

**SOCIAL ORGANISATION AND REPRODUCTIVE
BEHAVIOUR OF SABLE ANTELOPE (*HIPPOTRAGUS
NIGER* Harris, 1838): IMPLICATIONS FOR CAPTIVE
MANAGEMENT**

By

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Submitted in fulfilment of the requirements in respect of the Master's degree qualification Magister Scientiae Zoology in the Department of Zoology and Entomology, Faculty of Natural & Agricultural Sciences, University of the Free State, Bloemfontein, South Africa.

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Dedicated to my father, Danie Jacobs.

Thank you for all the support and love. Thank you for always believing in me and never giving up on me.

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CHAPTER 1: INTRODUCTION

Sable antelope (*Hippotragus niger*) are considered to be one of the most impressive antelope species found in southern Africa and one of the most sought after species for photographers and trophy hunters. The colloquial name originated from the description of the glossy black coat colour of adult males (Skinner & Chimimba 2005). Sable antelope are endemic to Africa and according to Estes (1999) four clearly distinguished subspecies exist, namely: *Hippotragus niger niger*; *H. n. kirkii*; *H. n. roosevelti* and *H. n. varianii*. The subspecies *H. n. kirkii* (Common sable antelope) has the largest geographical distribution, occurring throughout Tanzania, Malawi, Zambia, Zimbabwe, Mozambique, Angola and Namibia. *H. n. roosevelti* (Eastern sable antelope) occupies the coastal regions of Kenya, Tanzania and Mozambique. *H. n. varianii* (Giant sable antelope) has a very restricted historical geographic distribution being limited to central Angola within the Luando Integral Nature Reserve and the Cangandala National Park (Estes & Estes 1974). The subspecies *H. n. niger*, also referred to as the Southern subspecies, is comprised of populations in western Zambia, parts of Namibia, northern Botswana, Zimbabwe and in northern parts of South Africa. Research conducted by Jansen van Vuuren *et al.* (2010) on the geographic distribution of genetic groupings, indicates that genetic groupings generally conformed to the four subspecies recognised and defined according to morphology.

In terms of morphological characteristics, the Southern subspecies is considered to be the most distinct (Estes 2000). In populations of *H. niger niger* occurring south of the Zambezi River, females become as black as adult males, eliminating most of the sexual dimorphism prevalent in the other three subspecies (difference in coat colour) (Estes 2000). In the South African wildlife industry, this geographical race of Southern sable antelope is often referred to as the Matetsi race. The name "Matetsi" originates from a geographical area in Zimbabwe where this subspecies is often hunted. In the wildlife industry, populations of sable antelope of the Southern subspecies originating from Zambia, north of the Zambezi River, are referred to as Zambian sable.

According to Skinner & Chimimba (2005), sable antelope are a savanna woodland species, in which the availability of cover and water largely determines habitat utilisation. According to Bothma *et al.* (2010), the diet of sable antelope consists of 85% grasses, 10% browse and

5% forbs. Browse is predominantly utilised in the dry season (Estes & Estes 1974). Sable antelope are selective feeders that show selectivity at species, tuft and plant part levels (Wilson & Hirst 1977; Grobler 1981). The species shows a preference for green leaves (Estes & Estes 1974) while generally avoiding stems (Grobler 1981) especially during the dry season (Parrini 2006). According to Estes & Estes (1974), sable antelope do not feed on grass swards shorter than a few inches from the ground, but when utilising post-burn flush, they have been observed feeding on swards of two inches and shorter. Various literature sources state that burning parts of the home range with the onset of the dry season is of great importance to the maintenance of body condition during the dry months (Estes & Estes 1974; Grobler 1981; Parrini & Owen-Smith 2009; Le Roux 2010).

Contradictory to findings that suggest that sable antelope are selective feeders, Van Hoven (2010) suggests that sable antelope are bulk feeders that have very large rumens. According to Van Hoven (2010) their diet consists mainly of structural carbohydrates that contain an abundance of cellulose with very little cell content or juice. The low nutritional value of forage is compensated for by retaining food in the rumen for longer periods of time (facilitated by an enlarged rumen) thereby prolonging the exposure to microbial fermentation. The high level of structural carbohydrates in the diet is utilised by microbes, which in turn multiply into large numbers. Together with smaller digestible food particles, microbes are passed through to the omasum, compressed, and then passed to the true stomach (abomasum) for digestion. Microbial cells are broken down, and thereby the diet is supplemented with protein. The rate of digestion is therefore dependent on the quality of food ingested.

Sable antelope are considered as a water dependent species (Estes & Estes 1974; Wilson & Hirst 1977), in some cases not moving further away than two to four kilometres from water (Wilson & Hirst 1977). According to Estes & Estes (1974) water dependency also varies from the wet to the dry seasons. Herds at the Luando Natural Integral Reserve were observed visiting water holes more frequently in the dry season (Estes & Estes 1974). According to Estes & Estes (1974) the home range of an animal is its distribution over a period of time. The sizes of home ranges are affected by variations in rainfall and a number of other factors (Estes & Estes 1974) and may vary greatly from year to year, day to day, and between herds and populations. Home range sizes estimated from 95% minimum convex polygons (MCP's), on Transvaal nature reserves, include a 7.46 km² annual home range recorded for a population situated in the Percy Fyfe Nature Reserve, a 9.23 km² annual home range in the Loskop Dam Nature Reserve, and a 17.72 km² annual home range in the Kgaswane Nature Reserve (Wilson & Hirst 1977). Annual home ranges as large as 65 km² and 118 km² were recorded for two herds of sable antelope in Kruger National Park (Rahimi & Owen-

Smith 2007). Sable antelope in the Shimba Hills National Park had annual home ranges varying between 10 to 24 km² (Sekulic, cited in Dabengwa 2009). Sable antelope from Zimbabwe and Botswana have entirely separate wet and dry season home ranges (Estes & Estes 1974). Estes & Estes (1974) theorises that this is because these parts are the driest of the species' geographical range, occurring south of the preferred *Brachystegia* – *Julbernardia* woodland zone and that these populations could therefore be considered migratory to semi-migratory as a result. Though herd composition may vary seasonally and from day to day, a herd generally remains within a defined area over multiple generations (Estes & Estes 1974). Home ranges of neighbouring herds almost never overlap, and there is no exchange of individuals between neighbouring herds (Estes & Estes 1974). According to Estes & Estes (1974) the seasonal variation in the dispersal and aggregation of herd members and the range of daily herd movements is strongly correlated to seasonal variation in the availability of food and/or habitat preferences and the stage of reproduction. In Angola the largest aggregation occurred during the dry season and the amount of day to day movement was relatively small as large herds utilised burnt pastures. This was followed by herds breaking up into relatively stable subgroups settling in the wooded part of the home range with the onset of the rut season. At the end of the rains herd stability was at its lowest with subgroups breaking into smaller groups and wandering more widely. According to Estes & Estes (1974) the instability and restlessness, with expeditions of up to 10 km at a time, observed during this time were as a result of the search for higher quality forage just before the calving season. Restructuring of breeding herds occurred after calves left concealment.

The general activity pattern of sable antelope is determined by the species' foraging strategy, which in effect determines how much time is spent foraging and ruminating (Grobler 1981; Parrini & Owen-Smith 2009). However, according to Grobler (1981) physiological requirements such as water dependency and thermoregulation also have an effect. Herds of sable antelope are generally more active in the morning and late afternoon, separated by several hours of inactivity during which individuals mostly rest and ruminate (Grobler 1981; Estes 1992). Sable antelope herd members drink water collectively most often at midday (Grobler 1981) but also in the early morning, late afternoon and at night (Estes & Estes 1974).

According to Estes & Estes (1974) the same social organisation and grouping patterns are observed in all subspecies of sable antelope. Three social classes occur namely breeding herds (females and young), territorial males and bachelor herds (juvenile to sub-adult males) (Estes & Estes 1974; Grobler 1974). A linear hierarchy is maintained among female sable antelope and is based on seniority (Estes & Estes 1974; Thompson 1993). Estes & Estes

(1974) states that the oldest females are often the most dominant individuals and lead herd movements. Additionally according to Estes & Estes (1974) all immature individuals are dominated by adult individuals. Dominant – submissive relationships are maintained through frequent intimidation (Grobler 1974; Thompson 1993). According to Thompson (1993) the unidirectionality of aggressive interactions may contribute to the long term stability of linear hierarchies observed in the species, with dominant adult females initiating more aggression compared to sub-ordinate adult females. Additionally, adult females do not direct aggression towards their immediate sub-ordinate, instead a number of dominant females may direct their aggression towards one specific sub-ordinate female (Thompson 1993). According to Thompson (1993), in instances where food and shelter is limited, females receiving disproportionate amounts of aggression may suffer.

Bachelor herds are uncommon in sable antelope however, when they do occur, they only contain young sexually and/or socially immature males (Estes & Estes 1974). Sable antelope males are evicted from the breeding herd at the age of four years, which is late in comparison to other antelope species. At the age of two years, sub-adult males become more independent and tend to form sub-groups (Estes & Estes 1974). Between three and four years of age, these sub-groups separate from the herd, but tend to remain in the home range of the breeding herd (Estes & Estes 1974).

Between the ages of five and six years, sable antelope males mature socially and separate themselves from other males (Estes & Estes 1974). Socially mature males seek out areas to make their own which they patrol and demarcate by defecating, scraping and performing vegetation horning (Estes 1999). The home ranges estimated for territorial males are generally considered as their territories (Estes & Estes 1974; Grobler 1974). In populations under natural conditions, male territories are usually situated within the home range of at least one breeding herd depending on the status of the male (Grobler 1974). Most of the time of the territorial male is spent in a favoured area (core area), with some time spent on patrolling and demarcating boundaries (Estes & Estes 1974).

When accompanying a breeding herd, the territorial male exerts dominance over all members of the breeding herd (Estes & Estes 1974; Grobler 1974). The territorial male however does not lead the breeding herd, but brings up the back of the herd, where according to Estes & Estes (1974) he can more easily control the movements of the herd. Herd movements are controlled by a series of dominance and threat displays reinforced by the occasional chasing, horning, and head butting (Estes & Estes 1974; Grobler 1974). The territorial male tends to remain behind in his territory after a breeding herd leaves (Estes &

Estes 1974; Grobler 1974). According to Grobler (1974) territorial behaviour is most pronounced during the peak mating season.

Sable antelope reproduce seasonally in the case of populations situated in the southern part of the species' geographic range, with one distinct calving season coinciding with the peak or end of the rainy season (Estes & Estes 1974; Sekulic 1978; Wilson & Hirst 1977; Skinner & Chimimba 2005). Populations situated closer to the equator however, do not reproduce seasonally. For example, sable antelope from the Shimba Hills National Park in Kenya reproduced throughout the year not showing any seasonality in reproduction (Sekulic 1978). The author attributed the lack of seasonality to a lack in seasonal variation of day length, temperature and unpredictability of rainfall. According to Sadleir (as cited in Sekulic 1978) the significance of calving in the rainy season is related to the high nutritional need of late pregnancy and lactation and states that calves born during the rainy season will therefore have a better chance of survival.

Sable antelope populations in Zimbabwe, Botswana and South Africa show similar mating and calving seasons (Child, cited in Skinner & Chimimba 2005; Fairfall 1968; Grobler 1974; Wilson & Hirst 1977). Mating seasons generally occur between May and June with a peak in June and calving from January to March peaking in February. According to Thompson (1991), partial birth synchrony and not full birth synchrony is observed in sable antelope, with a strong correlation between temporal proximity of parturition and social rank. Flehmen is unusually common in both sexes and all ages of sable antelope (Thompson 1995a; Estes & Estes 1974) and according to Thompson (1995b) might be the mechanism through which female sable antelope reproduce synchronously. Flehmen, as defined by Estes (as cited in Thompson 1995b), is characterised by the retraction of the upper lip directly following olfactory investigation, which typically involves direct sampling of freshly voided urine. According to Estes (as cited in Thompson 1995b) the territorial male will test the receptiveness of a female by performing flehmen behaviour. If however the female is not receptive, and therefore not in oestrous, the territorial male will move on. However, if she is receptive, courtship behaviour continues until copulation takes place (Skinner & Chimimba 2005).

Female sable antelope become sexually mature at the age of two years and will normally calve for the first time in the third year (Estes & Estes 1974; Grobler 1974; Grobler 1980a), whereas males become sexually mature at around 18 months (Wilson & Hirst 1977). The gestation period as reported by previous studies include 240 to 248 days (Wilson & Hirst 1977) observed for sable antelope in South Africa and nine months (Grobler 1974) observed for sable antelope populations in Zimbabwe. However, Grobler (1980a) observed

a mean gestation period for sable antelope in the Rhodes Matopos National Park of 266 days ($n = 4$; range: 259 – 272).

Sable antelope are considered to be one of the most profitable wildlife species in southern Africa. According to Bothma & Van Rooyen (2005) wildlife production is defined as “*the optimal utilisation of renewable natural resources in harmony with the environment, with the intent to derive an income from it by sustainable consumptive and/or non-consumptive means*”. The production of wildlife in South Africa provides a number of consumable activities such as recreational hunting, trophy hunting, and the utilisation of meat, as well as non-consumable activities such as accommodation, breeding material and wildlife viewing.

Extensive wildlife production, also known as wildlife ranching, is defined as the management of wildlife in a fenced system, with minimal human intervention (Carruthers 2008). Minimal human intervention in this case refers to the provision of supplementation and water in the dry months only (Carruthers 2008). Intensive wildlife production on the other hand refers to the management of wildlife in a fenced area where management practices such as the provision of supplementation and water, not only in the dry season, the control of parasites, the provision of health care, and the supplementation of prey populations is practiced to increase productivity (Carruthers 2008). Wildlife farming however, is defined as intensive wildlife management strategies practiced in small enclosures (Bothma & Van Rooyen 2005). According to Bothma & Van Rooyen (2005) the extensive management of rare wildlife species often results in retarded growth rates as a result of deficiencies and mortalities. Therefore, for optimal production in populations of sable antelope in South Africa, most opt for the use of intensive management strategies, often resorting to wildlife farming to limit the space needed.

The effects of captive management on aspects of social and reproductive behaviour of sable antelope have been investigated by a few authors (Thompson 1991; Thompson 1993; Thompson 1995a; Thompson 1995b). These studies were however mostly conducted on populations housed in very small enclosures (10 to 20 ha) with management practices centred around conservation. Management implications of the intensive production of sable antelope have been suggested by Kriek (2005). However, no scientific data is available concerning the effects of intensive management practices used in the intensive production of sable antelope in South Africa. The main objective of this study was therefore to determine the effects of management strategies practiced specifically in intensive wildlife production in South Africa, on the social and reproductive behaviour of sable antelope.

Key Question: How are aspects of social and reproductive behaviour of sable antelope influenced by management strategies used for intensive wildlife production?

Objective 1:

To determine how the general activity pattern of sable antelope is affected by intensive management strategies.

Questions:

1. Does the activity pattern of intensively managed populations differ from that of an extensively managed population?
2. What are the consequences of such behavioural differences, if any, for the management of intensive sable populations?
3. How is the extent of the range used influenced by intensive management strategies?

Objective 2:

To determine the prevalence of aggression in social behaviour in intensively managed sable antelope populations.

Questions:

1. Do intensive management strategies in wildlife production influence the frequency of agonistic behaviour?
2. Do intensive management strategies in wildlife production influence the levels of aggression in agonistic interactions?
3. Does the frequency and level of aggression of social interactions pose a threat of injury in intensively managed populations?

Objective 3:

To determine the effect of intensive management on the reproductive behaviour of sable antelope.

Questions:

1. Do intensive management strategies of sable antelope influence their reproductive behaviour in terms of (a) flehmen, (b) courtship and (c) territorial behaviour?

2. Do intensive management strategies practiced in wildlife production of sable antelope result in increased levels of productivity?
3. What are the implications of intensive management strategies concerning the social and reproductive behaviour of sable antelope?
4. Do these implications of intensive management, support the viability of intensive wildlife production?

CHAPTER 2: STUDY AREAS

Three populations of sable antelope, located at three different localities (Figure 2.1) not more than 150 km apart were included in the study. All three study areas fall within the boundaries of the Savanna biome (Mucina & Rutherford 2006; Low & Rebelo 1996). The macroclimatic patterns of this biome are tightly linked to the climatic differences between the Atlantic and Indian Ocean coasts. Characteristic of vegetation units in the Savanna biome is seasonal precipitation, mostly occurring during summer, distinct dry winters, subtropical to tropical temperature regimes and a low incidence of frost (Mucina & Rutherford 2006). Climate data was obtained from the South African Weather Service.

2.1 Sandveld Nature Reserve

A free range, extensively managed population of sable antelope was studied on Sandveld Nature Reserve, which is approximately 10 km east of Bloemhof in the Free State Province, South Africa (Figure 2.2). The reserve is situated along the banks of the Bloemhof Dam and extends along the borders of the Vet and Vaal Rivers in the Free State. For discussion purposes, the reserve was divided into two management units namely the Northern- and Southern Vet management units. The Northern Vet management unit is separated from the Southern Vet management unit by the Bloemhof Dam in the north and by the Vet River in the south. The study population remained within the Northern Vet management unit (Figure 2.2) which covers an area of approximately 4947.25 ha with an elevation of approximately 1 240 m above sea level.

According to Mucina & Rutherford (2006), the veld type of the Sandveld Nature Reserve is described as Kimberley Thornveld. It has previously been described as Kimberley Thorn Bushveld by Low & Rebelo (1996) and Kalahari Thornveld and Shrub Bushveld by Acocks (1988). The Kimberley Thornveld region is largely defined by Andesitic lavas of the Allanridge formation in the north and west and fine-grained sediments of the Karoo subgroup

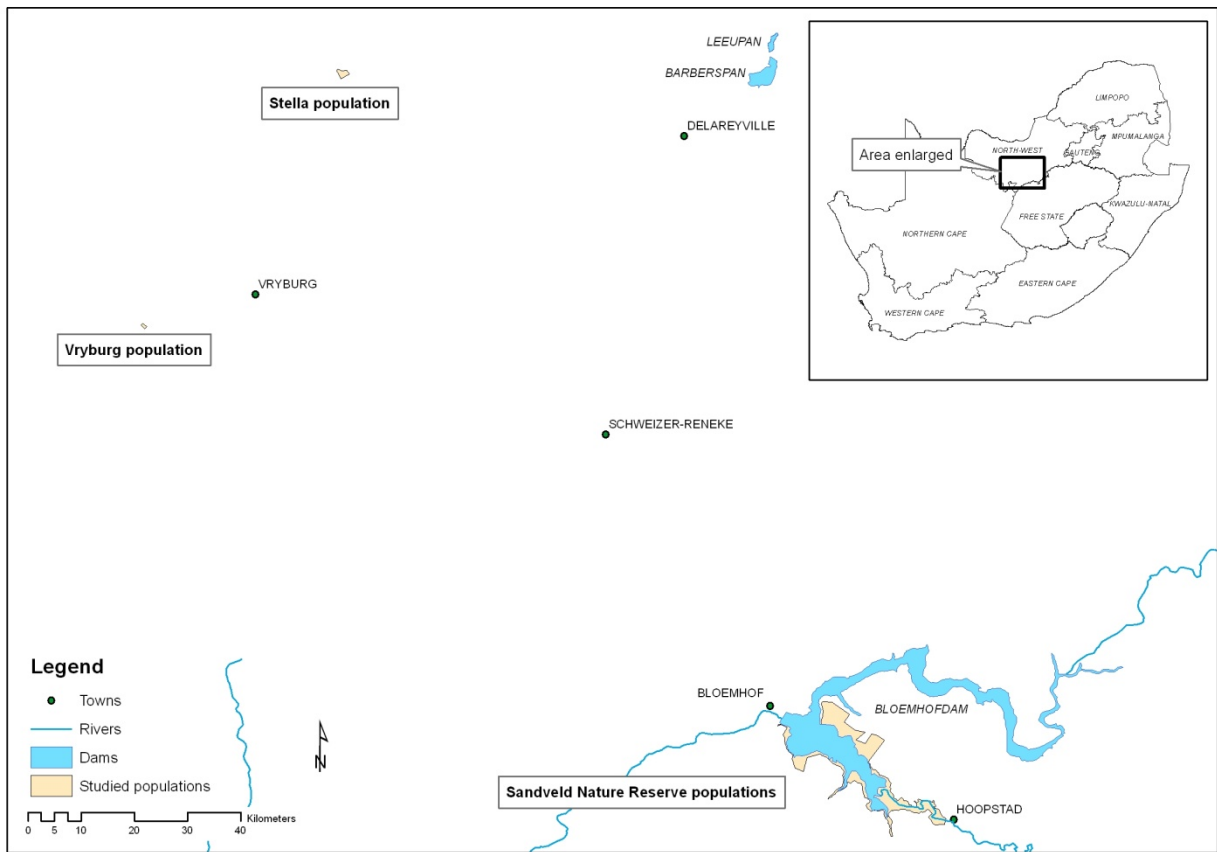


Figure 2.1 Geographical locations of the three study populations of sable antelope.

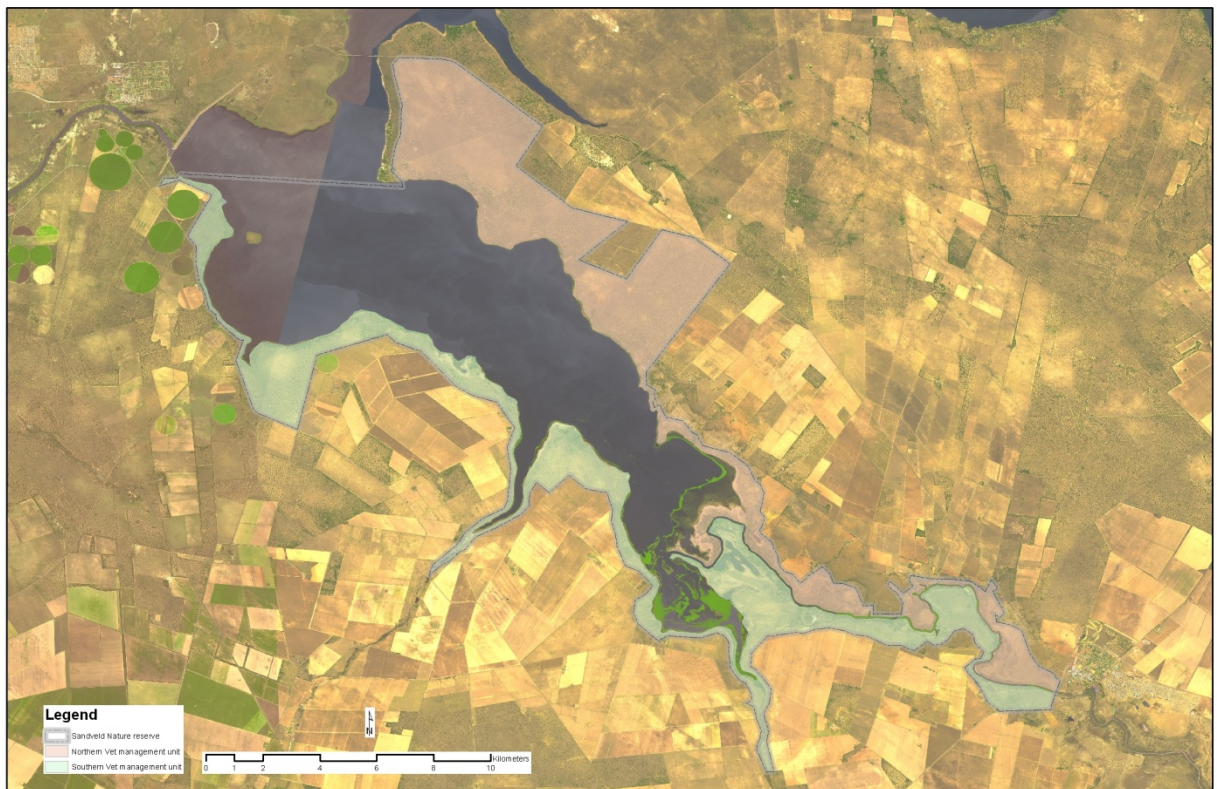


Figure 2.2 The Northern and Southern Vet Management units of Sandveld Nature Reserve, in the Free State Province, South Africa.

in the south and east. The region is situated on undulating sandy plains, with deep (0.6 – 1.2 m) sandy to loamy soils (Mucina & Rutherford 2006). The Sandveld Nature Reserve falls into a summer to autumn rainfall region, with very dry winters and frequent frost (Mucina & Rutherford 2006). A climatic diagram for the area, according to Walter (1979), was constructed using climate data obtained from the Bloemhof weather station (Figure 2.3). The mean annual rainfall for the area, from 1992 to 2010, was 501 mm. According to the climate diagram the wet season for the area is from October to May and the dry season from June to September, with the majority of precipitation occurring in December and January. Temperature for the region varies between a mean minimum value of -3.9 °C for July and a mean maximum value of 37.4 °C for January (Mucina & Rutherford 2006).

The area is savanna woodland with a well developed tree layer and a fairly well developed grass layer (Mucina & Rutherford 2006; Low & Rebelo 1996) (Figure 2.4). *Vachellia erioloba* is the dominant tree species. Abundant tree species include *Vachellia karroo*, *Vachellia hebeclada*, *Ziziphus mucronata*, *Searsia lancea* and *Diospyros lycioides*. The shrub layer is moderately well developed in places and is dominated by *Grewia flava*, *Ehretia rigida*, *Searsia pyroides*, *Asparagus laricinus* and *Asparagus sauveolens* (Viljoen 1979; Jooste 2000). According to Jooste (2000), the most important grass species are *Antheplora pubescens*, *Panicum kalaharensense*, *Panicum coloratum*, *Stipagrostis uniplumis*, *Brachiaria nigropedata*, *Digitaria eriantha*, *Eragrostis lehmanniana*, *Eragrostis trichophora*, *Schmidtia pappophoroides*, and *Aristida* spp.

In 1995, 15 years after the proclamation of the area as a Provincial Nature Reserve (1980), sable antelope were introduced for the purposes of breeding with scarce wildlife (Jooste 2000). In 1995 and 1996 a total of 31 females and seven males were translocated to the reserve from the farm Nietverdiend near the town Zeerust, North West Province, South Africa. Another group consisting of three males and four females was introduced from a farm located near Kuruman, Northern Cape Province, South Africa (Jooste 2000). Game counts for Sandveld Nature Reserve for 2011 and 2012 are listed in Table 2.1.

2.2 Stella

A second population included in the study, was located on a private game farm approximately 5 km south of Stella in the North West Province, South Africa (Figure 2.5). The enclosure is located at 26°34'56.87"S 24°52'48.67"E, at approximately 1 300 m above sea level and covers an area of 207 ha. This study area is geographically located in the Stella Bushveld vegetation unit (Mucina & Rutherford 2006).

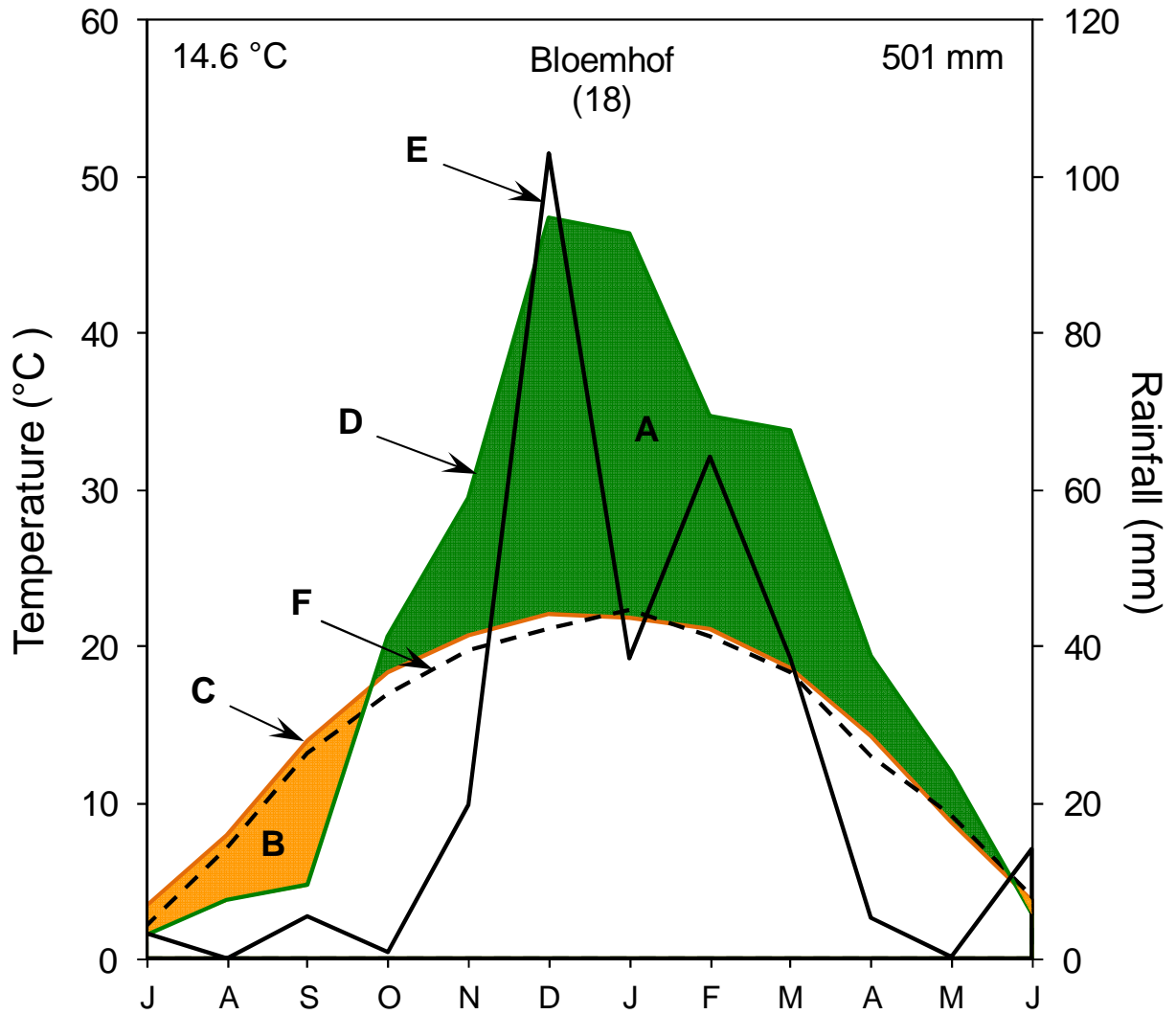


Figure 2.3 Walter's Climate diagram (Walter 1979), of Bloemhof for the years of 1992 to 2010. The number in brackets indicates the number of years observed. The mean annual temperature and the mean annual rainfall for the region are indicated in the top left and right corners respectively. A, wet season; B, dry season; C, mean monthly temperature; D, mean monthly rainfall; E, monthly rainfall during the study; F, mean monthly temperature during the study.



Figure 2.4 Savanna woodland area, utilised by sable antelope on Sandveld Nature Reserve, in the Free State Province, South Africa.

Table 2.1 Game counts of all conserved wildlife species on Sandveld Nature Reserve during the study period.

Game Species		Number of animals	
Common name	Scientific name	Year	
		2011	2012
Blue wildebeest	<i>Connocheates taurinus</i>	214	204
Buffalo	<i>Syncerus caffer</i>	90	89
Common Rheedbuck	<i>Redunca arundinum</i>	16	35
Eland	<i>Tragelaphus oryx</i>	102	84
Gemsbok	<i>Oryx gazelle</i>	93	72
Giraffe	<i>Giraffa camelopardalis</i>	19	21
Hippopotamus	<i>Hippopotamus amphibious</i>	2	2
Impala	<i>Aepyceros melampus melampus</i>	84	92
Kudu	<i>Tragelaphus strepsiceros</i>	61	75
Ostrich	<i>Struthio camelus</i>	50	52
Plains Zebra	<i>Equus quagga</i>	76	73
Sable antelope	<i>Hippotragus niger niger</i>	72	64
Springbok	<i>Antidorcas marsupialis</i>	87	73
Steenbok	<i>Raphicerus campestris</i>	17	22
Tsessebe	<i>Damaliscus lunatus</i>	90	84
Warthog	<i>Phacochoerus africanus</i>	48	162
Waterbuck	<i>Kobus ellipsiprymnus</i>	47	45
White Rhinoceros	<i>Ceratotherium simum</i>	22	17

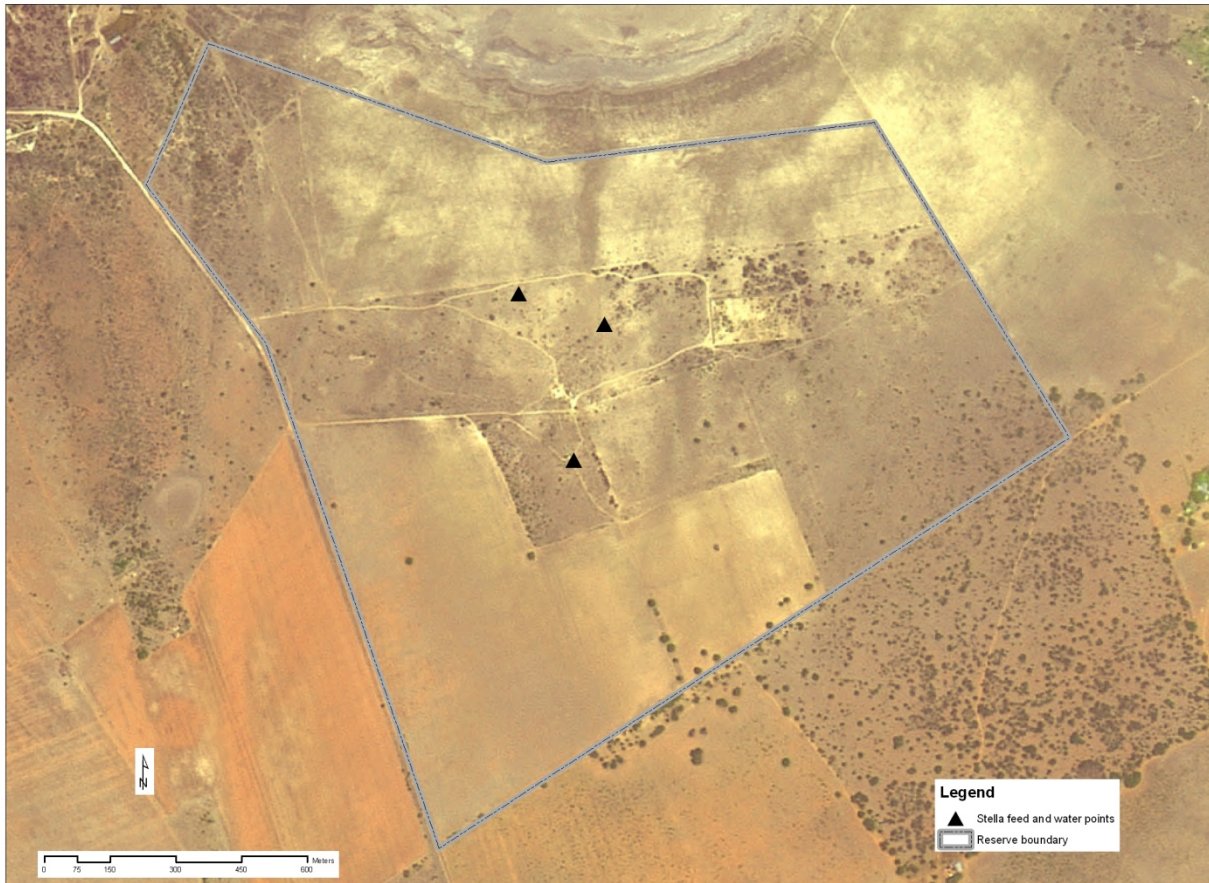


Figure 2.5 The private game farm situated outside Stella in the North West Province, with two water troughs and the location of feeding troughs shown.

The area was classified as Kalahari Plateau Bushveld by Low & Rebelo (1996) and as forming part of the Kalahari Thornveld and Shrub Bushveld vegetation unit by Acocks (1988). Andesitic lavas of the Allanridge Formation of the Ventersdorp Supergroup, sometimes covered by silcrete or calcrete of the Kalahari Group, with flat and hilly plains, are characteristic of the Stella Bushveld vegetation unit (Stella private game farm). Soils of this region are predominantly sandy and between 0.1 and 0.9 m deep.

The study area falls in a summer rainfall region with dry winters and frequent frost (Mucina & Rutherford 2006). A Walter's Climate diagram was constructed using climate data obtained from Vryburg (situated 57 km from this study area) (Figure 2.6). The area has a mean annual rainfall of 472 mm (1992 to 2010), with most of the precipitation occurring during January and February. The wet season is from November to May and the dry season from June to October.

