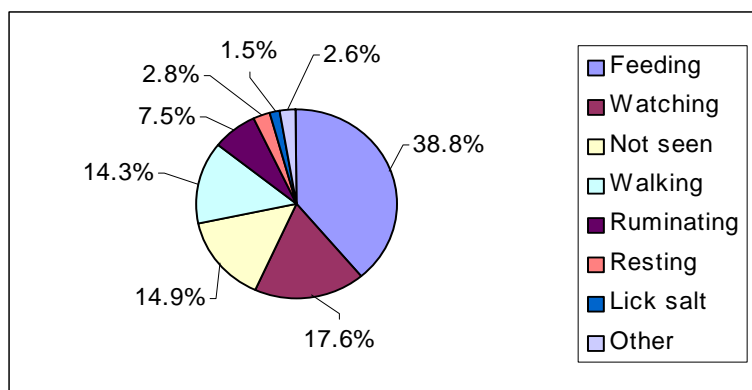
Figure 26 - Pie chart showing relative proportions of daily activity displayed by impala rams throughout the year.

The data obtained using scan and focal methods were both analysed on two levels using a GLM, comparing the relative time spent on different activities by territorial and non-territorial males, and how the proportion of time varied between the rut and non-rut. It is important to remember that those variables, whose length was measured by time, were also analysed by the number of times they occurred per day, so that they could be compared with variables recorded as counts.

Feeding – Grazing and Browsing

Table 5 shows the differences between the proportion of time territorial and bachelor rams spent feeding in the rut and non-rut. In separating out the feeding behaviour into grazing and browsing, the impala observed throughout the year grazed a mean of 37.0% of the time, and browsed 1.8% of the time. There was no significant difference in the proportion of time spent grazing between territorial and bachelor rams, or between the rut and non-rut. However, territorial rams appear to browse less (a mean of 1.7% of the time) than non-territorial rams (3.9%) in the non-rut, but no differences were found in the rut (F = 1.25, df = 12, p = 0.28). Bachelors also browse more (2.5% of the time) than territorial rams (1.1%) when the rut is ignored using a

67

between subjects analysis. All rams browse more in the non-rut (a mean of 2.8% of the time) than in the rut (0.9% of the time).

Table 5 - Significant differences found between territorial (T) and bachelor (B) rams feeding in the rut and non-rut. T<B signifies territorial rams perform the activity less than bachelors. Rut<Non-rut signifies all rams performed the activity less in the rut than non-rut.   NS signifies non-significant result.

BEHAVIOUR (method)	SIGNIFICANT DIFFERENCES FOUND BETWEEN RAMS:	REPORTED STATISTICS
Grazing (scan)		NS
Browsing (scan)	T < B - non-rut T < B - ignoring rut Rut < non-rut	F = 4.24, df = 12, P = 0.062 F = 6.94, df = 12, P = 0.022 F = 8.21, df = 12, P = 0.014

Watching / Vigilance

Field observations showed that the impala did not seem to notice or be bothered by the presence of the lions in the holding facility as they continued to be found nearby. Thus it is accurate to use the 'before and after' release to represent the absence and presence of lions in the study site. Table 6 shows the significant differences in vigilance and watching by territorial and bachelor rams in the rut and non-rut. Alert watching was the second most important behaviour for the impala rams, as shown using the scan sampling method. In the non-rut, territorial rams appear to watch more (a mean of 19.1% of the time) than non-territorial rams (12.1% of the time). However, this was not evident in the rut ($F = 1.02$, df = 12, $p = 0.33$). Vigilance (number of times the ram looks up) was also assessed using the focal method. There is no significant difference between the vigilance shown by territorial and bachelor rams, but all rams in the rut look less (38.29 times per hour) than in the non-rut (45.05 times).

Table 6 - Significant differences found between the vigilance and watching time of territorial (T) and bachelor (B) rams in the rut and non-rut. T>B signifies territorial rams perform the activity more than bachelors. Rut<Non-rut signifies all rams performed the activity less in the rut than non-rut.

BEHAVIOUR (method)	SIGNIFICANT DIFFERENCES FOUND BETWEEN RAMS:	REPORTED STATISTICS
Watching (scan)	T > B - non-rut	F = 4.39, df = 12, P = 0.058
Vigilance (focal)	Rut < Non-rut	F = 5.55, df = 8, P = 0.046

These differences were analysed further by including the presence and absence of lions, but this was difficult because the captivity and free-ranging periods of the lions overlapped closely with the rut and non-rut, so in most cases, too few rams existed across more than one condition. It seems that vigilance in the rut may be greater when the lions are free-ranging (44.67 times per focal hour), than when captive (37.75 times) but this is non-significant (F = 0.39, df = 2, P = 0.60), largely due to the extremely low sample size. The possible effect of lion release may explain the variation in vigilance between the rut and non-rut.

Chasing and being Chased

Table 7 shows the significant differences between the occurrence and length of time territorial and bachelor rams chased other impala and were chased by other rams in the rut and non-rut. Territorial rams appear to chase other impala for a greater proportion of the day than bachelors in the rut, and when the rut is ignored as they spend 1.3% of the observation time chasing *cf* 0.038% by bachelors. This difference is not evident in the non-rut (F = 0.68, df = 12, p = 0.43). Using the focal method, territorial males performed a mean of 12.1 chases per day in the rut, significantly more than the mean of 3.0 chases observed per day by bachelors. This also appears to be the case in the non-rut where territorial rams chase 10.6 times per day, *cf* 2.6 times by bachelors. Territorial males also chase more than bachelors when the rut is ignored, though interestingly again, no rut effect was seen (F =0.18, df = 12, P = 0.68). The length of chasing incidents were also measured. Territorial rams chase for

longer than bachelor rams in the rut, and also in the non-rut. When the rut is ignored, territorial rams chase a mean of 8.1s *cf* bachelors at 3.0 s.

Table 7 - Significant differences found between the occurrence and length of time territorial (T) and bachelor (B) rams chased other impala, and were chased by other rams in the rut and non-rut. T>B signifies territorial rams perform the activity more than bachelors. T<B signifies territorial rams perform the activity less than bachelors. Rut>Non-rut signifies all rams performed the activity more in the rut than non-rut.

BEHAVIOUR (method)	SIGNIFICANT DIFFERENCES FOUND BETWEEN RAMS:	REPORTED STATISTICS
Chase (scan)	T > B - rut	F = 4.68, df = 12, P = 0.051
	T > B - ignoring rut	F = 4.51, df = 12, P = 0.055
Chase (focal - count)	T > B - rut	F = 4.91, df = 12, P = 0.047
	T > B - non-rut	F = 4.54, df = 12, P = 0.054
	T > B - ignoring rut	F = 7.26, df = 12, P = 0.020
Chase (focal - time)	T > B - rut	F = 3.86, df = 12, P = 0.073
	T > B - non-rut	F = 3.24, df = 12, P = 0.097
	T > B - ignoring rut	F = 5.86, df = 12, P = 0.032
Chased (focal - count)	T < B - rut	F = 5.04, df = 12, P = 0.044
	T < B - non-rut	F = 5.60, df = 12, P = 0.036
	T < B - ignoring rut	F = 5.71, df = 12, P = 0.034
Chased (focal - time)	T < B - rut	F = 3.99, df = 12, P = 0.069
	T < B - non-rut	F = 4.08, df = 12, P = 0.066
	T < B - ignoring rut	F = 5.27, df = 12, P = 0.041
	Rut > Non-rut	F = 3.86, df = 12, P = 0.073

The opposite situation is true when looking at the number of times a ram was chased by other rams. Bachelors were chased a mean of 2.3 times during the rut, *cf* only 0.1 times in the case of territorial males. In the non-rut this is even clearer, as territorial rams were not chased at all, and hence this effect is evident over the year as a whole. Once again, there is no difference between the number of times rams were chased by other rams in the rut *cf* the non-rut (F = 0.75, df = 12, P = 0.40). Bachelor

males also appear to be chased longer than territorial rams in the rut, and of course in the non-rut during which territorial rams were not chased at all. Over the year ignoring the rut, territorial rams are chased for a mean of 0.1s a chase, *cf* 1.2s for bachelors. It also appears that rams are chased for longer in the rut (1.0s) compared to in the non-rut (0.3s).

Sparring

Table 8 shows the significant differences between the occurrence and length of time territorial and bachelor rams spar in the rut and non-rut. Sparring only occurred between bachelor males, although the time spent on this when sampled using the scan method was only significantly different to territorial rams during the non-rut, and when the rut was ignored. When using the focal sampling method, it was also clear that territorial males did not spar at all.

Table 8 - Significant differences found between the occurrence and length of time territorial (T) and bachelor (B) rams spar in the rut and non-rut. T<B signifies territorial rams perform the activity less than bachelors. Rut<Non-rut signifies all rams performed the activity less in the rut than non-rut.

