The role of territoriality in the mating system of the springbok *Antidorcas marsupialis* (Zimmerman 1780)

by

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ABSTRACT

The causes and consequences of territoriality were examined in the springbok *Antidorcas marsupialis*. Males retained territories for extended periods, which precluded them from responding to fluctuating ecological conditions as effectively as non-territorial males or females; their home ranges were smaller, they fed less effectively than non-territorial males in the dry season, and their density on the dry riverbeds remained independent of ecological conditions including vegetation biomass, rainfall and the distance from the nearest waterhole.

The social organisation of springbok exposed territorial males to the highest predation risk, whilst males in general risked a higher predation threat than females. This was reflected in both the observed predation and adult survivorship. Cheetahs were the main predator, taking twice as many adult males than females. The association of the two sexes within herds was modified by the agonistic behaviour of territorial males, which was lowest during the rut and highest at the end of the dry season.

Territories were maintained through the year, despite the restricted breeding periods. Territory take-up and loss were related to both prevailing environmental conditions and rutting periods. Most territories were established and abandoned passively. Males which had abandoned a territory generally returned to their former territories. Sometimes males would shift territories in a year, but only if they increased the number of ewes on their territory by doing so. Such long term territory holding probably increases males' chances of retaining their territories over rutting periods, subsequently improving their reproductive success.

Males held resource-based territories on the dry riverbeds and pans, where female numbers were highest. Only territorial males mated with females, though multiple matings by one or more males were common. Ruts were initiated by males and could potentially occur at any time of the year. A number of factors were involved in triggering rutting, though not all ruts led to successful matings, possibly because females were unable to respond. Ruts acted to co-ordinate mating and subsequently lambing periods, the benefits probably being enhanced male mating success at the time of the rut and an increase in offspring survival associated with the timing and synchrony of births.

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Chapter 1

Introduction

THEORETICAL BASIS

Originally this thesis was conceived due to our inadequate understanding, both from a theoretical and practical standpoint, of the breeding behaviour of the springbok *Antidorcas marsupialis.* This is surprising considering both its commercial importance, commonness and the ease with which it may be studied in some areas. Four major theoretical considerations form the basis of this thesis.

1. The mating system of the springbok; resource-defence polygyny

Some male springbok are territorial (Jackson *et al.* 1993) and it is thought that their breeding system is one of resource defence polygyny (Emlen & Oring 1977); by defending those resources most attractive to females, males will be able to monopolise any females within their defended area and thus increase their reproductive success. Extensive studies of this type of breeding system, taking into account our current understanding of animal mating systems, have been confined amongst the ungulates to the puku (Rosser 1987, Balmford *et al.* 1992), pronghorn antelope (Byers & Kitchen 1988, Byers *et al.* 1994) and red deer (Carranza *et al.* 1990). The impala (Murray 1981, 1982*ab,* Jarman, M. 1979, Jarman & Jarman 1973*ab*) red lechwe (Williamson 1990, 1992, 1994) blue wildebeest (Estes 1969), waterbuck (Spinage 1982) and Grevy's zebra (Ginsberg 1988) have been extensively studied, though not with such a full consideration of the theoretical principles underlying their breeding system.

Instead, research into the breeding behaviour of ungulates has concentrated on the other three systems observed; monogamy, lek breeding and female-defence polygyny (Emlen & Oring 1977). Both lek breeding and monogamy raise interesting evolutionary questions (Gosling 1986, Clutton-Brock *et al.* 1993), which are not presented by resource-defence or female-defence polygyny. The causes and consequences of monogamy have recently been investigated for the dik-dik (Brotherton 1994). All lekking species have lately received considerable attention; fallow deer (Apollonio *et al.* 1989, 1990, Clutton-Brock *et al.* 1988, 1989, Festa-Bianchet *et al.* 1990) topi (Gosling *et al.* 1987, Gosling & Petrie 1990), Uganda kob (Balmford 1990, 1992, Deutsch 1992, 1994), Kafue lechwe (Schuster 1976, Nefdt 1992) and white-eared kob (Fryxell 1987*b*). Detailed accounts of female-defence polygyny are given for the harem holding strategy of red deer (Clutton-Brock *et al.* 1982) and the 'follower' behaviour of the greater kudu (Owen-Smith 1984), reindeer (Espmark 1964) and bison (Komers *et al.* 1992), in which males will closely guard a series of oestrous females in a given season.

Thus there is a need to investigate resource-defence polygyny more comprehensively amongst ungulates, to parallel the advances which have been made in our understanding of their other mating systems. This is particularly important as it becomes apparent that mating systems may be flexible within a species (Byers & Kitchen 1988, Gosling 1986, 1991, Thirgood 1990, Alfarez *et al.* 1990), such that questions addressing how different systems evolved and how variation in the mating system of a species may occur can be addressed more comprehensively.

2. *Breeding synchrony*

Breeding synchrony may be defined as a phenomenon caused by biological interactions operating to produce a tighter clustering of breeding events than would have been imposed by environmental synchrony alone (Ims 1990). As springbok often produce a disproportionate number of lambs over a limited period (see account below) their breeding biology does show some degree of synchronisation. This is certainly the opinion of Skinner *et al.* (1992). Our understanding of reproductive synchrony is still limited (reviewed in Ims 1990). However it is becoming increasingly apparent that such synchrony is far more complicated than was previously assumed, and can be controlled by a combination of environmental, internal or social cues (Ims 1990).