Vegetation of the enclosure is made up of a combination between natural vegetation, recovering planted pastures and planted pastures of *Cenchrus ciliaris*. Recovering planted pastures are dominated by *Melinis repens*, and *Aristida congesta* with a few scattered *V. karroo* trees (< 2 m). Natural vegetation has a well developed open tree layer, with *Vachellia tortilis* and *V. erioloba* dominating and scattered individuals of *S. Lancea* (Figure 2.7). The shrub layer is well developed and consists predominantly of *G. flava*, *V. karroo* and *A. laricinus*. Dominant grass species are *C. ciliaris*, *Cymbopogon pospischilii*, *A. congesta*, *D. eriantha*, *Themeda triandra* and *E. lehmanniana*. The game farm was stocked with sable antelope, buffalo, springbok, blesbok and eland. The game counts for the enclosure at the start of the study are listed in Table 2.2.

2.3 Vryburg

The third population is kept in an enclosure of 44 ha on a game farm situated approximately 21 km west of Vryburg in the North West Province, South Africa (Figure 2.8). The enclosure is located at 27°0'17.11"S 24°32'20.54"E at approximately 1 265 m above sea level. According to Mucina & Rutherford (2006), the private game farm is geographically located in the Ghaap Plateau Vaalbosveld vegetation unit.

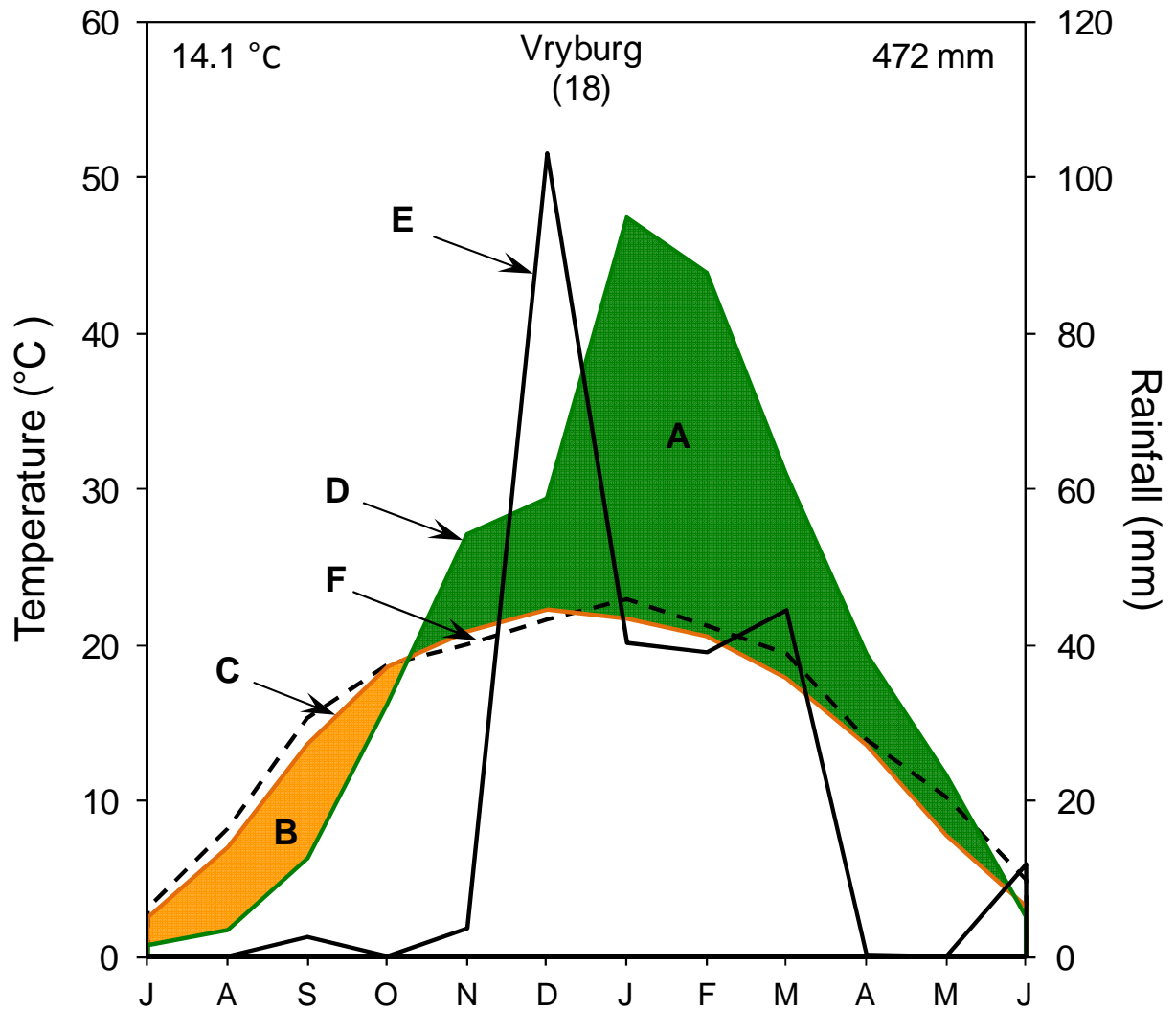


Figure 2.6 Walter's Climate diagram (Walter 1979), of Bloemhof for the years of 1992 to 2010. The number in brackets indicates the number of years observed. The mean annual temperature and the mean annual rainfall for the region are indicated in the top left and right corners respectively. A, wet season; B, dry season; C, mean monthly temperature; D, mean monthly rainfall; E, monthly rainfall during the study; F, mean monthly temperature during the study.



Figure 2.7 Natural vegetation in the enclosure on the private game farm situated near Stella in the North West Province, South Africa.

Table 2.2 Game counts at the start of the study (2011) for the private game farm situated approximately 5 km south of Stella in the North West Province, South Africa.

Game Species		
Common name	Scientific name	Number of animals
Blesbok	<i>Damaliscus pygargus phillipsi</i>	60
Buffalo	<i>Syncerus caffer</i>	10
Eland	<i>Tragelaphus oryx</i>	18
Sable antelope	<i>Hippotragus niger niger</i>	42
Springbok	<i>Antidorcas marsupialis</i>	15



Figure 2.8 The enclosure of the intensively managed population situated on a private game farm near Vryburg in the North West Province, South Africa.

This region was also classified as forming part of the Kalahari Plateau Bushveld vegetation unit (Low & Rebelo 1996) and the Kalahari Thornveld and Shrub Bushveld vegetation unit (Acocks 1988). The Ghaap Plateau Vaalbosveld vegetation unit features surface limestone of tertiary to recent age and dolomite and chert of the Campbell Group, supporting shallow soils between 0.1 and 0.25 m deep.

The study area falls in a summer to autumn rainfall region with dry winters and frequent to very frequent frost (Mucina & Rutherford 2006). The same climate diagram was used for the two intensive populations (Figure 2.6) (Walter 1979). The area has a mean annual rainfall of 472 mm (1992 to 2010), with most of the precipitation occurring during January and February. The wet season is from November to May and the dry season from June to October. Mean monthly minimum and maximum temperatures for the region ranged between -5.5 °C for July and 36.6 °C for January respectively (Mucina & Rutherford 2006).

The area has well developed shrub layer dominated by *Tarchonanthus camphoratus* with scattered individuals of *V. karroo*. The area's tree layer is open with sparsely occurring individuals of *Olea europaea africana*, *V. tortilis*, *Z. mucronata*, and *S. lancea*. The enclosure has a well developed shrub layer dominated by *T. camphoratus* and *G. flava* with *V. karroo* occurring sparsely (Figure 2.9). The tree layer of the enclosure consists of a few scattered individuals of *S. Lancea*. Dominant grasses of the study area include *C. pospischilii*, *Antheophora pubescens*, *Heteropogon contortus*, *Fingerhuthia africana*, *T. triandra*, *S. uniplumis* and *Sporobolus fimbriatus*.



Figure 2.9 The natural vegetation in enclosure situated on the private game farm near Vryburg in the North West Province, South Africa.

CHAPTER 3: METHODOLOGY

3.1 Study populations

Three different sable antelope populations under different management regimes were included in the study. To determine the effects of management strategies practiced on captive sable antelope, intensive managed populations were compared to an extensively managed population. One population situated on Sandveld Nature Reserve was considered to be an extensive population as these animals were free to breed under natural conditions without any human interference. Firstly males were not artificially selected, instead sexual and natural selection pressures remained undisturbed. Secondly rates of reproduction and survival were not manipulated through the provision of dry feed during the dry season, and depended entirely on resources available naturally. Thirdly mortality rates (especially of calves) were not minimised through the exclusion of predators. This is common practice in intensively managed populations where Jackal proof fencing is used to keep out small predators such as caracal (*Caracal caracal*) and black backed jackal (*Canis mesomelas*). Small predators, e.g. caracal and black backed jackal, occurred within the reserve and could move between the reserve and farmland surrounding the reserve. Two management strategies, that could however be considered as somewhat intensive, were included in the management strategy of the population, namely the provision of salt lick in the dry season and water by means of a small artificial round dam situated within the population's home range.

Sable antelope from Sandveld Nature Reserve are considered to be part of the Southern subspecies (*Hippotragus niger niger*, Harris 1838) and because female individuals of the population were dark brown to black in colour, they were considered to belong to a race originating from areas south of the Zambezi River (Estes 2000). In the game farming industry this race is often referred to as the "Matetsi" race. The exact genetic lineage of this population however is unknown. This study population will therefore hereafter be referred to as the Matetsi-extensive population. At the start of the study (August 2011) the study population consisted of 18 sexually mature females, of which two were sub-adults (under three years of age), one sub-adult male, one yearling, 10 juveniles, and the herd was accompanied by one adult male. The study population was identified by the presence of a dominant adult female with a distinct broken right horn and by the number of specific gender and age classes.

Another population situated on a private game farm outside Stella in the North West, were under semi-intensive management. In this population dietary supplementation was provided during late wet (once in the afternoon) and dry seasons (morning and afternoon), when animals showed physical signs of dietary stress. Supplementation was provided in the form of antelope cubes (5 kg per day for the whole sable antelope population) in tire troughs (n = 30) spaced evenly in a circle formation. Other game species that were interested in supplementation, such as the eland, were physically kept away from the feed during feeding times. The population drank water from two standard rectangular water troughs.

Due to the small size of the enclosure male sub-adults were removed at the age of 15 months to reduce aggression. Adult males were selected artificially, according to various aspects such as horn length, coat colour and body size. These males were cycled every two years as to prevent inbreeding. During the study four female yearlings and one sub-adult female were sold at a game auction. This population is considered to be part of the "Matetsi" race of the Southern subspecies (*H. n. niger*, Harris 1838) as females are black in colour, and will hereafter be referred to as the Matetsi-intensive population. This population was established five years prior to the study and at the start of the study consisted of 22 sexually mature female individuals, of which three were sub-adult females (two year olds), 19 yearlings, one juvenile and one adult bull.

Lastly a population situated on a private game farm near Vryburg, in the North West Province was also included in the study. The management strategies practiced in this population were the most intensive in comparison to the other two populations. Supplementation, in the form of antelope cubes, was provided throughout the year in the morning and afternoon in tire troughs (10% more troughs than individuals present in the herd) spaced evenly in two parallel rows. Water was provided in one standard rectangular water trough. Similar to the Matetsi-intensive population sub-adult males were removed at the age of 15 to 18 months, to reduce aggression and artificially selected adult males, were cycled every three years to prevent inbreeding. Due to the small size of the enclosure (44 ha) the management strategies practiced in this population can be described as game farming. This population was established nine years prior to the study and was the only game species present in the enclosure. At the start of the study (August 2011), the population consisted of 14 sexually mature females, of which five females were classified as sub – adults (under three years of age), six yearlings, ten juveniles and one adult male (Figure 2.12). In 2010 all eight adult females calved and of the eight calves two were male. In 2011 just before the study started the first yearling male was removed and the second yearling male was removed in August with the onset of the study. During the study period one male yearling (approximately 16 months) was removed after being targeted by the adult

male and females. Genetic testing indicates that this population is part of a lineage originating from Zambia (Southern subspecies *H. n. niger*, Harris 1838), with females remaining light in colour (chestnut) and will hereafter be referred to as the Zambian-intensive population.

3.2 Field observations and data collection

The location of the breeding herd, in all three populations, was recorded hourly by means of a Garmin eTrex Vista global positioning system (GPS). In order not to disturb the herd, initially its location was temporarily recorded relative to prominent features in the landscape. The GPS point was taken in the exact location after the herd had moved out of the area. Field observations were made from a vehicle on all three populations for 10 consecutive days during late dry season (September 2011), wet season (January 2012), late wet season (April 2012), and dry season (June 2012). Since the Matetsi-intensive population was only included in the study in January 2012 observations in the late dry season are lacking for this population. Study populations were observed from sunrise to sunset (11 to 14 hours daily, depending on the season). Observations were done from not more than 100 meters away with the aid of 10 X 50 Bushnell binoculars. The scan sampling method as described by Altmann (1974) was used and all activities were instantly recorded with the aid of an Olympus VN-8100PC digital voice recorder. The duration of scan sampling varied between 30 seconds and one minute. Continuous observation was used to determine the incidence of drinking water. The prevailing activity pattern, as described in Table 3.1, was recorded every 15 minutes for all individuals of the breeding herd, as well as for the territorial male.

Age determination was based on the external appearance of horns by focussing on the number of annulations and curvature of the horn as described by Grobler (1980b) and listed in Table 3.2. During field observations it was difficult to distinguish between two and three-year-old females. Since females reach sexual maturity at the age of two years (Grobler 1980a; Estes & Estes 1974), two-year-old females were included in the adult female class as done by Grobler (1974). All instances of social interaction were recorded as such and were done between scan sampling. Categories of social behaviour that were of importance in this study included: flehmen, courtship, territorial and agonistic behaviour. All social interactions occurring between two immature individuals for example among yearlings or between yearlings and juveniles were considered as play behaviour and were not included in further analysis. For every interaction, the time of the interaction, the gender and age class of individuals involved, the behaviour patterns exhibited and whether or not the initiator won the interaction was recorded. In instances where both individuals engaged in any other activity for at least one minute, the interaction was considered terminated.

Table 3.1 Age determination of sable antelope as described by Grobler (1980b).

Age category	Age	Horn characteristics
Juveniles	0 - 1 years	No annulations, horn length never exceeded the ear length, tips of horns become visible above the hairline at around two months
Yearlings	1 - 2 years	Between one and 10 annulations (less than a third of the horn length), with horn length equalling or exceeding ear length
Sub-adults	2 - 3 years	Annulations ranged from 10 to 20, horns of two-year-old males showed distinct curvature and were easily distinguishable from far away
Adults	3 years or older	Male horns tend to full curvature (20 to 30 annulations), females become difficult to place into an annual age class

Table 3.2 Activity patterns and descriptions used to determine the general activity pattern of all three populations of sable antelope. All activity patterns are mutually exclusive.

Activity Pattern	Description
Grazing	Foraging at ground level
Browsing	Feeding on trees and shrubs (not at ground level)
Walking	Movement without foraging or social interaction
Standing alert	Standing with an erect and alert body posture
Standing	Resting and ruminating while standing
Lying	Resting and ruminating while lying down
Drinking	Drinking water
Grooming	Removing dirt and parasites from the skin and fur with the teeth or by scratching
Social Interactions	Any intra-specific interaction between two individuals
Territorial displays	Performed by the dominant/territorial male: vegetation horning, herding, scraping and defecation
Utilising dry feed	Utilising dry feed, usually provided in feeding troughs
Supplementation	Geophagy and the utilization of salt lick

For agonistic interactions, the proportion of interactions containing displays of aggression was determined and compared between populations. Displays of aggression were defined and identified using the description of Estes (1992) as a guideline and are listed in Table 3.3. Following the explanation of Estes (1992), displays of aggression were further grouped into fighting, threat displays and dominance displays. According to Estes (1992) “fighting” includes aggression that involves physical contact between two opponents. Aggressive displays included in this category were *horning*, *horn hitting*, *head butting* and *sparing*. Estes (1992) considered *chasing* as the most intense form of aggression displayed by sable antelope and therefore it was also included in the category of “fighting”.

According to Estes (1992), dominance and threat displays occur in the same context, both are used to intimidate the opponent and can therefore easily be confused. For discussion purposes, displays of aggression included in this category were *supplanting*, *walk after*, *head rubbing*, *courtship imitation*, *lateral display* and *circling*. According to Estes (1992), a threat display includes exaggerated displays of movements and postures usually associated with fighting. These displays function as threats of attack. Behavioural patterns included in this category were *mock charging* and all of the described “static” threats (Table 3.3). In effect a threat display does not involve any physical contact and is more likely to end in an attack than in a dominance display.

Flehmen behaviour was defined as the evaluation of a female’s reproductive state through anogenital sniffing or the investigation of freshly voided urine, through analyses in the vomeronasal organ (Estes, as cited by Thompson 1995b). Flehmen was behaviourally defined as the outward curling of the upper lip directly following sampling (Estes, as cited by Thompson 1995b). All interactions containing flehmen were included in the analysis of flehmen behaviour. For all instances of flehmen, the gender and age of the individual urinating and of the individual responding, and whether or not urine was sampled directly from the urine stream or indirectly from the ground after the individual urinating had moved out of the vicinity, was recorded. All flehmen performed by the territorial male was recorded even if courtship continued after sampling. Interactions that were initiated by socially mature individuals and contained predefined behaviour patterns associated with courtship in sable antelope were included in the analyses of courtship behaviour. Courtship behaviour therefore included interactions between territorial males and adult females, as well as between territorial males and yearling females. According to Estes (1999), behaviour patterns associated with courtship include the dominant male following a female closely in the erect posture coupled with foreleg-lifting (“*Laufschlag*”), flehmen behaviour, mounting and, in the case of an unreceptive female, driving, chasing and courtship circling.

Table 3.3 Aggressive displays, their definitions and similar behaviours as described by Estes (1992).

Behavioural Pattern	Definition	Estes (1992)
Fighting		
Horning	Physical contact between the horn tip of dominant individual and any part of the submissive individual, may or may not be preceded by a charge	<i>Stabbing</i>
Head butting	Submissive individual is knocked with the base of the horns or head, normally on the flank or rump, always following a charge	-
Chase	Dominant individual chases the submissive individual (both individuals are running)	<i>Chasing</i>
Sparing	Either head to head or shoulder to shoulder - horns are rubbed and clashed together. A pushing contest normally determines the winner. In shoulder to shoulder sparing, individuals will throw their heads back in an attempt to stab the other individual (shoulder to shoulder sparing is normally only performed in sub-adult individuals (Estes, 1991))	<i>Clash - fighting and fencing, thrust - fighting, parallel fighting,</i>
Horn hitting/Pushing	Horns are hit/ pushed against any part of another individual	-
Dominant displays		
Supplant	Movement towards another individual (walking), with the second individual departing	<i>Supplanting</i>
Head rubbing	Dominant individual rubbing the head and horns against the rump, shoulders, neck or head (including the horns at times) of the submissive individual	<i>rubbing head/horns on opponent</i>
Walk after	Dominant individual walking after the submissive individual while often displaying dominance (both individuals are walking)	<i>Pursuit march</i>
Lateral display	Two individuals standing reverse parallel about one body length apart, displaying the lateral side of the body to the opponent (opponents are near equals)	<i>Lateral presentation</i>
Circling	In a lateral display, both individuals moving in a circle (is included in lateral display when opponents are even more equally matched)	Described as part of <i>Lateral presentation</i>
Courtship imitation	Most often seen between yearlings and calves, asserting dominance, includes mounting and fore leg lifting	-
Threat displays		
Mock Charge	Short running approach stopping short of the individual, fainted attack	<i>Rushing or charging</i>
"Static" threats	Listed below - can be displayed without movement towards the opponent (but is often displayed while moving towards, walking after, in lateral display or whilst chasing subordinate individuals)	
Horn threat	Including <i>high-, medial-, low- and angle- horn presentation</i> as described by Estes (1991)	<i>High-, medial-, low- and angle horn-presentation</i>
Nodding	Moving head up and down	<i>Symbolic butting</i>
Side sweeping	Head is jerked back to shoulder or flank - resembles grooming behaviour	<i>Horn - sweeping</i>
Scrapping	Dominant individual will scrape the ground with one of the front legs	-
Shake head	Shaking head - resembles grooming behaviour	<i>Head - shaking or twisting</i>
Vegetation horning	Displacement activity - thrashing vegetation	<i>Object – horning</i>

However, to determine when true rut occurred, courtship was divided into two categories according to the degree of interest by the territorial male. Interactions that were terminated by the territorial male after performing flehmen were analysed as part of the social category, flehmen behaviour, whereas interactions that continued after flehmen were defined as courtship behaviour. The true rut season was also determined by evaluating peak calving seasons. Peak calving times for all three populations were determined through the evaluation of calving dates. Birth dates of all juveniles present were determined during every observation period by examining hair moult as described by Grobler (1980a). Calving rate were calculated by dividing the number of calves born by the number of adult females older than three years as, according to Grobler (1981), sable female antelope only calve for the first time in their third year.

Territorial displays were defined as any act or intra-specific interaction by the territorial male that functioned in demarcating his territory, retaining a breeding herd within his territory and/or defending his territory against intruding sexually and socially mature males. Territorial displays function in intra-specific competition between territorial males and can therefore also be classified as agonistic behaviour, but for discussion purposes it was analysed separately from other agonistic behaviour. Three different types of territorial displays were identified namely vegetation horning, scraping and herding. Vegetation horning as defined by Estes (1992) is the thrashing/breaking of bushes and saplings with the horns. Branches are broken with the cleft of the horns and bark is scraped off with the outer ridges of the annuli. Herding was defined as the dominant bull forcing the breeding herd in a certain direction (normally away from a territorial boundary) by making use of dominant and threat displays or even physically blocking the way (Grobler 1974). Grobler (1974) also observed territorial males rounding breeding herds up into small compact groups. The most distinctive body postures displayed during territorial behaviour were the *erect posture*, defined as the neck raised above the horizontal sometimes accompanied by lifting the tail horizontally, *lowstretch* defined as the head and neck stretched out in a line with the horns pulled back (chin out), *horn sweeping* and *loud snorting* (Estes 1992). Territorial males also demarcate their territories by scraping and defecating (Estes 1974). For all instances of territoriality, GPS locations were recorded.

Since it is often difficult to determine the exact cause of an interaction, agonistic behaviour was behaviourally defined as all interactions that could not be classified as flehmen, courtship, territorial, mother-calf interactions or play behaviour, though these interactions may also contain agonistic components. Agonistic interactions are often referred to as “fighting” and might even seem to be without any direct benefits especially among females (“spiteful” as described by Stockley & Bro-Jørgensen 2010).

3.3 Data analysis

In all statistical analyses 95% and 99% confidence intervals were used to determine significance. For the analysis of the activity pattern, as the number of individuals observed per scan sample varied between consecutive samples, the counts of a particular activity pattern were expressed as a proportion (percentage) of the total number of observations. These proportions were referred to as the “incidence” of an activity pattern. The incidence of activity patterns was calculated for the wet and dry seasons separately for the comparison between seasons. Furthermore, incidences (percentage of time spent according to Altmann (1974)) of activity patterns for every hour of the day were calculated for the evaluation of daily variation in activity. The seasonal variation in the dietary selection of all three populations was determined by calculating the percentage of observations of browsing, grazing and utilizing dry feed from observations that pertained to feeding behaviour only.

The significance of variation within populations and between populations in multinomial data, including activity patterns and the percentage of interactions containing displays of aggression, was tested using the Pearson chi-square test (SAS procedure FREQ). The reported P-values were checked by estimating the exact P-values using Monte-Carlo simulation (EXACT option in SAS procedure FREQ).

The rate of specific social interactions was determined by dividing the count of observed interactions of the type in question by the relevant number of hours observed. Due to small values the rate per hour was converted to daily rate by multiplying by 24. Seasonal variation in the rate of social interactions was evaluated by calculating the rate per day (per individual, where applicable) for every observation period (late dry, wet, late wet and dry season). This was done because the number of adult females in the Zambian-intensive population increased throughout the study as individuals matured.

Comparisons of the rate of interactions between populations and seasons were carried out by fitting a Poisson regression model, namely a generalized linear model with the following specifications: a Poisson Error distribution; a logarithmic link function; and the logarithm of the product of the number of hours observed and the number of individuals present as the offset variable. From the Poisson regression model estimates of relevant rates were calculated, as well as estimates and associated 95% confidence intervals and p – values for relevant rate ratios (comparisons between populations and seasons).

The GENMOD procedure of SAS (2009) was used to carry out this analysis. To compare the incidence of fighting, threat displays and dominance displays, the same procedure was followed, except the reported P-values were checked by calculating exact P-values because

of small observed counts in some instances (Conditional Exact Test). Statistical analysis was verified by the Statistical Consultation Unit, Department of Mathematical Statistics, Faculty of Natural and Agricultural Sciences, University of the Free State, using the SAS software package (SAS 2009).

For each breeding herd, the annual, wet and dry season home ranges and core areas were calculated by constructing 95% (home range) and 50% (core area) fixed kernel density estimates. Fixed kernel density estimates were constructed using the Geospatial Modelling Environment (Version 0.7.4.4) in conjunction with statistical software R (Version 3.2.0). Maps were drawn using *ArcMap* 10.1. The smoothing parameter (bandwidth) was determined using the least square cross validation method. In order to compare populations the same cell size of 10 m was used for all three populations. Home ranges were also calculated by constructing 95% minimum convex polygons, for the comparison with previously published data on the home range size of sable antelope. Ranges of territorial males were determined using GPS coordinates obtained for breeding herd if the specific territorial male was sighted within 15 minutes before or after the location was documented. To determine where territorial behaviour was more pronounced, sightings of territoriality were compared to annual 95% kernel density estimates (territories) and 50% kernel density estimates (core areas) constructed for the three territorial males of the Matetsi-extensive population. For the Matetsi-intensive and Zambian-intensive populations these sightings were compared to the annual 95% and 50% kernel density estimates of the breeding herd as they almost never separated from breeding herds.

CHAPTER 4: ACTIVITY PATTERNS AND RANGE USE

4.1 General Activity Pattern

Results

In order to establish the influence of the use of management strategies on the general activity patterns of sable antelope, seasonal and daily variation in activity budgets of territorial males and breeding herds of all three populations were compared. Observations of the Matetsi-extensive, Matetsi-intensive and Zambian-intensive populations were carried out for a total of 287, 188 and 267 hours respectively. The seasonal and hourly incidence (percentage) of activity patterns was determined by dividing the count of a specific activity pattern, for the specified season or hour, by the total number of observations for the time period. Of all of the activity patterns observed, the least prevalent activities were drinking water; grooming and supplementation (*vide* Table 3.2) and due to very small sample sizes these activities were combined into an “other” category and were not included in statistical analysis.

In the two Matetsi populations, lying and grazing dominated wet and dry season activity patterns of breeding herds and territorial males (Figures 4.1 & 4.2). However in the Zambian-intensive population lying alone was the most pronounced activity for both the territorial male and breeding herd, with other activities such as grazing, standing and the utilisation of dry feed equally constituting substantial parts of the wet and dry activity patterns (Figure 4.3).

In comparing only the breeding herds of all three populations, the percentage of time spent grazing in both seasons significantly decreased as the intensity of management increased. The Matetsi-extensive population (dry season, 33.2%; wet season, 46.3%) grazed significantly more ($p < 0.01$) compared to the Matetsi-intensive population (dry season, 26.2%; wet season, 42.4%) which in turn, grazed significantly more ($p < 0.01$) than the Zambian-intensive population (dry season, 14.8%; wet season, 20.8%). Conversely, only in the wet season, the percentage of lying in the activity of breeding herds also increased significantly with the use of intensive management strategies ($p < 0.01$).

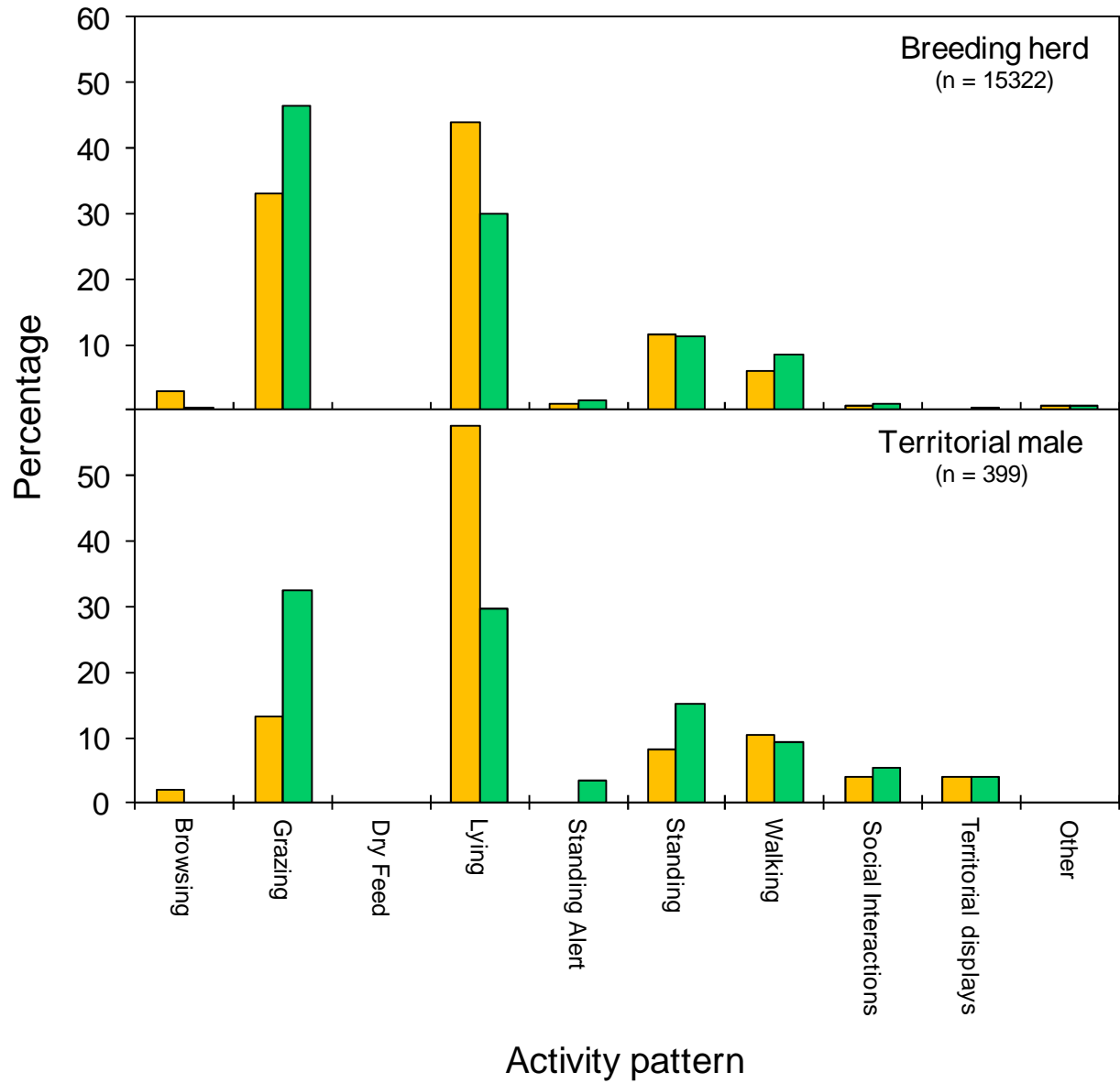


Figure 4.1 Seasonal variation in the general activity of the breeding herd and territorial male of the Matetsi-extensive population at Sandveld Nature Reserve for the dry (June – September, yellow bar) and wet seasons (October – May, green bar).

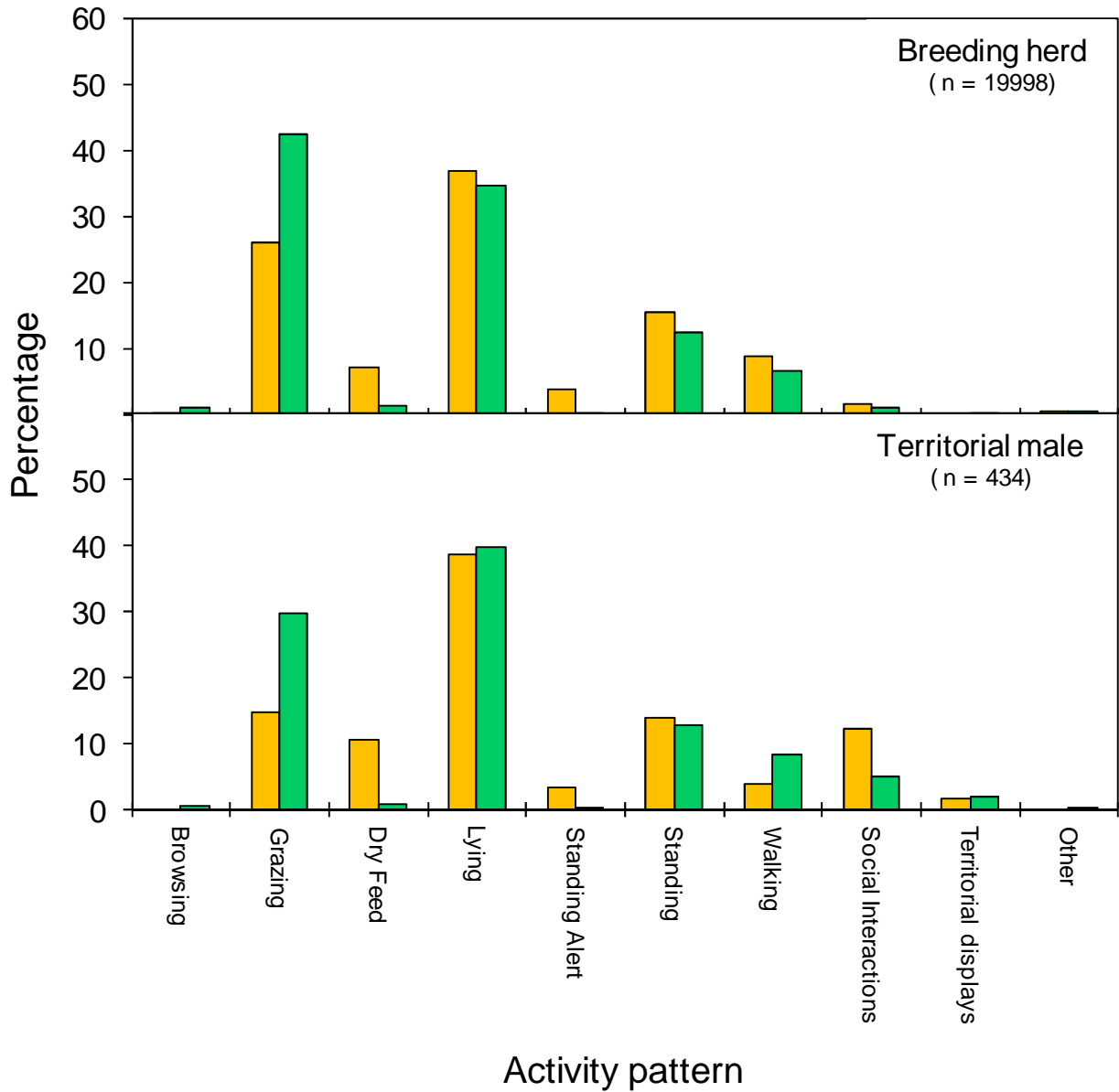


Figure 4.2 Seasonal variation in the general activity pattern of the breeding herd and territorial male of the Matetsi-intensive population at Stella for the dry (June – September, yellow bar) and wet seasons (October – May, green bar).