BEHAVIOUR (method)	SIGNIFICANT DIFFERENCES FOUND BETWEEN RAMS	REPORTED STATISTICS
Sparring (scan)	T < B - non-rut	F = 6.55, df = 12, P = 0.025
	T < B - ignoring rut	F = 7.84, df = 12, P = 0.016
Sparring (focal - count)	T < B - rut	F = 3.25, df = 12, P = 0.096
	T < B - non-rut	F = 5.48, df = 12, P = 0.037
	T < B - ignoring rut	F = 5.58, df = 12, P = 0.036
	Rut < Non-rut	F = 5.22, df = 12, P = 0.041
	Interaction b/w rut + territoriality	F = 5.22, df = 12, P = 0.041
Sparring (focal - time)	T < B - non-rut	F = 4.58, df = 12, P = 0.054
	T < B - ignoring rut	F = 6.88, df = 12, P = 0.022

As a result, bachelors sparred significantly more than territorial rams in all respects. However, as seen in Table 9, in the rut the mean occurrence of sparring by

bachelors is lower, and thus the difference between territorial and bachelor males is barely significant. Sparring only occurs between rams a mean of 0.57 times in the rut as opposed to 5.14 times in the non-rut. It is therefore not surprising that there is a significant interaction between the occurrence of sparring by territorial and bachelor rams in the rut and non-rut.

Table 9 - The mean number of sparring incidents performed by territorial and bachelor rams during focal periods in the rut and non-rut.

	TERRITORIAL	BACHELOR
RUT	0.00	1.14
NON-RUT	0.00	10.29

When analysing the length of time sparring takes place, there appears to be significant difference in the non-rut, but not in the rut ($F = 2.44$, df = 12, $P = 0.14$). Again, sparring is only seen in bachelor rams, lasting a mean of 20.1s per sparring occurrence in the rut and in the non-rut. In the rut sparring is rare, and therefore there is no significant differences between the length of time territorial and bachelor rams carry out this behaviour.

Grooming and Allogrooming

Table 10 shows the significant differences found between the occurrence and length of time territorial and bachelor males groom and allogroom in the rut and non-rut. Allogrooming was only ever observed in bachelor males. As a result, bachelor rams allogroom more and for longer than territorial rams, regardless of the method used or the period observed. However there is no significant rut effect observed using the scan (Wilks' Lambda $F = 2.4$, df = 12, $p = 0.15$) or focal methods. In cases where results are not fully significant (<0.05), it is likely that this is a result of the low occurrence or length of the allogroom occurrence in that period.

Table 10 - Significant differences found between the occurrence and length of time territorial (T) and bachelor (B) rams groom and allogroom in the rut and non-rut. T<B signifies territorial rams perform the activity less than bachelors. Rut<Non-rut signifies all rams performed the activity less in the rut than non-rut.

BEHAVIOUR (method)	SIGNIFICANT DIFFERENCES FOUND BETWEEN RAMS:	REPORTED STATISTICS
Allogroom (scan)	T < B - rut	F = 4.37, df = 12, P = 0.058
	T < B - non-rut	F = 4.50, df = 12, P = 0.054
	T < B - ignoring rut	F = 5.71, df = 12, P = 0.034
Allogroom (focal - count)	T < B - rut	F = 6.19, df = 12, P = 0.029
	T < B - non-rut	F = 5.25, df = 12, P = 0.041
	T < B - ignoring rut	F = 6.82, df = 12, P = 0.023
Allogroom (focal - time)	T < B - rut	F = 3.80, df = 12, P = 0.075
	T < B - non-rut	F = 6.23, df = 12, P = 0.028
	T < B - ignoring rut	F = 4.58, df = 12, P = 0.054
Grooming (scan)	Rut < non-rut	F = 6.41, df = 12, P = 0.026
Grooming (focal - count)	T < R - rut	F = 8.99, df = 12, P = 0.011
	T < B - ignoring rut	F = 7.17, df = 12, P = 0.020
	Rut < Non-rut	F = 5.35, df = 12, P = 0.039
	Interaction b/w rut + territoriality	F = 3.68, df = 12, P = 0.079

When using scan sampling, there was no significant difference in the mean time spent grooming by territorial and bachelor males in the rut, non-rut, or over the year when the rut was ignored (F = 1.42, df = 12, p = 0.26). However, rams spent only 0.39% of time grooming in the rut, as opposed to 1.3% of the time in the non-rut. Grooming, being a short behaviour, is more likely to be accurately recorded as the number of occurrences counted per hour using the focal method. It was found that bachelor males groomed more (5.7 times per hour) than territorial rams (2.3 times per hour) during the rut, but not during the non-rut (F = 1.57, df = 12, P = 0.23). When the rut was ignored, bachelor rams again groomed more (5.79 times per hour), than territorial rams (3.51 times per hour). All rams also groom less in the rut (mean of 4.00 times per hour) than in the non-rut (5.33 times per hour). There also appears to

be a significant interaction between the rut and territoriality, in respect to the time
spent grooming.

Roaring

Table 11 shows the significant differences in roaring performed by territorial
and bachelor rams in the rut and non-rut. The occurrence of roaring is significantly
greater in territorial rams than bachelors, both in the rut (12.6 times per hour *cf* 1.0
times per hour), and in the non-rut (8.3 times per hour *cf* 0.10).   This effect is
therefore highly significant over the year when the rut is ignored.

Table 11 - Significant differences in the occurrence of roaring by territorial (T) and bachelor (B) rams
in the rut and non-rut. T>B signifies territorial rams perform the activity more than bachelors

BEHAVIOUR (method)	SIGNIFICANT DIFFERENCES FOUND BETWEEN RAMS:	REPORTED STATISTICS
Roaring (focal - count)	T > B - rut	F = 5.86, df = 12, P = 0.032
	T > B - non-rut	F = 9.63, df = 12, P = 0.009
	T > B - ignoring rut	F = 12.4, df = 12, P = 0.004

Interestingly, there is no significant difference between the roaring of rams in
the rut or non-rut (F = 0.97, df =12, P = 0.34). However, the mean number of roars
performed was 6.8 per hour in the rut *cf* 4.2 per hour in the non-rut, showing that
roaring does indeed seem to be performed at a lower rate in the non-rut, even if it is
not significant.

Object Aggression

Table 12 shows the significant differences between the occurrence and length
of object aggression performed by territorial and bachelor males in the rut and non-
rut. As object aggression is often a short behaviour, it is not surprising that no
significant differences were found when using the scan sampling method. When
using focal sampling, no significant difference occurred between territorial and

bachelor rams in the rut, non-rut or when the rut is ignored (F = 1.18, df = 12, P = 0.30). However, object aggression occurred less in the rut (a mean of 0.5 times per hour) than in the non-rut (1.7 times per hour). When looking at the length of time object aggression was performed, no significant difference was found between territorial and bachelor males in the rut (F = 0.70, df = 12, P = 0.42), but in the non-rut, territorial rams certainly carried out longer object aggression performances than bachelor males, as shown in Table 13.

Table 12 - Significant differences found between the occurrence and length of time territorial (T) and bachelor (B) rams perform object aggression in the rut and non-rut. T>B signifies territorial rams perform the activity more than bachelors. Rut<Non-rut signifies all rams performed the activity less in the rut than non-rut. NS signifies differences are non-significant.

BEHAVIOUR (method)	SIGNIFICANT DIFFERENCES FOUND BETWEEN:	REPORTED STATISTICS
Object aggression (scan)		NS
Object Aggression (focal - count)	Rut < Non-rut	F = 6.37, df = 12, P = 0.027
Object Aggression (focal - time)	T > B - non-rut Interaction b/w rut + territoriality	F = 6.40, df = 12, P = 0.026 F = 10.0, df = 12, P = 0.008

There is also a highly significant interaction between the rut and territoriality, which shows that in the rut, bachelors show longer object aggression than territorial rams, whilst in the non-rut this is reversed. In the same way, territorial rams show an increase in the length of object aggression going from the rut to the non-rut, whilst the opposite is true of bachelors.

Table 13 - Mean length (s) of object aggression performance by territorial and bachelor rams in the rut and non-rut.

	TERRITORIAL	BACHELOR
RUT	10.3	15.6
NON-RUT	14.6	4.5

Salt Licks

Table 14 shows the significant differences between the amount of time
territorial and bachelor rams were observed licking salt in the rut and non-rut. Rams
spent less time licking salt in the rut (a mean of 0.2% of the time) than the non-rut
(2.8% of the time). In contrast, there was no significant difference between the
proportion of time spent at this by territorial and non-territorial rams in the rut, non-
rut or when the rut was ignored using a between subjects analysis (F = 3.01, n = 8, p =
0.12).