The springbok is the most vocal of the gazelles (Walther *et al.* 1983), such that any tendency of the females to begin cycling could be modified by a social stimulus; the behaviour of the breeding males. Certainly it is well known that increased stimulation by males may promote oestrous activity amongst domestic stock (Watson & Radford 1960, Oldham *et al.* 1978, Ott *et al.* 1980); the 'ram effect'. However evidence that male behaviour may affect female receptivity in wild ungulates is very limited. McComb (1987) showed that the vocalisations of red deer stags could advance the time of oestrus in females.

3. *The costs of resource-defence polygyny to males*

In species other than the springbok it has been established that territory holding greatly enhances the breeding success of males (Jarman & Jarman 1973*b*, Kitchen 1974, Floody & Arnold 1975, Wirtz 1981, Murray 1982, Baharav 1983*a*, Miura 1984, Thirgood 1990, Williamson 1994) and may even be a pre-requisite for males to breed at all. However whilst the ultimate goal of holding a territory is presumably to enhance access to oestrous females, this does not mean that it can be achieved without imposing costs on these males, related directly to their territorial status. Certainly the males of many polygynous species lose weight rapidly during the breeding season and must enter subsequent periods of nutritional deprivation in poor condition (Clutton-Brock 1991).

Whilst such weight losses relate directly to the breeding period itself, species such as the springbok may maintain their territories throughout the year (David 1978*b*, Jackson *et al.* 1993). Males presumably experience extra costs through their extended territory tenure. Some of these costs have been considered by Jackson *et al.* (1993) and relate to two principle factors. First, the disadvantage of spending more time alone, a characteristic of territorial individuals (Estes 1969, Leuthold 1978*a*, Rosser 1992). This may lead to both increased predation threat (Schaller 1972, Hornocker 1970, Mills 1984, Fitzgibbon 1990) and decreased foraging efficiency (Dehn 1990).

Second, the handicap of remaining bound to a specific area, the territory and its immediate vicinity. Springbok are highly mobile, capable of moving large distances in search of food or water, responding rapidly to rainfall and the subsequent growth of herbaceous plants (Mills & Retief 1984*b*, Williamson 1985, Knight *et al.* 1988). The ability of the population to respond rapidly to changing environmental conditions is contrasted by the constraints territorial males impose upon themselves by being territorial.

4. Territorial dynamics and territory maintenance

A study of the territorial behaviour of springbok would be incomplete without considering the mechanisms by which males establish and maintain their territories. Territory dynamics amongst ungulates are poorly studied or understood and have raised more questions than answers (Gosling 1986, Rosser 1987). This thesis therefore considers territory establishment and turnover for the springbok. It also considers those mechanisms whereby males are able to maintain their territorial status. These include both the agonistic behaviour of territorial males as well as their methods of territory demarcation.

THE STUDY SPECIES

The springbok is a medium-sized antelope, indigenous to the western arid zone of southern Africa (Figure 1). Its distribution extends from the south-western Cape, through from the Karoo and the Orange Free State, to the Kalahari and Namib and up into southern Angola (Skinner & Smithers 1990). Its preferred habitat is open grassland (Bigalke 1972, Mason 1976) together with pans and dry riverbeds (Bigalke 1972, Bigalke *et al.* 1975, Williamson 1985). Springbok show an aversion towards rocky and mountainous areas within their range (Skinner & Smithers 1990). Though roaming freely in many of these areas, it is also kept in enclosed paddocks by farmers in both South Africa and Namibia. Here it is exploited for commercial use (Skinner 1989), because of its excellent venison (Skinner *et al.* 1971), low management requirements, ability to coexist with domestic stock (Davies, Botha & Skinner 1986, Davies & Skinner 1986*a*) and high productivity (Skinner & van Zyl 1970*a*).