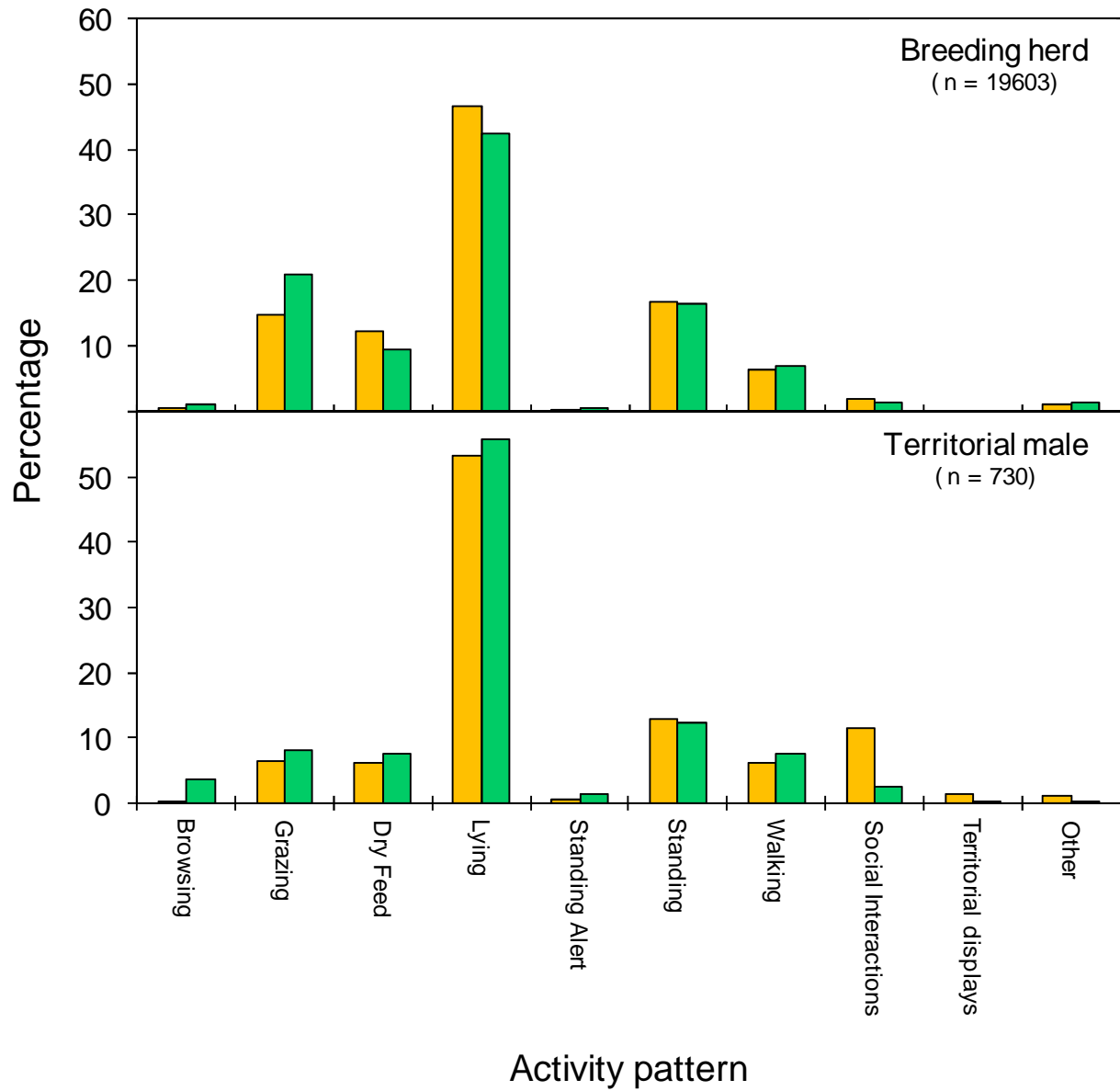


Figure 4.3 Seasonal variation in the general activity pattern of the breeding herd and territorial male of the Zambian-intensive population near Vryburg for the dry (June – September, yellow bar) and wet seasons (October – May, green bar).

However, in the dry season, though the incidence of lying was still the highest in the Zambian-intensive population, the percentage of time spent lying by the breeding herd of the extensively managed population at Sandveld Nature Reserve was significantly higher ($p < 0.01$) than that of the Matetsi-intensive population. In comparing breeding herds, the highest incidence of standing alert was observed in the Matetsi-intensive population in the dry season. This breeding herd was significantly more vigilant in the dry season compared to both the Matetsi-extensive and Zambian-intensive populations ($p < 0.01$). In both seasons the incidence of standing also increased as the extent of intensive management increased. However, in the wet season the percentage of time spent standing by the breeding herd of the Matetsi-intensive population was similar ($p > 0.05$) to that observed for the breeding herd of the extensively managed population at Sandveld Nature Reserve and, in the dry season it was more comparable to the percentage of time spent standing by the breeding herd of the Zambian-intensive population.

In the wet season the breeding herd of the Matetsi-extensive population was observed spending significantly more ($p < 0.01$) time walking compared to the breeding herds of the two intensive populations, with intensive breeding herds spending similar percentages of time walking ($p > 0.05$). However in the dry season the breeding herd of the Matetsi-intensive population spent significantly more ($p < 0.01$) time walking than the breeding herd of the Matetsi-extensive and the Zambian intensive populations, with the percentage of time spent walking in these two populations not differing significantly ($p > 0.05$).

In comparing territorial males, in both seasons the percentage of time spent grazing by the Matetsi-intensive territorial male did not differ significantly from that observed for the territorial male of the Matetsi-extensive population ($p > 0.05$). However the incidence of grazing observed for the territorial male of the Zambian-intensive population was significantly lower ($p < 0.05$) than the incidences of grazing observed for territorial males of the other two populations in both the wet and dry seasons. For territorial males, the incidence of lying in the wet season only, increased significantly ($p < 0.01$) as the degree of intensive management increased, constituting as much as 55.8% of the wet season activity pattern of the territorial male of the Zambian-intensive population. However in the dry season territorial males of the Matetsi-extensive population spent significantly ($p < 0.01$) more time lying down compared to the territorial male of the intensively managed population at Stella, not differing significantly from the territorial male of the Zambian-intensive population ($p > 0.05$). In the dry seasons lying constituted as much as 57.6% of the activity pattern of the Matetsi-extensive territorial male.

In comparing social classes, in all three populations in both seasons breeding herds were observed grazing significantly more than territorial males ($p < 0.01$). In evaluating the percentage of time spent lying down, the territorial male of the Zambian-intensive population spent significantly more time lying compared to the breeding herd in both seasons ($p < 0.05$). In the Matetsi-intensive population though the percentage of time spent lying down in both seasons was slightly more for the territorial male compared to the breeding herd, these differences were not significant ($p > 0.05$). In the Matetsi-extensive population in the dry season the territorial male spent significantly more time lying down compared to the breeding herd ($p < 0.01$). In the dry season territorial males of the Matetsi-extensive population were slightly more vigilant compared to the breeding herd. Additionally the territorial male of the Zambian-intensive population was also observed standing alert significantly more often compared to the breeding herd in the wet season ($p < 0.01$). However, in the Matetsi-intensive population there were no significant differences between the breeding herd and territorial male in the percentage of time spent standing alert in the dry or wet season ($p > 0.05$).

The only difference in the percentage of time spent standing observed between a breeding herd and territorial male was in the Zambian-intensive population, in which the breeding herd spent significantly more time standing in the wet season compared to the territorial male ($p < 0.05$). In the dry season the territorial male of the Matetsi-extensive population spent significantly more time walking compared to the breeding herd ($p < 0.05$). In both of the Matetsi populations the percentage of time spent on social interactions, was significantly higher for territorial males compared to breeding herds ($p < 0.01$). However in the Zambian-intensive population only during the dry season, and not in the wet season, did the territorial male spend significantly more time on social interactions compared to the herd ($p < 0.01$).

A distinct pattern in the seasonal variation in the percentage of time spent grazing and lying was observed when comparing breeding herds and territorial males of all three populations. For all three breeding herds grazing was significantly more pronounced in the wet season compared to the dry season ($p < 0.01$), and conversely lying was significantly more pronounced in the dry season compared to the wet season ($p < 0.01$). Similarly for territorial males of the Matetsi-extensive population the proportion of observations noted as grazing was significantly ($p < 0.01$) higher in the wet season compared to the dry season and conversely the incidence of lying was significantly ($p < 0.01$) higher in the dry season compared to the wet season. However for territorial males of the two intensive populations both grazing and lying was more pronounced in the wet season compared to the dry season.

In the smallest enclosure (Zambian-intensive population) the percentage of time spent walking by the territorial male and breeding herd did not differ significantly between the wet and dry seasons ($p > 0.05$). However in the larger enclosure of the Matetsi-intensive population the territorial male was observed walking more in the wet season compared to the dry season, whilst the breeding herd spent significantly ($p < 0.01$) more time walking in the dry season compared to the wet season. In the extensively managed population at Sandveld Nature Reserve the breeding herd also spent significantly ($p < 0.01$) more time walking in the wet season compared to the dry season. The percentage of time spent on social interactions by territorial males of the two intensive populations was significantly ($p < 0.01$) higher in the dry season compared to the wet season, whereas for the territorial male of the Matetsi-extensive population it was slightly higher in the wet season. The incidence of standing alert for both the breeding herd and the territorial male of the Matetsi-intensive population was significantly higher in the dry season compared to the wet season ($p < 0.01$). Conversely, the breeding herd and territorial male of the Matetsi-extensive population were significantly more vigilant in the wet season compared to the dry season ($p < 0.05$). The levels of vigilance in the Zambian-intensive population were much lower compared to the other two populations.

Dietary preferences were evaluated in more detail by estimating proportions of grazing, browsing and, in the intensive populations, dry feed, from observations pertaining to feeding behaviour only. Sable antelope at all three study sites showed a preference for grazing as a means of obtaining daily nutrition (Figures 4.4, 4.5 & 4.6). Dietary selection of breeding herds in the two intensive populations differed significantly ($p < 0.01$) compared to that of the extensively managed population. In both seasons a larger proportion of the diet of the breeding herd of the Matetsi-extensive population consisted of grass. The breeding herd of the Matetsi-extensive population also showed a higher preference for browse in the dry season compared to breeding herds of the two intensive populations whereas in the wet season both intensive breeding herds showed a higher preference for browse compared to the breeding herd of the Matetsi-extensive population.

The proportion of grass, browse and dry feed in diets of breeding herds of the Matetsi-intensive and Zambian-intensive populations also differed significantly ($p < 0.01$). In both seasons the proportion of the diet that consisted of grass was higher in the Matetsi-intensive population compared to that the breeding herd of the Zambian-intensive population, whereas in both seasons the proportion of dry feed and browse was higher in the diet of the breeding herd of the Zambian-intensive population. In the dry season, the proportion of grazing and browsing allocated to the diet did not differ significantly ($p > 0.05$) between territorial males of all three populations.

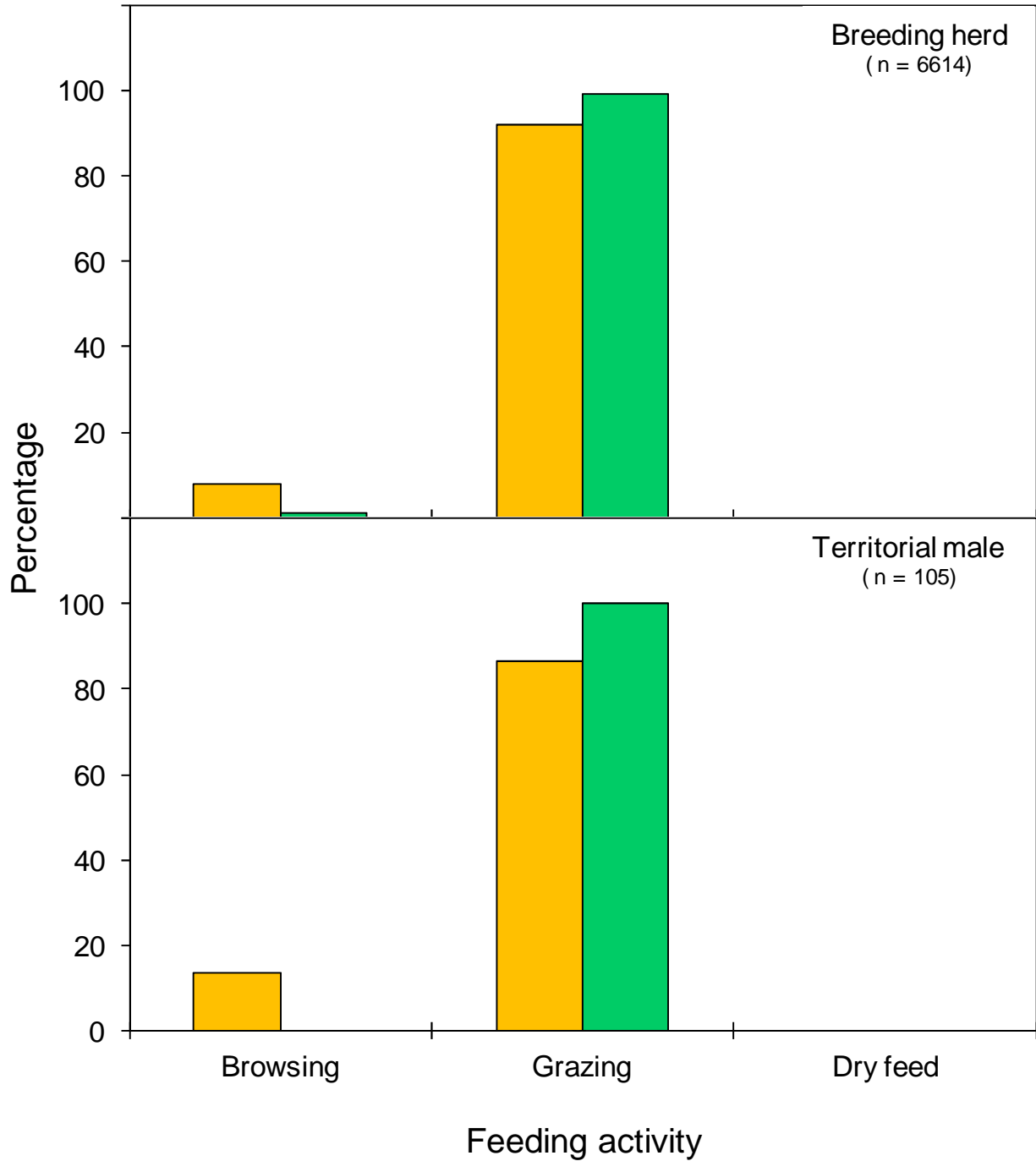


Figure 4.4 Seasonal variation in the dietary preferences of the breeding herd and territorial male of the Matetsi-extensive population at Sandveld Nature Reserve for the dry (June – September, yellow bar) and wet seasons (October – May, green bar).

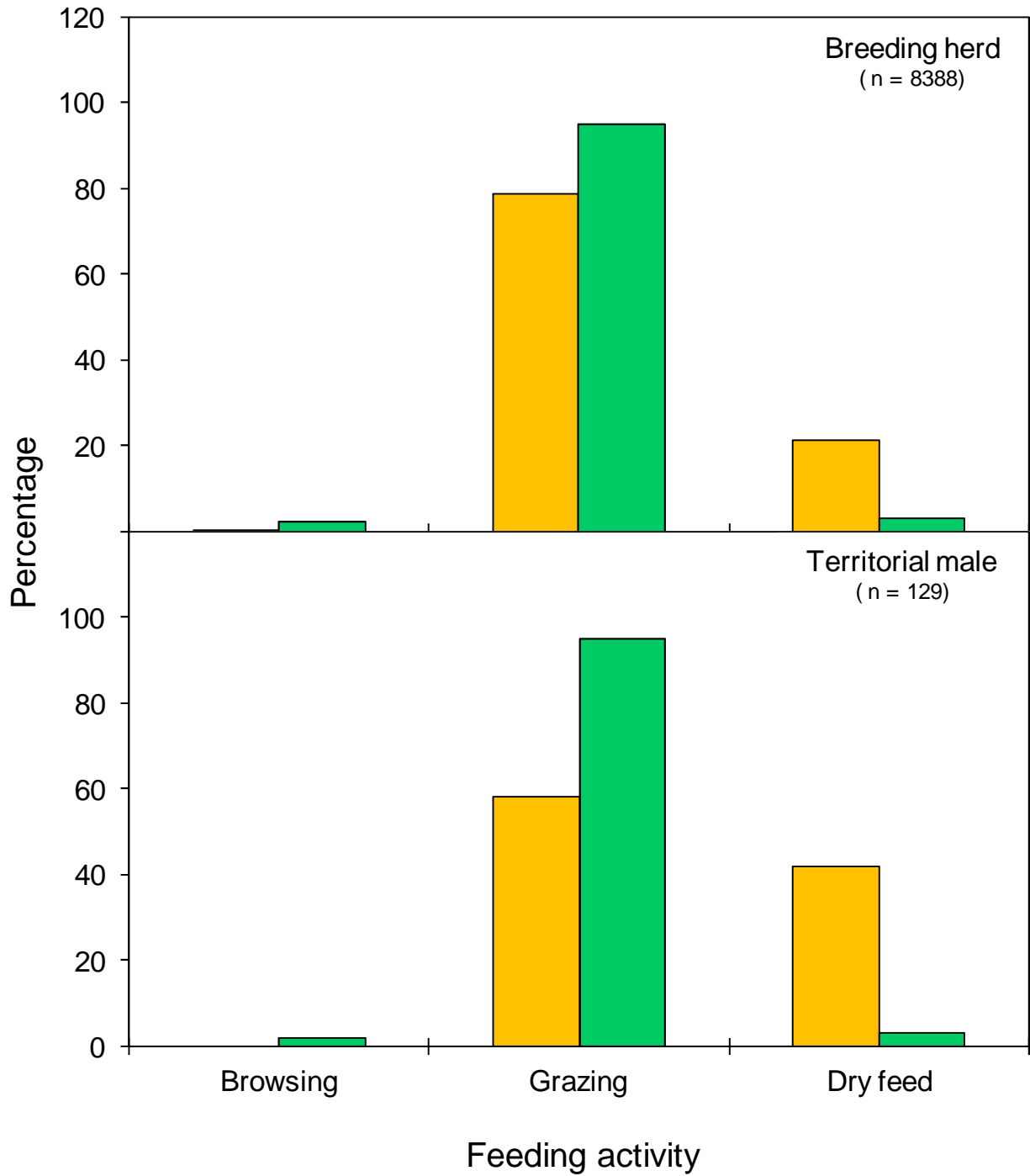


Figure 4.5 Seasonal variation in the dietary preference of the breeding herd and territorial male of the Matetsi-intensive population at Stella for the dry (June – September, yellow bar) and wet seasons (October – May, green bar).

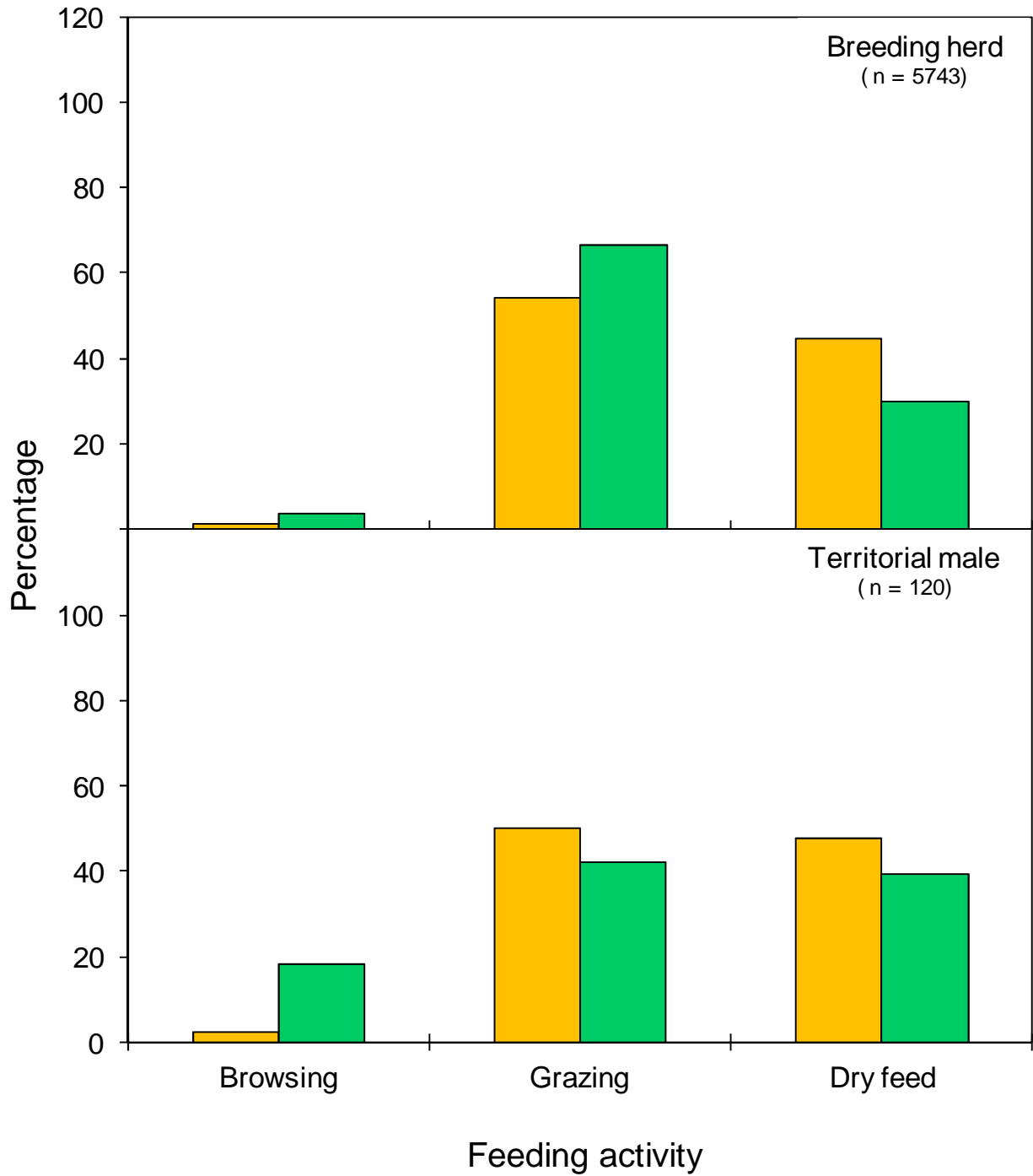


Figure 4.6 Seasonal variation in the dietary preference of the breeding herd and territorial male of the Zambian-intensive population situated near Vryburg for the dry (June – September, yellow bar) and wet seasons (October – May, green bar).

However in the wet season the diet of the territorial male of the Matetsi-extensive population differed significantly ($p < 0.01$) from the territorial male of the Zambian-intensive population. The territorial male of the Matetsi-extensive population showed a higher preference for browsing and grazing in the wet season compared to the territorial male of the Zambian-intensive population.

The dietary selection of the territorial male and breeding herd of the Matetsi-extensive population did not differ significantly for both seasons ($p > 0.05$). However for the Matetsi-intensive population in the dry season a significantly larger ($p < 0.05$) part of the territorial male's diet was composed of dry feed compared to the diet of the breeding herd. In effect, the breeding herd relied more on grazing and browsing to meet their nutritional demands. Additionally a larger proportion of the diet of the territorial male of the Zambian-intensive population consisted of dry feed compared to the diet of the breeding herd in both the wet and dry seasons, but these differences were not significant (*vide* Figure 4.6).

Although the breeding herd of the Matetsi-extensive population utilised browse throughout the year, the territorial male only browsed in the drier months of June to September. Browse however made up significantly smaller ($p < 0.01$) proportions of the diet of the breeding herd in the wet season compared to the dry season. In the two intensive populations for territorial males and the breeding herds the diet was supplemented with browse more in the wet season compared to the dry season. Seasonally, dry feed constituted more of the dry season diets compared to the wet season diets of both social classes of the Matetsi-intensive population, whereas for the Zambian-intensive population dry feed made up a significantly larger ($p < 0.01$) part of the breeding herd's dry season diet compared to in the wet season.

Diurnal activity patterns of breeding herds of all three populations were evaluated by calculating the hourly proportions of grazing, lying, walking and standing for the dry and wet seasons. In general, daily activity patterns portrayed similar trends during both seasons for all three sable populations (Figures 4.7 – 4.9). Grazing activity in the Matetsi-extensive population peaked in the early morning and evening, with a third peak at midday, in the 14th hour in the dry season and in the 13th hour in the wet season (Figure 4.7). A higher level of grazing was maintained at midday in the wet season compared to the dry season. Concerning the intensive managed population of sable at Stella, feeding seems to be more sporadic and only seems to decrease during the mornings and early afternoon (Figure 4.8). In the wet season the breeding herd of this population also spent the most time grazing in the early morning and evening and also around midday (14th hour), although with a much higher rate of incidences in comparison to the Matetsi-extensive population.

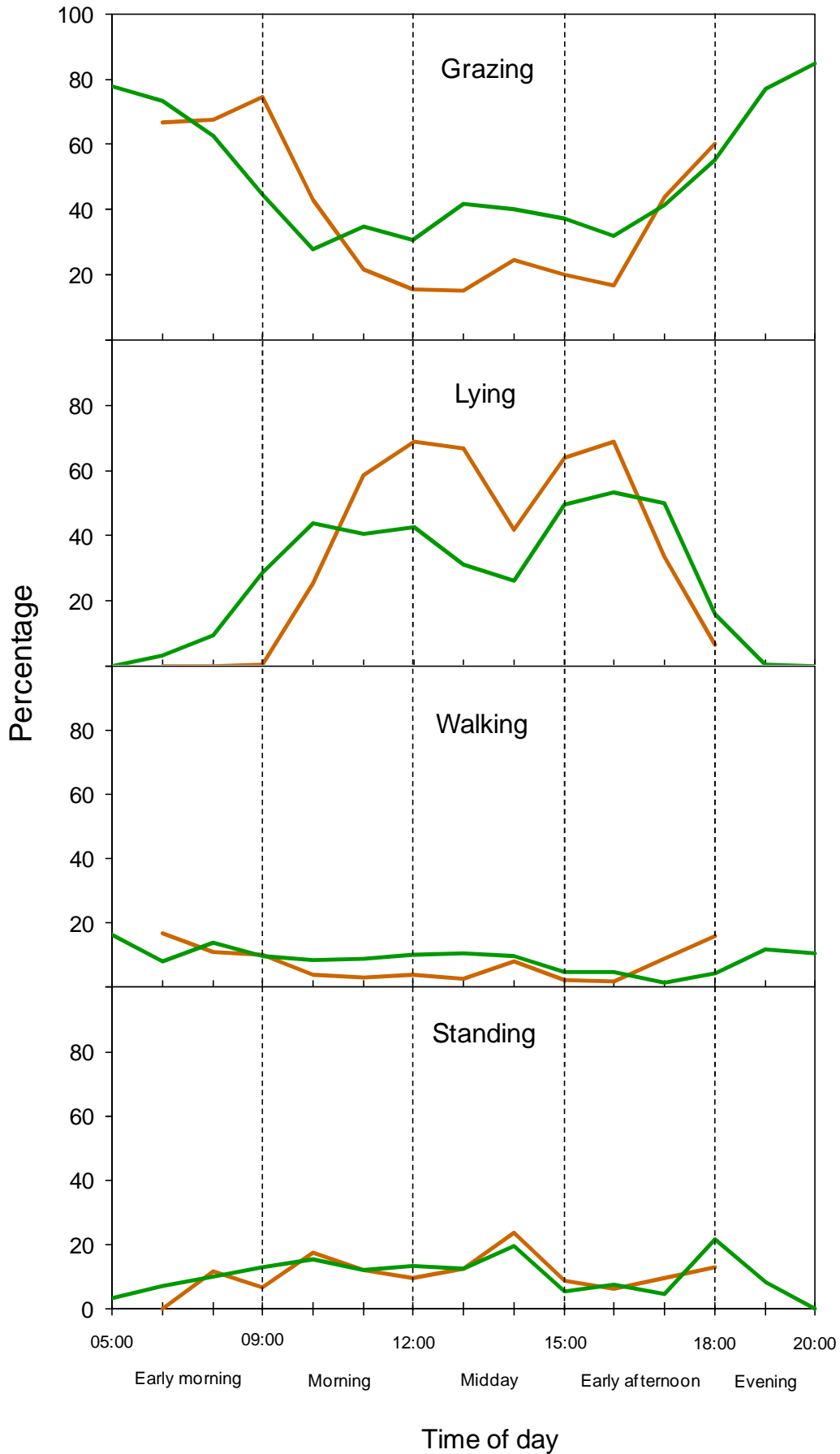


Figure 4.7 The daily variation in the incidence of grazing, lying, walking and standing by the breeding herd of the Matetsi-extensive population for the dry (June – September, orange line) and the wet seasons (October – May, green line).

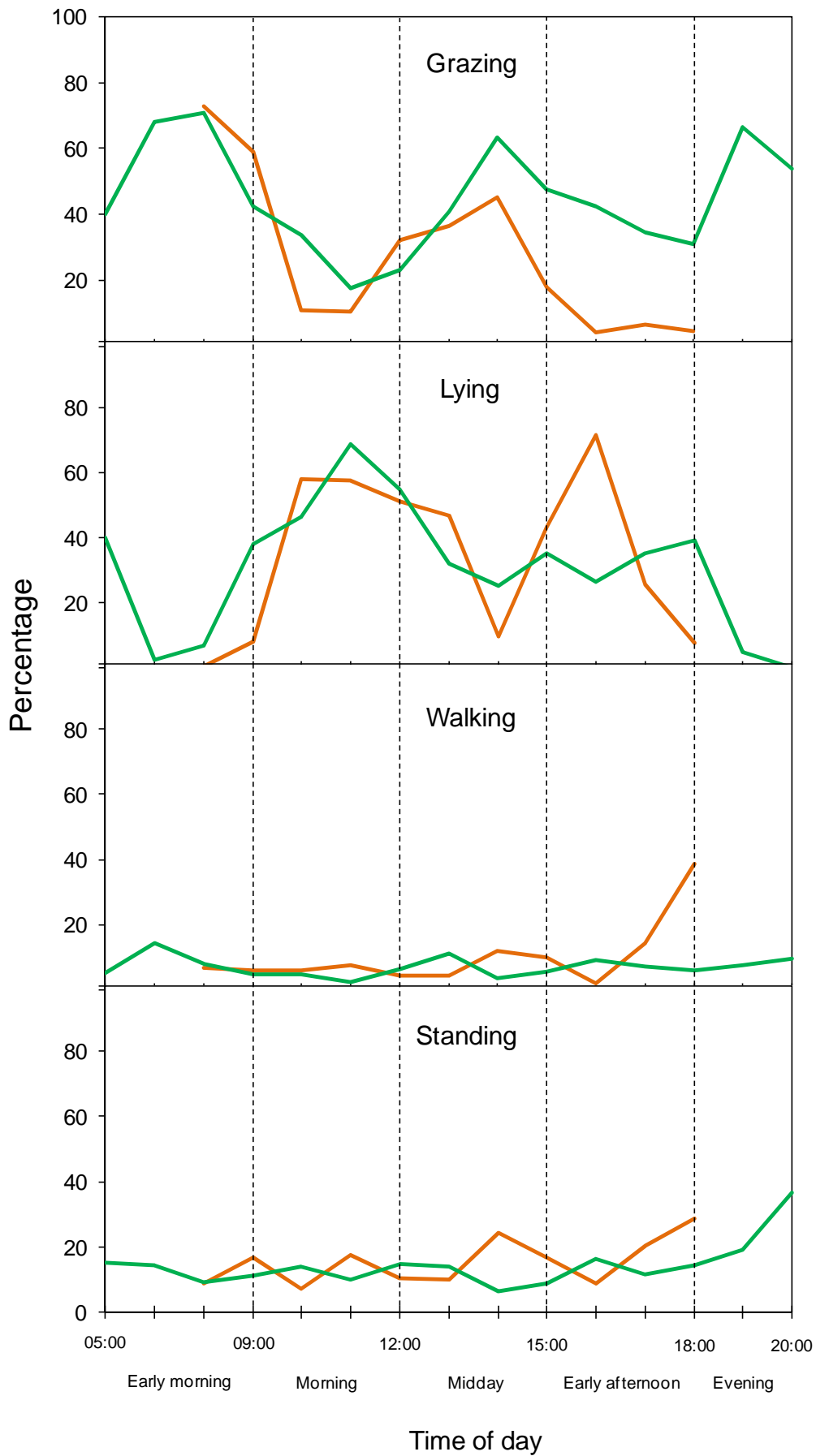


Figure 4.8 The daily variation in the incidence of grazing, lying, walking and standing by the breeding herd of the Matetsi-intensive population for the dry (June – September, orange line) and the wet seasons (October – May, green line).

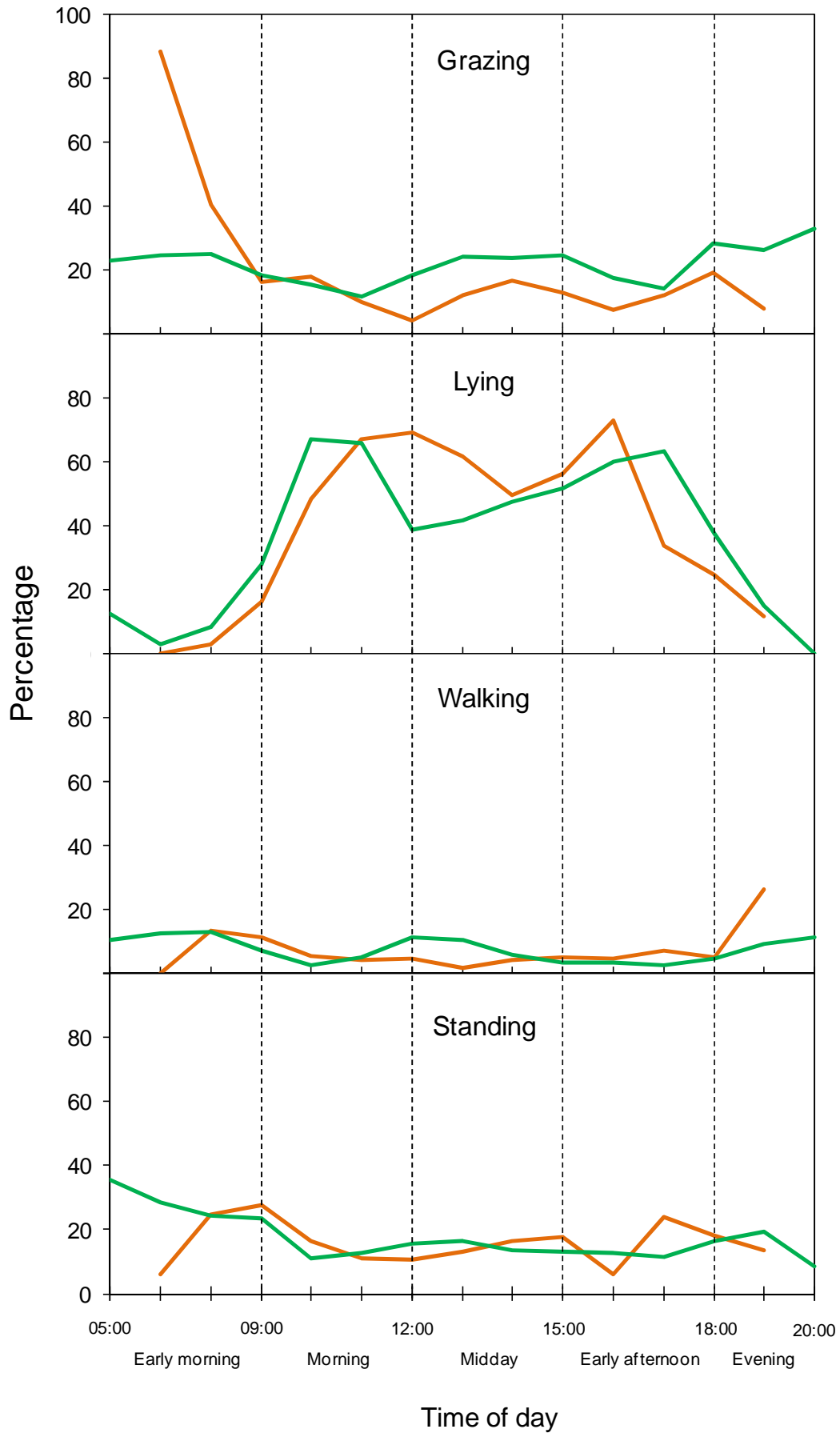


Figure 4.9 The daily variation in the incidence of grazing, lying, walking and standing by the breeding herd of the Zambian-intensive population for the dry (June – September, orange line) and the wet seasons (October – May, green line).

However, grazing in the Zambian-intensive population does not follow the same trend in the wet season but remains constant throughout the day (Figure 4.9). In the dry season, grazing of the breeding herd occurred predominantly in the early morning with a steady decline towards the end of the morning periods. During the middle of the day grazing increased slightly after which a second decline in this activity was observed until it increased again towards the evening.

Lying in the wet season for the Matetsi-extensive population reached two pronounced peaks from 08:00h to 12:00h (9th to the 12th hour) and from 14:00h to 17:00h (15th to 17th hour). In the dry season lying commenced slightly later, and was terminated earlier in the afternoon with two peaks, in the morning (09:00h to 13:00h) and early afternoon (14:00h to 16:00h). In the Matetsi-intensive population, lying also peaked twice daily from the 10th to the 13th hour (morning and midday) and in the early afternoon (15th to the 16th hour) in the dry season and in the wet season in the morning (9th to 12th hour) and around early afternoon (15th and 18th hour). In both seasons the proportion of lying in the Zambian-intensive population also peaked in the morning (10th to 11th hour in the wet season and 10th to the 12th hour in the dry season) and in the early afternoon (16th and 17th hour in the wet season and in the 16th hour in the dry season). In all three populations the proportion of time spent lying in both the wet and the dry seasons dropped significantly around midday (in the 13th and 14th hour) coinciding with a peak in grazing.