Table 14 - Significant differences found between the amount of time territorial (T) and bachelor (B)
rams lick salt in the rut and non-rut. Rut<Non-rut signifies all rams performed the activity less in the
rut than non-rut.

BEHAVIOUR (method)	SIGNIFICANT DIFFERENCES FOUND BETWEEN RAMS:	REPORTED STATISTICS
Lick Salt (scan)	Rut < non-rut	F = 18.9, df = 8, P = 0.0025

Other Main Activities

The other main activities of walking, ruminating and resting all showed no
significant differences between territorial and bachelor males in the rut and non-rut.
There were no differences found in the percentage of time rams were 'not seen'
during scan sampling, showing that the method was reliable and consistent to measure
the other behaviours in all rams throughout the year. Behaviours such as defecating /
urinating, displaying, drinking and fighting were all non-significant, showing that they
were equally performed by all rams in the rut and non-rut. The same can be said for
the reproductive behaviours such as flehmen, whilst rearing was only seen on one
occasion, as was licking the genitalia of a female, in both cases performed by a
territorial male.   Laufschlag was never witnessed in impala. The mount and
copulation behaviour were also rare, and are analysed and discussed in Chapter 3.
The fact that these behaviours were only rarely performed and that the sample size of

rams performing these behaviours was relatively small, contributes to non-significant differences in some cases.

Discussion

The daily diurnal activity of 14 impala (7 territorial and 7 bachelors) was analysed using scan data, to show the proportion of time spent in various behaviours. Focal data were best for short acting behaviours, and showed the relative number of occurrences of the behaviour in the conditions stated. In some activities, the time a particular behaviour took place was analysed to show the relative length of time a performance was carried out. Unfortunately 14 animals is a relatively small sample size, and resulted from the fact that many of the known rams did not fit comfortably into the territorial or bachelor categories, or had limited data as a result of them not remaining for long enough periods in the study site. As territorial males were only territorial for limited periods, it is also important to note that the data for these animals will be less than those for bachelors for whom data from the whole year can be used. All this will inevitably mean that many results or effects that show big differences may not be shown as statistically significant. As a result, although the standard procedure is to only reject the null hypothesis when $P < 0.05$, results that produce a P value of slightly over this will be discussed as showing a tendency to appear to be statistically significant, as earlier mentioned.

In the diurnal period that the impala in this project were examined, feeding was the most prevalent activity, taking 38.8% of the time which compares to the mean of 49% of the time observed by Jarman & Jarman (1973a) for a female herd in the Serengeti. The second most common behaviour was watching (17.6%), which is higher than Jarman & Jarman's (1973a) estimate averaged at 9.7% of the day spent standing, presumably a similar behaviour. Walking is only slightly different, and resting (lying down as described by Jarman & Jarman (1973a) occupies a very similar proportion of time in both studies. However, the observed estimate for ruminating of 7.5% is less than Jarman & Jarman's (1973a) mean of 23.7% for females. It is possible that males do carry out this behaviour less than females in the diurnal hours, and it is also likely that the males spend more time on other behaviours as a result of the rut which thus effects the means across the year. Just as importantly, the different

definitions of behaviours between this and the other study can cause a variation in the balance of overall daily behaviour observed. The reduced time spent ruminating in this study can be balanced by the increased time they were observed standing, which these aside would mean that overall, the daily behaviour of rams fitted with Jarman & Jarman's (1973a) guidelines.

Of more interest however, are the differences found between territorial and bachelor males, because it is these that reflect the costs and resulting adaptations of territoriality in the impala. To facilitate discussion, the various activities and behaviours have therefore been split up and dealt with separately.

Feeding – Grazing and Browsing

Feeding was separated into grazing and browsing as best as possible, and the fact that no significant differences were found between the grazing of territorial and bachelor males is presumably due to the fact that it is such a common and vital behaviour and is performed throughout the year. This does however, contradict the various observations by researchers such as Jarman & Jarman (1973a) that territorial males feed (and therefore presumably graze) less than bachelor males during the rut. Browsing on the other hand was rated as only occurring for an average of 1.8% of the day over the year, yet bachelors appeared to browse far more than territorial males in the non-rut and clearly when the rut is ignored. This coincides with the observations of Anderson (1972a) and van Rooyen & Skinner (1989) who suggest that the restriction of bachelors to less good grazing areas means they have to browse more on dicotyledons. It also reflects the fact that territorial rams have less time to browse than bachelors when grazing is scarce, due to the time taken up by territorial defence. One would expect these effects more in the rut when inter-male aggression is at its greatest, but it is possible that this restriction is apparent more when territoriality occurs outside the rut, especially in the drier non-rut when grazing is less available. The fact that there is also a rut effect shows that, as noted by Meissner *et al.* (1996), browsing must increase heavily in the dry season which would have had the greatest effect in the months after the rut in June, July, August and even September.

Watching / Vigilance

Watching, or standing alert was the second most common behaviour performed, yet the fact that territorial males spend more time watching than bachelors in the non rut is difficult to explain. It is possible that it is simply due to the fact that territorial males spend more time alone (Dasmann & Mossman, 1962) and therefore according to the work of Pulliam (1973) and Dehn (1990), would spend more time being vigilant due to the increased predation risk. Dunham (1979) found that during the rut, impala showed an increase in scanning that lasted up until almost the end of the dry season, which he also attributed to increased vulnerability to predators. However, Hunter & Skinner (1998) and Alados (1985) observed increased vigilance by all rams during the rut as a result of the social interactions taking place in the mating season. Thus, a general increase in vigilance by all males as a result of the interactions during the rut, may reduce any differences between territorial and bachelor males. The presence of territorial males who set up territories early in the year in the non-rut, and also those that continued to hold territories well into the dry season, may mean that this increased vigilance by territorial rams due to increased risk of predation is more evident in the non-rut.

.

One would expect a rut effect as described by Dunham (1979) and Alados (1985) with increased watching in the rut. However, this effect may be confounded by the lion release programme, which saw the lions placed in a holding facility just before the rut began, and released just before it ended. Hunter & Skinner (1998) observed that vigilance increased when a predator was introduced into a naïve population. Thus, as the lions were released into the study site in the post-rut, non-rut, it is possible that this increase balances the higher vigilance in the rut associated with mating behaviour, thus reducing the overall rut effect of watching behaviour as obtained by scan sampling. Using the focal data, it was found that rams look up more during the non-rut than in the rut. The lions were captive for virtually the whole rut, and were free-ranging for the whole post-rut. Thus the higher vigilance rates in the non-rut seem to confirm Hunter & Skinner's (1998) finding that introduced predators lead to increased vigilance. The means obtained for the vigilance of rams in the rut being greater when the lions were free-ranging as opposed to captive would seem to support this, although it is difficult to use these means with much confidence due to

the small degrees of freedom used to create them. In addition, the fact that there was no difference between territorial or bachelor rams using the focal data observations would indicate that all adapted to the presence of free ranging lions by increasing vigilance. Focal data are likely to give a more accurate perspective on vigilance, due to the short nature of 'looking up'. However, standing watching may also be very important, and so the two methods should be used to support and compliment each other, rather than operating as separate entities.

Chasing and being Chased

Chasing is another behaviour that, although taking up a relatively small proportion of daily activity analysed using the scan method, is nonetheless important. Understandably, it appeared to be a significantly more common act performed by territorial than bachelor males, both in the rut and when ignoring the rut, over the year as a whole. Bearing in mind the different roles played by territorial and bachelor rams, and thus the increased herding of females and dominating of other males by territorial rams, these differences are not surprising. They also agree with findings by Murray (1982b) who found that most aggression involved high-ranking (territorial) males, whilst less dominant rams only showed 'contagious' chasing and 'mass roaring' as aggression increased in the rut. The fact that no significant difference is found between rams of different social status in the non-rut, reflects the lower incidence of aggressive interactions in impala out of the rut. The overall differences ignoring the rut show that over the year, territorial males chase more.

When the focal method was used to analyse counts, the same patterns were observed with territorial rams all carrying out more chases than bachelors in the rut, non-rut, and thus ignoring the rut. Once again the significance in the non-rut was slightly over the recognised $P = 0.05$ boundary, but it is accepted as being likely. Again no rut effect was seen. The mean lengths of chases that occurred also appeared to be significantly higher in territorial rams than bachelors in the rut and non-rut, although barely so. However, where the rut is ignored, there is a significant difference. These results coincide with the fact that territorial rams also show a greater proportion of time chasing other impala as shown by the scan data, confirming the role of chasing in the dominance displays of territorial rams throughout the year.

80

These differences are also reflected in the fact that when chased, it appears that bachelor rams are chased more and for longer than territorial rams. Looking at the means, it is evident that territorial rams were never chased during the non-rut, and that this was a rare occasion in the rut. It is therefore clear that, whilst territorial rams chase other rams more and for longer, they are chased less and for a much shorter time. This fits with field observations. Bachelor rams were chased when they intruded and took too much interest in females, or when the territorial male decided to show his dominance. In some cases where two rams were displaying against each other, they would both chase bachelors for extended periods, rather than fight and chase each other which would lead to dangerous conflict. The only time territorial males were chased was when they lost their territories, and in most cases they fled resulting in the chases being short.