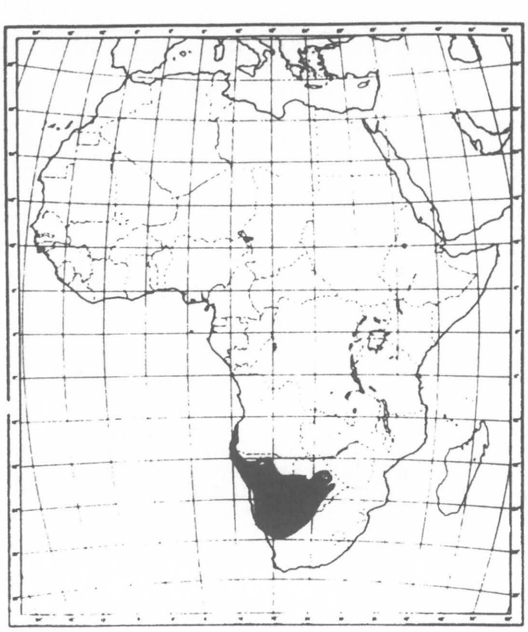

Figure 1 The distribution of springbok in southern Africa

Springbok are gregarious by nature and may be found in large herds, most famously so during their mass treks (Child & le Riche 1969, Skinner 1993). However some males are territorial (Williamson 1985) and rams may hold their territories at all times of the year (Mason 1976, David 1978*b*). Whilst territorial males have been observed to mate this has not been recorded for non-territorial males (Williamson 1985, Skinner *et al.* 1986, Skinner & Smithers 1990), though no detailed records have ever been collected. The appearance of territorial males does not differ greatly from that of non-territorial rams, the only significant difference recorded being in neck thickness (Skinner *et al.* 1995). In the southern Kalahari males weigh approximately 42 kg and stand 86 cm at the shoulder (Skinner & Smithers 1990). There is however considerable variation in the morphometrics of individuals from different regions, which is largely attributable to differences in nutrition, with little evidence for a genetic basis (Robinson 1975). Adult females are smaller weighing 35 kg, with a shoulder height of 71 cm (Skinner & Smithers 1990). The maximum recorded ages of springbok, measured in the Kimberley area, are nine and a half years for a ewe and seven and a half years for a ram (Liversidge pers comm.[*]). Both sexes are horned, though the horns of males are markedly thicker than those of females.

The sexual cycle of the springbok ram is not as pronounced as that in seasonally breeding species (Skinner *et al.* 1974). Whilst males may show decreased spermatogenesis at certain times of the year (Skinner & Van Zyl 1970*b*), they remain reproductively active at all times (Skinner *et al.* 1974). Similarly ewes may conceive at any time of the year. Gestation periods have been estimated at 167 days (Brand 1963), 24 weeks (Van Zyl & Skinner 1970) and 174-180 days (Liversidge & de Jager 1984).

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[*] Dr. R. Liversidge, 92 Central Road, Kimberley, 8301

Females sometimes show a post-partum oestrus 9-15 days after parturition (Liversidge & de Jager 1984). The oestrous cycle lasts for 14-17 days (Liversidge & de Jager 1984).

Ewes normally give birth to a single lamb (Skinner *et al.* 1971), though rare records of twins have been made (Brand 1963). New-born lambs are hidden for their first day or two of life (Bigalke 1972). There is a tendency for females with young to form their own nursery herds, or crèches (Bigalke 1972). Lambs are weaned after a period of approximately four months (Liversidge & de Jager 1984) and lambing rates usually reach 100 %, though this may increase when large numbers of lambs are cropped (Skinner & van Zyl 1970*a*) or when favourable conditions allow females to conceive twice in a year (Bigalke *et al.* 1975). However springbok generally lamb once a year, as indicated by the single annual parturition peak observed in many areas, showing that springbok may synchronise their breeding efforts (Bigalke 1970).

Female springbok are capable of conceiving at 28 weeks of age (Skinner & van Zyl 1970*a*), though many probably do not conceive until about one year old (Liversidge & de Jager 1984), dependent on the underlying environmental conditions. At 28 weeks of age females have reached 83 % of mature weight, whilst males will only have reached 57 % by the same age and 75 % by 64 weeks (Skinner *et al.* 1971). Males only reach sexual maturity when 16 months old, physical maturity not being achieved until approximately 2½ years old. The adult sex ratio, in common with other ungulates, is female biased both in free-ranging (Bigalke 1970, David 1978*a*) and farmed (Crowe & Liversidge 1977) populations. However, Penzhorn (1974) recorded a male biased adult sex ratio in a shot sample and Skinner *et al.* (1971) recorded an even adult sex ratio.

Springbok are mixed feeders, predominantly grazing after rainfall, but tending to browse more as the dry season progresses. They will drink when water is available to them, but survive in water-free areas such as the central Kalahari by supplementing their diet with water-rich roots and tubers (Williamson 1985).

The Kalahari Gemsbok National Park was originally chosen as a study site by J.D. Skinner and the present study, making use of individuals which had been immobilised by him, has concentrated on the same area and individual springbok. The open habitat with which springbok are associated in the Park makes them an ideal study animal; they are very conspicuous and easily followed. Furthermore, the Park supports a natural predator population not found in the farming areas. The disadvantages farm areas have over the Kalahari Gemsbok National Park site are the restrictions imposed by both hunting and fences on animals. These increase the springbok's flight distance considerably and severely restrict seasonal movement between areas.

In this thesis I use the springbok as a suitable study species to examine resource-defence polygyny as a mating system amongst ungulates. I examine the benefit to individuals of such a mating system as well as trying to evaluate both the cause and function of the springbok rut in the southern Kalahari. I also try and establish why males should maintain year round territories when their breeding efforts are restricted to short rutting periods. Finally I explore the potential costs to males in becoming territorial relative to non-territorial males, together with the ways in which these rams advertise and maintain their territorial presence. Also included with this thesis are the two scientific papers which have so far emanated in conjunction with this study.

PRINCIPLE AIMS OF THE STUDY

To summarise, the principle aims of this thesis focus on the following questions:

1. Are springbok resource-defence polygynists, and if so how does their behaviour relate to similar species ?

2. What are the benefits to males of holding territories, relative to non-territorial males ?

3. What factors are important in determining territory take-up and turnover ?

4. How do males maintain their territories ?

5. Do the demography and daily maintenance activities of territorial males differ from those of non-territorial males and females, and if so are these limiting ?
6. Does the alternative behaviour of territorial males to that of non-territorial males and females represent a potential cost of territoriality ?
7. What are the key factors important in synchronising the timing of breeding ?