Walking in the Matetsi-extensive population in the wet season remained relatively constant throughout the day, whereas in the dry season it occurred more in the early morning and early afternoon with a slight peak in the 14th hour (midday) coinciding with the peak in grazing. In the Matetsi-intensive population walking also remained constant throughout the day but in the dry season more time was spent walking in the early afternoon. The breeding herd of the Zambian-intensive population walked more in the early morning and evening in the wet and dry seasons, with a third peak in the early afternoon (11:00 to 13:00h) in the wet season. The incidence of standing by the breeding herd of the Matetsi-extensive population remained fairly constant throughout the day in the wet season, whereas in the dry season it was lowest during the early morning and late afternoon with a slight peak in the 14th hour. In the Matetsi-intensive population standing also remained relatively constant throughout the day for the wet and dry seasons and similar to walking, standing peaked in the late afternoon in the dry season. For the breeding herd of the Zambian-intensive population standing peaked early morning and decreased as the day progressed, whereas in the dry season standing peaked slightly in the early morning and late afternoon.

The Matetsi-extensive population was observed drinking water at least once every other day between 07:00h and 08:00h (8th hour) but mostly between 11:00h and 14:00h (12th, 13th and 14th hours). The Matetsi-intensive population was observed drinking water once daily either between 12:00h and 13:00h (13th hour) or between 15:00h and 16:00h (16th hour). In the Zambian-intensive population water was utilised at all hours of every day, normally by only a few individuals at a time. The utilization of water peaked in the 9th hour, coinciding with the provision of dry feed.

Discussion

The Matetsi-extensive population grazed significantly less and spent significantly more time lying down in the dry season compared to the wet season. Similar results in the time spent grazing and lying was found in a study done on blesbok (*Damaliscus pygargus phillipsi*) on the Transvaal highveld (Novelli 1978). According to Novelli (1978) the daily foraging budget provides some clues as to what foraging strategy the species relies on. In the dry winter months when low-quality forage is in abundance, a species can either respond by feeding selectively, thereby spending more time foraging as high-quality forage is more sparsely dispersed. A ruminant can also respond by lowering its plain of selection, accepting a relatively large quantity of forage from one feeding site, thereby reducing the time needed to fill the rumen. The reduced quality in forage would therefore force a grazer to ruminate more in the dry season compared to the wet season.

According to Blaxter *et al.* (1961), the appetite of a ruminant is affected by how full the rumen is. As low-quality forage will take longer to digest it will consequently limit the intake of more forage. Novelli (1978) suggests that shorter foraging periods and increased ruminating time observed for blesbok in the dry season is a good indication that the latter foraging strategy is applied. Results from a study done on Cape buffalo (*Syncerus caffer*) in the Willem Pretorius Game Reserve (Winterbach 1999) also indicated that dietary selectivity decreased in the dry season as buffalo accepted lower-quality forage and that it resulted in longer ruminating and resting periods and subsequently less grazing activity. The fact that sable antelope spend less time grazing in the dry season in comparison to the wet season could therefore be an indication that sable antelope at Sandveld Nature Reserve are forced to lower their plain of selection in the dry season, ingesting a large quantity of low-quality forage. This is supported by the fact that significantly more time is spent resting and ruminating while lying down in the dry season. A study done on the feeding ecology of sable antelope at Sandveld Nature Reserve revealed that sable accepted a wider variety of grass

species during the dry months (Jooste 2000), indicating that sable antelope on Sandveld Nature Reserve were furthermore less selective on species level, in the dry season compared to the wet season. However selectivity on a finer scale, for example selection of sward greenness of grass as well as plant parts was not investigated.

In a study done on sable antelope in the Kgaswane Mountain Reserve (Parrini & Owen-Smith 2009) also reported that sable antelope were more selective during the late dry season compared to the early wet season. In addition, Parrini & Owen-Smith (2009) mentioned that sable increased their daily foraging time to compensate for lower quality forage in unburned areas and for a reduced intake rate of high-quality forage in burnt areas.

Furthermore sable antelope are known to take advantage of green leaves when available (Estes & Estes 1974; Grobler 1981; Parrini 2006; Macandza 2009; Le Roux 2010). According to Estes & Estes (1974) the movements of giant sable in the Luando Natural Integral Reserve were largely determined by the quest for bunch grasses at a tender growth stage. During the dry season these herds spent most of their time moving between areas that retained enough moisture to support continuous growth. Giant sable antelope also took advantage of new growth on burnt areas in the late dry season (Estes & Estes 1974).

The differences observed, in the time spent foraging and ruminating, between studies can possibly be explained by the availability of higher-quality forage in the landscape during the dry season. When available, the quest for and intake of higher quality forage could result in higher foraging times than expected. Burnt areas on the Transvaal highveld were also utilised by blesbok and as a result a higher proportion of time was spent foraging in the dry season than expected (Novelli 1978). Buffalo at Willem Pretorius Nature Reserve in the Free State Province (South Africa) also took advantage of the continuous production of green grass in the vlei grassland during the warm, dry season when food was most scarce. The intake of higher-quality forage also resulted in an increase in time spent foraging. According to Estes & Estes (1974), though sable antelope are generally selective for green pastures but can also subsist on dry hay if necessary, this could have been the case for sable on Sandveld Nature Reserve.

When considering the overall activity (*vide* Figures 4.1, 4.2 & 4.3), the two intensive populations grazed significantly more in the wet season compared to the dry season. However in contrast to the Matetsi-extensive population, territorial males of the intensive populations spent slightly more time laying down in the wet season compared to the dry season and when considering feeding behaviour only the dry season diet of the territorial male of the Zambian-intensive population consisted of a larger proportion grazing compared to the wet season (*vide* Figure 4.6), which could be due to the provision of dry feed.

Considering feeding behaviour only, in both the wet and dry seasons the territorial males of the two intensive populations were observed utilizing dry feed significantly more compared to the breeding herds. According to Estes & Estes (1974), a territorial male accompanying a breeding herd within his territory will always be dominant over all individuals of the breeding herd. Because of their high rank, territorial males dominate feeding troughs and are able to maximise the intake of dry feed thereby decreasing the need to forage naturally. The digestibility of antelope cubes could be higher than the available grasses, therefore the time spent ruminating would not be as high as expected during the dry season.

On the other hand, members of the breeding herd need to compete with each other as well as with the territorial male for dry feed. This could result in the breeding herd not satisfying as much of their nutritional need by utilizing dry feed compared to the territorial male. A larger proportion of the dry season diet is therefore obtained from grazing, forcing them to ruminate significantly more in the dry season compared to the wet season. Members of the breeding herd, especially subordinate individuals, are therefore more reliant on available grass and browse. The activities patterns of breeding herds, in terms of the incidence of grazing and lying, are therefore more reflective of the extensively managed population than that of the territorial male.

In all three populations, especially in the Matetsi-extensive population, the territorial male spent less time grazing and more time resting and ruminating in comparison to the breeding herd. This could be due to the higher nutritional demand of adult females as a result of pregnancy and lactation (Owen-Smith 1988; Ben-Shahar & Fairal 1978), possibly forcing the breeding herd to spend slightly more time searching for higher quality forage compared to the territorial male, thus grazing more and spending less time ruminating. Estes & Estes (1974), observed not only instability in herd composition just before parturition but groups of females were also observed to wander more, and in some instances travelled up to 10 km at a time without stopping. They explained that this might be in search of better quality forage for maintaining nutritional status during late pregnancy and parturition (Estes & Estes 1974). This theory is supported in this study, by the fact that female sable antelope from Sandveld Nature Reserve spent significantly more time walking in the wet season compared to the dry season, which was when parturition peaked.

The seasonal variation in the utilization of dry feed in the Matetsi-intensive population is reflective of the rate and consistency of the provision thereof. Dry feed was provided consistently in the dry season in the morning and afternoon, but was provided inconsistently during the late wet season (April 2012). This could explain why the territorial male and the breeding herd utilised significantly more dry feed in the dry season compared to the wet

season. On the other hand, for the Zambian-intensive population dry feed was provided religiously throughout the year (morning and afternoon), therefore seasonal variation in the utilization thereof is more representative of their changing nutritional need and seasonality of available forage. As expected the utilization of dry feed peaked in the dry season as the population compensated for a lower nutritional value in available grasses.

According to Estes & Estes (1974) though sable antelope are primarily grazers they do utilise small amounts of browse throughout the year but substantially more during the dry season. In accordance with this, the Sandveld Nature Reserve population utilised browse throughout the year, although more in the dry season. However, both populations that were managed intensively at Stella and Vryburg utilised more browse in the wet season. This could be as a result of the provision of antelope cubes that are high in crude protein, therefore eliminating the need to supplement the diet with browse in the dry season. Though this could explain the trend of browsing in the Matetsi-intensive population, it does however not explain the large proportion of time spent utilising browse by the territorial male as well as the breeding herd of the Zambian-intensive population in the wet season when dry feed was also provided. It could be that this population took advantage of new growth in the wet season.

When considering breeding herds only, the incidence of standing in both the dry and wet seasons increased as the enclosure size decreased (*vide* Figures 4.1 – 4.3). The higher incidence of standing in the breeding herd of the Matetsi-intensive population during the dry season compared to wet season, could be as a result of the time spent standing before and after dry feed was provided. This corresponds to the higher incidence of standing alert in the whole Matetsi-intensive population in the dry season.

The higher incidence in standing alert in the dry season by the territorial male of the Matetsi-intensive population (*vide* Figure 4.1) could indicate that territorial males were more vigilant to intruding males during this time. It could also be as a result of the more open savannah woodland occupied in the wet season compared to the closed woodland utilised in the dry season, as this was also observed for the breeding herd. The small number of observations for standing alert by the Zambian-intensive population (*vide* Figure 4.3) could be explained by the fact that the population was habituated to human activity, and that they had no exposure to predation.

Though still present, territorial behaviour was significantly less in the two intensive populations compared to the Matetsi-intensive population (*vide* Figures 4.1 – 4.3). This could be attributed to the absence of other adult males. For the Matetsi-intensive population social behaviour was displayed only slightly more ($p > 0.05$) in the wet season. In

contrast, the same interactions were displayed significantly more ($p < 0.05$) during the dry season in both intensive managed populations. This could be explained by the fact that the rut season for the Matetsi-extensive population peaked in the wet season whereas for the two intensive populations rut took place in the dry season. In the daily variation of activity patterns, feeding behaviour in the Matetsi-extensive and Matetsi-intensive populations peaked during the early morning and late afternoon, with the exception of the absence of the dry season afternoon peak in the Matetsi-intensive population (*vide* Figures 4.7 – 4.9). A third peak was observed in both of these populations around midday. This is similar to the findings of a study done by Grobler (1981), at Rhodes Matopos National park, Zimbabwe, where the foraging behaviour of sable peaked between 06:00h and 09:00h in the morning and between 16:00h and 17:00h and between 14:00h and 17:00h in the dry and wet seasons respectively. The author also observed an additional peak around midday, and explained that this peak in feeding was associated with drinking water (Grobler 1981). This could have been the case for the Sandveld and Matetsi-intensive populations as grazing peaked around the same time that water was utilised the most. The peaks in foraging behaviour in the early morning, midday and late afternoon in the Zambian-intensive population was less pronounced and could be explained by the fact that a substantial proportion of the diet consisted of dry feed.

In this study inactive behaviour (lying and standing) increased as ambient temperature increased (*vide* Figures 4.7 – 4.9). This indicates that the high incidence of inactivity at midday could be attributed to thermoregulation. Similar results were found by Ben-Shahar & Fairall (1987) in a comparative study between blue wildebeest (*Connochaetes taurinus*) and red hartebeest (*Alcelaphus buselaphus*). Two pronounced peaks for lying was observed during the hottest part of the day for the blue wildebeest. A peak in grazing was also observed around midday. The authors suggests that ambient temperature could be related to changes in activity and that the blue wildebeest seemed to fit the model of a true bulk feeder that quickly fills its rumen and for efficient digestion spends sufficient amounts of time resting and ruminating (Ben-Shahar & Fairall 1987).

According to Estes & Estes (1974) sable antelope are a water dependent species frequently visiting waterholes even during the wet season when available forage is green and high in moisture. Most herds of sable antelope drink daily, often at midday (Grobler 1981; Grobler 1974), but they have also been observed drinking in the early morning, late afternoon and sometimes at night (Estes & Estes 1974). Sable antelope of the Sandveld Nature Reserve population were the only population that were not observed drinking water every day. It could be that the population frequented the waterhole at night.

Various studies observed sable antelope to remain within travelling distances of water sources. In a study done at Rhodes Matopos National park, Zimbabwe, sable antelope remained within one kilometre from water (Grobler 1981). According to Wilson and Hirst (1977) sable antelope never seem to move further than two to four kilometres from water. Both of the Matetsi populations remained within 2 km of a water source throughout the study whereas the Zambian population spent most of their time within only 0.4 km of the water trough even though the furthest they could move away was 0.64 km. Furthermore, drinking water in the Sandveld and Matetsi-intensive populations was a collective function involving the whole herd, whereas in the Zambian-intensive population only a few individuals drank water at a time, numerous times throughout the day. As the enclosure is only 44 ha in size, the herd remained in the vicinity of the feeding troughs and water trough (within 0.4 km) for most of the day allowing individuals to frequent the water trough at any time. In the other two populations walking, standing and grazing peaked around the time water was utilised the most, indicating an increase in activity as the population moved to and from the water source.

4.2 Range use

Results

The effects of a number of abiotic and biotic factors, operating at different scales, on the extent of range use, temporal patterns in range use, extent of daily movements and habitat utilisation of sable antelope have been studied extensively by a number of authors (Wilson & Hirst 1977; Gureja & Owen-Smith 2002; Chirima 2009; Macandza 2009; Le Roux 2010; Capon 2011). In effect, the extent of range use and temporal patterns in range use is indicative of the interplay between resource availability and distribution, stage of reproduction and habitat requirements of the species. The evaluation of range use could therefore shed some light on the interaction between these components in the environment of the population in question and offer some explanation for seasonal variation observed in activity patterns and social behaviour of the population. Annual wet (wet and late wet seasons combined) and dry season (late dry and dry seasons combined) home ranges and core areas of breeding herds of all three populations were estimated by constructing 95% and 50% fixed kernel density estimates. Home ranges were also estimated by constructing 95% minimum convex polygons, to directly compare home range and core area estimates of this study to previously published data on range use of sable antelope.

The breeding herd of the Matetsi-extensive population utilised an annual home range of 8.02 km² (kernel density estimate) and core area of 1.12 km². The annual home range estimated by constructing a minimum convex polygon was 7.34 km². In evaluating the annual home range, the Matetsi-extensive population only utilised 15% of the total area available (Figure 4.10). In the Matetsi-extensive population the home range estimated for the wet season (8.47 km²) was larger compared to the dry season home range (4.82 km²) (Figures 4.11 & 4.12 respectively). The wet and dry season home ranges of the breeding herd of the population at Sandveld Nature Reserve overlapped considerably, with 46% of the annual home range being utilised in both seasons. Of the annual core area, 35% was utilised in both the wet and dry seasons.

The core areas of sable antelope at Sandveld Nature Reserve were compared to a vegetation map compiled for the Northern Vet management unit (unpublished report 2015) (Figure 4.13). The wet and dry season core areas were situated in close proximity to water and were predominantly concentrated in the *Vachellia erioloba* – *Panicum maximum* and the *Vachellia erioloba* – *Stipagrostis uniplumis* plant communities. Both of these plant communities have well developed tree and shrub layers dominated by *Vachellia erioloba*.

Other prominent tree and shrub species present in the plant communities include *Vachellia karroo*, *Vachellia hebeclada*, *Ziziphus mucronata*, *Searsia lancea*, *Searsia pyroides*, *Grewia flava*, *Diospyros lycioides*, *Boscia albitrunca*, *Ehretia rigida* as well as various *Asparagus* species. A distinguishable characteristic of the *Vachellia erioloba* – *Panicum maximum* community is the presence of dense stands of *Panicum maximum*, *Setaria verticillata* and *Eragrostis biflora* occurring under tall (> 3m) *V. erioloba* trees.

In areas of this community where woody cover occurs at lower densities, *Eragrostis lehmanniana*, *Eragrostis trichophora*, *Eragrostis pallens*, *Stipagrostis uniplumis* and *Cynodon dactylon* are also prevalent. In the *Vachellia erioloba* – *Stipagrostis uniplumis* community a well-developed tree layer is dominated by *V. erioloba*, with an understory of grasses dominated by *Stipagrostis uniplumis*, *Eragrostis pallens*, *Tragus koelerioides* and *Aristida mollissima*. Forbs in the community include *Hermannia tomentosa*, *Elephantorrhiza elephantina* and *Indigofera daleoides*, however, the large shrub layer is poorly developed consisting only of a few scattered clumps of *Vachellia hebeclada*. In the wet season the home range of Sable antelope extended into the open *Eragrostis pallens* – *Panicum kalaharensis* grassland community, which was almost entirely avoided in the dry season (Figure 4.14).

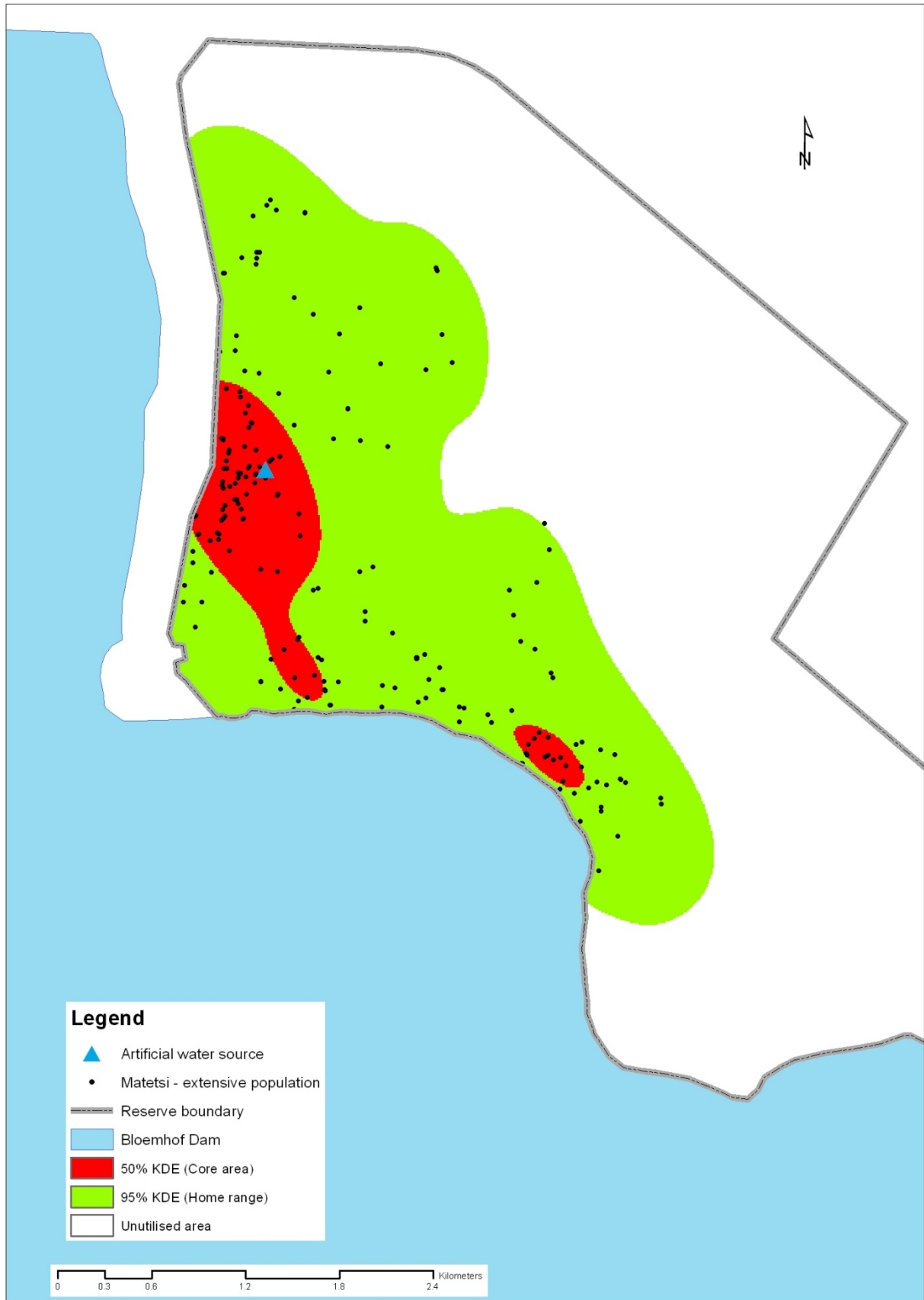


Figure 4.10 Annual range use of a breeding herd from the Matetsi-extensive population at Sandveld Nature Reserve in the Free State Province.

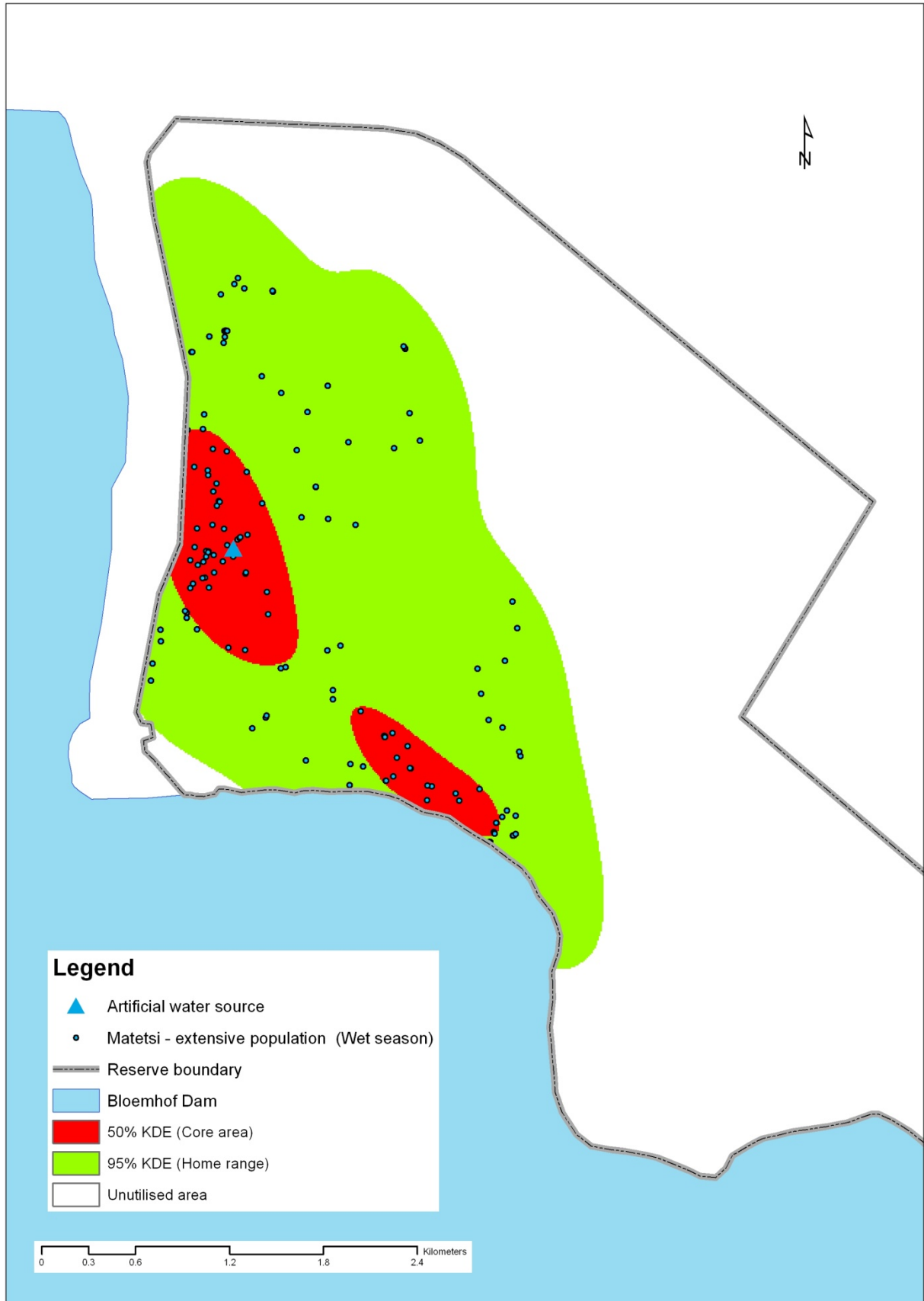


Figure 4.11 Range use of the breeding herd of the Matetsi-extensive population during the wet season at Sandveld Nature Reserve in the Free State Province.

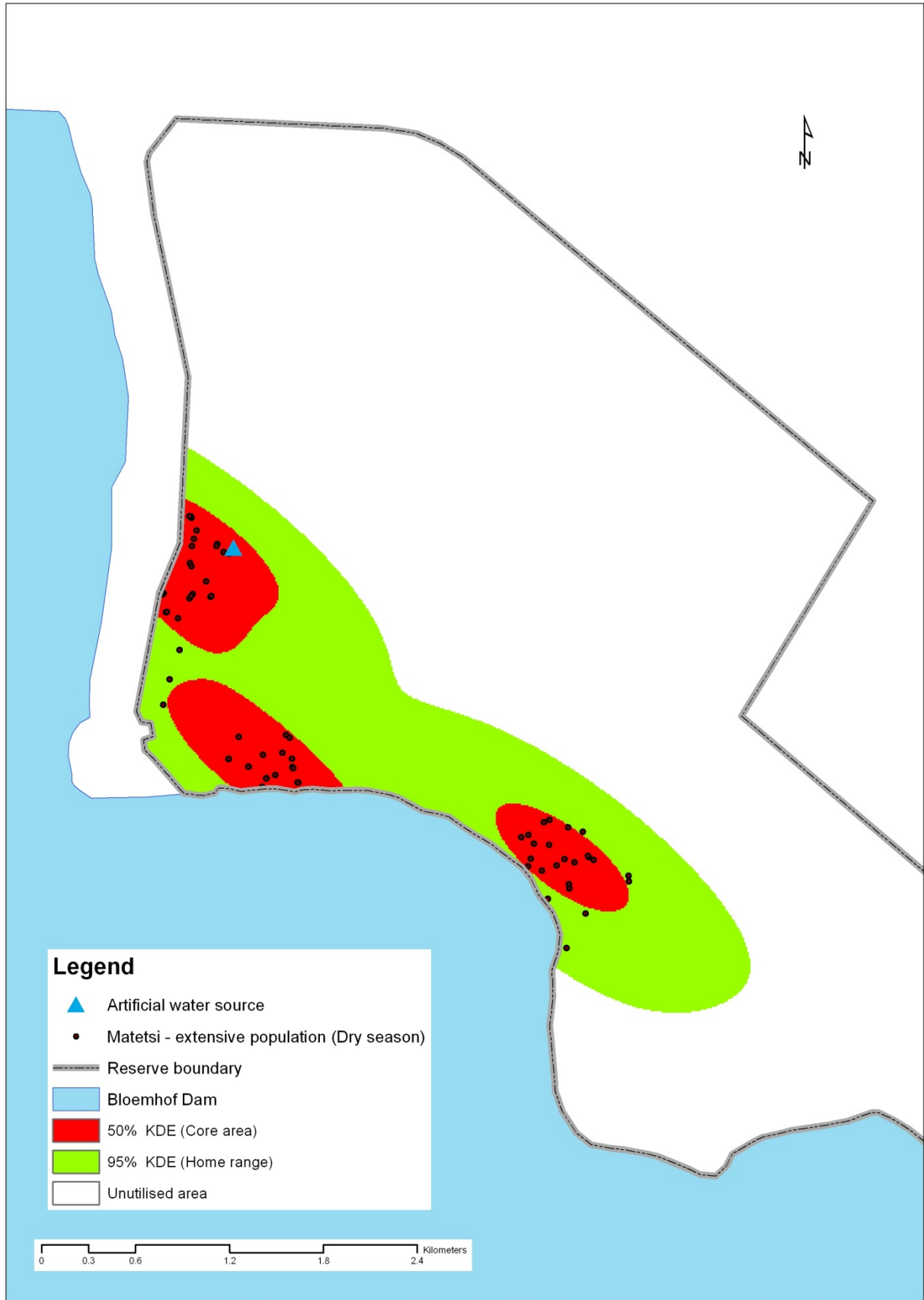


Figure 4.12 Range use of the breeding herd of the Matetsi-extensive population during the dry season at Sandveld Nature Reserve in the Free State Province.

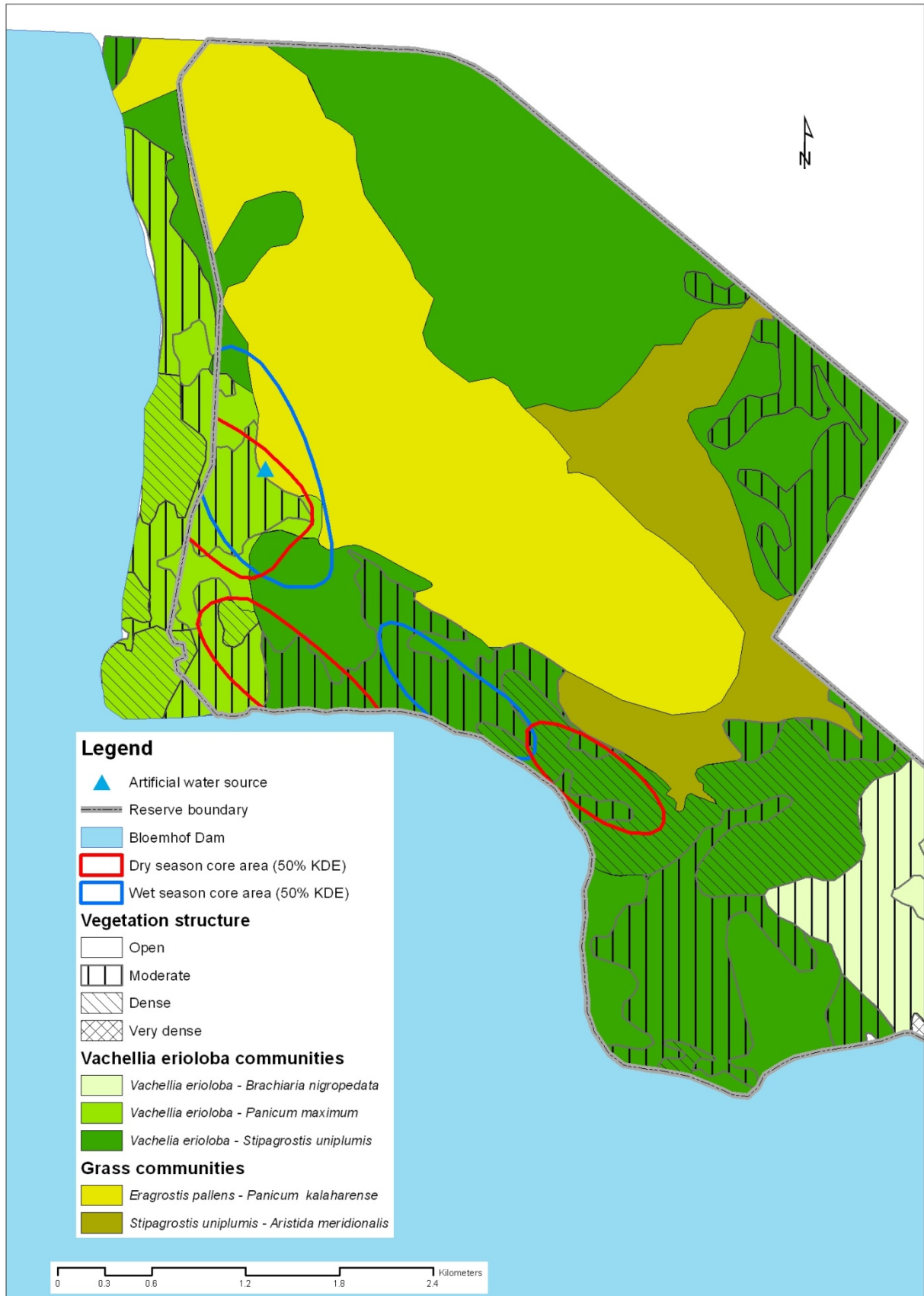


Figure 4.13 Core areas of the breeding herd of sable antelope at Sandveld Nature Reserve during both the wet and dry seasons in different plant communities.

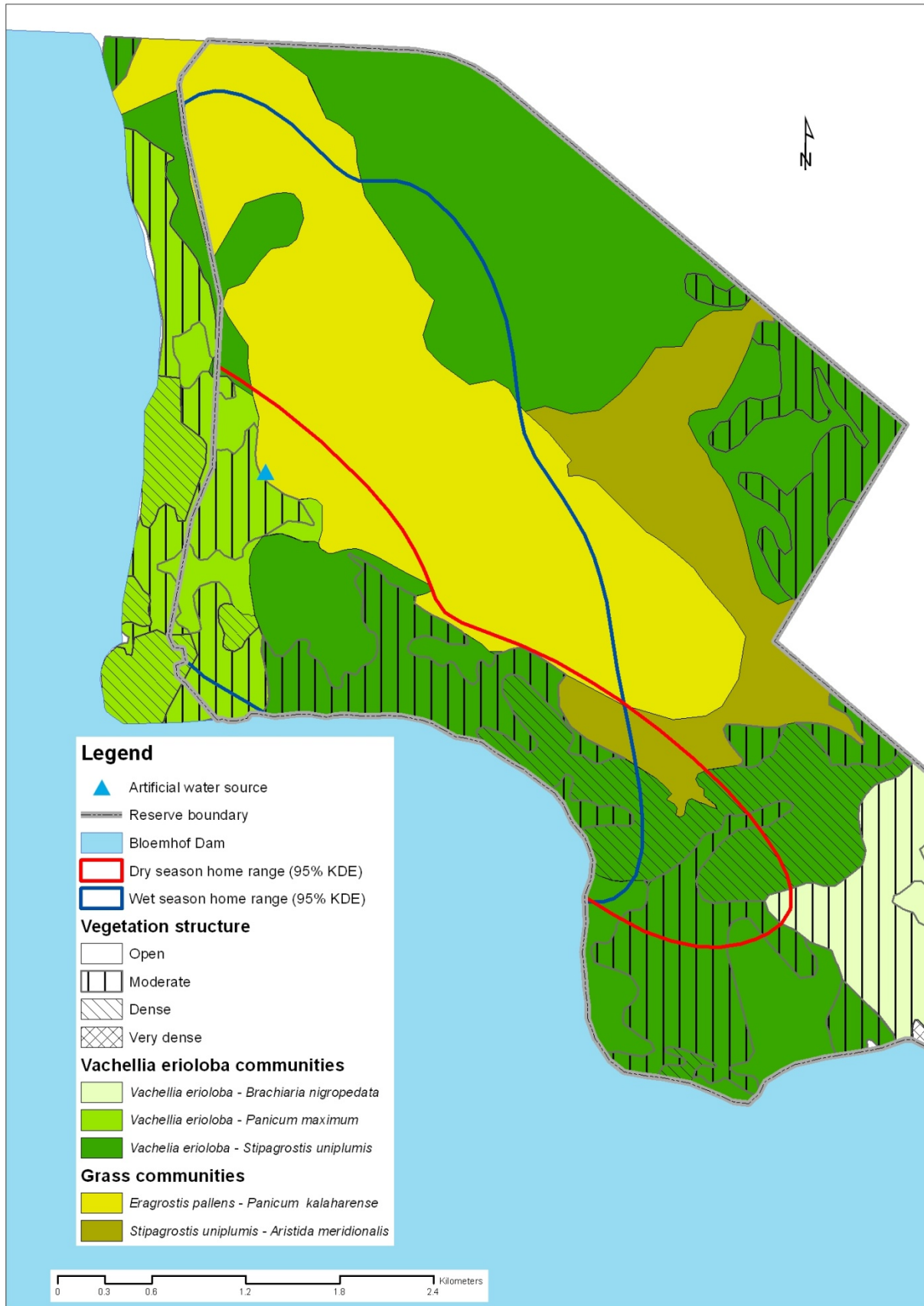


Figure 4.14 Home ranges of sable antelope at Sandveld Nature Reserve during both wet and dry seasons in different plant communities on the reserve.

This community has a well-developed grass layer characterised by *Panicum kalaharensense*, *Eragrostis gummiflua*, *Tristachya rehmannii* and dominated by *Eragrostis pallens*. Woody species present in the community are limited to a few scattered individuals of *Vachellia erioloba* less than 0.5 m in height occurring at an average density of 12 individuals / ha and a few large *Vachellia erioloba* trees occurring at an average density of 4 individuals / ha. Core areas of sable were situated in areas with moderate cover (11 to 30% tree cover) during the wet season whereas in the dry season, core areas included areas with 31 to 75% woody cover (“dense” in Figure 4.13).

The annual home range estimated for the Matetsi-intensive population was 1.86 km², which constituted as much as 76% of the whole enclosure (Figure 4.15). The home range estimated by constructing a minimum convex polygon was 1.58 km². Similar to the Matetsi-extensive population the wet season home range (0.32 km²) was larger than that of the dry season (0.21 km²) home range estimated for the population. However, the difference observed between seasons was not as pronounced as in the Matetsi-extensive population (Figures 4.16 & 4.17 respectively).