Sparring

Sparring was only seen between bachelor males, a difference that was significant when analysed by scan data in the non-rut and when ignoring the rut. This can be explained by the fact that sparring described the testing of each other between rams, more than outright fighting which occurred with a greater intensity and intent to harm. This fits with the fact that territorial rams remain on their own, and are aggressive to other rams. It is therefore highly unlikely that they would interact in sparring with other rams. This doesn't occur between territorial males to test each other because, as observed in the field, this would simply be too dangerous due its likely escalation into a full-blown fight. As a result, territorial males assess each other using ritualised displays such as yawning and parallel walking to assess each others condition (Murray, 1982b), rather than sparring. When analysed using the focal data which are liable to be more accurate for the shorter lasting sparring behaviour, bachelor rams sparred significantly more in the rut, non-rut and when the rut was ignored. They also sparred for longer when the rut was ignored, and appeared to do so in the non-rut, once again explained by the fact that territorial males did not spar. In addition, a significant rut effect was shown, with more sparring incidents occurring in the non-rut than in the rut. Even in bachelor males, the increased aggression between rams as a result of the rut could mean that sparring might escalate into a

81

fight. Thus it remains at a lower level in the rut than in the non-rut as bachelors can then spar without so much risk that things will get too aggressive.

Grooming and allogrooming

Allogrooming is only seen amongst bachelor males, because territorial rams are intolerant of the presence of other rams and are more interested in mating with females. It was a relatively rare event amongst males, and it is for this reason that the differences found using the scan method only just appear to be statistically significant in the rut and non-rut. When the rut is ignored, the difference is far more evident, as is the difference in the rut, non-rut and when ignoring the rut using the focal method instead. These results agree with those of Mooring *et al.* (1996) who noted that territorial males never engaged in allogrooming.

Mooring *et al.* (1996) also observed that territorial males orally groomed themselves much less than bachelor males or females. This was not evident in the present study using the scan method, as the only significant difference in grooming occurred between the rut and non-rut. Perhaps this can be explained by the fact that the increased social interactions and aggression of the rut influenced all males, and thus all showed a reduced amount of grooming compared to the non-rut when things were more relaxed. Bramley & Neaves (1972) stated that higher testosterone levels in territorial males suppressed oral grooming, whilst vigilance and rutting behaviour would also have an effect. It is likely that this would affect all males to a greater or lesser extent compared to the non-rut, and would therefore explain the decreased grooming observed. Lightfoot & Norval (1981) found that impala seldom carry large numbers of adult ticks, but become heavily infested with the larval and nymphal stages during the dry season in Zimbabwe. Horak (1982) found that whilst adult ticks peaked around the December to February wet season, larvae peaked around April to July, and nymphae from June to October. As a result, plenty of grooming is necessary both in the pre- and post-rut when grooming is less suppressed. It may be even more important post-rut if grooming decreased in the rut, and if animals are in poor body condition as a result of decreased nutrition and extra energy expenditure.

The story is made more complete however when looking at the focal data, which measures the number of times grooming occurs during an observation hour. During the rut, bachelor males groom significantly more than territorial males, and this is also the case when the rut is ignored. As predicted by Mooring *et al.* (1996) territorial males orally groom themselves less, and as a result support a higher density of ticks than either bachelor males or females. This would then contribute highly to loss of condition in territorial rams. No significant differences were found in the proportion of time spent grazing between territorial and bachelor males. It may therefore be likely that the larger tick burden and thus associated tick irritation described by Lightfoot & Norval (1981) plays a large role in the ultimate decline in the body condition of the territorial ram. This eventually results in him losing his territory to another ram, who has been acting as a bachelor and therefore grooming more. The fact that this difference occurs even when the rut is ignored reflects the fact that territorial rams suffer this cost even outside the rut when they had set up territories earlier or maintained them later than the rut. However the difference between territorial and bachelors is less in the non-rut when reproductive and aggressive behaviours are somewhat diminished. The fact that a significant rut effect was also seen shows that the scan data were accurate, and that it is likely that the increased interactions during the rut affects the grooming of all rams. There also appears to be an interaction between the rut and territoriality which reflects these differences between the territorial and bachelor rams, as well as the rut and non-rut.

Roaring

Roaring behaviour is something that can only be picked up by the focal method due to its short occurrence. As expected, territorial rams roared significantly more in the rut, non-rut and thus when rut was ignored, a finding that agrees with that of Jarman (1979). This is of course one of the characteristics associated with territorial males and, as described in Chapter 3, has been observed by Murray (1982b) as peaking at mating time, with Warren (1974) suggesting that at night, roaring occurred most during the full moon period. Leuthold (1970) observed far less roaring displays in East Africa, and it is likely therefore that the shortening diurnal season is important in stimulating the roaring by rams, which in turn helps to advance the onset and synchronisation of oestrus in females, as suggested by Skinner *et al.* (1992).

Schenkel (1966) described roaring as an "expression of activated male dominance", and the fact that it was largely only performed by territorial males reflects this. Roaring by bachelors was mainly limited to 'mass roaring' (Jarman, 1979) and occurred when they got excited and started chasing each other. It is surprising that there is no significant difference between the occurrence of roaring in the rut and non-rut. This may be once again due to the fact that territorial males who were roaring more, held territories from early in the year until July / August, and thus continued roaring in the pre-and post-rut periods. All territorial rams seemed to roar when herding females, regardless of the time of the year.

Object Aggression

No significant differences were found in the proportion of time spent in object aggression by rams in the scan data, but when analysed using the focal method, some appeared. Territorial males carried out longer object aggression acts than bachelors in the non-rut, but interestingly not in the rut. When looking at occurrences of object aggression, a significant rut effect shows that object aggression occurred more in the non-rut. To explain this is rather difficult. Jarman (1979) describes bush horning as a way of rubbing an oily secretion from the head onto bushes to define a territory, but also suggests that the object aggression itself is a strong visual display. This would be expected more and presumably longer during the rut when strong territorial defence is required. However, the present study shows that object aggression occurs more often in the non-rut, suggesting that this behaviour is used to determine territories as a less aggressive visual display. In the rut, it is possible that other aggressive displays make object aggression less important, whilst may use it as a display against other males, thus resulting in no significant difference between rams. The fact that bachelor males decrease the length of object aggression in the non-rut therefore reflects a reduction in their aggressive activity. Thus for bachelors, object aggression becomes shorter in the non-rut. Territorial rams continue object aggression for as long as they hold territories, and may find it more a important display during the non-rut.

Salt Licks

The scan data shows that rams spent far longer licking salt during the non-rut than the rut. This can simply be explained by the fact that the salt licks are extremely important in the dry season when nutritional demands are not being met and thus can be supplemented by the use of licks. Thus, the non-rut portion covering the dry season of June to September can easily account for this increased use of salt licks, compared to the rut when there was less demand for the licks, and also less time for rams to spend supplementing their feeding behaviour at the expense of partaking in social interactions. It may also reflect the reduced aggression involved in the non-rut between rams, that may effect the time spent by rams at a salt lick that requires them to move through and even remain in the vicinity of a territorial male. Even if the waterhole and salt lick are neutral areas in terms of territoriality, it would be understandable that more time could be spent in this area when general aggression between males is lower during the non-rut.

Other main activities

The other main activities shown by impala using the scan method showed no significant differences between territorial and bachelor males. This can be most easily explained by the fact that in most cases, they are necessary essential behaviours such as ruminating and resting which are required to take place for at least a portion of each day. However, the fact that more of these are not reduced by territorial males to a significantly lower level during the rut is slightly surprising, but is mostly consistent with the observations of Jarman & Jarman (1973a) for the individual behaviours described.

Behaviours showing no significant differences when analysed using the focal method are in many cases over the year, extremely rare. Defecating / urinating, fighting, display and flehmen behaviours all show no differences, and seem to be fairly evenly spread between territorial and bachelor males in the rut and non-rut. Other behaviours such as licking female genitalia and rearing were only observed on one or very few occasions, and this, combined with the low sample size, made them extremely hard to detect.

CHAPTER 5

<u>CONCLUSIONS</u>

In conclusion, this research has tackled two main areas of impala ram behaviour. First there is the dynamics of territoriality throughout the non-rut and rut periods in a certain study site area. Which rams are territorial, how long for, which mate and when, are all interesting questions that will aid the management of impala in the South African regions of the impala range. On the other hand, the general behaviour analyses serve to aid our understanding of impala, in an effort to determine what can be expected at different times of the year, and how different situations and conditions effect this.