Chapter 2

Study area

LOCATION

The Kalahari is an ancient depositional environment with a complex history. The Mega Kalahari sand sea is the largest on earth, covering 2 500 000 km^2, stretching from the Congo basin through to northern South Africa (Thomas & Shaw 1993). The more poorly defined Kalahari desert forms the area of surface exposure of these sands. This exposed area extends through most of Botswana, north-east Namibia, much of Angola and Zambia, north-west South Africa and even into parts of Zimbabwe (Parris 1976). It represents the largest exposed sand area in the world (Eloff 1984) covering 1 630 000km^2. This forms part of the South West Arid biome of Africa (Eloff 1984), to which the springbok is endemic. The Kalahari desert is divided by the Bakalahari rise which extends north-westerly from Kanye to Kuli in Botswana (Parris 1976, Knight 1991) at an elevation of 1100-1270 m. This determines the drainage pattern of the region. To the north-east of the rise the land form gradually dips to the Makadikgadi depression, elevation 880 m, (Parris 1976) in the central Kalahari. This is drained by the northwards running fossil Okwa riverbed, which is now made up of a series of sandy depressions (Knight 1991). To the south-west of the rise drainage is via the four predominantly dry riverbeds of the Nossob, Auob, Molopo and Kuruman. These used to drain southwards towards the Orange river (Knight 1991). However, for at least the past 1000 years the Molopo, into which the other three rivers flowed, has been blocked by dunes near the Orange river and today all the rivers in the Kalahari are usually dry (Mills 1977). During the present study none of these rivers flowed. The Auob last flowed in 1973 and 1974 and the Nossob in 1963 (Mills 1977, Mills & Retief 1984*b*), whilst both the Auob and Nossob flowed simultaneously in 1934 (van Wyk & le Riche 1984).

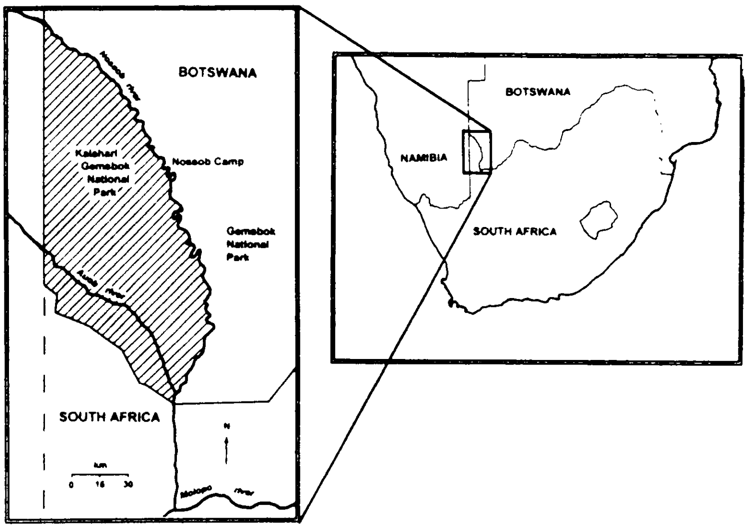

Figure 2 Southern Africa, showing the location of the Kalahari Gemsbok National Park.

Together the Kalahari Gemsbok National Park (KGNP, Figure 2) of South Africa and Gemsbok National Park (GNP) of Botswana form the core of the southern Kalahari (Mills 1990). The KGNP covers an area of 9 591km^2 and was proclaimed a national park in 1931 (van Wyk & le Riche 1984). The western boundary of the Park forms the border between South Africa and Namibia. Access between the two countries is restricted by an electrified game fence. The southern boundary between Mata Mata and Twee Rivieren is also demarcated by a game fence which separates it from the adjacent Mier settlement. The Nossob riverbed forms the northern and eastern boundary and is unfenced. The riverbed also defines the international boundary between South Africa and Botswana and consequently the borders of the KGNP and GNP. In 1938 a 40 km wide strip of land adjacent to the Nossob, encompassing 6 035km^2 of land in Botswana, was proclaimed a nature reserve (van Wyk & le Riche 1984). The area was elevated to National Park status and increased to its present size of 24 800km^2 in 1972 (Mills 1977). Together with the adjoining Botswanan Mabuasehube Game Reserve and Wildlife Management Areas the total conservation area covers 80 000 km^2, one of the largest in the world (Knight 1991). The present study was conducted in the vicinity of Nossob Camp in the KGNP, particularly the riverbed between Kwang and Kaspersdraai waterholes (Figure 3).