There was considerable overlap of home ranges in the wet and dry season with 42% of the annual home range being utilised in both the wet and dry seasons. Core areas of the Matetsi-intensive population during the wet and dry seasons only overlapped slightly, with only 7% of the annual core area being utilised in both seasons. In the wet season the Matetsi-intensive population utilised planted pastures and recovering planted pastures, however in the dry season these areas were mostly avoided whilst the population concentrated in areas with natural vegetation which provided more cover. A part of the core area of the dry season range was also situated in the area where dry feed was provided.

Surprisingly the Zambian-intensive population housed in the smallest enclosure only utilised 52% of the available area (Figure 4.18). The annual home range estimated for the Zambian-intensive population was a mere 0.34 km², with home range of 0.23 km² estimated by constructing a minimum convex polygon. As observed in the other two populations the wet season home range (0.24 km²) was slightly larger than the home range estimated for the dry season (0.1 km²) (Figures 4.19 & 4.20 respectively). There was considerable overlap between wet and dry home ranges, with as much as 91% of the annual home range utilised in both the wet and dry season. However, the wet and dry season core areas of the Zambian-intensive population were entirely separate. In both the wet and dry season space used by the Zambian-intensive population was concentrated around feeding troughs in close proximity to the water trough.

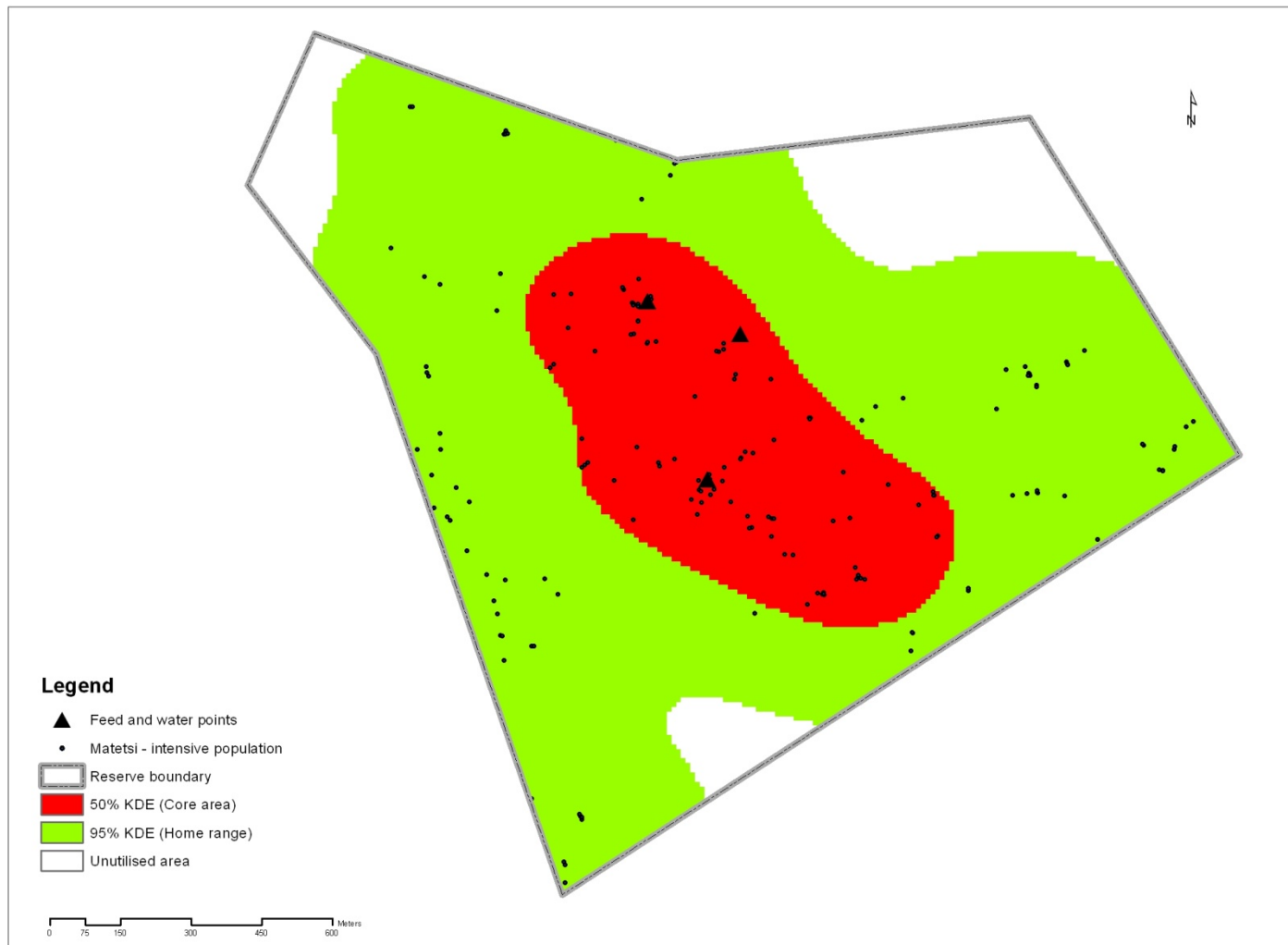


Figure 4.15 Annual range use of the breeding herd of the Matetsi-intensive population located close to Stella in the North West Province.

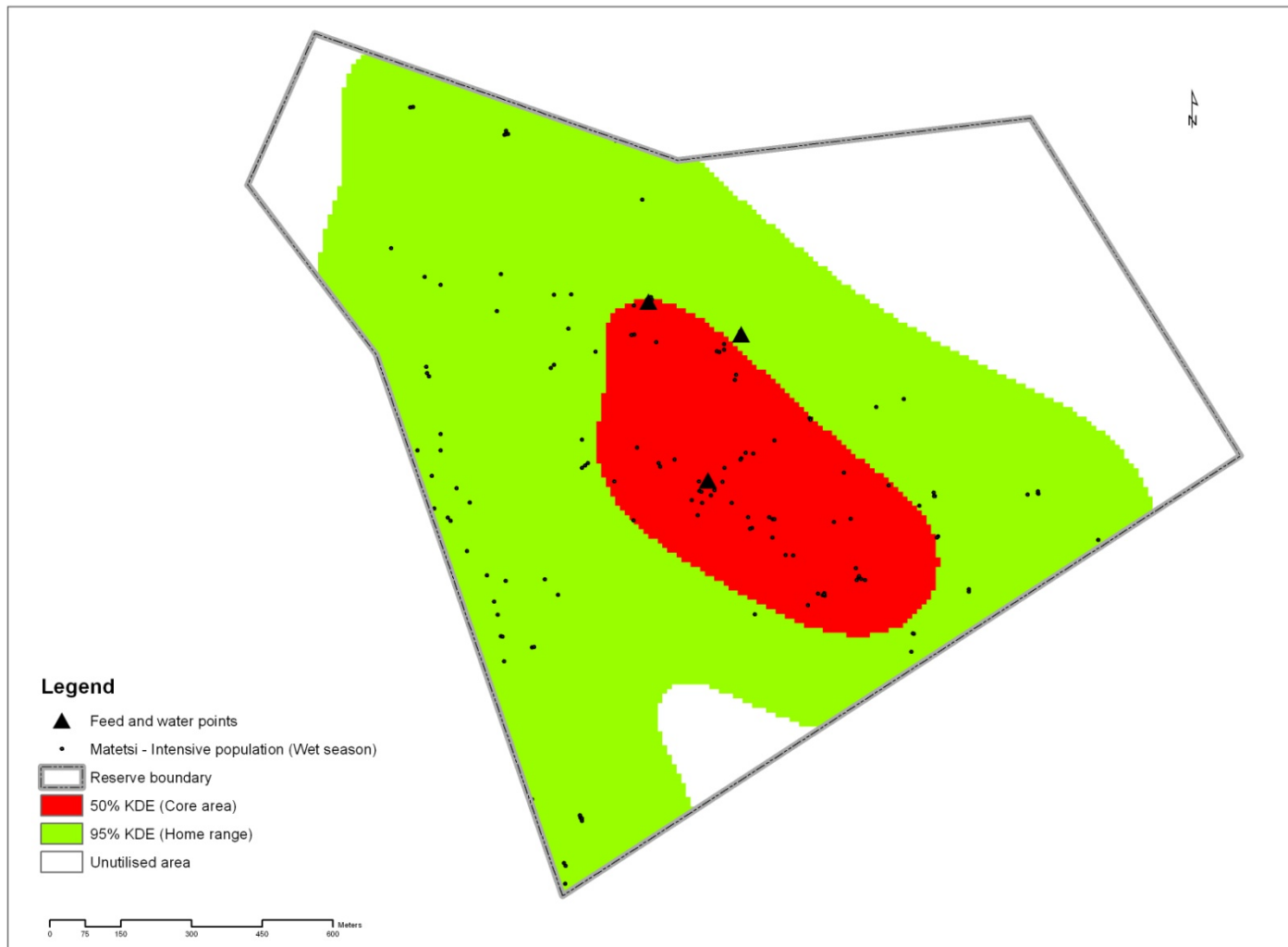


Figure 4.16 Range use of the breeding herd of the Matetsi-intensive herd during the wet season close to Stella in the North West Province.

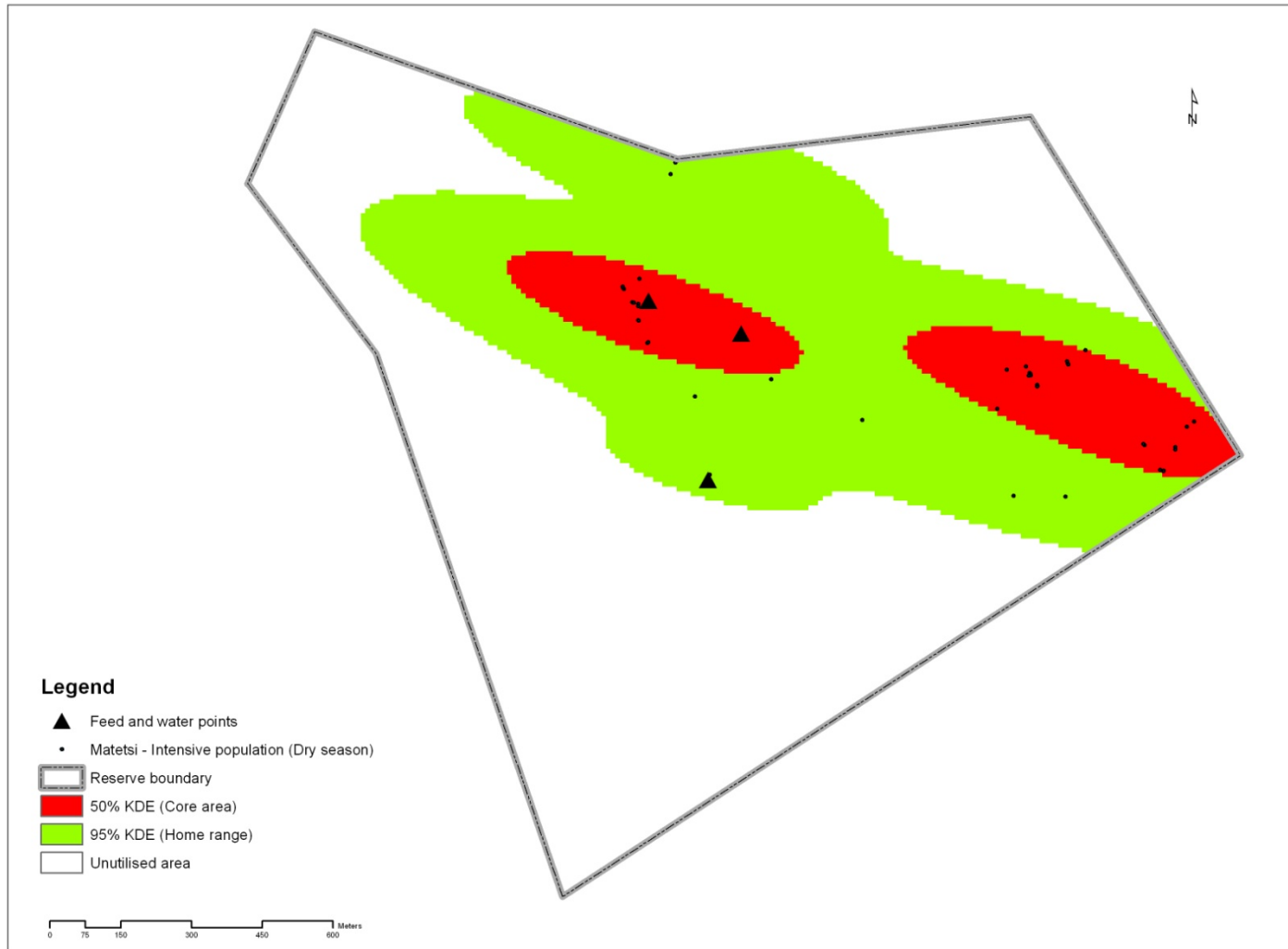


Figure 4.17 Range use of the breeding herd of the Matetsi-intensive herd during the dry season close to Stella in the North West Province.

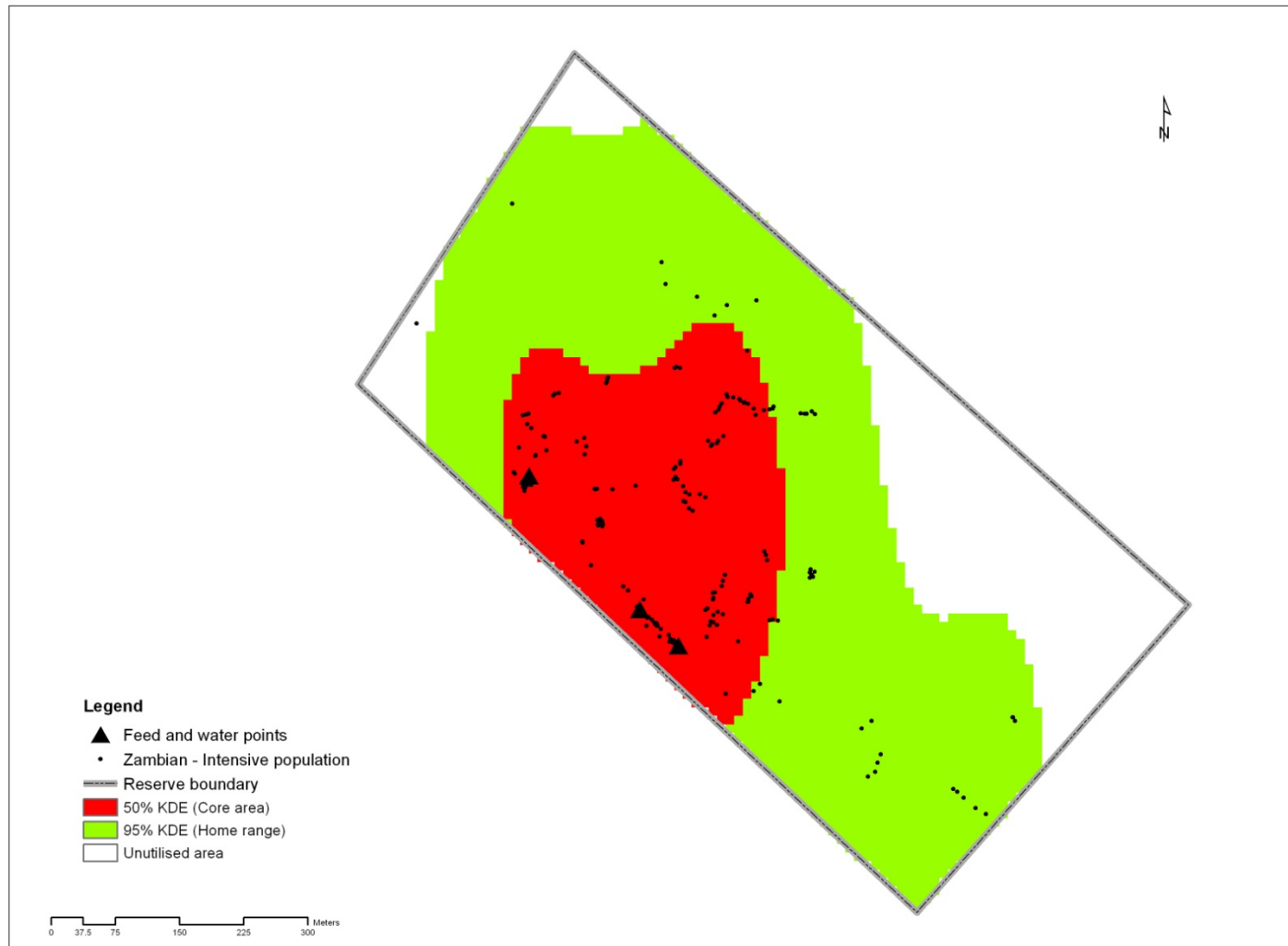


Figure 4.18 Home range and core area estimated for the breeding herd of the Zambian-intensive population at Vryburg in the North West Province.

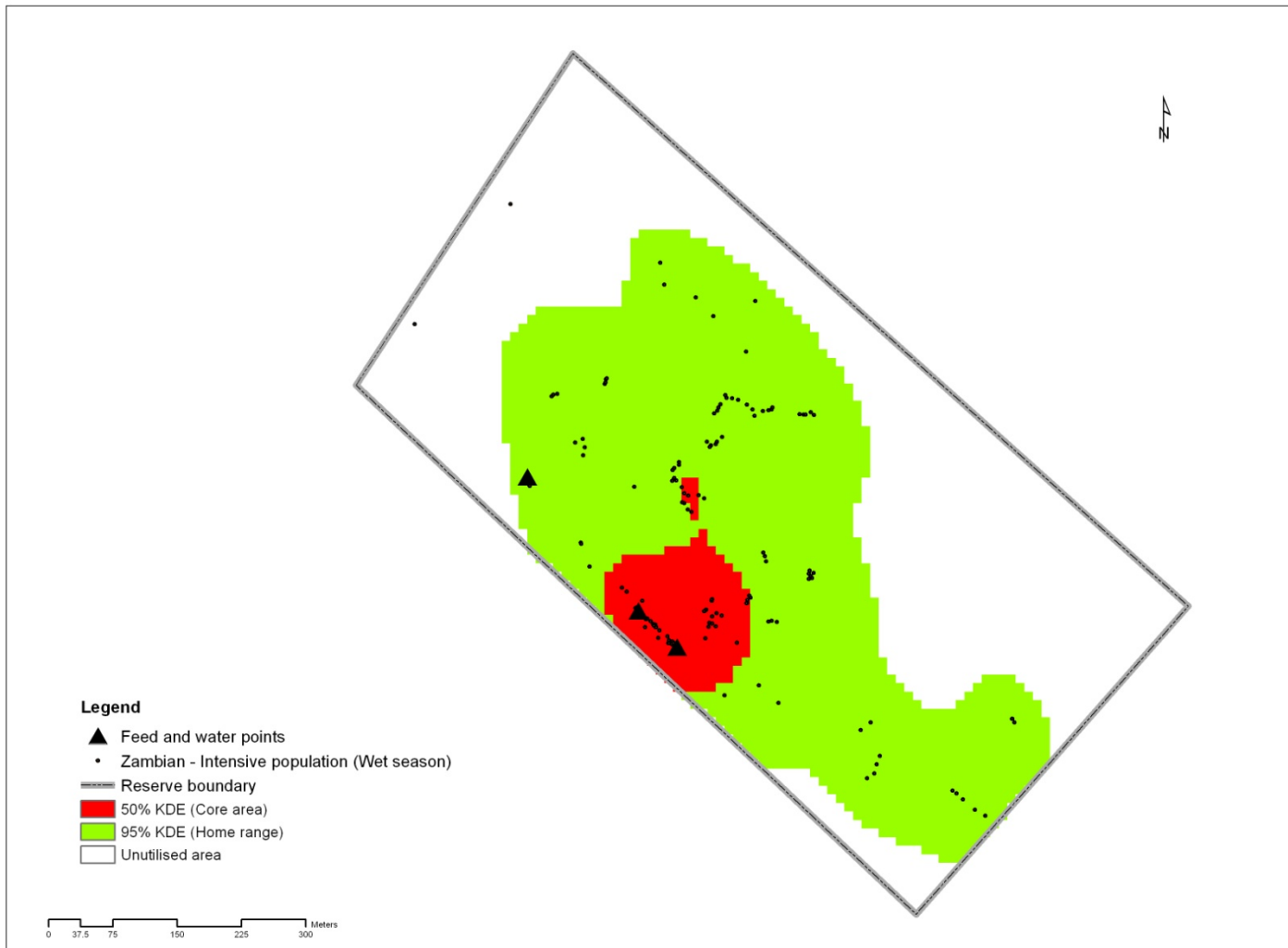


Figure 4.19 Range use of the breeding herd of the Zambian-intensive population during the wet season near Vryburg in the North West Province.



Figure 4.20 Range use of the breeding herd of the Zambian-intensive population during the dry season near Vryburg in the North West Province.

Discussion

According to previous studies, annual home range sizes vary greatly across the geographical distribution of sable antelope. The annual home range for the Matetsi-extensive population estimated by constructing a minimum convex polygon is comparable to results obtained by Wilson & Hirst (1977) on Transvaal nature reserves. Contradictory to previous studies (Wilson & Hirst 1977; Parrini 2006; Rahimi & Owen-Smith 2007; Macandza 2009) wet season home ranges of all three populations covered larger areas compared to the dry season home ranges. According to Parrini (2006), a larger dry season home range suggests a more selective feeding strategy adopted in the dry season to compensate for the decreased quality of forage and a decrease in the quantity of good forage, which would also result in increased daily feeding time as discussed in Chapter 4.1. However, according to Macandza (2009) as soon as energy gains obtained from increasing home range sizes are less than the costs of the expansion, especially during times of food scarcity, then the extent of the home range may decrease as the availability of food decreases. In a study done on sable antelope in the Malilangwe Wildlife Reserve in Zimbabwe (Capon 2011), smaller dry season home ranges compared to wet season home ranges was also observed. Capon (2011) attributed the temporal variation in the extent of the home range to the selection of high quality foraging patches which would restrict their home range.

This could definitely explain the smaller dry season ranges observed in the two intensive populations as most activities were concentrated in the areas where the dry feed was provided during the dry season. Rahimi & Owen-Smith (2007) attributed larger home ranges observed in the dry season compared to the wet season, for sable antelope in the Kruger National Park, to the extension of home ranges through the use of corridors towards nearby water sources. At Sandveld Nature Reserve the dry season home range was situated on the banks of the Bloemhof Dam and the population would therefore not have to travel great distances to water during the dry season, which could explain why the dry season range was not larger than the wet season range.

In all three populations there was overlap between wet and dry season home ranges as well as core areas in the two Matetsi populations. According to Wilson & Hirst (1977) that fact that breeding herds utilised areas throughout the year indicates that forage might be available year round in those areas. Additionally the more wet and dry season home ranges separate, the more likely it is that the palatability of forage, in those areas, changes throughout the year with rainfall, new growth and phenology (Wilson & Hirst 1977). The degree of overlap is therefore dependent on the distribution and variability of quality forage within the landscape. The utilisation of areas in the wet and dry seasons indicates that

resources within these areas are important in sustaining populations throughout the year. The core areas of the wet and dry seasons in the Zambian-intensive population were separate and could be explained by the movement of the feeding troughs as part of the management strategy.

In both the Matetsi-extensive and Matetsi-intensive populations dry season activity areas were concentrated in wooded areas, while mostly avoiding open areas. However in the wet season, though core areas were still situated in relatively dense communities, both populations extended the home ranges into open grasslands. Woodland communities utilised in the dry season were denser compared to areas utilised in the wet season. The use of areas with density measured at around 25% has previously been documented by a number of authors (Estes & Estes 1974; Wilson & Hirst 1977; Parrini 2006). There are a number of reasons why sable antelope would prefer areas with moderate woody density. Firstly grasses growing beneath tree canopies are sheltered from environmental extremes such as frost and loss of water in surrounding soil through evaporation and therefore remain greener for longer. Soil beneath tree canopies are also enriched with nutrients through the nutrient pump effect (Scholes 1990). The selection of greener foraging areas and of greener tufts in foraging areas has been observed by a number of authors (Estes & Estes 1974; Grobler 1981; Parrini 2006; Macandza 2009; Le Roux 2010).

Additionally *Panicum maximum* has been documented as not only a preferred foraging species for sable antelope (Grobler 1974; Grobler 1981; Wilson & Hirst 1977; Gujera & Owen-Smith 2002; Parrini 2006; Le Roux 2010), but also as an important resource in the dry season (Parrini 2006). *Panicum maximum* prefers to grow beneath trees and shrubs (van Oudshoorn 1999) and therefore this could also have contributed to the selection of the *Vachellia erioloba* – *Panicum maximum* community on Sandveld Nature Reserve. Other than the availability and quality of food in these areas, cover might also provide some shelter from the cold for the animals themselves and may even play an important part in anti-predator strategies (Macandza 2009). In both seasons the activity of the Zambian-intensive population was concentrated in the vicinity of feeding troughs. Even though the wet season home range extended further away from water and feeding troughs, due to the homogeneity of vegetation, and only a few scattered trees present in the enclosure, no real habitat selection was observed.

CHAPTER 5: SOCIAL BEHAVIOUR

5.1 Reproductive behaviour

Results

Intensive management strategies are generally applied in wildlife production to improve reproductive success of a population. In order to determine the effect of intensive management strategies on the incidence and nature of reproductive behaviour of sable antelope, the seasonality and rate of reproduction as well as the reproductive success of populations were evaluated. Seasonality of reproduction was determined by evaluating peaks in calving, courtship behaviour, and flehmen behaviour. The reproductive success of all three populations was determined by calculating the calving and survival rate for each population.

Flehmen behaviour

Flehmen, as defined by Estes (as cited in Thompson 1995b), is the olfactory investigation typically involving the direct sampling of freshly voided urine to evaluate female reproductive status. A total of 81 (daily rate = 6.8), 75 (daily rate = 9.6) and 105 (daily rate = 9.4) interactions containing flehmen behaviour were observed in the Matetsi-extensive, Matetsi-intensive and Zambian-intensive populations respectively. The daily rate of flehmen behaviour observed for both intensively managed populations was significantly more ($p < 0.05$) compared to the extensively managed population at Sandveld Nature Reserve. In comparing the two intensive populations, no significant differences were calculated in the overall daily rate of flehmen behaviour ($p > 0.05$). In all three populations flehmen behaviour occurred in response to adult and yearling females urinating and urine was mostly sampled directly from the urine stream, with the exception of adult females in the Matetsi-extensive and Matetsi-intensive populations, which mostly took advantage of sampling freshly voided urine from the substrate/ground (Figure 5.1).

Seasonality of reproduction was determined by calculating the incidences of flehmen behaviour, displayed by sexually mature individuals (adult females and territorial males) during all seasons. Although no significant differences could be established in the daily rate

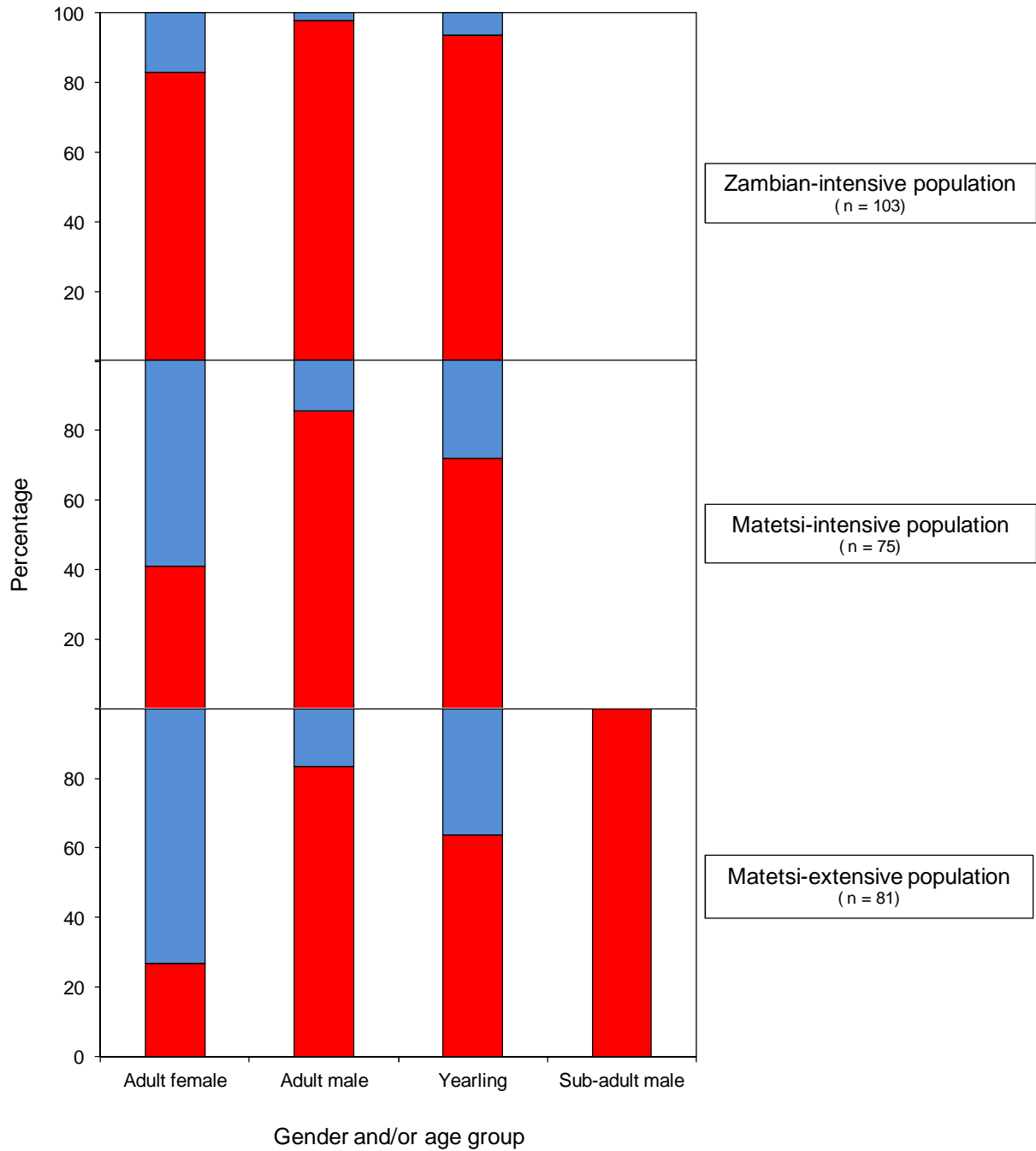


Figure 5.1 Flehmen behaviour performed by different gender and age groups of sable antelope under different management strategies. Red bar, sampling urine directly from the urine stream; blue bar, sampling urine indirectly from the ground/substrate.

of flehmen behaviour performed by the territorial male of the Matetsi-extensive population, between seasons, subtle dissimilarities were observed (Figure 5.2). During August and January, which fall in the late dry and wet season respectively, the daily rate of flehmen behaviour was almost equal with more than three occurrences per day. During late wet season (April) however, the average daily rate dropped to only one incident. The highest daily rate of flehmen behaviour took place during June which falls in the dry season.

The territorial male of the Matetsi-intensive population at Stella sampled urine and performed flehmen behaviour significantly more in the dry season compared to the remaining two (wet and late wet) seasons ($p < 0.05$) (Figure 5.2). In contrast, the daily rate of flehmen behaviour performed by the territorial male of the Zambian-intensive population at Vryburg remained more or less constant throughout the different seasons ($p > 0.05$). Although no significant differences were calculated for this behaviour between seasons, there was however a decrease in daily rate of flehmen behaviour in the wet season.

Though no flehmen behaviour was performed by any adult females of the extensively managed population in the late dry season (August), the daily rate of flehmen behaviour per adult female distinctly peaked during the wet season (January) ($p < 0.01$). During the consecutive late wet and dry seasons, this behaviour as observed per adult female per day declined dramatically (Figure 5.3). In the Matetsi-intensive population, the daily rate of flehmen per adult female peaked in the dry season (June), and reached a low in the late wet (April) season (Figure 5.3). In contrast to the previous two sable populations, a distinct peak ($p < 0.01$) in incidence of flehmen performed by adult females of the Zambian-intensive population occurred during the late dry season (June), with the lowest daily rate observed in the late wet season (April).

Courtship behaviour

When considering actual courtship, a comparable number of courtship interactions were observed in the Matetsi-extensive ($n = 20$) and the Matetsi-intensive ($n = 25$) populations. Almost double the number ($n = 47$) of the same behaviour was observed in the Zambian-intensive population. The daily rate of courtship interactions also differ between the various populations. Where the extensive population at Sandveld Nature Reserve displayed the least (1.67) interactions per day, the intensively managed population at Stella exhibited almost double (3.19) the number of interactions per day. In the intensively managed Zambian population, the most (4.21) courtship interactions was observed per day. Similar to flehmen behaviour, the overall daily rate of courtship behaviour was significantly more ($p < 0.01$) in the intensive populations compared to the extensively managed population at Sandveld Nature Reserve, with no significant difference ($p > 0.05$) between the

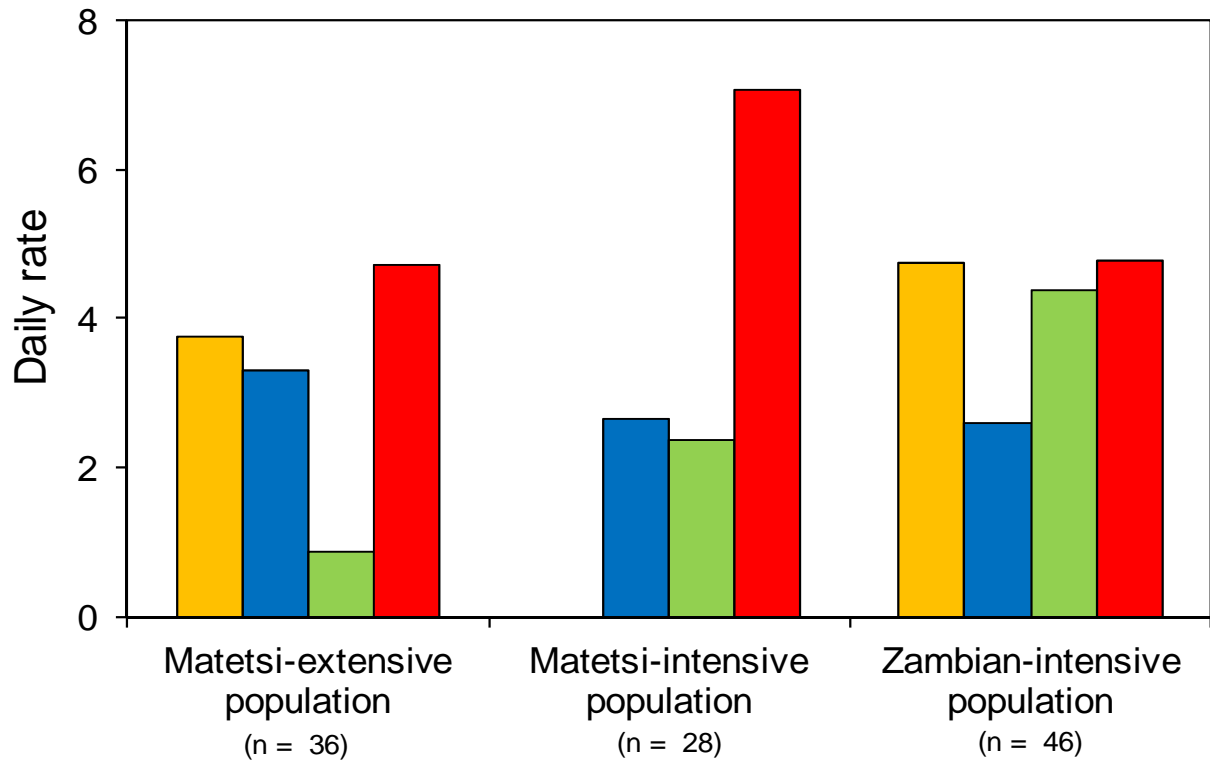


Figure 5.2 Seasonal variation in the daily rate of flehmen behaviour performed by territorial males of all three study populations for the late dry (August 2011, yellow bar), wet (January 2012, blue bar), late wet (April 2012, green bar) and dry seasons (June 2012, red bar). No observations were carried out during the late dry season for the Matetsi-intensive population.