Rams appear to hold territories for shorter periods in southern Africa, in comparison to those in eastern Africa. This would reflect the shorter breeding season induced by shortening days in autumn, allowing pregnancy over winter and births after the summer rains. Mating opportunities are therefore restricted to a certain time period, and thus the benefits of holding a territory are reduced by associated costs. It is interesting that some impala rams set up territories earlier in the year but lose them in the rut. It is proposed that these are younger males who 'practice' holding territories. Bearing in mind the costs of territory ownership, they are more than likely to suffer a loss in body condition as a result, and this explains why they do not succeed in maintaining their status to a point when mating begins. The loss of territories on or around the first day of mating contradicts the observations of Murray (1982b), who suggested that relations between territorial males stabilise at this time. Territory sizes are smaller than those recorded in east Africa. Whilst the observed home range sizes are smaller than in east Africa, the estimates may be affected by the study site and the limits to observation. The recorded territory sizes are however likely to be more accurate due to the restricted movement of these rams. It is likely that smaller territories reflect the increased competition between males to hold an area during the short breeding season. From a management point of view, having a useable area of at least 60 ha for an impala ram's home range and within this for territories of at least 20 ha per territorial ram, is recommended in the Waterberg. The

smaller the area, the greater the conflict between males will occur and thus, the greater the chance of fatalities. Female home range was estimated at 75 ha, and though this may be an underestimate, it shows that almost half of the study site area was used on a regular basis.

The rut, determined by an increase in roaring and chasing, appeared to occur from the middle of April through until the middle of June. Within the rut, mating was first recorded on 16th May, and was last recorded on 4th June. These dates are likely to remain fairly consistent from year to year due to the timing being regulated by daylength (Skinner & Skinner, 2001). There was no evidence that the lunar cycle has any role to play in timing, but such a role is not impossible. Field observations show that when a territorial male loses his territory, there is approximately a week of upheaval before he is replaced. Results seem to confirm Jarman's (1979) theory that the greater the territorial tenure, the shorter time it takes for the ram to join bachelors, termed indeterminate. Using the breeding period established, it would be wise for managers to heed the advice of Young (1992) when he states that lone rams should not be culled at this time, so as to reduce the chances of removing a territorial male. As the territorial ram is likely to be one of the fittest and strongest individuals (although depending on the length of time he has been holding the territory, he may be showing a temporary loss in condition), it is also unwise to remove him, as this opens up mating opportunities for other males who may not be as genetically fit. In the resultant upheaval, oestrous females may also be missed, thus reducing the number of next season's young. There is a chance that any lone male may be an aspirant ram, who is non-territorial but testing the territorial rams to see if he can replace them. The lone male could also be indeterminate, who has recently lost his territory and is yet to join a bachelor herd. However these other statuses are less likely and can be identified by examining the behaviour.

It is important to note that, unlike in springbok where non-territorial rams show no interest in mating (Skinner & Skinner, 2001), all mature impala rams show interest and the capability of mating should they be in a position to do so. It is difficult to assess what proportion of matings non-territorial males are responsible for, but it is clear that they certainly account for some. The nature of the mating behaviour ensures that it is extremely difficult for a non-territorial ram to participate

in a 'sneak' mating, but it is possible if the territorial ram is occupied by a herd of oestrous females, and a female leaves the herd. Even young sexually mature males are kept away from the female herd, implying that, if given the opportunity, they will mate. This means that, should an impala population lose its territorial males for reasons such as culling, predation or disease, it is extremely likely that any sexually mature male would be capable of mating with the females.

Four main territories existed, the boundaries of which remained approximately the same between the earlier and later territorial rams. However, three of the four territorial rams who took over territories in the rut and thus held them in the later part of the year, held larger territories, which may reflect the greater need to access water and salt licks in the dry season. The qualities of a good territory are extremely debatable, but as a result of this study, some conclusions can be made. As a territory is ultimately designed to enable a ram to claim mating rights with females, it must contain characteristics attractive to females. These include the favoured ecotone habitat that was abundant in the study site, due to the large open areas surrounded by denser bush. This habitat provides a large amount of grazing during the summer, and during the dry season, a plentiful amount of browse. However, it is likely that the most desirable quality within the study site was the water source that the water-dependent impala females visited everyday. The provision of a salt lick during the dry season, on the banks of the waterhole, further attracted the females. The most important territories to be held were those bordering onto the water hole, allowing daily access to females. As a result, the territories nearer the waterhole were smaller, perhaps reflecting the increased competition between males in this area. As expected, all males (territorial and non-territorial) were observed at the dam, and although some aggressive interactions such as displaying were observed, in general it did not seem as though one ram was dominant. It is therefore likely that these important areas are 'neutral' as suggested by Dasmann & Mossman (1962), which therefore reduces the aggression that rams would otherwise have to endure. Instead the aggression occurs over territories that surround these important sites. As a result, one can conclude that the greater the number of important features such as water holes and salt licks, the more territories there are that females may visit. This would perhaps enable more rams to mate, and would increase genetic diversity, which is particularly recommended in small impala populations.

In this study, it is evident that in the site of approximately 200 ha, four territorial rams were present to compete for approximately 40 females. This gives a very rough sex ratio recommendation of 1 ram per 10 females. With four territorial rams present at one time, this left approximately 15 non-territorial rams. Four of these took over territories during the rut, replacing the original owners, and three other rams also showed brief territorial behaviour. As a result, it would be theoretically possible to remove half of the 15 non-territorial rams, and still ensure that all females were successfully mated. Clearly these estimates will vary as a result of many variables such as the type and quality of habitat, and the number of important, available resources. It is likely that with no competition from other rams, one territorial male could mate far more than 10 females. However, with competition the costs increase, and thus the number of females a male can successfully mate with may be reduced.

The general behaviour of impala discussed in Chapter 4 produced some interesting results. In terms of the proportion of time spent on a diurnal activity, feeding was the most important, followed by watching, walking, ruminating, resting and licking salt. Both browsing and licking salt increases in the non-rut, dry period reflecting the changing vegetation at this time of year, and the benefits of supplying salt licks to supplement nutrient intake. Time spent grazing did not vary over the year, which contrasted with the findings of others such as Meissner *et al.* (1996). Bachelors generally spent more time browsing than territorial rams, reflecting that they are sometimes restricted by territorial males who hold the prime feeding sites, whilst territorial males have less time to browse. This is significant because it suggests that in times of greatest food shortage in the dry season, territorial rams get to feed less, and thus their condition would be expected to decrease. This was shown by Jarman (1979), amongst others, but was not found here due to the difficulty in gaining a large enough sample size.

Territorial males chase other impala more often and for longer than bachelors, and are chased by other rams less, reflecting the fact that it is a behaviour heavily involved in territorial defence. Roaring is also more common in territorial males, although surprisingly it seemed to continue at least in part throughout the year. This

may suggest that it is not only used for stimulating females to come into oestrus, but also plays a role in territorial advertisement. In the same way it confirms the findings of Jarman (1979), whilst agreeing with Leuthold (1970) who found that roaring occurred less in east Africa. Object aggression was found to occur more in the non-rut than the rut, and in the non-rut, longer acts were carried out by territorial rams than bachelors. This behaviour is clearly also important in stating dominance, and is more important in the non-rut in comparison to the rut, during which other aggressive behaviours predominate.   Defecating and urinating do not seem to be used in territorial marking, at least in the frequency in which the behaviours were performed, as no difference was seen between the number of times this occurred in territorial and bachelor rams. However, territorial males defecate and urinate in particular places as dung piles were evident, and these piles may therefore mark the territorial boundaries. Unfortunately this was not investigated, and thus whether only territorial males use these piles is unknown. Sparring was only carried out by bachelor males, who presumably used it to test each other's strength. Territorial males refrained from this activity, partly because they do not socialise with other males, and also because if it occurred, it could escalate into a full fight. Fights were extremely rare due to the greater chance that injury may result, and occurred between both territorial and bachelor males. Likewise, the display behaviour between males was performed by both territorial and bachelor rams, where it replaced the more aggressive sparring or fighting behaviours in enabling rams to assess each other.

Grooming behaviour seems to be extremely important, confirming the reason for extensive work done in this area on impala by researchers such as Mooring *et al.* (1996).   Allogrooming only occurs between bachelors and not territorial males, showing again that only bachelors and not territorial males socialise with other males. As discussed, the tick burden impala suffer can be extremely high and, as a result, grooming is important to make this burden manageable. It is however clear that territorial behaviour interferes with time spent grooming and, as a result, territorial rams are forced to spend less time grooming than bachelors. In the same way, during the rut all rams are forced to reduce their grooming time in comparison to the non-rut, presumably due to the increased aggressive activity in the rut. It is suspected that, especially in view of the fact that no significant decreases in grazing time or in physical condition were observed, tick burden and the associated irritation could be a

significant contributing factor to the length of territorial tenure and thus the likely changeover from territorial to bachelor status. It would be interesting in the future to examine whether there is any relationship between the amount of time a territorial ram is able to spend grooming, and the length of time he is able to hold his territory. It is possible that oxpeckers play a large role in tick control. It would be interesting to see if oxpeckers frequent territorial rams more due to their higher tick loads, or whether the reverse is true as a result of the increased activity shown by territorial rams which would thus disturb the oxpeckers feeding.