CLIMATE

The southern Kalahari is a semi-arid region (van Rooyen 1984, Mills 1990, Knight 1991) receiving low, irregular and often localised rainfall. The KGNP falls between the 200 mm and 250 mm isohyets (Mills & Retief 1984*a*), with rainfall increasing to

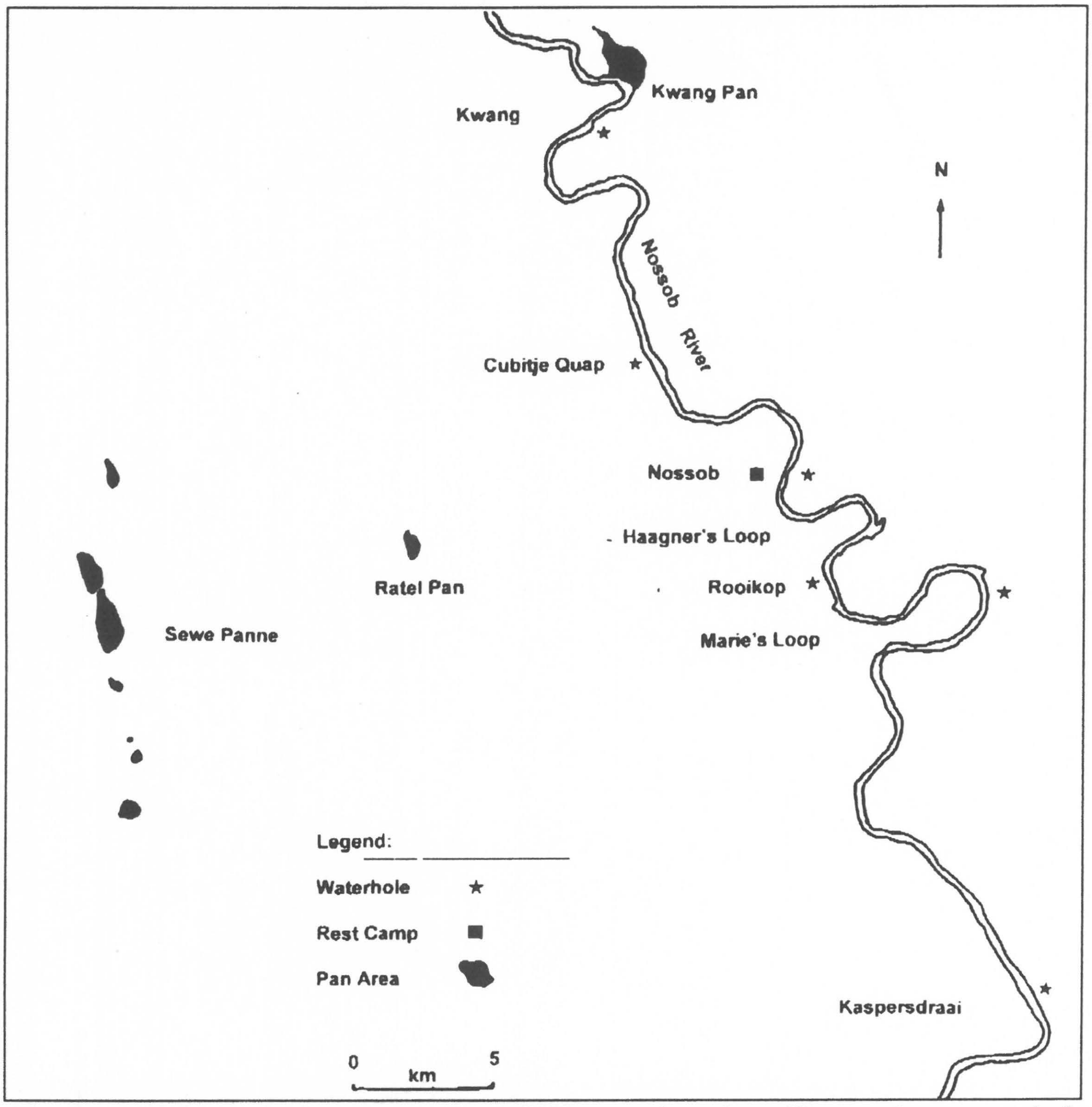

Figure 3 The core study area in the KGNP extending from Kaspersdraai waterhole to Kwang pan. Most behavioural observations were made on Haagner's and Marie's loops.

the north-east (Parris 1976, Knight 1991). Precipitation is often as short duration, high intensity thundershowers (Parris 1984). The majority of rain falls between November and April (van Rooyen 1984) with 70% or more falling between January and April (Mills 1981). Evaporation far exceeds precipitation in the area and has been estimated as more than 3 000 mm per annum (Parris 1976, van Rooyen 1984). Free standing water is only found temporarily on pans and along the fossil riverbeds following exceptional rain.

During the summer months daytime temperature normally reaches 30-40°C, falling to 10-20°C. Winter temperatures reach a maximum of approximately 20°C, declining to 5°C or less at night (Mills 1990). Frost is common in the winter. Winds are frequent and most violent from August until the end of the dry season (Parris 1984), coming most regularly from the north-west.

HABITAT TYPES

The southern Kalahari can be divided into a number of different habitat and microhabitat types. Three broad habitat types were recognised as being pertinent to the present study. These are the dunes, calcareous pans and fossil riverbeds. Differences between these habitat types are based on their geomorphology and consequently on the plant and animal communities they support.