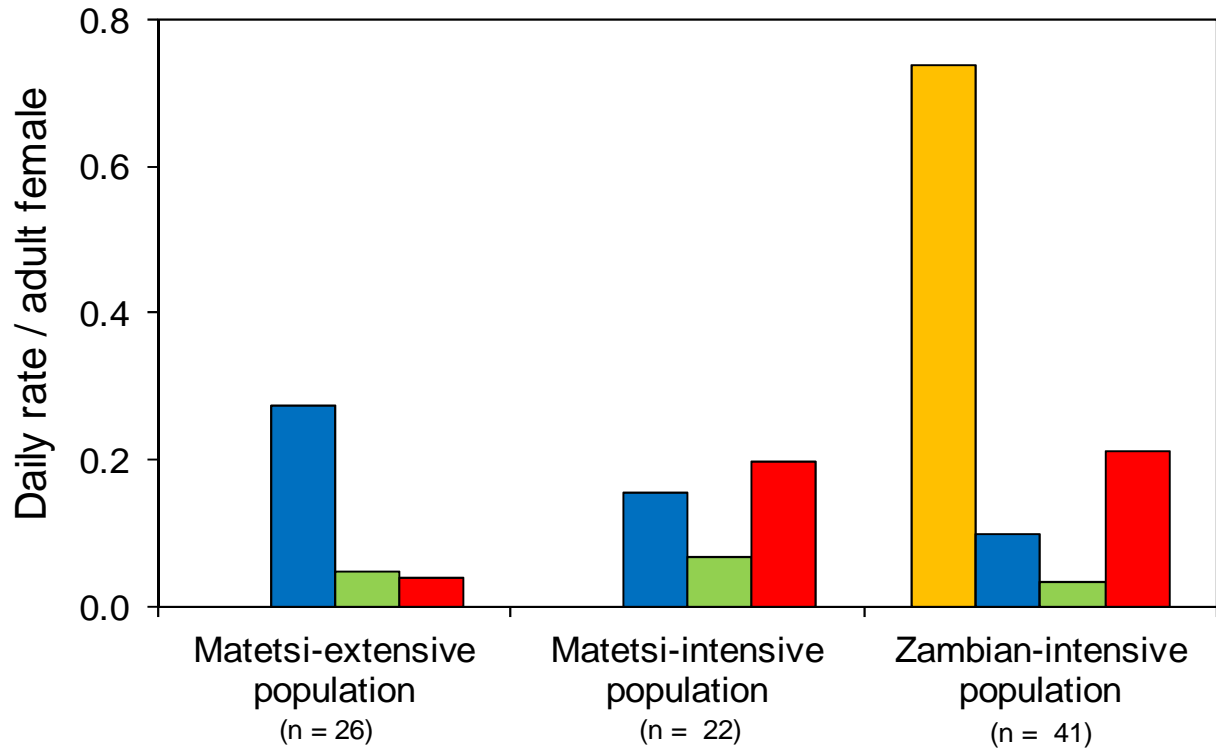


Figure 5.3 Seasonal variation in the daily rate of flehmen behaviour performed by adult females of all three study populations for the late dry (August 2011, yellow bar), wet (January 2012, blue bar), late wet (April 2012, green bar) and dry seasons (June 2012, red bar). No observations were carried out during the late dry season for the Matetsi-intensive population.

two intensively managed populations. In all three populations over 80% of all courtship behaviour was directed at adult females, with only a small proportion occurring between the territorial male and yearling females.

In comparing seasonal variation in the daily rate of courtship behaviour between the territorial male and adult females (Figure 5.4) in the Matetsi-extensive population courtship occurred most in the dry season, with the Zambian-intensive population also showing a secondary peak in courtship behaviour during the dry season (June). However, in the Zambian-intensive population courtship behaviour occurred the most during the late dry season. In the Matetsi-intensive population a distinct peak in the daily rate of courtship behaviour per adult female was observed in the late wet season ($p < 0.05$) (April).

The monthly distributions of births for all three populations are illustrated in Figure 5.5. The Matetsi-extensive population showed a clear calving season between November and January (2011/2012) with one calf born in July 2011 and another in April 2012. In the Matetsi-intensive population a calving peak was observed from January to April, with the most births occurring in February. However it should be taken into account that no observations were done on this population between July and December so it is possible that a second calving peak occurred. At the end of the study period in June 2012 a number of females were heavily pregnant, which could suggest that a second smaller peak could have occurred from July to August. In the Zambian-intensive population, calves were born throughout most of the year although a distinct peak in calving was observed from June to August. Monthly distributions of births for three consecutive years were also compiled for the Zambian-intensive population (Figure 5.6). Reproduction in the Zambian-intensive population showed no signs of seasonality occurring at different times each year.

The reproductive success of each sable population was calculated by dividing the number of births in a one year cycle by the number of adult females over three years of age. In the Zambian-intensive population a calving rate of 100% was observed for the year 2011-2012. Additionally three sub-adults aged between 24 and 36 months, also calved for the first time. All calves born in the year 2010 survived to the age of one year. As the Matetsi-intensive population was only observed for part of the year, the number of yearlings from the previous year (2010-2011) was used to determine the reproductive success of the population. For the previous year all 19 adult females older than three years calved indicating a 100% calving and/or survival rate in the year prior to the study. The reproductive success of the Matetsi-extensive population was only 75% for the year 2011-2012 as only 12 out of 16 mature females had calves at foot. All calves born during that year survived to the end of the study in June 2012.

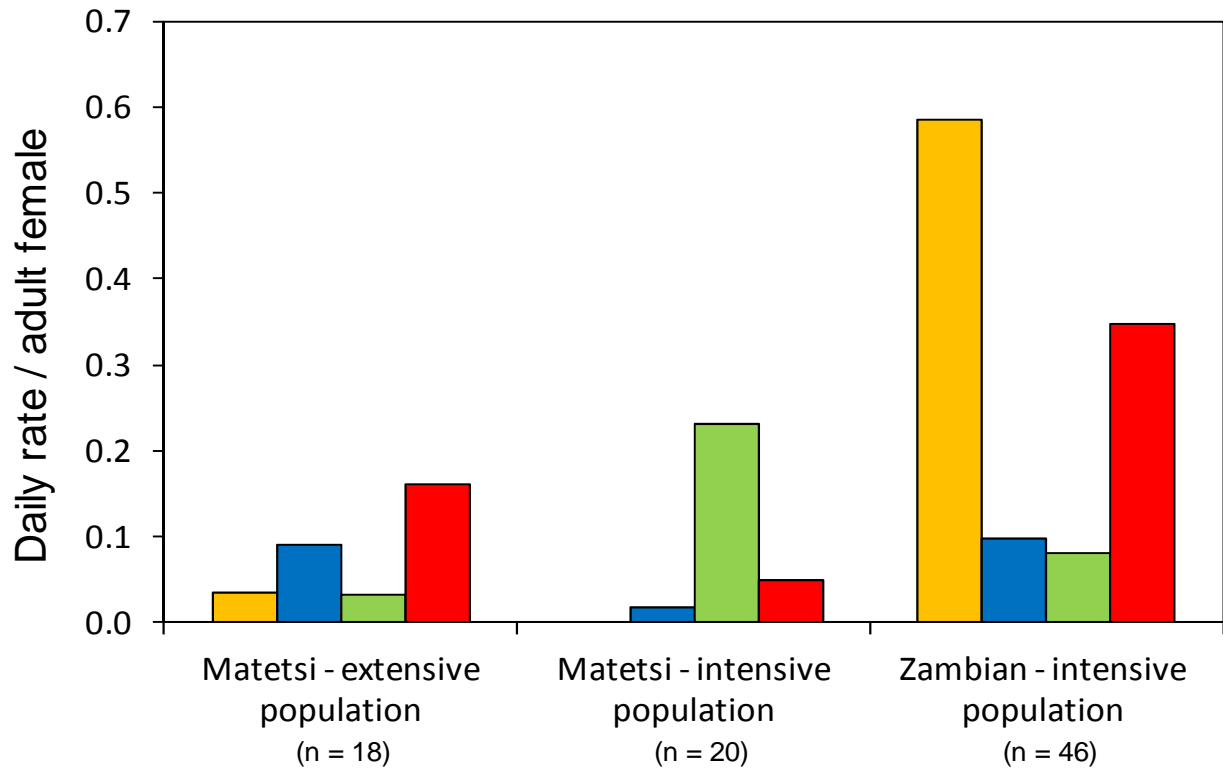


Figure 5.4 Seasonal variation in the daily rate of courtship behaviour directed at adult females of all three study populations for the late dry (August 2011, yellow bar), wet (January 2012, blue bar), late wet (April 2012, green bar) and dry seasons (June 2012, red bar).

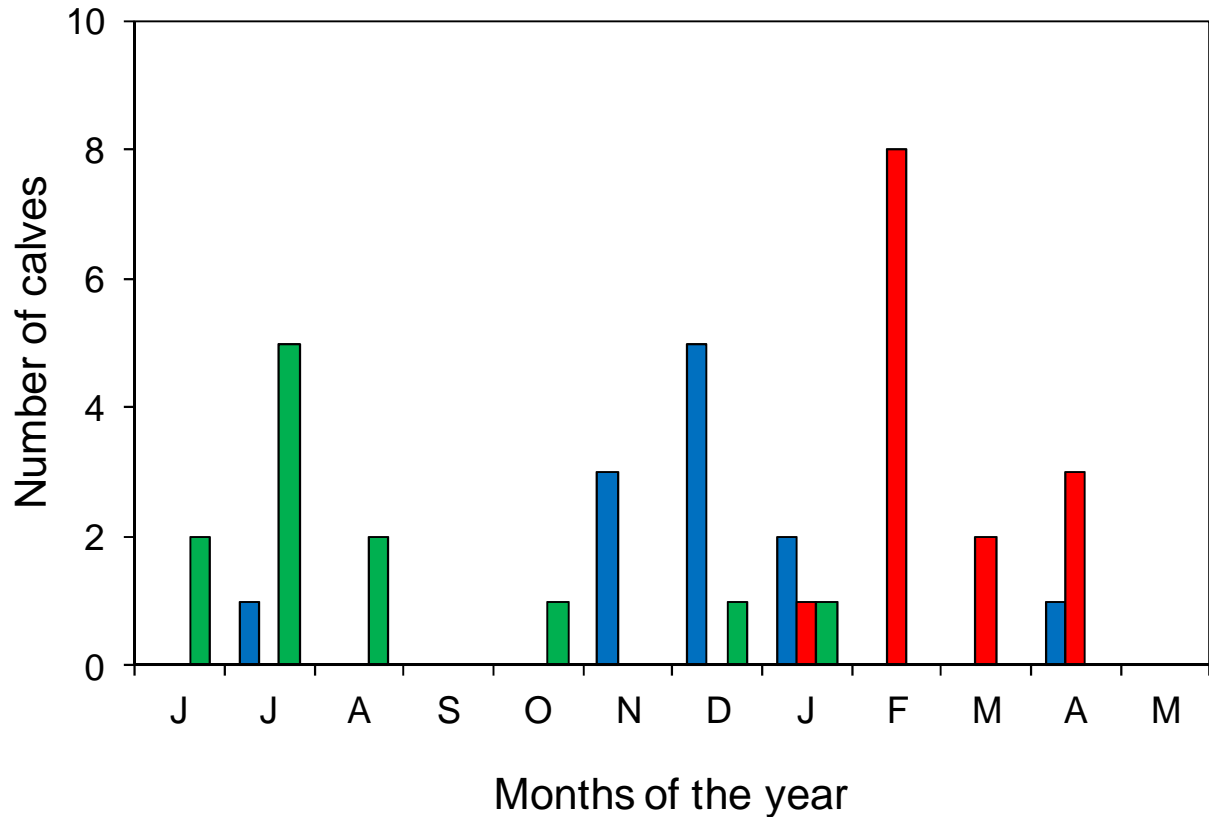


Figure 5.5 Number of calves born in the year 2011/2012 for the Matetsi-extensive (blue bar), Matetsi-intensive (red bar) and Zambian-intensive (green bar) populations.

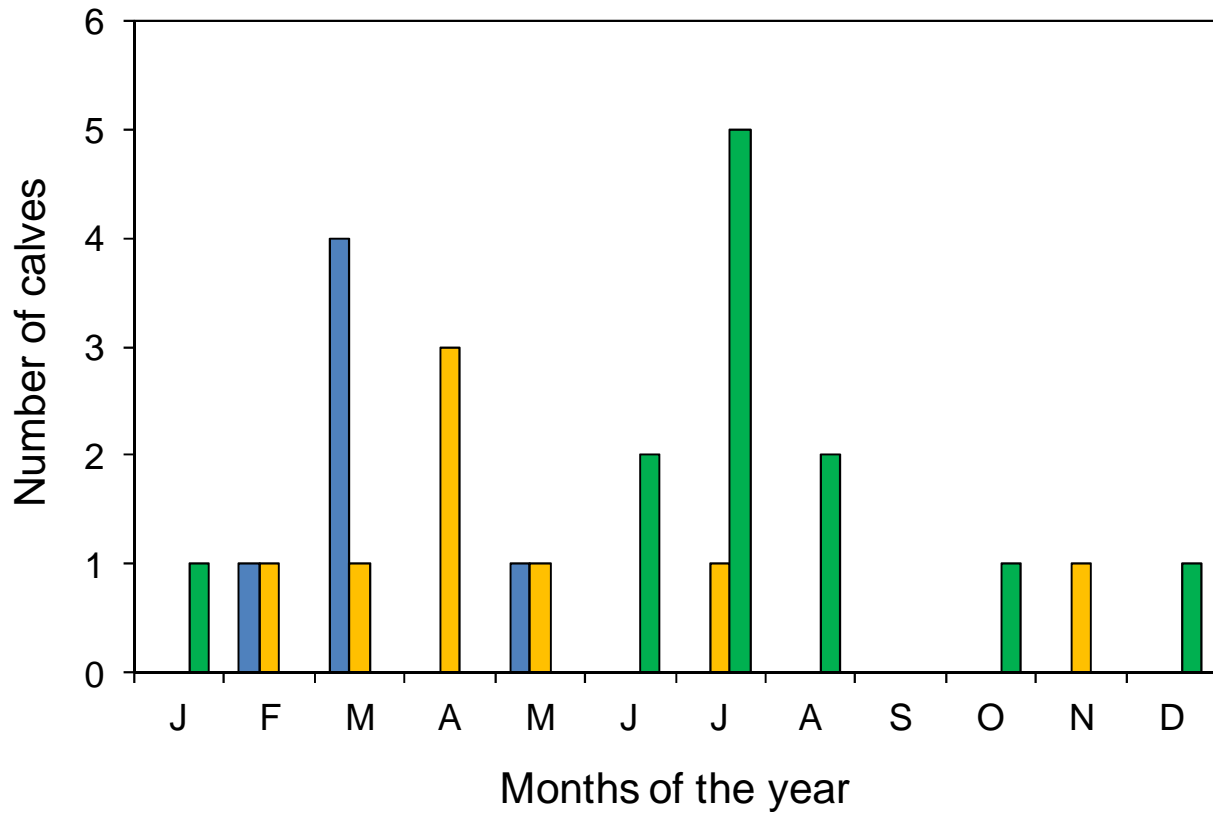


Figure 5.6 Number of calves born in the Zambian-intensive population for the years 2009 (blue bar), 2010 (yellow bar) and 2011 (green bar).

Discussion

The overall rate of reproductive behaviour was significantly higher in the two intensively managed populations compared to the Matetsi-extensive population. Dörgeloh *et al.* (1996) found that supplementary feeding significantly correlated to the growth rate of populations of roan antelope (*Hippotragus equinus*) under intensive management. Therefore the provision of dry feed in the dry seasons of the two intensive populations could explain the higher rate of courtship interactions observed in these two populations.

According to Sekulic (1978), populations of all African antelope species further away from the equator are inclined to have a single well defined calving peak which normally coincides with a single rainy season. The peak in calving in December, in the Matetsi-extensive population, coincided with the highest peak in rainfall for the region (*vide* Figure 2.3). Published data (Grobler 1974; Wilson & Hirst 1977) indicate that the range in gestation period for sable antelope varies between 8 and 9 ½ months. According to this, the peak mating season for the Matetsi-extensive population would have occurred from March to May. However, the rate of courtship behaviour observed in the late wet season (end of March) was very low (*vide* Figure 5.4) and therefore the peak in mating could have occurred in April and May (no observations), resulting in the calving peak observed in December and suggesting a gestation period of eight months. Observations of sable antelope on Transvaal nature reserves also indicated a gestation period of only eight months (Wilson & Hirst 1977).

The proposed seasonal rut for the Matetsi-extensive population, from April to June, was partly confirmed by the seasonal variation in courtship behaviour and flehmen performed by the territorial male, which peaked in the dry season (*vide* Figure 5.2). The highest peak in flehmen performed by adult females however, coincided with a second peak in courtship behaviour in the wet season (January 2012), closely following parturition, which would result in a calving peak in August 2012. Assuming that reproduction in this population is seasonal, it is highly unlikely that this would have happened as no peak in calving was observed in August of the previous year (2011). According to Sadleir (as cited in Sekulic 1978) the nutritional need of reproducing females is the highest during late pregnancy and lactation and therefore calves born during months of highest rainfall would have the best chance of survival. According to Sekulic (1978) females that are in good condition should be able to conceive shortly after giving birth, but in areas with only one rainy season this would result in calves being born during the dry season decreasing their chances of survival. In effect, individuals reproducing immediately after parturition would be eliminated by the process of natural selection.

In a study done in the National Zoological Park, Front Royal, Virginia (USA), captive female sable antelope showed no sign of seasonal variation in ovarian cyclicity, even though birth records indicated some degree of seasonality in reproduction (Thompson *et al.* 1998). According to Thompson *et al.* (1998), birth patterns could be as a result of a variety of factors other than the seasonality in ovarian cyclicity, such as seasonal variation in the fertility of males and the behavioural inhibition of reproductive behaviour by the female. According to Wilson & Hirst (1977) sperm obtained from herd bulls outside the active breeding season, showed little difference in appearance to sperm obtained in active breeding seasons and concluded that male sable antelope are capable of breeding throughout the year. According to Thompson (1995b), frequencies in flehmen performed by adult females reach a peak at the approximate time of oestrous. Therefore the peak in flehmen performed by adult females in the wet season (*vide* Figure 5.3) might suggest that females in the Matetsi-extensive population could have come into oestrous shortly after a peak in parturition. Wilson & Hirst (1977) also noted that though sexual behaviour by territorial males was displayed throughout the year, peaking during active mating season, females were only receptive (allowing courtship to commence) during oestrous in the breeding season. Unfortunately very small sample sizes of the incidence of behavioural patterns associated with behavioural oestrous such as mounting and tail lifting, hampered the evaluation of seasonality in female receptiveness. It is therefore uncertain what factors could have contributed in the inhibition of conception in the wet season in the Matetsi-extensive population. The absence of a peak in flehmen performed by adult females in the dry season (June 2012) could be explained by the lack of observations in April and May of 2012, as according to Thompson *et al.* (1998), oestrous cycles in sable antelope last on average only 24.2 days.

A previous study done on sable antelope on Sandveld Nature Reserve reported on a peak mating season from June to July and two peak calving seasons, from February to March and from September to October (Jooste 2000). This however, does not correspond with results of this study. Similarly, inconsistencies in aspects of reproductive behaviour existed between neighbouring herds in the Shimba Hills National Reserve in Kenya (Sekulic 1978). After calving in the dry season one herd was the only herd out of four in which partial birth synchrony took place. Sekulic (1978) suggested that the synchrony in this herd could have been facilitated by the mowing and burning of grassland within their range. It is therefore possible that aspects of reproductive behaviour can differ between two neighbouring herds at a particular time and for one herd over time, depending on resources available in its home range. Sekulic (1978) therefore suggest that individual herds should be considered as

separate reproductive units especially when resource partitioning varies greatly in space and in time.

Calving in the Matetsi-intensive population occurred from January to April, coinciding with the end of the rainy season (*vide* Figure 2.6) which suggests a mating season from May to August, with a peak in June. This is supported by the fact that the rate of flehmen performed by the territorial male and adult females peaked in the dry season. However courtship behaviour for the population did not peak in the dry season. Again the true rut season for the Matetsi-intensive population could have occurred before or after observation periods. The calving season and proposed rut season is congruent to other studies done on extensively managed sable antelope in the southern parts of the species' range (Fairfall 1968; Grobler 1974; Wilson & Hirts 1977). The presence of heavily pregnant females in June 2012 suggests that a second peak in calving could have occurred from July to August. This second peak in calving could be explained by the seasonal provision of dry feed in times of food scarcity during the drier winter months. According to Estes (1999) populations of antelope that do not experience extended periods of food scarcity can breed throughout the year. Similarly, in parts of sable antelope's northern range, for e.g. Kenya, populations either reproduced throughout the year with no evidence of seasonality in reproduction (Sekulic 1978) or two peaks in calving was observed coinciding with two rainy seasons (Estes & Estes, cited in Sekulic 1978). In the Zambian-intensive population, calving peaked from June to August in 2011 suggesting a peak in courtship behaviour from October to January. In this population a peak in courtship behaviour coincided with a peak in flehmen performed by territorial males (*vide* Figure 5.2) and adult females (*vide* Figure 5.3) in the late dry season (August 2011), which could have been the start of the breeding season. However when evaluating peak calving seasons in the Zambian-intensive population for three consecutive years it is evident that reproduction in this population is not seasonal. This is similar to results found by Sekulic (1978) and Thompson *et al.* (1998) and could be as a result of dry feed being provided throughout the year.

Calving and survival rates of the two intensively managed populations indicated a higher level of reproductive success compared to the extensively managed population at Sandveld Nature Reserve. In the two intensively managed populations, a survival rate of 100% was maintained, however, in the Matetsi-extensive population the survival rate of calves born the year prior to the study could not be determined due to a lack in records of births and mortalities. According to Estes & Estes (1974) about 15% of calves born in populations of large antelope under natural conditions, die within the first year. In the Matetsi-extensive population the calving rate was calculated from the percentage of calves present in the herd after the hiding phase and therefore some calves could have died prior to being integrated

into the breeding herd. The reproductive success estimated for the Matetsi-extensive population could therefore rather be referred to as the “survival rate” as described by Estes & Estes (1974), which is the ratio of immature individuals to a 100 adult females. In the Matetsi-extensive population a 75% percent calf survival rate was calculated indicating that either some adult females did not reproduce or 25% of calves did not survive the first month. In the Zambian-intensive population three of the five sub-adult females calved at the age of two years. Female sable antelope reach sexual maturity at the age of two years and normally have their first calve at the age of three years (Estes & Estes 1974; Grobler 1974). Grobler (1974) states that if females had to come into oestrous before two years of age, they would probably be too small or light to be mounted by an adult male. This is obviously not the case. According to Skinner & Chimimba (2005), female sable antelopes in captive populations may reach sexual maturity a year earlier compared to females of populations occurring under natural conditions. Wilson & Hirst (1977) also found that protein and mineral supplementation of pregnant and lactating females resulted in notable improvements in body condition and nutritional status and this in return is transferred to calves.

5.2 Territorial displays

Results

In game ranch industries, where sable antelope populations are managed intensively the absence of competitive territorial males, which form part of breeding strategies, may have an effect on the territorial behaviour of dominant animals. The lack of contesting males can influence the number of incidences as well as the spatial characteristics of dominance displays or territorial behaviour of game species. Although the wider concept of territorial behaviour or displays include demarcation of territories as well as rituals of dominance, for this part of the study it referred to actions displayed by dominant sable antelope males only in the presence of mature breeding females. As this study focused on the effects of intensive breeding with sable antelope, territorial displays in the absence of breeding females were not investigated.

The effect of certain intensive management strategies on the seasonality, daily rate, and spatial characteristics of territorial displays was determined by comparing such behaviour between populations. In the sable population at Sandveld Nature Reserve where breeding is not controlled and competition between dominant males occurred naturally, more incidences (79) of territorial displays in the presence of breeding females were observed

compared to the two sable populations which are managed intensively at Stella (8) and Vryburg (16).

Dominancy and territorial displays amongst adult male individuals to claim mating rights, can take place in the form of various anatomical features or rituals. Apart from horn length or body stature, female herding, vegetation horning and soil scraping were identified as the major territorial displays exhibited by male sable antelope during this study. Female herding included any attempts to keep the breeding herd from leaving the male's territory by driving them in a certain direction or even by blocking the way. The percentages of occurrence of the identified territorial displays were calculated for each population (Figure 5.7). Territorial displays performed by the dominant Matetsi-extensive population territorial male consisted predominantly of female herding. On occasion, in the Matetsi-extensive population, the territorial male was observed herding the breeding herd into a small compact group and fetching and returning with females that tried to escape by stampeding. Vegetation horning made up less than 20% of all territorial displays and though limited to only a few incidences, soil scraping as territorial display was observed only in this population. Considering the intensively managed populations where competition for mating rights were absent, the percentages of incidences where female herding occurred decreased as the enclosure size decreased. Interestingly enough, the proportion of vegetation horning increased as enclosure size got smaller. In the Zambian-intensive population where the enclosure is a mere 44 ha, more than 50% of all territorial displays were comprised of vegetation horning.

As could be expected, territorial displays were more dominant during certain seasons. The competitiveness of additional males is further evident in the increased daily rate of territorial behaviour observed in the Matetsi-extensive population which was significantly more compared to both the intensively managed populations ($p < 0.01$) (Figure 5.8). Although the number of territorial displays by the territorial male of the Zambian population were double the number observed in the Matetsi-intensive population at Stella, no statistical significant differences were calculated between the daily rates of territorial displays observed for these two sable populations ($p > 0.05$). Seasonal territorial displays differ completely between the three sable populations. In the Matetsi-extensive population the daily rate of territorial displays were highest during the wet season with almost 20 displays per day (Figure 5.8). The daily rate of territorial displays declined during the late wet season but increased again towards the dry season. In contrast, territorial displays in the Matetsi-intensive population were highest during the late wet season and the least displays were observed during the wet season. It seems that territorial displays in the Zambian population are more restricted to the drier seasons of the year with only a few incidences recorded during both the wet and late wet season.

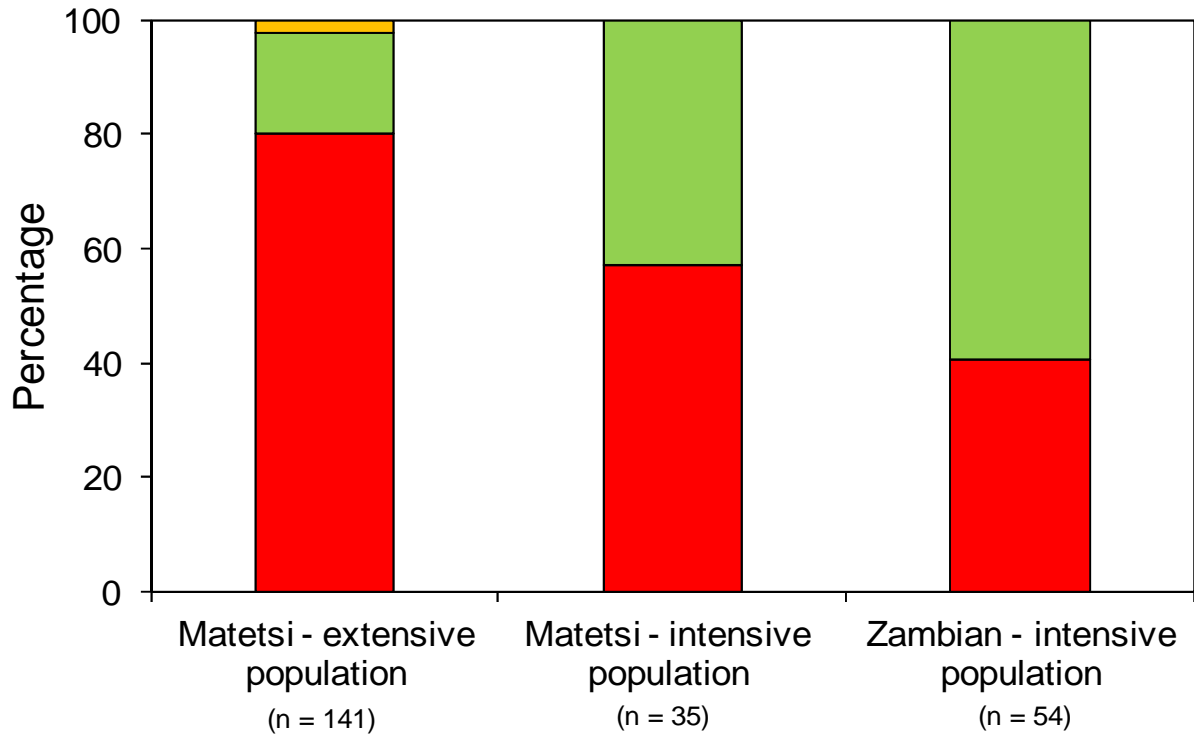


Figure 5.7 Territorial behaviour by territorial males in the form of herding (red bar), vegetation horning (green bar), and scraping (yellow bar) in three different sable antelope populations.

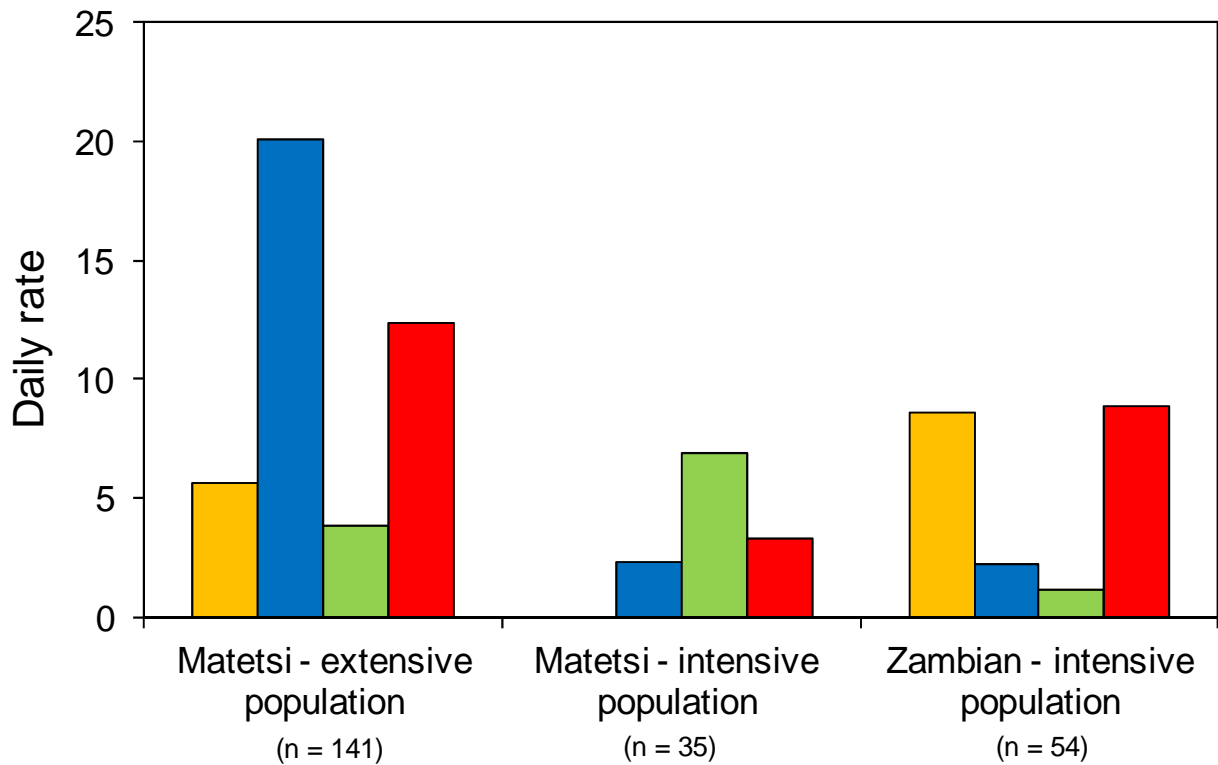


Figure 5.8 Seasonal variation in the daily rate of territorial behaviour observed in all three study populations for the late dry (August 2011, yellow bar), wet (January 2012, blue bar), late wet (April 2012, green bar) and dry seasons (June 2012, red bar).

Home range (95% kernel density estimates) and core area (50% kernel density estimates) sizes as well as areas of overlap between territorial males in home ranges and core areas were calculated for the three territorial males of the Matetsi-extensive population. In order to compare the area covered (km²) by each territory with previously published data, sizes of territories were also estimated from 95% minimum convex polygons. The 50% and 95% kernel density estimates calculated for breeding herds of the Matetsi-intensive and Zambian-intensive population, were used to describe territories and core areas of territorial males in these two populations. For all three populations localities of territorial behaviour were mapped against annual home ranges and core areas to determine where territorial behaviour was more pronounced. The territories of the three territorial males of the Matetsi-extensive population were all situated within the home range of the breeding herd observed (Figure 5.9). These males were referred to as territorial male one (TM1), two (TM2) and three (TM3) according to dominance rank which in turn was based on the number of interactions won and lost. The loser of an interaction was identified as the individual leaving the site of the interaction, displaying any submissive displays as described by Estes (1991)

Home ranges of TM1, TM2, and TM3 were estimated at 4.61, 1.86 and 2.70 km² respectively (fixed kernel density estimate). There was considerable overlap in the home ranges of territorial males at Sandveld Nature Reserve. As much as 44% of TM2's home range was situated in the territory of TM1. Additionally, the whole core area of TM2 was situated in the home range of TM1. The core areas of the two territorial males also overlapped, with 44% of TM2's core area overlapping with 19% of TM1's core area. A considerable overlap in home ranges of TM2 and TM3 also occurred with an overlap of 17% of TM2's and 12% of TM3's territory being shared by the two males. Only 39% of the home range of TM2 did not overlap with another territorial male. The overlap in home ranges of TM1 and TM3 however was not as large, with less than 1% of each territorial male's home range overlapping with the other.

In the Matetsi-extensive population two territorial disputes, between TM2 and TM3 and between TM1 and TM2 were observed. During the wet season the breeding herd moved through all three territories, though most time was spent in TM1 and TM2's territories. Whilst accompanied by TM2, on one occasion, TM3 approached the breeding herd, whilst resting under cover in the midday sun, and started rounding up females. TM2, also resting some distance from the herd facing in the other direction, eventually noticed and immediately charged TM3, who took flight, TM2 following in full pursuit. TM2 returned a while later limping. This interaction was initiated in the 95% kernel overlap between the territories of these two males. A second territorial dispute was observed in the 50% kernel overlap between TM1 and TM2. The herd was accompanied by TM2 in the late wet season when

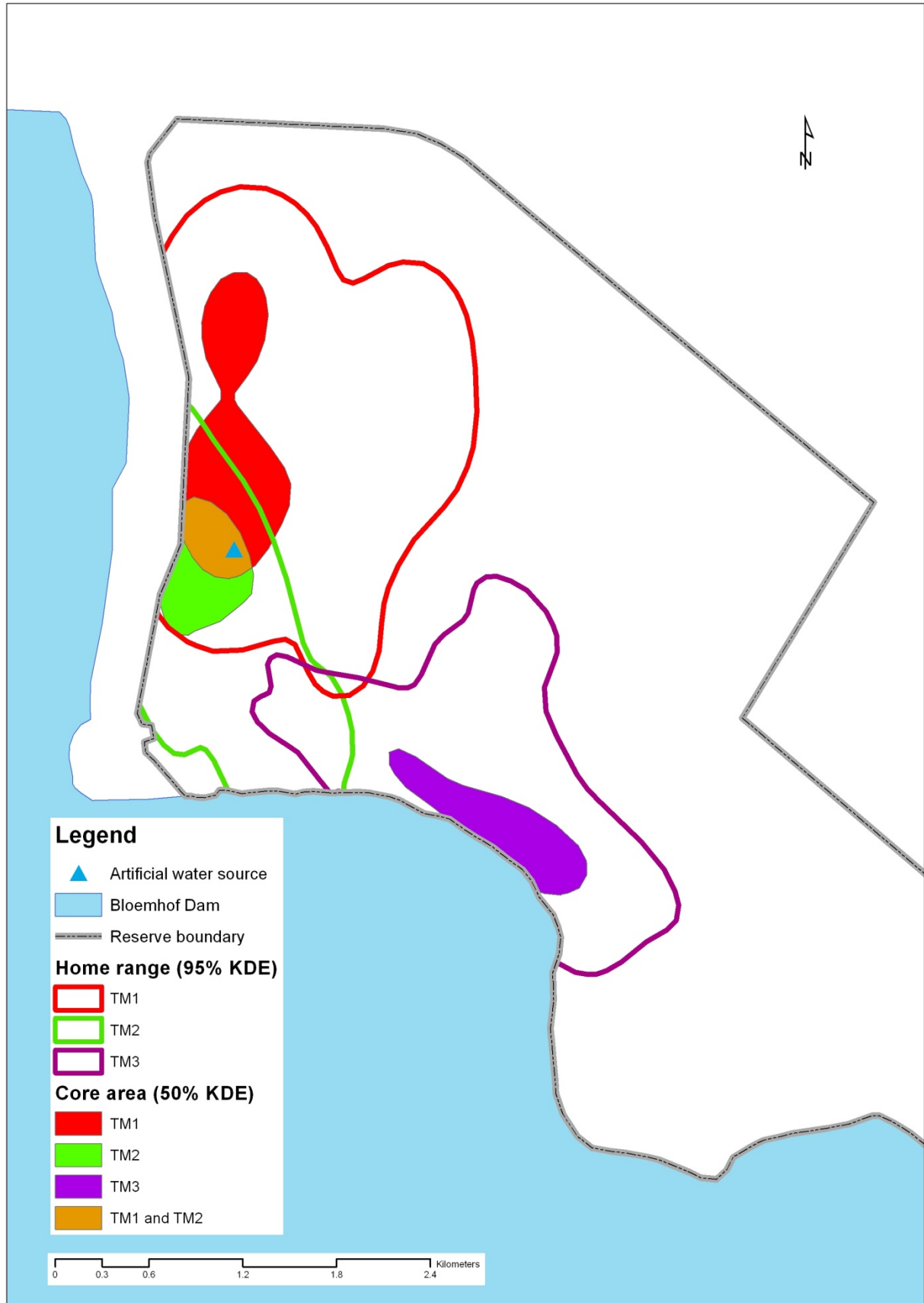


Figure 5.9 Range use of three territorial males of the Matetsi-extensive population at Sandveld Nature Reserve in the Free State Province, South Africa.