Finally, the introduction of lions onto Touchstone Game Ranch has had an effect on the vigilance of impala rams. It seems likely that both territorial and bachelor rams are effected by the release of lions, as the post-rut shows a significant increase in vigilance, correlating largely with the lions being free-ranging. The fact that territorial rams were more vigilant than bachelor rams in the post-rut (when the lions were free) may also reflect that territorial rams are alone more and therefore must be more vigilant. The differences between territorial and bachelor rams may also be greater in the non-rut as bachelors are behaving normally, whilst territorial rams still show increased vigilance for females and invading males. From a management point of view, it is perhaps advisable that predators such as lions should not be released during the rut where all rams are involved in inter-male aggression. This is especially true if they start catching lone males which may be more vulnerable, as any loss of territorial males will invariably stimulate a change in territory holder, with the associated aggression, and perhaps a drop in fecundity.

In conclusion then, it is apparent that although similar, impala in southern Africa behave differently in some aspects, than those in east Africa. The territorial system evident in southern Africa's short breeding season is fundamental to the reproductive activity and success of the impala, and this causes rams to compete for ownership of territories whilst suffering a number of costs that effect their condition and ultimate health. As a result, the strongest and most healthy rams are those carrying out the matings and providing the highest quality genes to the next generation. An understanding of this system therefore enables managers to make plans in order to maintain the survival and abundance of the impala species, as well as the rest of the ecosystem in which the impala play such an important role.

SUMMARY

The territorial behaviour of impala rams was investigated to provide information on the reproductive behaviour of impala in southern Africa. Rams were identified, and their locations in the study site were recorded and mapped, whilst their associations with other impala were noted throughout the year. Ram behaviour was also recorded using scan and focal sampling methods.

The rut was established using the occurrences of chasing and roaring by rams, which peak between 10th April through until 10th June. Rams were defined as territorial or bachelors, whilst aspirant and indeterminate categories were also devised for rams that did not fit these categories comfortably. The average territorial tenure was 67.25 days, with mating observed on 16th May, 21st May and 4th June. In one case, the mating ram was rated as aspirant, but the others were territorial. There was no evidence that the lunar cycle has any role in the timing of matings. The home ranges and territory sizes were estimated using 95% Minimum Convex Polygon and 95% fixed kernel methods. The latter seemed to give greater, more realistic areas, with a mean home range of 34.1 ± 9.03 ha for territorial rams and 58.8 ± 33.35 ha for bachelor rams, figures that were not statistically significantly different. Territorial rams were restricted to territories of a mean size of 21.0 ± 11.27 ha. Within the study site, four main territories seemed to exist, and the boundaries remained consistent across different territory owners. It is suspected that areas such as water holes and salt licks are neutral in terms of territoriality, with the surrounding areas being the most desirable territories to occupy.

The activity of impala was examined, and showed that the most important diurnal behaviour was feeding, followed by watching, walking, ruminating, resting and licking salt. No differences were found between the amount of time territorial and bachelor rams grazed throughout the year. All rams browsed more in the non-rut, and bachelors browsed more overall. All rams were more vigilant in the post-rut, non-rut period when the lions were free-ranging, than in the rut when they were captive. Territorial rams chased other impala more and were chased by other males less, than bachelor rams. In the same way, roaring was seen far more in territorial males. On the contrary, sparring and allogrooming were only seen in bachelor rams,

as territorial males do not socialise with other males. Although all rams showed oral grooming, it was reduced in the rut due to the increased aggression and activity shown by all males. Territorial rams groom less than bachelors, and thus are likely be affected by the tick burden which may therefore contribute to their loss in condition. Object aggression occurred significantly more in rams in the non-rut than in the rut, and was performed over longer periods by territorial than bachelor rams in the non-rut, showing its role in dominance displays. Other activities such as display and flehmen behaviours seem to be performed by both territorial and bachelor males in the rut and non-rut.

REFERENCES

Alados, C.L. (1985) An analysis of vigilance in the Spanish ibex (*Capra pyrenaica*). *Zietschrift für Tierpsychologie* 68, 58-64.

Anderson, J.L. (1965) Annual change in testis and kidney fat weight of impala (*Aepyceros melampus*). *The Lammergeyer* III, 56-59.

Anderson, J.L. (1972a) Seasonal changes in the social organisation and distribution of the impala in Hluhluwe Game Reserve, Zululand. *Journal of South African Wildlife Management Association* 2,16-20.

Anderson, J.L. (1972b) The impala rut. *African Wildlife* 27 (2), 78-82.

Anderson, J.L. (1975) The occurrence of a secondary breeding peak in the southern impala. *East African Wildlife Journal* 13, 149-151.

Berger, J., & Cunningham, C. (1988) Size-related effects on search time in North American grassland female ungulates. *Ecology* 69,177-183.

Berger, J., Daneke, D., Johnson, J., & Berwick, S.H. (1983) Pronghorn foraging economy and predator avoidance in a desert ecosystem: implications for the conservation of large mammalian herbivores. *Biological Conservation* 25, 193-208.

Boulanger, J.G., & White, G.C. (1990) A comparison of home-range estimators using Monte Carlo simulation. *Journal of Wildlife Management* 54, 310-315.

Bourgarel, M., Fritz, H., Gaillard, J-M., De Garine-Wichatitsky, M., & Maudet, F. (2002) Effects of annual rainfall and habitat types on the body mass of impala (*Aepyceros melampus*) in the Zambezi Valley, Zimbabwe. *African Journal of Ecology* 40, 186-193.

Bowen, W.D. (1982) Home range and spatial organisation of coyotes in Jasper National Park, Alberta. *Journal of Wildlife Management* 46, 201-216.

Bramley, P.S. & Neaves, W.B. (1972). The relationship between social status and reproductive activity in male impala, *Aepyceros melampus*. *Journal of Reproduction and Fertility* 31, 77-81.

Burger, J., & Gochfeld, M. (1994) Vigilance in African mammals: differences among mothers, other females, and males. *Behaviour* 131, 153-169.

Burt, W.H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24, 346-352.

Child, G. (1964) Growth and ageing criteria of impala (*Aepyceros melampus*). *Occasional Papers of the National Museums of Southern Rhodesia,* Series B 4, 128-135.

Dasmann, R.F., & Mossman, A.S. (1962) Population studies of impala in Southern Rhodesia. *Journal of Mammalogy* 43, 375-395.

Dehn, M.M. (1990) Vigilance for predators: detection and dilution effects. *Behavioural Ecology and Sociobiology* 26, 337-342.

Dunham, K. (1979) The feeding ecology of impala (*Aepyceros melampus*) in the Sengwa region of Rhodesia. Unpublished M. Phil. Thesis, University of Rhodesia.

Dunham, K.M. (1980) The diet of impala (*Aepyceros melampus*) in the Sengwa Wildlife Research Area, Rhodesia. *Journal of Zoology,* London 192, 41-57.

Dunham, K.M. (1982) The foraging behaviour of impala *Aepyceros melampus*. *South African Journal of Wildlife Research* 12, 36-40.

Dunham, K.M. & Murray, M.G. (1982) The fat reserves of impala, *Aepyceros melampus*. *African Journal of Ecology* 20, 81-87.

Du Plessis, S.S. (1972) Ecology of blesbok with special reference to productivity. *Wildlife Monographs* 30, 1-70.

Du Toit, J.T. (1990) Home range – body mass relations: a field study on African browsing ruminants. *Oecologia* 85, 301-303.

Elgar, M.A. (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Review* 64, 13-33.

Fairall, N. (1969a) The use of the eye lens technique in deriving the age structure and lifetable of an impala population. *Koedoe* 12, 90-96.

Fairall, N. (1969b) Prenatal development of the impala *Aepyceros melampus* Licht. *Koedoe* 12, 97-103.

Fairall, N. (1983) Production parameters of the impala, *Aepyceros melampus*. *South African Journal of Animal Science* 13, 176-179.

Fairall, N. & Braack, H.H. (1976) Growth and development of the impala *Aepyceros melampus*. *Koedoe* 19, 83-88.

FitzGibbon, C.D. (1989) A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. *Animal Behaviour* 37, 508-510.

Hanks, J., Cumming, H.M., Orpen, J.L., Parry, D.F., & Warren, H.B. (1976). Growth, condition and reproduction in the impala ram (*Aepyceros melampus*). *Journal of Zoology,* London 179, 421-435.