The dunes cover 95% of the southern Kalahari (Werger 1978) and are aeolian in origin (Knight 1991). They cover most solid geological formations present in the area. Today most dunes are stabilised by the vegetation growing on them. The majority are linear, with a north-west to south-east orientation though some are transverse, particularly further from the fossil riverbeds (Malherbe 1984, van Rooyen 1984). Virtually all rainfall is immediately absorbed by the dunes and retained by the sand as capillary water (Parris 1984). These soils are infertile, being low in available phosphate, as well as having relatively low levels of the exchangeable cations magnesium and potassium. Cattle introduced into the area suffered from bovine parabotulism as a result of eating bones because of a phosphate deficiency (van Rooyen 1984). The vegetation of the dunes is described as an open to very open tree or shrub savannah (Werger 1978). The tree *Boscia albitrunca* is common in the dune habitat, together with smaller *Acacia erioloba* and *Acacia haematoxylon*, the shrubs *Acacia mellifera* and *Grewia flava* and a herb layer of tall perennial grasses including *Eragrostis lehmanniana*, *Asthenatherum glaucum*, *Aristidia meridionalis*, *Stipogrostis obtusa*, *Stipogrostis ciliata* and the annual *Schmidtia kalahariensis* (Leistner 1967, Mills 1981, Knight 1991).

The calcareous pans are scattered unevenly over the dune habitat (Parris 1984), though the main concentration lies in the Kokong-Tshane area of Botswana. Here their density reaches up to one per 30 km^2. The pans form shallow sub-circular depressions in the dunes and may reach five kilometres across and 10-15 m deep (Lancaster 1974). These pans were initially formed by deflation in more arid times as indicated by the material forming adjacent crescent dunes. Following their formation these depressions were occupied by shallow lakes, as indicated by lacustrine clays, carbonates and marls in the pan depressions (Lancaster 1974). Pan soils are rich in minerals, particularly sodium, potassium and magnesium (Werger 1978) and have a pH value of 7-10 (van Rooyen 1984). Important features of the pans to antelope are their salt licks, seasonal waterholes and grasses of significantly higher nutritional quality than those associated with the dunes (Parris 1984). A number of grasses, trees and shrubs are associated with the pans. These include *Acacia mellifera*, *Acacia newbrownii*, *Rhighozum trichotomum*, the commonest grasses being *Cenchrus ciliaris*, *Cynodon dactylon*, and *Setaria* spp. with *Eragrostis truncata*, *Panicium coloratum* and *Sporobulus* spp. associated with the pan floors (Parris 1976).

Kwang pan, unlike the majority of pans, is of alluvial origin. It was formed because a tributary could not transfer its sand load quickly enough to the Nossob river, which it consequently dumped, damming the tributary against the higher base level of the Nossob river (Malherbe 1984).

The most recent soils of the fossil riverbeds have been dated to 12-19 000 years before present. Prior to this the rivers actively eroded the land and carried their sediment loads towards the Orange river. The Nossob was at one time a mature river as indicated by the meanders at Kwang pan as well as Marie's and Haagner's loops. The rivers eroded into the underlying bedrocks, but the Nossob riverbed was filled between Unions End and Kaspersdraai when it did not have sufficient water to flow further and deposited its sand load (Malherbe 1984). These alluvial deposits have produced a compact and poorly drained soil rich in nutrients (Werger 1978, Parris 1984). Available phosphates are relatively low, but higher than in the adjacent dune sands (van Rooyen 1984). The soils are not as mineralised or alkaline (pH 7-8) as the calcareous pans. As with the pans the vegetation community is different to that of the dunes and generally more nutritious (Parris 1984). Common vegetation on the riverbeds is described in some detail in chapter three. The Nossob riverbed may reach one kilometre wide in the north of the KGNP, narrowing to 100-500 m in the south. Together the calcareous pans and fossil riverbeds occupy less than five percent of the southern Kalahari.

Another important feature of the KGNP is the presence of perennial water. This is available from a series of wind and solar pumps in both the Auob and Nossob riverbeds as well as several points in the surrounding dunes. Along the riverbeds pumps are situated at intervals of 4-24 km. Some of this water is highly mineralised and these waterholes are utilised both as salt licks and drinking points (Knight *et al.* 1988).

FAUNA

Seven species of antelope are indigenous to the southern Kalahari. Of these the steenbok, eland and grey duiker are predominantly found in dune habitat. Springbok, gemsbok, blue wildebeest and red hartebeest use the fossil riverbeds to a varying degree at different times of the year (Mills & Retief 1984*b*). Several species of carnivore inhabit the area. These include the black-backed jackal, lion, leopard, cheetah, caracal, spotted hyaena and brown hyaena. Wild dogs are rare visitors to the area and were not seen personally during the course of the study.

Chapter 3

Materials and methods

The general methodology which has been used throughout the study is detailed in this chapter. These techniques are therefore pertinent to various chapters of the thesis, whilst more specific methods are described in detail at the start of the relevant chapters. Basic methods covered the collection of three broad data types; environmental variables, population censussing and animal behaviour. Fieldwork was conducted from May 1990 until August 1993.

ENVIRONMENTAL VARIABLES

1. Temperature

Daily maximum and minimum temperatures records were noted at Nossob camp's weather station. The station was situated within the camp, slightly elevated from the riverbed (less than 10 m), and temperatures were assumed to represent a good estimate of riverbed temperature; the difference between the riverbed and the camp's weather station was normally less than 0.5°C. These records were used to determine mean monthly temperatures. They were also taken when considering behavioural activity which may have been related to temperature. Temperatures were noted to the nearest half degree centigrade.