TM1 approached the breeding herd late afternoon. TM1 repeatedly approached TM2 who continued to move away. TM1 continued to drive TM2, in an erect posture, tail lifted horizontally to the body, frequently reinforcing the pursuit by nodding, head shaking and side sweeping. TM2 kept avoiding TM1 but did not move out of the vicinity of the breeding herd, but instead every now and then approached a female in the low stretch posture and tried to initiate courtship behaviour through lining up and performing "*Laufschlag*". A few times TM1 would do vegetation horning, possibly as a displacement activity. The dispute continued for almost an hour without any physical contact between the two territorial males. Finally after a pursuit by TM1, TM2 ran out of sight.

In the Matetsi-extensive population 88% of territorial displays performed by TM1 and 79% performed by TM2 occurred within or on the boundary of their core areas (Figures 5.10 & 5.11). Only three instances of territorial displays were observed for TM3 of which two occurred within the boundaries of the core area (Figure 5.12).

In the Matetsi-intensive population the territorial male mostly remained with the breeding herd, with 67% of the territorial displays performed occurring within the annual core area of the population (Figure 5.13). Most (70%) of the territorial displays in the Zambian-intensive population also occurred within the core area of the annual range use of the breeding herd. However, territoriality was more concentrated on the North-western side of the enclosure which faced the enclosure of another breeding herd and territorial male (Figure 5.14). Similar to the Matetsi-intensive population, movements of the territorial male mostly coincided with the breeding herd, however every now and then the male would disappear to the North-western boundary presumably to demarcate his territory and/or investigate the possibility of an intrusion by another male.

Discussion

The rate of territorial displays in the Matetsi-extensive population was significantly more than that observed in the two intensive populations. This could be attributed to the fact that only one territorial male was present in the two intensive populations. The Zambian intensive population also had a slightly higher daily rate of territoriality, however not statistically significant, which could be explained by the presence of another territorial male in a neighbouring camp. According to Grobler (1974), territories are most clearly defined during the mating season. Peaks in the rate of territorial displays per day in the Matetsi-extensive population coincided with peaks in other reproductive behaviour in the wet and dry

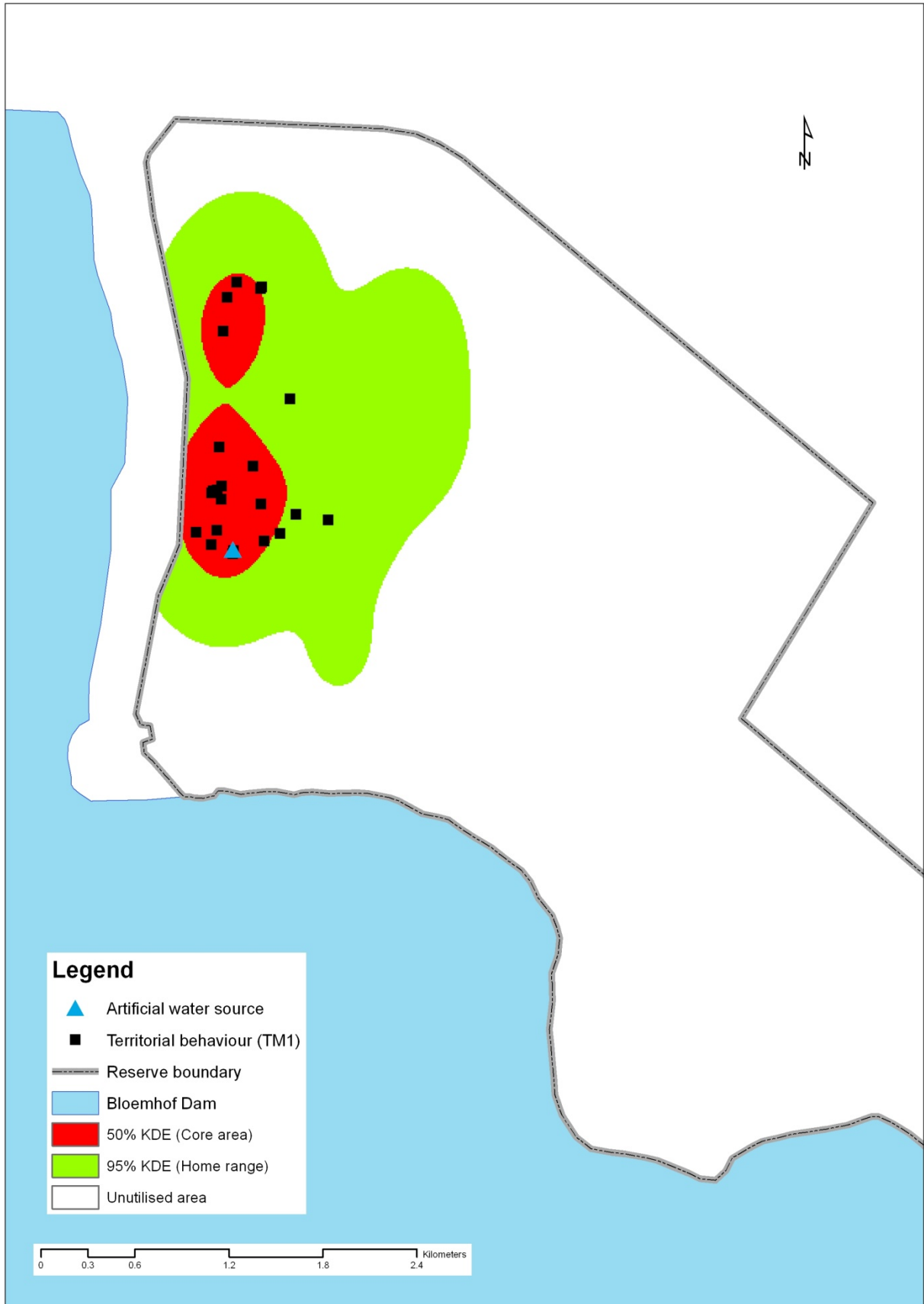


Figure 5.10 Spatial distribution of territorial behaviour performed by TM1 of the Matetsi-extensive population.

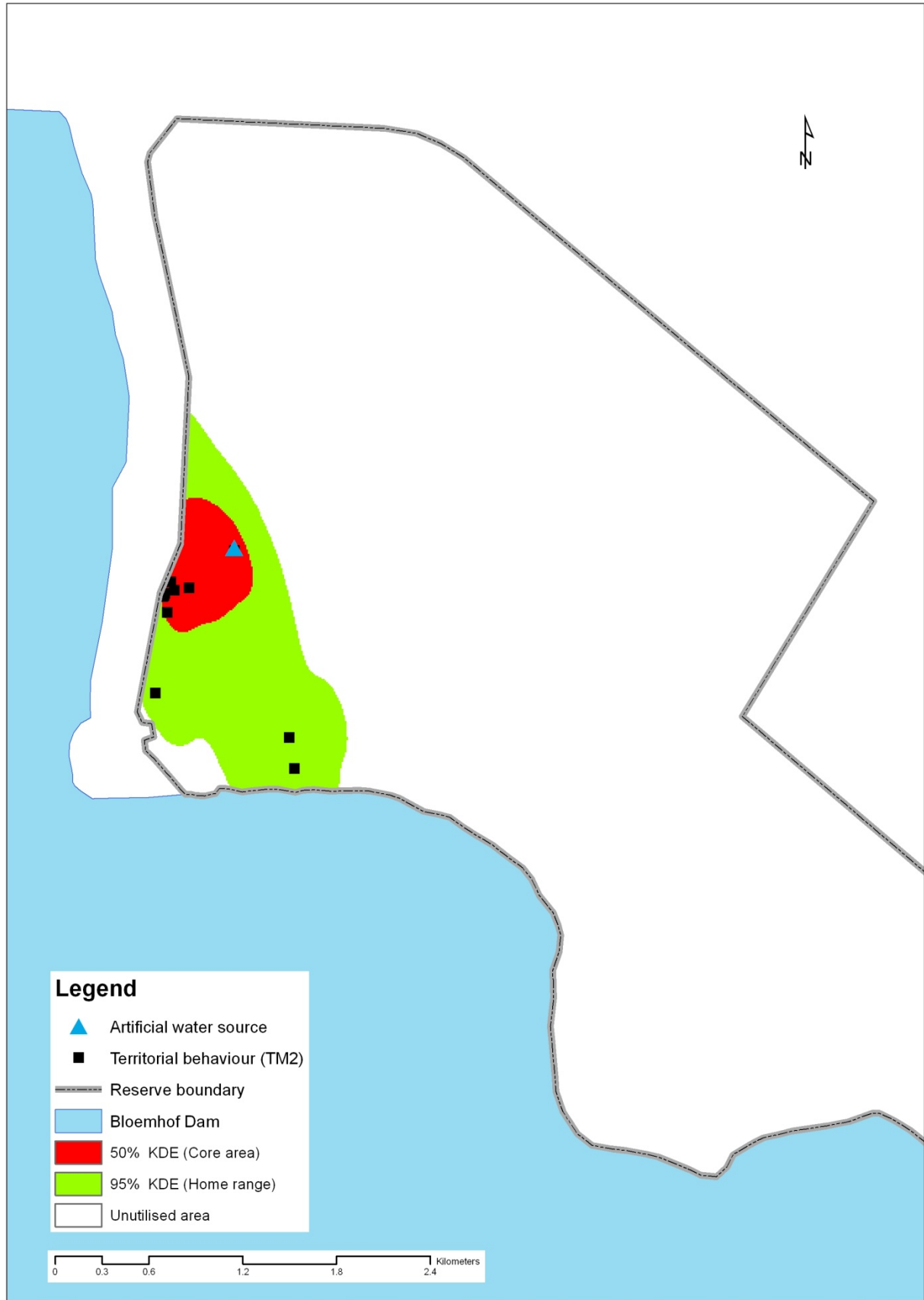


Figure 5.11 Spatial distribution of territorial behaviour performed by TM2 of the Matetsi-extensive population.

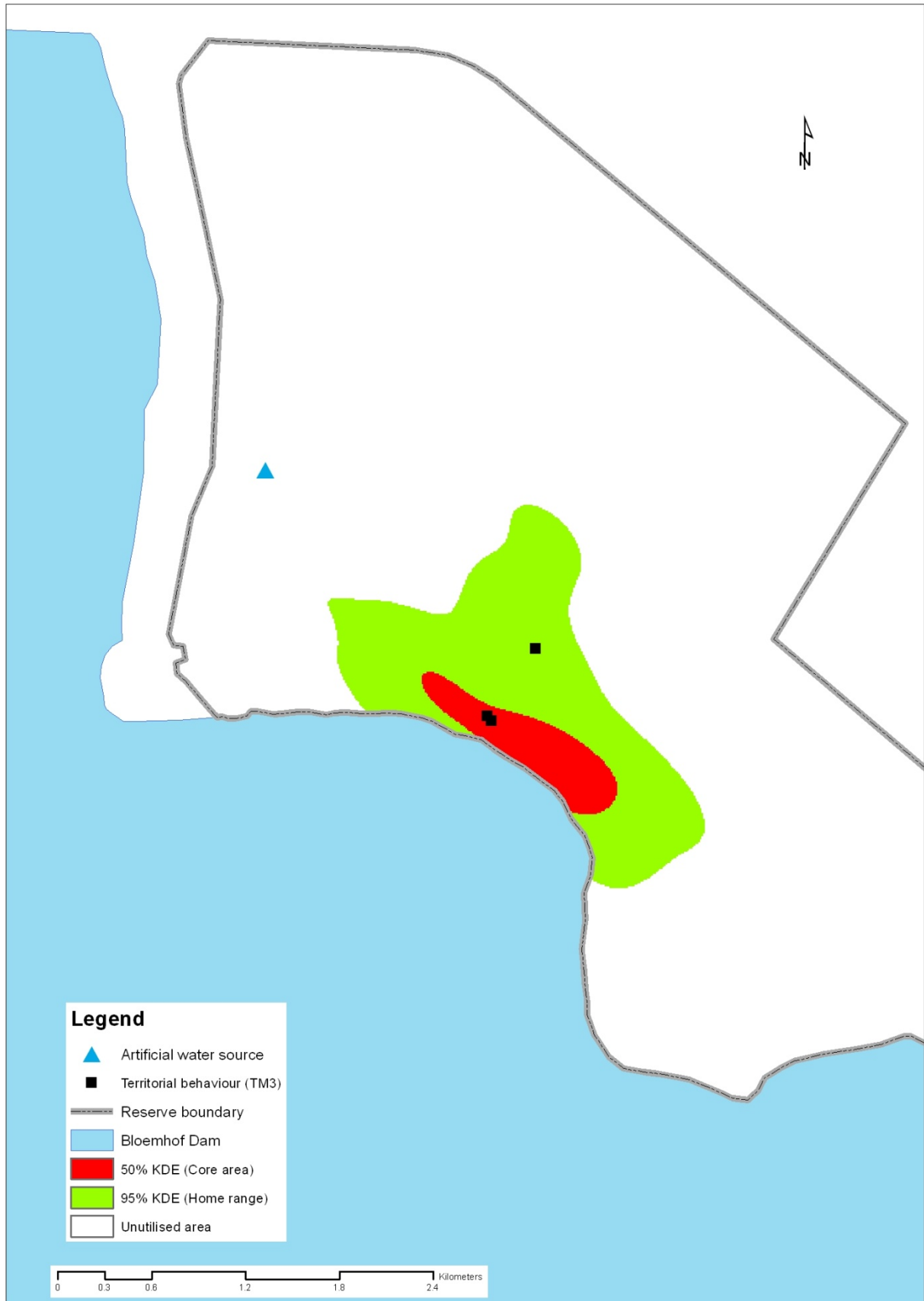


Figure 5.12 Spatial distribution of territorial behaviour performed by TM3 of the Matetsi-extensive population.



Figure 5.13 Spatial distribution of territorial behaviour performed by the territorial male of the Matetsi-intensive population.

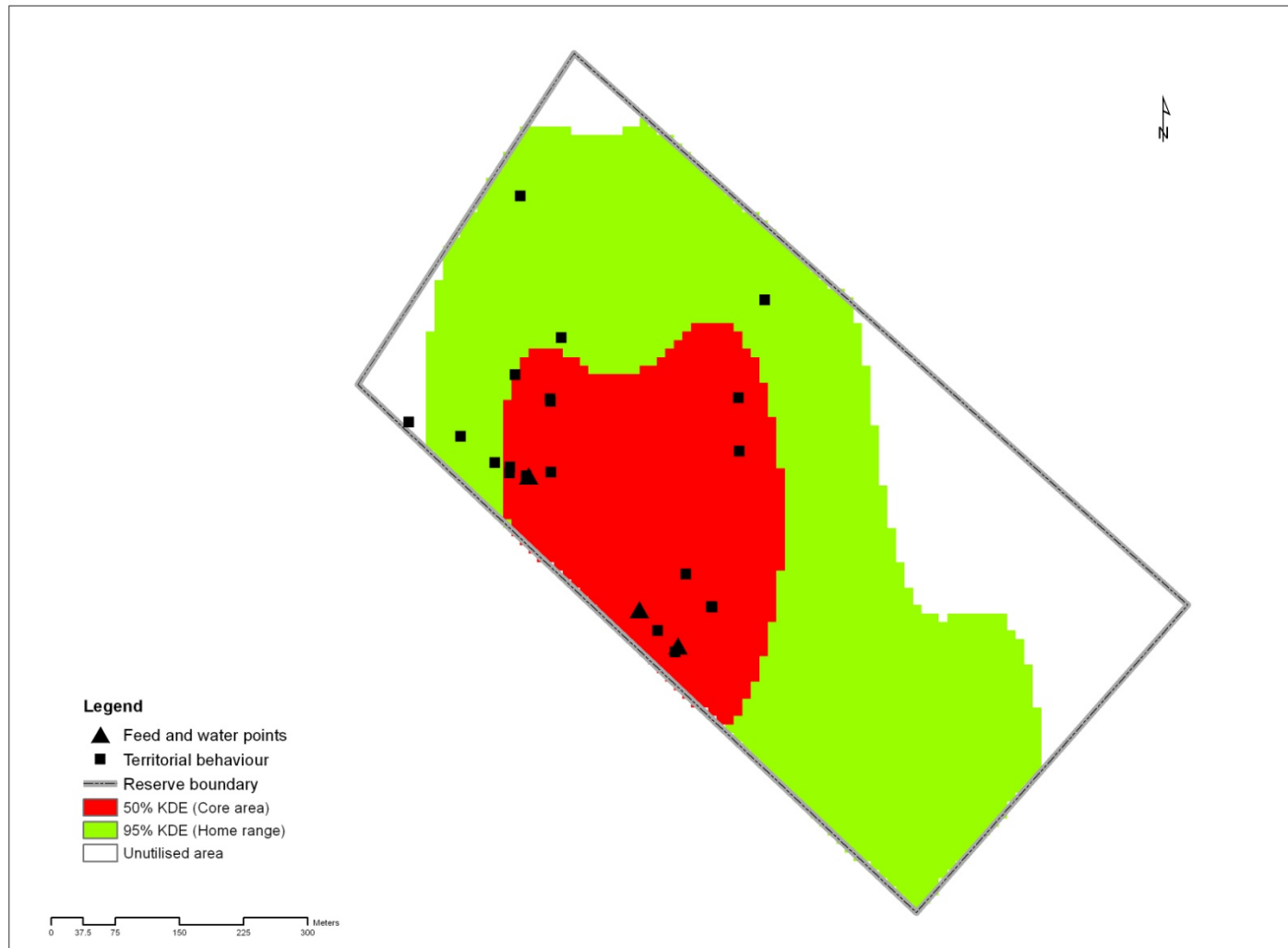


Figure 5.14 Spatial distribution of territorial behaviour performed by the territorial male of the Zambian-intensive population.

seasons. However the rate observed in the wet season was significantly more than that observed for the dry season. Similar patterns were observed in the seasonal variation in the rate of flehmen performed by adult females. This again indicates that adult females of the Matetsi-extensive population could have come into oestrous shortly after the peak in parturition observed in December 2011. In both the Matetsi-intensive and Zambian-intensive populations territorial behaviour was reflective of the rate of courtship behaviour.

The decreasing incidence of herding, as the enclosure size decreased, could have been due to the limitation of the breeding herd's movements (in effect the range) and the absence of other territorial males. Territorial males in the Matetsi-extensive population have to actively herd breeding herds to prevent them from moving into a neighbouring male's territory, and in doing so actively compete for the chance to mate. As the enclosure size decreases, a breeding herd's movements should become more localised, and therefore the need to herd might not be elicited as much. Additionally the presence of competitors in the Matetsi-extensive population might also have elicited higher frequencies in herding. However a more plausible explanation could be that in the extensively managed population at Sandveld Nature Reserve, territorial behaviour associated with demarcating territories such as vegetation horning and scraping could have occurred more during times when territorial males were solitary, which occurred more often compared to the intensively managed populations. Herding on the other hand only occurs in the presence of a breeding herd and may therefore appear to occur at higher frequencies as the activity of territorial males were not observed when separated from the breeding herd.

Additionally, according to Grobler (1974) vegetation horning correlates well with the boundaries of territories, which was not the case for territorial behaviour observed in this study. The majority of territorial behaviour observed in the Matetsi-extensive population occurred within core areas of territorial males. This could therefore be explained by the lack of observations on solitary males. However in the intensive populations where territorial males remained with breeding herds and were observed for most of the time, territoriality was still concentrated in the annual core area of the population.

The general description of herding by territorial males of this study was similar to that observed by Grobler (1974). In the Matetsi-extensive population during the wet season a number of females tried to escape and move out of the territory as a number of them had calves in hiding. This eventually resulted in part of the herd continually stampeding. The territorial male (TM2) eventually stopped trying to fetch herd members that moved out of his territory but continued to focus his aggression on individuals that he managed to block. As described by Estes & Estes (1974), all territorial males observed in this study brought up the

rear of the breeding herd as the population moved from one location to the next. Estes & Estes (1974) explain that it is easier for the territorial male to direct intended movements of the breeding herd from this position.

In the Matetsi-extensive population the home range sizes of territorial males estimated from minimum convex polygons, were comparable to territories recorded by Estes & Estes (1974), of 3 to 4 km² for sable in the Luando Natural Integral Reserve in Angola. However again, as the range use of territorial males at Sandveld Nature Reserve was only recorded in relation to the breeding herd studied, home ranges estimates for territorial males could be under or over estimated. There was significant overlap not only in the home ranges of all three males, but surprisingly also in the core areas of TM1 and TM2. Core areas of TM1 and TM2 were situated in the same areas as wet and dry seasons core areas estimated for the breeding herd of the population (*vide* Figure 4.12).

Territories of sable antelope normally included sufficient cover (Estes & Estes 1974), favoured grazing areas, and a drinking site (Grobler 1974). As discussed in Chapter 4.2, this area was considered a preferred foraging area due to the presence of dense stands of *Panicum maximum*, with a sufficient percentage of woody cover and a water source. Though the estimated core areas of territorial males were related to the areas favoured by the breeding herd and were not necessarily representative of areas favoured by territorial males when alone it could be that aside from the presence of a breeding herd this area would have been favoured by solitary territorial males as well.

5.3 Agonistic Behaviour

Results

All animals compete for resources such as food, water, shelter and breeding partners. However, when resources like these are limited, competition increases. In intensively managed sable antelope populations, a number of factors could therefore have an effect on the rate and nature of agonistic interactions. While a total of 176 agonistic interactions were observed in the Matetsi-extensive population (15 interactions per day), more than twice the number (432) of such agonistic encounters were observed in the Zambian-intensive (39 interactions per day) populations and more than three times the number (633) in the Matetsi-intensive population (81 interactions per day). Agonistic interactions in all three populations were almost always initiated by the eventual winner (85% of interactions in the Matetsi-extensive population, 96% of interactions in the Matetsi-intensive population and 90% of agonistic interactions in the Zambian-intensive population).

The daily rates of agonistic interactions between different gender and age class combinations are summarised in Table 5.1. In all three populations most of these interactions involved adult females. Agonistic behaviour displayed by adult females seemed furthermore to be directed more towards older age classes for example sub-adult males and yearlings and less towards younger individuals. The same trend of the relatively insignificant number of incidences of agonistic interactions towards younger herd members was observed where adult males were involved. When comparing populations (Table 5.1), significantly higher daily rates of agonistic interactions among adult females, between adult females and yearlings and between adult females and juveniles, were observed for the Matetsi-intensive population compared to the Matetsi-extensive and Zambian-intensive populations ($p < 0.01$). For these three types of agonistic interactions a significantly higher daily rate was also observed for the Zambian-intensive population compared to the extensively managed population at Sandveld Nature Reserve ($p < 0.01$). For agonistic interactions between adult males and adult females and between adult males and yearlings the daily rate was also significantly more in the Matetsi-intensive population compared to the other two populations. However, there was no significant statistical difference ($p > 0.05$) between the daily rates observed for the Matetsi-extensive and Zambian-intensive populations.

In all three populations only one agonistic interaction between a territorial male and juvenile was observed in the Matetsi-intensive population. The daily rate of agonistic interactions involving sub-adult males in the Matetsi-extensive population were relatively low compared to other types of agonistic interactions, with interactions between adult females and sub-adult males occurring more often than between sub-adult males and the territorial male.

Seasonal variation in the rate of agonistic interactions was evaluated for interactions among adult females only (Figure 5.15). For the Matetsi-extensive population, the daily rate of agonistic interactions per female reached a high in the wet season (January 2012) decreasing as the year progressed and was at its lowest in the late dry season of the previous year (August 2011). The incidence of agonistic interactions among adult females in the Matetsi-intensive population was the lowest in the wet season and significantly increased from the wet to the late wet season and exponentially from the late wet to the dry season. In the Zambian-intensive population the daily rate of agonistic interactions per female remained relatively constant throughout the year however, the daily rate dropped significantly in the late wet season. In the wet season the Matetsi-intensive population had a similar daily rate of agonistic interactions per adult female to the Matetsi-extensive population, both

Table 5.1. Daily rate of agonistic interactions observed between different gender and age classes of different sable antelope populations (n = number of interactions observed).

Interactions	Matetsi-extensive Population		Matetsi-intensive population		Zambian-intensive Population	
	n	Daily rate	n	Daily rate	n	Daily rate
Adult female/ Adult female	113	9.4495	415	52.9787	308	27.6854
Adult female/Sub-adult male	17	1.4216	-	-	-	-
Adult female/Yearling	31	2.5923	148	18.8936	87	7.8202
Adult female/Juvenile	2	0.1672	26	3.3191	18	1.6180
Adult male/ Adult female	7	0.5854	25	3.1915	15	1.3483
Adult male/ Sub-adult male	3	0.2509	-	-	-	-
Adult male/Yearling	3	0.2509	18	2.2979	4	0.3596
Adult male/Juvenile	0	0.0000	1	0.1277	0	0.0000

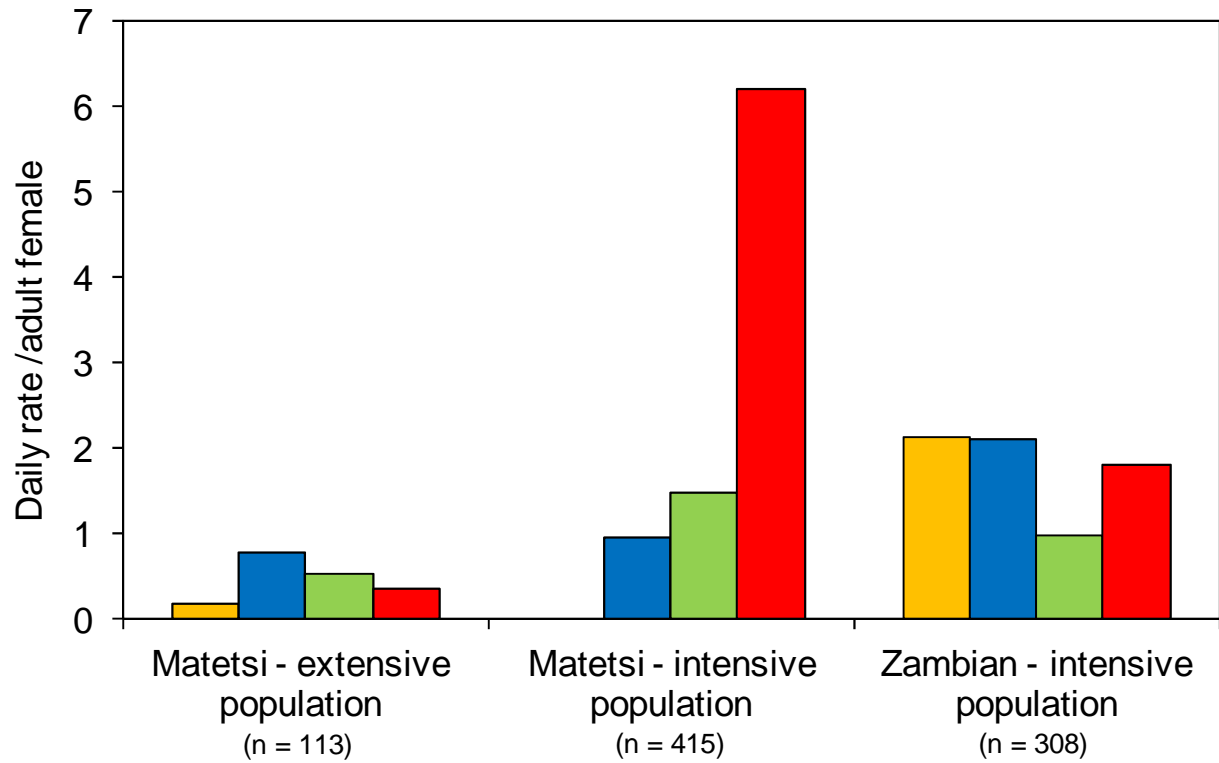


Figure 5.15 Seasonal variation in the daily rate of agonistic interactions among adult females, of all three populations, for the late dry (August 2011, yellow bar), wet (January 2012, blue bar), late wet (April 2012, green bar) and dry seasons (June 2012, red bar).

significantly lower than that observed for the Zambian intensive population (*vide* Figure 5.15). However in the late wet and dry seasons the daily rates observed for the Matetsi-intensive population were significantly more compared to the extensively managed population at Sandveld Nature Reserve.

For all three populations the hourly rate of agonistic interactions among adult females was compared to the hourly incidence of grazing, lying, walking, browsing, drinking water, territorial behaviour performed by the territorial male and, in the intensive populations, the utilisation of dry feed (Figures 5.16, 5.17 and 5.18). For the Matetsi-extensive population, in all four seasons, the hourly rate of agonistic interactions among adult females increased at the start and end of resting periods. Higher hourly rates of agonistic interactions also coincided with an increase in territorial behaviour in both the late dry and wet seasons. In the wet, late wet and dry seasons, increased hourly rates of agonistic interactions coincided with an increase in the amount of time spent walking. An increased rate in agonistic behaviour was observed in the wet, late wet and dry seasons around the time the breeding herd was observed drinking water. However in the late dry season, though the breeding herd drank water in the 12th hour, no increase in the hourly rate of agonistic behaviour was observed for this hour. In the late dry season increased amounts of time spent browsing also coincided with increases in the rate of agonistic interactions among adult females.

In the Matetsi-intensive population, during the wet, late wet and dry seasons, increases in the hourly rate of agonistic interactions among adult females coincided with increased incidences of walking. This is seen especially around midday in all three seasons, as the population moved to and from the water trough. In all three seasons the hourly rate of agonistic interactions also increased as the population drank water. In both the late wet and dry seasons the daily variation in the rate of agonistic interactions among adult females is positively correlated to the utilisation of dry feed ($R^2 = 0.8565$ & $R^2 = 0.7783$, respectively).

In the Zambian-intensive population during the late dry season the hourly rate of agonistic interactions among adult females was positively correlated to the incidence of walking ($R^2 = 0.7852$). An increase in the incidence of walking, in the early morning during the late wet season also coincided with an increase in the hourly rate of agonistic interactions among adult females. In all four seasons, the hourly rate of agonistic interactions among adult females increased as the population utilised dry feed. This was similar to what was observed in the Matetsi-intensive population. However, during the wet and dry seasons the daily variation in the hourly rate of agonistic interactions among adult females was positively correlated to the

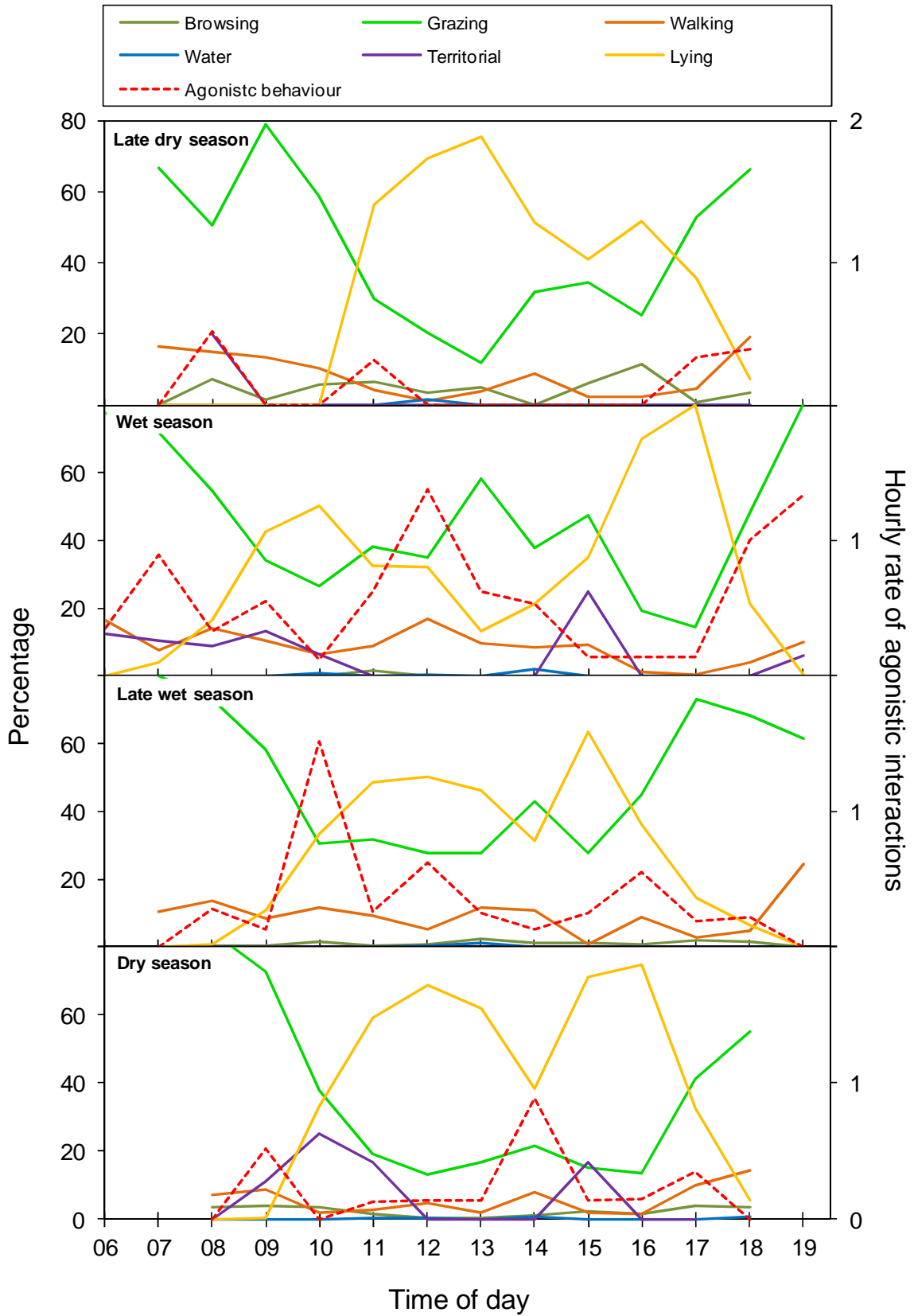


Figure 5.16 Hourly incidence of activity patterns compared to the hourly rate of agonistic interactions among adult females in the Matetsi-extensive population during different seasons at Sandveld Nature Reserve.

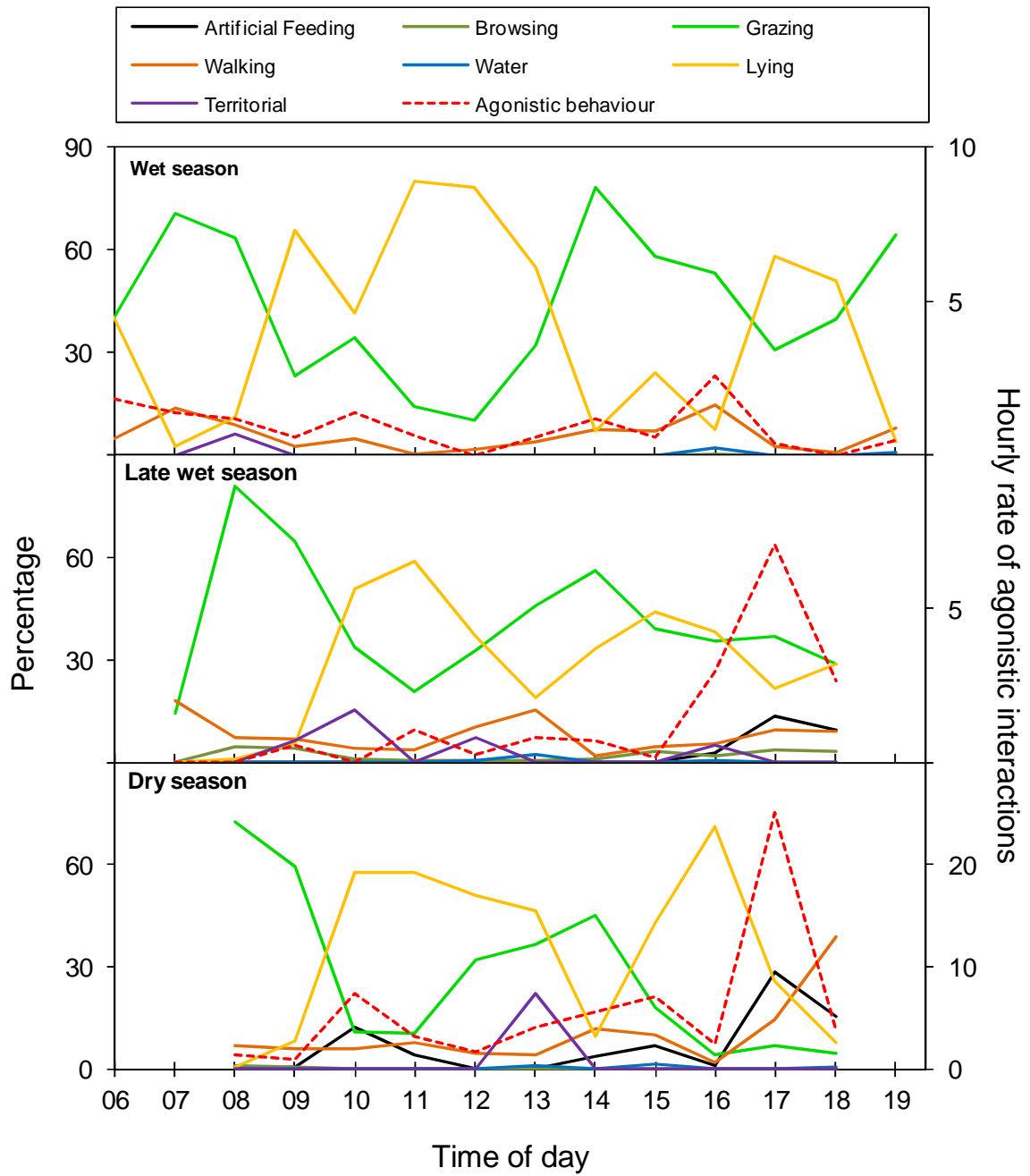


Figure 5.17 Hourly incidence of activity patterns and hourly rate of agonistic interactions among adult females in the Matetsi-intensive population during different seasons at Stella.