Harker, K.W., Taylor, J.I. & Rollinson, D.H.L. (1954) Studies on the habits of zebu cattle. 1. Preliminary observations on grazing habits. *Journal of Agricultural Science* 44, 193-198.

Hart, B.L., Hart, L.A., & Mooring, M.S. (1990) Differential foraging of oxpeckers on impala in comparison with sympatric antelope species. *African Journal of Ecology* 28, 240-249.

Hofmann, R.R. & Stewart, D.R.M. (1972) Grazer or browser: a classification based on the stomach-structure and feeding habits of East African ruminants. *Mammalia* 36, 226-240.

Hooge, P.N., & Eichenlaub, W.M. (1998) *Animal movement extension to ArcView version 1.1*. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, AK, USA. Available: http://www.absc.usgs.gov/glba/gistools.htm.

Horak, I.G. (1982) Parasites of domestic and wild animals in South Africa. XV. The seasonal prevalence of ectoparasites on impala and cattle in the northern Transvaal. *Onderstepoort Journal of Veterinary Research* 49, 85-93.

Hunter, L.T.B. (1998) The behavioural ecology of reintroduced lions and cheetahs in the Phinda Resource Reserve, Kwazulu-Natal, South Africa. Unpublished PhD Thesis, University of Pretoria.

Hunter, L.T.B., & Skinner, J.D. (1998) Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour* 135, 195-211.

Jackson, T.P. (1995) The role of territoriality in the mating system of the springbok *Antidorcas marsupialis* (Zimmerman, 1780). Unpublished PhD Thesis, University of Pretoria.

Jackson, T.P., Skinner, J.D., & Richardson, P.R.K. (1993) Some costs of maintaining a perennial territory in the springbok, *Antidorcas marsupialis*. *African Journal of Ecology* 31, 242-254.

Jarman, M.V. (1970) Attachment to home area in impala. *East African Wildlife Journal* 8, 198-200.

Jarman, M.V. (1979) *Impala Social Behaviour, Territory, Hierarchy, Mating and the Use of Space.* Parey, Hamburg, 1-93.

Jarman, M.V. & Jarman, P.J. (1973a) Daily activity of impala. *East African Wildlife Journal* 11, 75-92.

Jarman, P.J. (1972) The development of a dermal shield in impala. *Journal of Zoology,* London 166, 349-356.

Jarman, P.J., & Jarman, M.V. (1973b) Social behaviour, population structure and reproductive potential in impala. *East African Wildlife Journal* 11, 329-338.

Lane, E.P., Kock, N.D., & Hill, F.W.G. (1994) Age determination in free-ranging impala (*Aepyceros melampus*). *Zimbabwe Veterinary Journal* 25, 14-25.

Leuthold, W. (1970) Observations on the social organisation of impala (*Aepyceros melampus*). *Zeitschrift für Tierpsychologie* 27, 693-721.

Lightfoot, C.J. & Norval, R.A.I. (1981) Tick problems in wildlife in Zimbabwe.1. The effect of tick parasitism on wild ungulates. *South African Journal of Wildlife Research* 11, 41-45.

Lincoln, G.A. (1971) The seasonal reproductive changes in the red deer stag (*Cervus elaphus*). *Journal of Zoology,* London 163, 105-123.

Loomis, M.R. & Wright, J.F. (1989) Systemic infections in impala (*Aepyceros melampus*) calves following ear tagging. *Journal of Zoo and Wildlife Medicine* 20, 370-372.

Marais, A.L., & Skinner, J.D. (1993) The effect of the ram in synchronisation of oestrus in blesbok ewes (*Damaliscus dorcas phillipsi*). *African Journal of Ecology* 31, 255-260.

Mason, D.R. (1976) Observations on social organisation, behaviour and distribution of impala in the Jack Scott Nature Reserve. *South African Journal of Wildlife Research* 6, 79-87.

McComb, K. (1987) Roaring by red deer stags advances the date of oestrus in hinds. *Nature* 330, 648-649.

McKenzie, A.A. (1990) The ruminant dental grooming apparatus. *Zoological Journal of the Linnean Society* 99, 117-128.

McKenzie, A.A., & Weber, A. (1993) Loose front teeth: radiological and histological correction with grooming function in the impala *Aepyceros melampus*. *Journal of Zoology,* London 231, 167-174.

Meissner, H.H., Pieterse, E., & Potgieter, J.H.J. (1996) Seasonal food selection and intake by male impala *Aepyceros melampus* in two habitats. *South African Journal of Wildlife Research* 26, 56–63.

Monro, R.H. (1980) Observations on the feeding ecology of the impala. *South African Journal of Zoology* 15, 107 –110.

Monro, R.H., & Skinner, J.D. (1979) A note on condition indices for adult male impala, *Aepyceros melampus*. *South African Journal of Animal Science* 9, 47-51.

Mooring, M.S. (1995) The effect of tick challenge on grooming rate by impala. *Animal Behaviour* 50, 377-392.

Mooring, M. (1999) The living fossil. *Africa – Environment and Wildlife* 7, 5, 52-61.

Mooring, M.S. & Hart, B.L. (1992) Reciprocal allogrooming in dam-reared and hand-reared impala fawns. *Ethology* 90, 37-51.

Mooring, M.S. & Hart, B.L. (1993) Effects of relatedness, dominance, age, and association on reciprocal allogrooming by captive impala. *Ethology* 94, 207-220.

Mooring, M.S. & Hart, B.L. (1995a) Differential grooming rate and tick load of territorial male and female impala, *Aepyceros melampus*. *Behavioural Ecology* 6, 94-101.

Mooring, M.S. & Hart, B.L. (1995b) Costs of allogrooming in impala: distraction from vigilance. *Animal Behaviour* 49, 1414-1416.

Mooring, M.S., McKenzie, A.A., & Hart, B.L. (1996) Role of sex and breeding status in grooming and total tick load of impala. *Behavioural Ecology and Sociobiology* 39, 259-266.

Mooring, M.S. & Mundy, P.J. (1996) Interactions between impala and oxpeckers at Matobo National Park, Zimbabwe. *African Journal of Ecology* 34, 54-65.

Murray, M.G. (1982a) Home range, dispersal and the clan system of impala. *African Journal of Ecology* 20, 253-269.

Murray, M.G. (1982b) The rut of impala: aspects of seasonal mating under tropical conditions. *Zeitschrift für Tierpsychologie* 59, 319-337.

Novellie, P.A. (1975) Comparative social behaviour of springbok, *Antidorcas marsupialis* (Zimmermann, 1780), and blesbok, *Damaliscus dorcas phillipsi* Harper, 1939, on the Jack Scott Nature Reserve, Transvaal. Unpublished MSc Thesis, University of Pretoria.

Pulliam, H.R. (1973) On the advantages of flocking. *Journal of Theoretical Biology* 38, 419-422.

Riney, T. (1960) A field technique for assessing physical condition of some ungulates. *Journal of Wildlife Management* 24, 92-94.

Ritter, R. (1993) Behaviour and land usage of water dependent herbivores in arid grasslands. Unpublished PhD Thesis, St. John's College, Oxford.

Ritter, R.C., & Bednekoff, P.A. (1996) An aseasonal impala birth in Botswana. *Journal of African Zoology* 110, 65-67.

Rodgers, W.A. (1976) Seasonal diet preferences of impala from south east Tanzania. *East African Wildlife Journal* 14, 331 – 333.

Roettcher, D., & Hofmann, R.R. (1970) The ageing of impala from a population in the Kenya Rift Valley. *East African Wildlife Journal* 8, 37-42.

Schenkel, R. (1966) On sociology and behaviour in the impala (*Aepyceros melampus*). *Zeitschrift für Säugetierkunde* 31, 177-205.

Seaman, D.E., & Powell, R.A. (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77, 2075-2085.

Seebuck, R.M., Springel, P.H., & O'Kelly, J.C. (1971) Alterations in host metabolism by the specific and anorectic effects of the cattle tick (*Boophilus microplus*) 1. Food intake and body weight growth. *Australian Journal of Biological Science* 24, 373-380.

Skinner, D.C., Cilliers, S.D., & Skinner, J.D. (in press) The effect of ram introduction on the oestrous cycle of springbok ewes (*Antidorcas marsupialis*). *Reproduction*.

Skinner, J.D. (1971) The sexual cycle of the impala ram, *Aepyceros melampus*. *Zoologica Africana* 6, 75-84.

Skinner, J.D., & Bonsma, J.C. (1964) The effect of early introduction of vasectomised bulls upon the sexual activity of the breeding herd. *Proceedings of the South African Society of Animal Production* 3, 60-62.

Skinner, J.D. & Hofmeyr, H.S. (1969) Effect of the male goat and of progesterone and PMSG treatment on the incidence of the anoestrous boer goat doe. *Proceedings of the South African Society of Animal Production* 8, 155-156.