Temperature differences between the riverbed and the surrounding dunes were also monitored. These were recorded using max-min mercury thermometers which were placed on the south facing (shade side) of trees in both the riverbed and on the crest of a dune bordering the riverbed. Readings were taken every morning of both maximum and minimum temperatures for the preceding day. The thermometers were calibrated against each other to ensure that any temperature differences between them were not due to any inherent bias.

2. Precipitation

Precipitation was measured using conical rain gauges. These were positioned in the tops of dead trees to prevent damage by lions or spotted hyaenas. They were checked directly after any rain had fallen to minimise any losses due to evaporation. Four rain gauges were set up over a 17 km stretch of riverbed, incorporating the central study area, and data were supplemented by measurements taken from the rain gauge at Nossob Camp.

3. Vegetation biomass

Vegetation biomass was measured on a monthly basis. The area of riverbed in which biomass was monitored was half way along Haägner's loop, in which both annual and perennial grasses and herbs were common. Dominant grasses included *Chloris virgata, Eragrostis porosa, Setaria verticulata and Tragus racemosus. Schmiditia kalahariensis*, predominant in the surrounding dunes, also fringed the borders of the riverbed in the sample area. Other common plants included the herbs *Amaranthus thunbergii*, *Cucumis africanus*, *Enneapogon brachystachyus*, *Heliotropium lineare* and *Tribulis terrestris* and the dwarf shrub *Lebekia linearfolia.* Larger shrubs (*e.g. Acacia mellifera*, *Galenia africana*, *Grewia flava*, *Rhigozum trichotomum*) found in other areas of the riverbed were absent from the sampling area.

As grasses and herbs predominated in the sampling area a disc pasture meter was used to provide an estimate of vegetation biomass (Bransby & Tainton 1977, Bransby *et al.* 1977, Dankwerts & Trollop 1980). The technique involves measuring the height to which vegetation is crushed under a sliding disc, which is allowed to drop down a rod from a fixed height. The mean crush height is then fed into a regression plot of disc height versus plant mass to obtain an estimate of the biomass. Any records in which the only tree present on the riverbed, *Acacia erioloba*, was recorded were omitted from the final regression analysis. The disc pasture meter was calibrated each month for the study area. Four complete transects were made perpendicularly across the riverbed with a reading being taken every twenty paces. To maintain a straight line a point was fixed on the far side of the riverbed towards which I would walk. No transect was ever terminated part way across the river due to the uneven distribution of vegetation across the riverbed. Records were made on a monthly basis and always on the same stretch of riverbed. In this way any change in the biomass could be attributed to a seasonal variation and not a random variation from sampling different areas of the riverbed in different months.

POPULATION CENSUSSING

1. Population density

The population census began with the censussing of the springbok population in the immediate vicinity of the study area, covering some 20 km of riverbed. Notes were taken of the size and structure of herds on a daily basis. It soon became apparent however that I was recounting the same individuals (*e.g.* animals with recognisable horn abnormalities), and it was decided to extend the survey over a much larger area of the riverbed to increase the sample size and the independence of results. Two days were set aside each month for this purpose, one to count north along the river from Nossob Camp, and the other to count south. In this way individuals were counted at most once per month. Counts were made over a fixed distance from Dikbaardskolk to six kilometres north of Bedinkt waterhole, a total distance of 129 km. This was the total distance which could be traversed in the two day count during the peak population density on the riverbed, recorded in April 1991.

As animals tended to move away from the riverbed and into the surrounding dune areas overnight in the cooler months, observations at this time of year began a few hours after sunrise to allow animals to move back on to the river for the day. All counts covered the width of the riverbed and an area 50 m to its sides, which represented the area where males were seen to show territorial behaviour. Due to the good visibility afforded by the open habitat it was considered that all individuals could easily be counted; in more enclosed areas the incidence of sighting different groups varies with observer distance (Underwood 1982*b*). In order to make a comparison between different months results are presented in a standardised format (*e.g.* as springbok per km riverbed, percentage of total count *etc.*).

The population was also censused on pan areas. These included both Kwang pan, adjoining the riverbed, and the Seven Pans (Sewe Panne) complex in the dune habitat. The number of springbok on Kwang pan was recorded on several occasions over the course of a month but never more than once in a single day. Counts were made at random times of the day. Knowing the area of the pan a mean springbok density on the pan could be calculated for different months.

These data were supplemented by a monthly count of springbok numbers at the Seven Pans complex. The number of springbok present on these pans was counted and their density calculated. These pans were isolated 25 km from the riverbed, but clustered together in the dunes. In addition the number of springbok present was monitored at Ratel pan situated on the dune road approximately half way to Seven Pans from Nossob, and at a single pan 3.7 km NNE of the Seven Pans complex. Thus a total of nine pans were monitored in the dunes.

The trip to and from the pans allowed a count to be made of springbok in the dune areas. A strip count was made to the same approximate width as the riverbed (300 m). A total distance of 40 km was covered in this way. From this a monthly estimate of the density of springbok in the dunes could be made for comparison with that on the riverbed and pans.