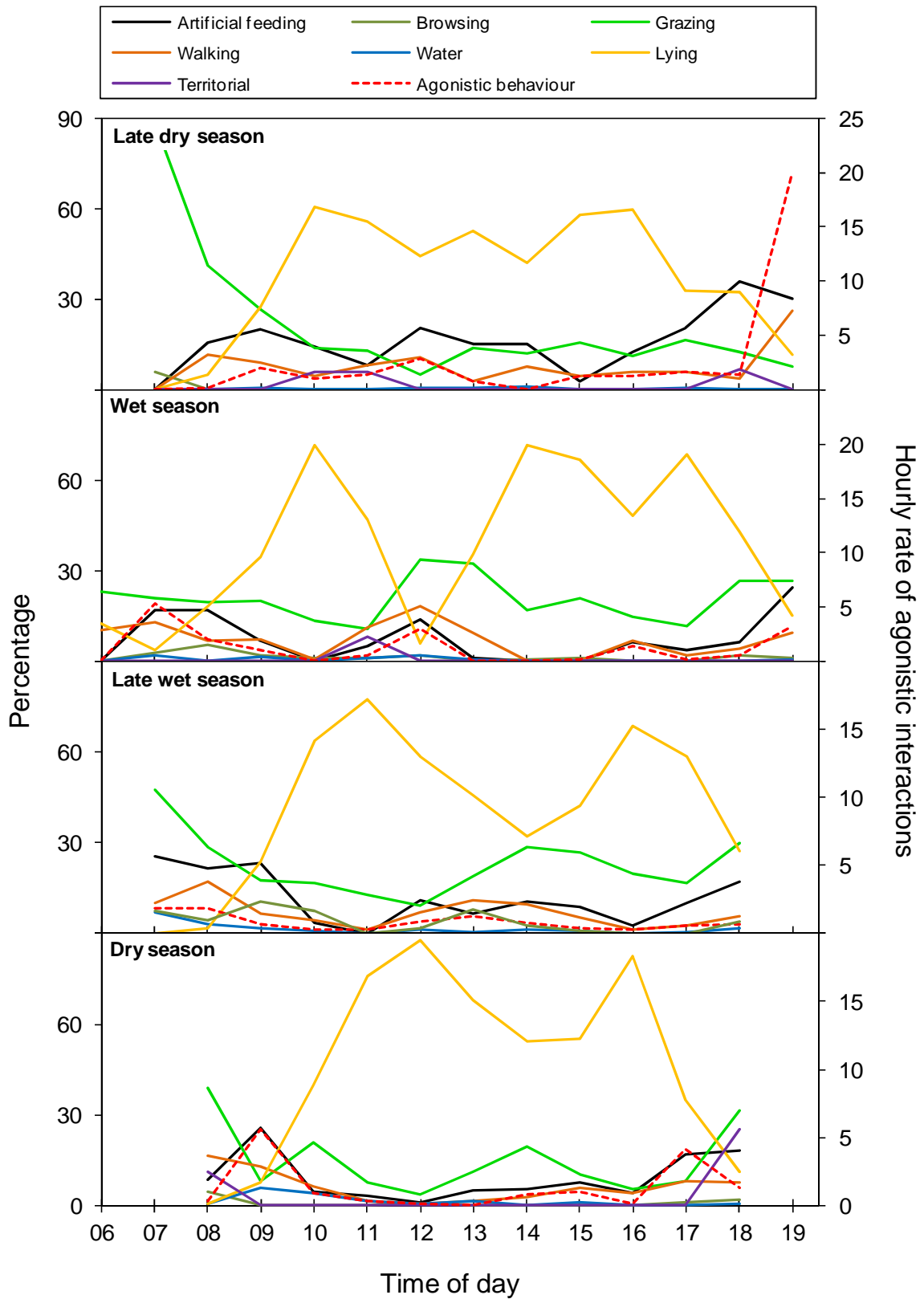


Figure 5.18 The hourly incidence of activity patterns and hourly rate of agonistic interactions among adult females, in the Zambian-intensive population during different seasons at Vryburg.

utilisation of dry feed ($R^2 = 0.7458$ & $R^2 = 0.7766$, respectively). During the wet and dry seasons the incidence of drinking water coincided with an increase in the utilisation of dry feed and therefore also coincided with increased hourly rates in agonistic interactions among adult females. However in the late dry and late wet seasons there was no relation between the incidence of drinking water and the hourly rate of agonistic interactions among adult females. In the late wet season an increase in the incidence of agonistic interactions among adult females coincided with an increase in time spent browsing. Similar to what was observed in the Matetsi-extensive population, in all four seasons an increase in the hourly rate of agonistic interactions was observed in the afternoon at the end of a resting period, as the activity of the breeding herd started to increase.

The percentage of agonistic interactions which contained behavioural patterns defined as fighting, dominance displays and threat displays (*vide* Table 3.2) were calculated for all types of agonistic interactions in all three populations (Figure 5.19). When considering agonistic interactions among adult females, these interactions in the Matetsi-extensive population consisted of almost equal parts fighting, dominance displays and threat displays. In the Matetsi-intensive population adult females relied firstly on threat displays, secondly on dominance displays and lastly on fighting to compete for resources. In the Zambian-intensive population, agonistic interactions among adult females consisted predominantly of dominance displays followed by threat displays, with fighting used as a last resort.

In the Matetsi-extensive population agonistic interactions among adult females, contained proportionately more fighting compared to both of the intensively managed populations, with differences observed being highly significant ($p < 0.01$). The two intensive populations however, did not differ significantly from each other when considering the incidence of fighting in these interactions ($p > 0.05$). These interactions contained significantly more *chases* and *horning* in the Matetsi-extensive population compared to the two intensive populations. Agonistic interactions among adult females of the Zambian-intensive population also contained significantly more *head rubbing* compared to the other populations, therefore the incidence of dominance displays observed in these interactions for the Zambian-intensive population was also significantly more compared to the Matetsi-extensive and Matetsi-intensive populations ($p < 0.05$).

In all three populations agonistic interactions between adult males and adult females were dominated by dominance displays, with the adult females of the Zambian-intensive population using dominance displays significantly more compared to adult females of the other two populations ($p < 0.05$). Though not significant ($p > 0.05$), fighting was also more pronounced in the Matetsi-extensive population compared to the two intensive populations

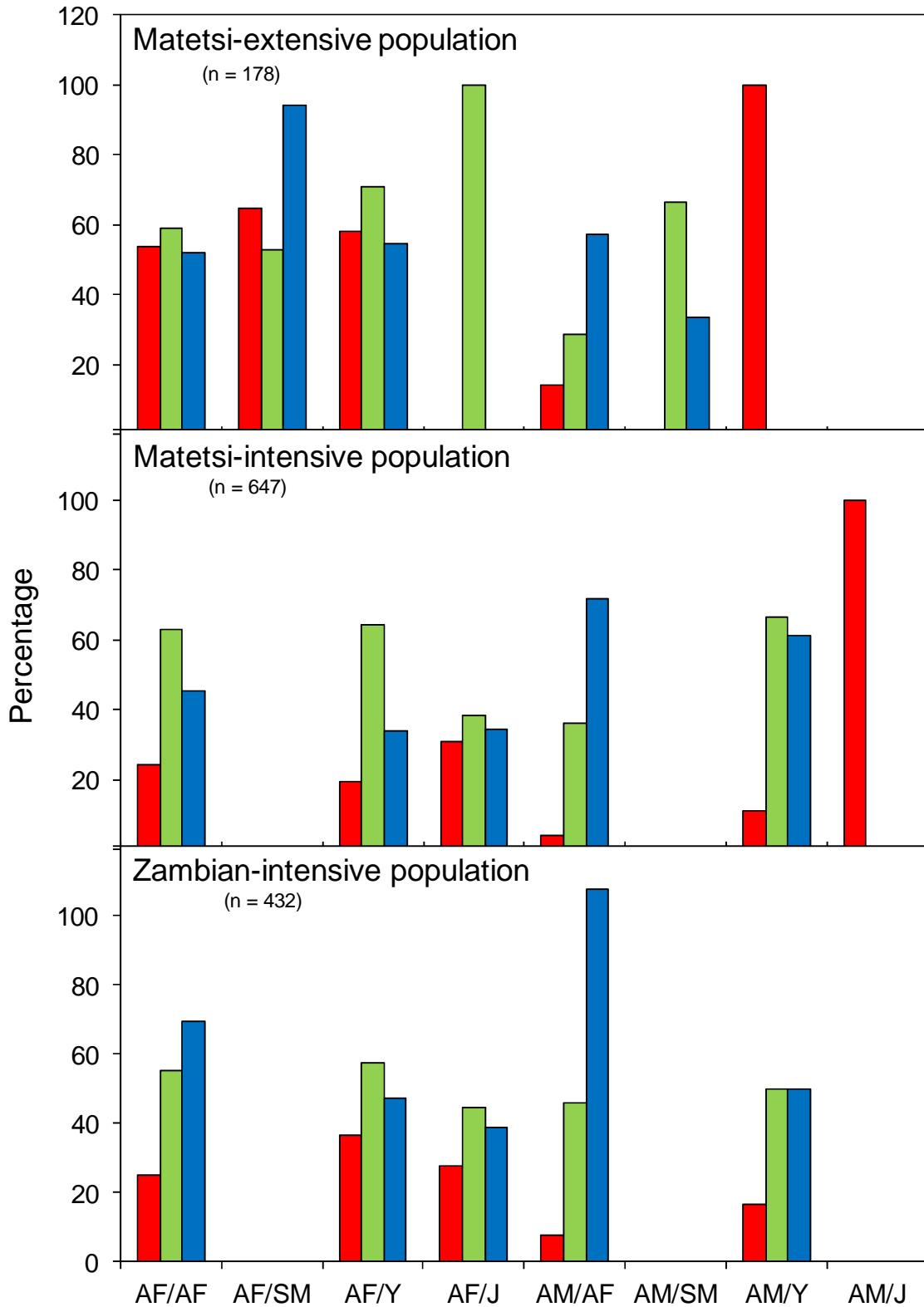


Figure 5.19 Agonistic interactions containing behaviour patterns classified as fighting (red bar), threat displays (green bar) and dominance displays (blue bar) in interactions among different age classes and gender in different sable antelope populations. AF, adult female; AM, adult male; SM, sub-adult male; Y, yearling; and J, juvenile

when considering agonistic interactions between adult males and adult females and, between adult males and yearlings. The incidence of behavioural patterns considered as fighting, in agonistic interactions between adult females and yearlings, was also significantly more in the Matetsi-extensive population compared to the Matetsi-intensive population ($p < 0.05$). However the incidence of fighting in agonistic interactions between adult females and yearlings observed in the Matetsi-extensive and Zambian-intensive populations were found to be similar ($p > 0.05$). The higher incidence of fighting in these interactions observed in the Matetsi-intensive population can be attributed to significantly more *horning* and *head butting* ($p < 0.05$). Agonistic interactions between the territorial male and yearlings in the Matetsi-extensive population was comprised only of fighting, but with a very low sample size of only two interactions this might not be representative of what these interactions are truly comprised of. Whereas, in the Matetsi-intensive and Zambian-intensive populations, in these types of interactions the incidence of fighting is much lower and threat and dominance displays are more prevalent.

Agonistic interactions between adult females and juveniles in the Matetsi-extensive population were only comprised of threat displays, whereas in the two intensive populations these interactions also included fighting and dominance displays. Furthermore, the one interaction that took place between an adult male and a juvenile was in the Matetsi-intensive population and contained *horning*, which falls into the fighting category.

Discussion

Agonistic interactions in all three populations were almost always initiated by the eventual winner. Similar results were obtained by Thompson (1993), who stated that this trait is particularly pronounced in bovids. According to Thompson (1993) a linear hierarchy is established in sable antelope and remains stable over time. Thompson (1993) suggests that the unidirectionality of interactions could contribute to the long term stability of hierarchies observed in this species as subordinate individuals rarely challenge dominant individuals.

When comparing populations, for most of the types of agonistic interactions, the Matetsi-intensive population had the highest rate, followed by the Zambian-intensive population and then lastly the Matetsi-extensive population. In all three populations the most agonistic interactions took place among adult females. This is not surprising as according to Stockley & Bro-Jørgensen (2010), female mammals frequently compete for not only mates, but also for other resources such as food, shelter, and constituents of time and space that might provide anti-predator advantages etc., all to ultimately improve their reproductive strategies.

When evaluating agonistic interactions among adult females only, though the daily rate observed for the Matetsi-extensive population was significantly lower compared to both of the intensively managed populations, the proportion of agonistic interactions among adult females containing fighting was significantly more in the extensively managed population compared to that of both intensively managed populations. Therefore in the Matetsi-extensive population though agonistic interactions occurred at significantly lower rates interactions appear to be more aggressive. However, when considering the extremely high rate of agonistic interactions in the two intensive populations the chances of injury was still higher compared to the Matetsi-extensive population.

The higher rate of agonistic interactions observed in the intensively managed populations could be explained by the provision of dry feed. When examining the seasonal variation in the daily rate of agonistic interactions among adult females, it is evident that even though in the wet season the Matetsi-intensive population's rate was similar to that of the Matetsi-extensive population, in the late wet and dry seasons it increased greatly, exceeding even that of the Zambian-intensive population. This exponential increase in the rate of agonistic interactions among adult females coincides with the provision of dry feed. Dry feed was provided for the first time in the late wet season, though intermittently, but without fail in the mornings and afternoons of every day in the dry season. This is furthermore supported by the fact that positive correlations were detected between the daily variation of the utilisation of dry feed and the daily variation in the rate of agonistic interactions among adult females in both of the intensive populations. In both intensive populations, a set portion of dry feed per day was provided for every individual of the population. Even though enough dry feed was provided for every herd member, certain individuals over utilised, or were forced to underutilise dry feed. Additionally in the Matetsi-intensive population dry feed was almost always finished by the time the population moved away and if not, was utilised by other game species present in the enclosure. Therefore individuals of the Matetsi-intensive population would need to compete to acquire enough dry feed before it was finished and before the herd moved out of the area. However, in the Zambian-intensive population some dry feed was almost always left over and as the population remained within the vicinity of the feeding troughs throughout the day, subordinate individuals could revisit feeding troughs whilst the majority of the herd was lying down.

Additionally, in the Matetsi-intensive population, in all seasons observed, the rate of agonistic interactions also increased whilst the population frequented the water trough, which was not the case for the Zambian-intensive population. Under natural conditions water is in theory only a limited resource in the dry months, when some water sources dry up. In the case of the use of a water trough however, water is continuously provided and is

thus never a limited resource. The increase in the rate of agonistic interactions whilst drinking water could therefore not be as a result of water being a limited resource, but could be related to the limited space around the water trough as well as the limited amount of time spent by the herd in the vicinity of the water trough.

In theory, if the activity of members of a breeding herd is synchronized, all individuals would utilise water together within a short period of time before the population moved off again. Individuals would therefore compete to drink water first as to avoid being left behind which could increase the risk of predation. This was observed in the Matetsi-intensive and Matetsi-extensive populations, but in the Zambian-intensive population, as a result of the population remaining in the vicinity of the water trough for most of the day, individuals would drink water more sporadically throughout the day. Therefore the time available to drink water whilst still remaining in the herd was not limited in the Zambian-intensive population. Therefore when the time available to utilise resources, for example dry feed and water, is limited it could result in increased levels of agonistic interactions. This could have been why the incidence of agonistic interactions in the Zambian-intensive population was lower than that of the Matetsi-intensive population.

In the Matetsi-extensive population the utilisation of water in the late dry season had no effect on the rate of agonistic interactions among adult females whereas, in the wet, late wet and dry seasons an increase in the incidence of agonistic interactions was observed when the population drank water. This can be explained by the fact that in the late dry season the herd drank water from the banks of the Bloemhof dam, whereas during the wet, late wet and dry seasons a small artificial water source was frequented by the breeding herd. According to Du Toit (2010), grazers are generally more water dependent compared to browsers, as a result of the moisture content of grasses falling below 10% in the dry season. In the dry season the incidence of agonistic interactions, which coincided with the Matetsi-extensive population drinking water, was more pronounced compared to other seasons. This could therefore be as a result of the low moisture level of forage consumed. According to Estes & Estes (1974) in the dry season sable antelope of the Luando Natural Integral Reserve were observed drinking water at least once daily compared to frequenting water holes every other day in the wet season.

In the Matetsi-extensive population in the late dry season the incidence of browsing seemed to have an effect on the rate of agonistic interactions among adult females. Browsing constituted a substantial part of the dry season diet of the breeding herd and could have been an important resource needed to maintain body condition and nutritional status throughout the dry season.

Increases in the incidence of territorial behaviour in the Matetsi-extensive population also coincided with an increased rate of agonistic interactions among adult females in the late dry and wet seasons. During territorial behaviour the territorial male would round up the breeding herd, herding them into a compact group, thus decreasing the space between individuals of the breeding herd. According to Estes (1991), individuals of the tribe Hippotragini (horse-like antelopes) like to maintain individual distances, as to remain beyond the reach of another individual's horns. Individuals herded together could possibly feel the need to compete with each other for personal space, thereby increasing the rate of agonistic interactions. Similarly when the population moves from one location to the next the space between individuals also decreases and could result in an increased rate of agonistic interactions as individuals compete for space. Additionally whilst moving herd members may also compete for favourable positions in the centre of the herd that would be less exposed to predators.

In the Matetsi-extensive population an increase in the rate of agonistic interactions among adult females was observed at the start and end of resting periods in all four seasons. This was also observed for the Zambian-intensive population, however only at the end of resting periods as the population's activity increased. According to Grobler (1974), individuals of the breeding herd always rest in close proximity to each other. The increase observed at the onset of the resting period could be as a result of individuals competing for lying space that is less exposed to predators. However, this does not explain the increase observed at the end of a resting period. According to Thompson (1995b) activity patterns of females within a breeding herd is highly synchronised and females are generally observed urinating within several minutes of the herd transitioning from rest to activity. Thompson (1991) found that higher ranked females would give birth in closer temporal proximity to other females compared to lower ranked females, and as a result only partial birth synchrony is observed in this species. Thompson (1991) suggests that reproductive synchrony in sable antelope is achieved through the performance of flehmen by sexually mature females. According to Thompson (1991) the rate of flehmen performed by a female was positively correlated to her rank, which is generally maintained through direct aggression. Therefore higher ranked females would have more opportunities to investigate freshly voided urine and would therefore be able to give birth in closer proximity to other herd members, whereas low-ranking females would have less access to olfactory cues and would therefore be less likely to give birth in close proximity to other herd members.

According to Thompson (1991), for females the optimal reproductive strategy would be to give birth in close temporal proximity to only a few other females and not all females present in the herd. According to Estes & Estes (1974) sable antelope calves born around the same

time tend to form crèches, therefore hiding together. The optimal number of calves present in a crèche should be small enough not to be detected by predators and large enough to provide social cover (safety in numbers) whilst still in the hiding phase and during integration into the herd. As dominance relationships are maintained through direct aggression and adult females should in theory compete for flehmen opportunities to give birth synchronously, this could explain the increased rates of agonistic interactions among adult females observed at the end of resting periods.

In the Matetsi-extensive population the daily rate of agonistic interactions involving sub-adult males was relatively low. Sable antelope are tolerant of sub-adult males in breeding herds up to four years of age (Estes & Estes 1974; Grobler 1974). According to Wilson & Hirst (1977), male sable antelope reach sexual maturity at the age of 18 months and can successfully breed in the absence of a territorial male. Grobler (1980) however found that male sable antelope reach sexual maturity at the age of 3 years and are sexually active throughout the year. The two sub-adult males present in the Matetsi-extensive population were between two and three years of age and were also observed to be sexually active during the study period. This was however in the presence of the territorial male. On one occasion, both the territorial male and a sub-adult male were engaged in courtship behaviour with reproductively mature females within meters of each other. The sub-adult males were also observed bringing up the back of the breeding herd alongside the territorial male, with no obvious aggression between the territorial male and sub-adult males.

However, in the Zambian-intensive population a yearling male (17 months) was removed in the first observation period (August 2011) after enduring numerous aggressive attacks by the territorial male. Wilson & Hirst (1977) noted aggressive interactions between the territorial male and yearling males at the age of 17 – 19 months, often violently driving them away from the breeding herd. They also noted that intra-specific aggression of this nature should be considered as a limiting factor on smaller reserves. The high tolerance of sub-adult males in the Matetsi-extensive population could also lend some evidence to a theory of andromimicry proposed by Estes (2000). Estes (2000) hypothesised that the mimicking of male secondary characters, such as the darkening of coat colour in adult females, might function in decreasing sexual dimorphism among herd members. Therefore young maturing males of darker females are less conspicuous to a territorial male and might be able to remain within the breeding herd for longer, increasing its chances of survival.

CHAPTER 6: MANAGEMENT IMPLICATIONS & RECOMMENDATIONS

The importance of higher quality forage, available in vleis areas, burnt areas or scattered across the landscape in the dry season, has been confirmed for sable antelope (Estes & Estes 1974; Grobler 1981; Parrini 2006; Macandza 2009; Parrini & Owen-Smith 2009; Le Roux 2010). Parrini (2006) noted that sable antelope were able to adapt their foraging behaviour depending on the availability and distribution of resources during the dry season. The results of this study indicate that sable antelope at Sandveld Nature Reserve possibly subsisted on dry grass due to the absence of higher quality forage in the landscape during the dry season. However, the calving rate observed was still high and comparable to populations of sable antelope in other studies where higher quality forage was available in the dry season (Estes & Estes 1974). Therefore sable antelope at Sandveld Nature Reserve might not have been negatively affected by the absence of good quality forage in the dry season. Sable antelope are therefore able to adapt their feeding strategy in sub-optimal habitats outside their natural range, given that the area is not overstocked.

Even though dry feed was provided throughout the year in the Zambian-intensive population, a substantial part of the diet still consisted of natural forage. This was especially true for the breeding herd which was observed utilising less dry feed compared to the territorial male in both seasons. Sub-ordinate individuals would also benefit from the availability of natural forage, as they are often forced to under-utilise dry feed. Therefore enclosures should contain sufficient amounts of natural forage throughout the year. This could however be effected by the size of the enclosure as small enclosures are usually overstocked and could therefore lead to overgrazing. This challenge can be overcome with the implementation of an enclosure rotation system, which could be practically implemented through the use of adjacent enclosures. The movement of herds from one enclosure to the next could be achieved by luring the herd through gates with the provision of dry feed. By periodically resting the vegetation in some of the enclosures overgrazing could be avoided. In areas where overgrazing has already occurred, the establishment of planted pastures is recommended, for example *Cenchrus ciliaris* and *Digitaria eriantha*, as this will dramatically increase the carrying capacity of the enclosure.

In intensively managed populations, when providing dietary supplementation high in crude protein, browse made up a much smaller part of the diet and therefore the presence of woody plant species in enclosures might not be as important. However, in areas that experience cold winters with frost, wooded areas may provide protection from the cold. Wooded areas might also be important for providing shade at midday during hot summer months. The nutritional need of reproducing females is the highest during late pregnancy and lactation and therefore calves born during months of highest rainfall would have the best chance of survival. Due to the provision of dry feed, intensively managed populations never experienced periods of food scarcity and were therefore able to reproduce during the dry season as well. Extreme temperatures in winter months may also influence calf survival rate. However, in the current study no calf mortalities were reported as a result of low temperatures for either of the intensively managed populations.

There is no doubt that the provision of dry feed in the two intensively managed populations resulted in increased productivity of 100% compared to 75% observed for the extensively managed population at Sandveld Nature Reserve. In the Zambian-intensive population subordinate individuals benefited from having access to dry feed left over after feeding periods. This is confirmed by the fact that two sub-adult females calved for the first time, at the early age of 26 months, compared to the age of at least 36 months observed in naturally occurring populations (Estes & Estes 1974; Grobler 1980a). However, according to Kriek (2005) calving at an early age could lead to dystocia problems. Additionally, the teeth of old sable antelope females, from the age of thirteen years, are worn down to the gums and will result in the loss of body mass, eventually leading to death (Kriek 2005). However due to the provision of dry feed in intensively managed populations, old females remain productive for longer. One specific adult female in the Zambian-intensive population calved at the age of 18 years. According to Kriek (2005) the life expectancy of sable antelope under natural conditions varies between 13 and 15 years. Therefore the provision of dry feed not only increases life expectancy of an adult female but also productivity. When considering higher calving rates observed for intensive populations, the fact that female start reproducing at an earlier age and remain productive for longer, could lead to major financial gains.

Though dry feed may increase productivity it also results in increased rates of agonistic interactions. However, the level of aggression observed in agonistic interactions among adult females was not increased by the provision of dry feed but due to extremely high rates of agonistic interactions around feeding troughs, the chances of injury were still higher in the intensive populations compared to the extensively managed population at Sandveld Nature

Reserve. Additionally, agonistic interactions directed at immature individuals were also more pronounced and more aggressive in the intensively managed populations, presumably due to the provision of dry feed. Additionally, behavioural patterns that would not normally result in injury under extensive management could result in injury in the vicinity of feeding troughs. From personal observations, the use of numerous tire troughs, instead of the conventional large rectangular steel troughs, seems to help in avoiding injuries associated with utilising dry feed. Tire troughs are less obscure and more pliable and therefore less likely to cause injury when collided with. Furthermore, the rates of agonistic interactions could be reduced by increasing the space between feeding troughs. Increased rates of agonistic interactions around artificial water sources is however difficult to avoid, but may be decreased through the provision of water in a larger artificial round dam, situated just above ground level as to avoid injury.

When comparing the two intensive populations, the rate of agonistic interactions observed was lower in the Zambian-intensive population compared to the rate observed for the Matetsi-intensive population, even though in the Zambian-intensive population dry feed was provided throughout the year and not only in the dry season. The lower rate of agonistic behaviour could be related to the fact that the Zambian-intensive population remained within the vicinity of feeding troughs and the water trough throughout the day and therefore subordinate individuals were able to utilise dry feed and drink water intermittently reducing the need to compete for these resources at a specified time. This would suggest that housing sable antelope in smaller enclosures could lower increased levels of aggression caused by the provision of dry feed. However overstocking, which is almost always the case in small enclosures, leads to overgrazing. This could in turn increase competition between individuals when utilising dry feed as no other resources are available, increasing rates of agonistic behaviour even more. A viable solution would be the use of small enclosures (50 to 100 ha) in conjunction with an enclosure rotation system, as described previously.

Feeding according to a strict time schedule, twice daily, may have decreased the need to compete for scraps left over in the Zambian-intensive population. Additionally, in the Matetsi-intensive population competition with other game species present in the enclosure could also have resulted in higher levels of competition among individuals of the sable antelope population. It is therefore recommended that if sable antelope are fed, it should occur at the same times every day, and that this intensive management strategy be practiced in the absence of other game species.

Kriek (2005) however forewarns that if the intake rate of antelope cubes is too high, animals may suffer from acidosis which leads to death. Additionally according to Van Hoven (2010)

a sudden change in the diet of wild ungulates, from natural forage to concentrated feed, results in the rapid increase of bacteria such as, *Streptococcus bovis*, in the rumen. This in turn leads to an overproduction of lactic acid and therefore a subsequent drop in the pH of the rumen. The decreased pH levels in the rumen kills off other micro-organisms and more importantly also effect the muscles in the rumen wall, to the extent that contraction and subsequent mixing of food is hampered and can lead to death. Van Hoven (2010) therefore suggests that sudden changes from a natural diet to concentrated feed and vice versa should be avoided. Accordingly, care should be taken not to provide too much antelope cubes, and the introduction and removal of concentrated feeds to or from the diet of sable antelope should be done progressively. The rate of agonistic interactions, directed at sub-adult males at Sandveld Nature Reserve, was relatively low compared to other types of agonistic interactions. However a yearling male (17 months) had to be removed in the Zambian-intensive population with the onset of the study to avoid injury, due to increased levels of aggression directed at the yearling by the territorial male. Wilson and Hirst (1977) also noted aggressive interactions between the territorial male and yearling males at the age of 17 – 19 months and suggests that intra-specific aggression of this nature should be considered as a limiting factor on smaller reserves. It is therefore recommended that yearling males should be removed from the breeding herd before the age of 17 months to avoid injury and mortalities.

Territoriality was less pronounced in the two intensive populations compared to the extensively managed population at Sandveld Nature Reserve. The presence of a territorial male in a neighbouring camp of the Zambian-intensive population could have resulted in slightly increased territoriality compared to the Matetsi-intensive population. Territorial herding is generally quite intense and often contains very aggressive behavioural patterns such as chasing, and may therefore be detrimental for populations in small enclosures, as levels of social stress increases. Therefore sable antelope enclosures containing breeding herds and territorial males should preferably not be adjacent to one another. From observations on social and reproductive behaviour in this study it can be concluded that though intensive management strategies could adversely affect aspects of social behaviour of sable antelope in intensively managed systems, in practice these management strategies definitely succeed in increasing productivity. However, there are a number of other adverse effects of intensive management strategies that have not been discussed in this dissertation and therefore it is recommended that the information provided be used in conjunction with recommendations of other studies to truly determine the viability of intensive wildlife production.

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SUMMARY

Sable antelope (*Hippotragus niger*) are considered to be one of the most profitable wildlife species in southern Africa favoured by photographers and trophy hunters. Intensive wildlife production of sable antelope is practiced to improve reproductive rate which would normally be retarded by deficiencies and mortalities in extensive management systems. Intensive wildlife production refers to the management of wildlife in a fenced area where management practices such as the provision of dietary supplementation and water (throughout the year), the control of parasites and the provision of health care are implemented in order to increase productivity. Up to now studies investigating the effects of captivity on social and reproductive behaviour of sable antelope, have been focused on populations in zoos and conservancies where management practices are centred on conservation. Additionally, no published scientific data is available concerning the effects of intensive management practices used in the wildlife ranching industry of South Africa. The main objective of this study was therefore to determine the effects of management strategies practiced specifically in intensive wildlife production in South Africa, on aspects of social and reproductive behaviour of sable antelope. To determine the effects of different management strategies, the social and reproduction behaviour of three sable antelope populations under different management regimes were investigated. Interactions pertaining to reproductive behaviour, territorial displays, and agonistic behaviour were evaluated and compared between populations. The success of management strategies practiced was evaluated by determining the reproductive rate of each population. To determine why these behavioural patterns were affected, differences in the activity pattern and range use of breeding herds and territorial males of populations were also assessed. Populations in intensively managed systems showed 100% calving and survival rates compared to a 75% survival rate observed for the extensively managed population. Though the implementation of intensive management strategies resulted in increased production, it also resulted in increased rates of agonistic interactions. However, the occurrence of aggressive displays that could result in injury was not abnormally high in the intensively managed populations compared to that observed in the extensively managed population. However, in the two intensive populations agonistic interactions directed at immature individuals were not only more numerous but also contained a larger percentage of aggressive displays. Increased rates of agonistic behaviour were primarily as a result of the provision of dry feed. Other factors that could have influenced the rate of agonistic interactions in both the extensively and intensively managed populations included, the artificial provision of water, activities that result in decreased personal space, the rate of territorial displays and limited resources. Therefore it

can be concluded that though intensive management strategies definitely succeed in increasing productivity, in practice these strategies could adversely affect aspects of social behaviour of sable antelope in intensively managed systems.

Keywords: *agonistic behaviour, aggression, intensive wildlife production, extensive wildlife production, activity pattern, range use, reproductive rate, territorial displays, flehmen behaviour, courtship behaviour*

OPSOMMING

Die swartwitpens (*Hippotragus niger*) word beskou as een van die mees winsgewende wild spesies in Suider-Afrika en is 'n gunsteling onder fotografe en trofeeë jagters. Intensiewe wildboerdery met swartwitpense is gemik op die verbetering van aanteel sukses wat gewoonlik vertraag word deur tekortkominge en vrektes in ekstensiewe stelsels. Intensiewe wildboerdery verwys na die bestuur van wild in 'n omheinde gebied waar bestuurspraktyke soos die voorsiening van byvoeding en water dwarsdeur die jaar, die beheer van parasiete en beter gesondheidsorg, alles gemik is om produktiwiteit te verbeter. Vorige studies wat die effek van aanhouding op die sosiale en reprodktiewe gedrag van swartwitpense nagevors het, was gebaseer op bevolkings in dieretuine waar bestuur gemik was op die bewaring van wild. Daar bestaan ook geen wetenskaplike data wat gepubliseer is rakende die moontlike effek van intensiewe bestuurspraktyke wat toegepas word gedurende wildboerdery in Suid-Afrika nie. Die hoofdoel van die studie was dus om te bepaal wat die moontlike effek van bestuurspraktyke, spesifiek in intensiewe wildboerdery in Suid-Afrika, is op die sosiale en reprodktiewe gedrag van swartwitpense. Om die effek van verskillende bestuurspraktyke te bepaal, is die sosiale en reprodktiewe gedrag van drie swartwitpens bevolkings wat onder verskillende bestuurspraktyke bedryf word, bestudeer. Interaksies aangaande reproduksie, territoriale gedrag en kompetisie was tussen bevolkings vergelyk en geëvalueer. Die sukses van bestuurspraktyke was geëvalueer deur die reproduksie tempo van elke bevolking te bepaal. Om te bepaal waarom gedragpatrone geaffekteer was, is verskille in die aktiwiteitspatroon en benutting van loopgebiede bepaal vir beide teeltroppe asook territoriale bulle. Bevolkings onder intensiewe bestuurstelsels het 100% kalf- en oorlewingsstempos gehad teenoor 'n 75% oorlewingsstempos vir die bevolking wat ekstensief bestuur word. Alhoewel die implementering van intensiewe bestuursstrategieë, verhoogde produksie tot gevolg het, lei dit ook tot verhoogde interaksies wat met kompetisie te make het. Die voorkoms van aggressiewe teenoestellings wat beserings tot gevolg kan hê, was egter nie abnormaal hoog in die bevolkings wat intensief bestuur word in vergeleke met die bevolkings wat ekstensief bestuur word nie. Interaksies in die bevolkings wat intensief bestuur word, wat te make het met kompetisie en gemik was op onvolwasse individue, was egter meer en het 'n groter persentasie aggressiewe teenoestellings getoon. Verhoogde tempos van interaksies wat met kompetisie te make het, kan hoofsaaklik toegeskryf word aan die verskaffing van droë voer. Ander faktore wat die tempo van interaksies in beide bevolkings wat intensief en ekstensief bestuur word, wat met kompetisie te make het, kon *beïnvloed* het, sluit in: die verskaffing van water; aktiwiteite wat lei tot nouer kontak tussen individue; die tempo van territoriale teenoestellings asook beperkte hulpbronne. Die

gevolgtrekking kan dus gemaak word dat, alhoewel intensiewe bestuurs strategieë wel daarin slaag om verhoogde produksie te verseker, dit moontlik in die praktyk newe effekte op sosiale gedrag van swartwitpense onder intensiewe bestuurs stelsels tot gevolg kan hê.

Sleutelwoorde: *kompetisie, aggressie, intensiewe wildboerdery, ekstensiewe wildboerdery, aktiwiteitspatroon, benutting van loopgebiede, reprodktiewe tempo, territoriale tentoonstellings, flehmen reaksie, hofmakery*