Skinner, J.D., Jackson, T.P., & Marais, A.L. (1992) The 'ram effect' in three species of African ungulates. In: *Ongules / Ungulates 91*. Eds. F. Spitz, G. Janeau, G. Gonzalez, and S. Aulagier. SFEPM-IRGM, Toulouse, France.

Skinner, J.D., Monro, R.H., & Zimmermann, I. (1984) Comparative food intake and growth of cattle and impala on mixed tree savannah. *South African Journal of Wildlife Research* 14, 1-9.

Skinner, J.D., & Skinner, D.C. (2001) Significance of aseasonal breeding in arid adapted antelope in southern Africa. In: Prakash, I. (ed.) *Ecology of Desert Environments*. Jodhpur: Scientific Publishers (India), 391-403.

Skinner, J.D., & Smithers, R.H.N. (1990) *The Mammals of the Southern African Subregion*. 2nd Edition. University of Pretoria, Pretoria.

Skinner, J.D., Van Aarde, R.J., Knight, M.H., & Dott, H.M. (1996) Morphometrics and reproduction in a population of springbok *Antidorcas marsupialis* in the semi-arid southern Kalahari. *African Journal of Ecology* 34, 312-330.

Skinner, J.D., & Van Jaarsveld, A.S. (1987) Adaptive significance of restricted breeding in southern African ruminants. *South African Journal of Science* 83, 657-663.

Skinner, J.D., Von La Chevalliere, M. & Van Zyl, J.H.M. (1971) An appraisal of the springbok for diversifying animal production in Africa. *Animal Breeding Abstracts* 39, 215-224.

Spinage, C.A. (1968) A quantitative study of the daily activity of the Uganda defassa waterbuck. *East African Wildlife Journal* 6, 89-93.

Spinage, C.A. (1971) Geratodontology and horn growth of the impala (*Aepyceros melampus*). *Journal of Zoology,* London 164, 209-225.

Spinage, C.A. (1973) The role of photoperiodism in seasonal breeding in tropical African ungulates. *Mammal Review* 3, 71-84.

Talbot, L.M. & McCulloch, J.S.G. (1965) Weight estimates for East African mammals from body measurements. *Journal of Wildlife Management* 29, 84-89.

Tufto, J., Andersen, R., & Linnell, J. (1996) Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *Journal of Animal Ecology* 65, 715-724.

Turner, H.G. & Short, A.J. (1972) Effects of field infestation of gastrointestinal helminths and of the cattle tick (*Boophilus microplus*) on growth of three breeds of cattle. *Australian Journal of Agricultural Research* 23, 177-193.

Underwood, R. (1982) Vigilance behaviour in grazing African antelopes. *Behaviour* 79, 81-107.

Van Rooyen, A.F. (1990) The diet, habitat selection and body condition of impala and nyala in Zululand. Unpublished MSc Thesis. University of Pretoria.

Van Rooyen, N. & Bredenkamp G. (1996) Waterberg Moist Mountain Bushveld. In: Low, A.B. & Rebelo, A.G. (eds) *Vegetation of South Africa, Lesotho and Swaziland*. Dept. Environmental Affairs and Tourism, Pretoria.

Van Rooyen, A.F., & Skinner, J.D. (1989) Dietary differences between the sexes in impala (*Aepyceros melampus*). *Transactions of the Royal Society of South Africa* 47, 181-185.

Warren, H.B. (1974) Aspects of the behaviour of the impala male, *Aepyceros melampus* during the rut. *Arnoldia Rhodesia* 6, 1-9.

Worton, B.J. (1987) A review of models of home range for animal movement. *Ecological Modelling* 38, 277-298.

Worton, B.J. (1989) Kernel methods for estimating the utilisation distribution in home range studies. *Ecology* 70, 164-168.

Worton, B.J. (1995) Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management* 59, 794-800.

Young, E. (1970) Water in game management. Paper read at Convention: *Water for the future, Water Year 1970 Proceedings*, University of Pretoria, 16-20 November.

Young, E. (1972). Observations on the movement patterns and daily home range size of impala, *Aepyceros melampus* (Lichtenstein) in the Kruger National Park. *Zoologica Africana* 7, 187-195.

Young, E. (1992). *Game Farming and Wildlife Management*. Eddie Young Publishers, Nylstroom. 35-37.

APPENDIX 1

Definition of social category of all observed rams throughout study period

RAM	SOCIAL CATEGORY	DATES	NO. OF DAYS
Angry *	Bachelor	15/05 – 16/05	2
	Territorial	17/05 – 24/05	8
	Bachelor	27/06 – 04/09	70
Black	Aspirant	08/05 – 12/05	5
	Territorial	14/05 – 05/06	23
	Indeterminate	06/06 – 20/06	15
	Bachelor	02/07 – 26/09	87
Black5	Aspirant	06/02 – 22/02	17
	Territorial	26/02 – 16/05	80
	Indeterminate	17/05 – 22/05	6
	Bachelor	29/05 – 26/09	124
Blue4	Aspirant	05/02 – 06/02	2
	Territorial	07/02 – 16/05	99
	Indeterminate	17/05 – 22/05	6
	Bachelor	28/05 – 26/09	121
Bly7	Aspirant	08/02 – 13/02	6
	Bachelor	14/02 – 26/09	226
Broken *	Bachelor	22/03 – 18/05	58
Cheeky?	Aspirant	17/04 – 07/05	21
	Territorial	08/05 – 11/05	11
	Indeterminate	12/05 – 18/05	7
	Bachelor	24/05 – 25/09	125
Circle	Bachelor	14/05 – 10/09	120
Dark *	Aspirant	16/05 – 18/05	3
	Bachelor	21/05 – 28/05	8
Dunny	Bachelor	14/02 – 26/09	226

Eary	Bachelor	15/03 – 01/05	48
Face	Bachelor	01/05 – 16/07	77
Horney	Bachelor	14/02 – 26/09	226
NH	Bachelor	09/05 – 21/09	137
Nosey	Aspirant	09/04 – 11/04	3
		16/05 – 21/05	6
	Bachelor	22/05 – 07/09	109
Patch	Bachelor	04/04 – 25/05	52
	Aspirant	29/05 – 04/06	7
	Territorial	05/06 – 07/08	64
	Relaxed	08/08 – 26/09	50
Radio *	Bachelor	24/04 – 07/06	45
Radiogr *	Bachelor	04/05 – 21/05	18
Rambo	Bachelor	05/03 – 18/05	75
	Territorial	21/05 – 20/07	61
	Relax	21/07 – 26/09	68
Roman *	Territorial	14/05 – 21/05	7
	Indeterminate	22/05	1
Scarry	Bachelor	14/02 – 10/09	110
Stripe	Territorial	21/05 – 25/07	66
	Relax	27/07 – 24/09	60
Teary	Bachelor	15/02 – 26/09	225
White Eye	Territorial	14/02 – 12/05	88
	Indeterminate	14/05 – 15/05	2
	Bachelor	16/05 – 25/09	133
Y6	Bachelor	10/03 – 06/06	89
	Territorial	07/06 – 02/08	57
	Relaxed	07/08 – 26/09	51

* - signifies ten observation days or less.

? - signifies data which does not correlate closely with field observations and is therefore not reliable in places

APPENDIX 2

Territory and home range sizes for territorial (T) and bachelor (B) rams.

Rams	Home range - 95% fixed kernel (ha)	Home range - 95% MCP (ha)	Territory size - 95% fixed kernel (ha)	Territory size - 95% MCP (ha)
Black (T)	44.9	44.1	17.4	7.8
Black5 (T)	30.4	25.5	8.6	4.3
Blue4 (T)	19.0	21.2	10.7	7.3
Patch (T)	29.3	24.2	16.2	11.0
Rambo (T)	26.8	20.3	13.7	7.8
Stripe (T)	39.1	20.2	36.2	12.8
White Eye (T)	42.7	31.6	36.8	14.0
Y6 (T)	40.2	38.6	28.7	19.3
MEAN	34.1	28.2	21.0	10.5
STANDARD DEVIATION	9.03	9.03	11.27	4.76

Rams	Home range - 95% fixed kernel (ha)	Home range - 95% MCP (ha)	Territory size - 95% fixed kernel (ha)	Territory size - 95% MCP (ha)
Dunny (B)	34.1	29.5	*	*
Circle (B)	115.9	59.3	*	*
Eary (B)	64.5	22.5	*	*
Face (B)	64.4	19.0	*	*
Horney (B)	29.1	29.6	*	*
Narrow Horn(B)	29.5	27.2	*	*
Scarry (B)	98.1	59.3	*	*
Teary (B)	35.0	32.5	*	*
MEAN	58.8	34.9	*	*
STANDARD DEVIATION	33.35	15.67	*	*