2. *Springbok age and sex classes*

All observations during the course of the riverbed count were made from a vehicle with the help of a pair of 10x50 binoculars. Care was taken not to disturb springbok whilst driving and most animals could be approached to within 30 m before they started to move off. Animals were considered to be part of the same herd if they were within 100 m of one another. Notes were taken on the number of animals in a herd, their sexes and ages.

Age structure was classified according to horn structure, with five classes being recognised in accordance with Rautenbach's criteria of horn development (Rautenbach 1971). This discriminated between new-born lambs up to two months of age, two classes of juveniles, sub-adults and adults over 15.5 months old. Lambs were considered to be those animals whose hornbuds could not yet be clearly seen. These animals were not sexed as it is a very time consuming procedure due to the relatively small phenotypic differences between the sexes at this age. By the time the lambs reached two months old sexing became much easier as the horn buds emerged. Thus young were first sexed at this age in the knowledge that the horns of the males erupt slightly before those of the females and are slightly thicker. The penis sheath of the rams is another obvious sexing feature and as the young continue to grow so does the dimorphism in horn structure and body size, making sexing of individuals less difficult in older animals. It was important to establish the sex ratio as early as possible after birth to compare it to that of the adult population.

Three subsets of adult springbok were recognised; territorial males, non-territorial males and females. Males were considered to be territorial if they were alone on the riverbed; territorial males spent much of their time alone (see chapter seven). Herds of springbok in the riverbed were also considered to contain at least one territorial ram (if a ram was present). If more than one ram in a herd was seen to be behaving in a manner associated with territorial males they were also classified as being of territorial status. These behavioural patterns included sexual and aggressive activity, as well as the linked urination-defecation sequence and horn rubbing which are all activities performed predominantly by territorial rams, in both the springbok as well as other antelope species (Walther 1978*a*, pers. obs.).

3. Distance from water

Permanent water is found in the KGNP in the form of water troughs supplied by windpumps. These are spaced along the course of the riverbeds as well as in the surrounding dune system. Note was made of the distance between each windpump using the vehicle's odometer. Distances were measured to the nearest 100 m. The distances of herds from water were also recorded. If a herd extended over several hundred metres, the midpoint was taken as the average group distance from water. In this way the distance of animals from the nearest waterhole could be calculated. Animals were classed as either being 1 km or less from, or at a distance of greater than 1 km from water.

4. *Identification of individuals*

Almost all territorial and some of the non-territorial rams watched were identifiable individuals to whom radio transmitters had been attached by means of a neck collar. To fit radio collars animals first had to be immobilised. This was done in conjunction with J.D.Skinner's work (Skinner *et al.* 1995), which necessitated anaethetising adult males. The immobilisation darts used contained 1 mg etorphine HCl (M99®, R&C Pharmaceuticals) and 10 mg xylazine HCl (Rompun®, Bayer). The antidote was composed of diprenorphine HCl (M50-50®, R&C Pharmaceuticals) and doxapram HCl (Dopram-V®, R&C Pharmaceuticals). Animals were darted at a distance of 30 m using a 'Telinject'™ variable power remote applicator.

Some territorial and non-territorial rams were identified by ear tags. These were applied to either the left or right or both ears of animals. A number of different colours of ear tag were used. Each tagged animal was uniquely identifiable by its combination of colour tags. Blue, green, yellow and orange were all found to be good colours. Problems were found with white tags which discoloured to cream, making them difficult to distinguish from yellow tags at a distance, and red tags which were hard to tell apart from orange tags. The first rams were immobilised and fitted with radio collars in June 1990. Radio collars consisted of a Telonics or AVM radio transmitter, powered by a 3.6 v lithium battery. These were embedded in dental acrylic, whilst the collar itself was of industrial conveyor-belting, which was riveted in place. Radio life was approximately three years. No ewes were fitted with radio collars or ear tags for both logistical and financial reasons.

5. *Location of known individuals*

All sightings of known individuals were recorded. These included both radio-collared and ear-tagged animals. Consequently re-sightings were restricted to rams. Where possible individuals were actively located by means of radiotelemetry, using a Yaesu transceiver together with a whip and Yagi four element antennae. The position of an individual was recorded either as a bearing and distance from a fixed point or as a radio bearing from two fixed points. The former was the most common form of relocation. This had the advantage of being a visual record and further information could also be collected on the status of the individual (territorial or non-territorial), whether the animal was on or off its territory, the time of day and the number of adult male and female springbok in its company. Markers were fixed at 500 m intervals in the central study area along the border of the riverbed. These consisted of steel posts driven into the ground. In the peripheral areas 'markers' were taken as distances in 500 m intervals on the vehicles odometer to the nearest waterhole along the riverbed. Additionally geographic beacons were used as marker points. An attempt was made to relocate individuals once a day and at different times of the day. From May 1993 until the end of the period of fieldwork additional information on the habitat-type (riverbed or dune) on which an individual was resighted was also made. From this period onwards both diurnal and nocturnal locations were also recorded.

Further to this tracking of individuals, records were also kept of animals which were resighted during the course of other work. These included ear-tagged individuals and those whose radio-transmitters had failed.

ANIMAL BEHAVIOUR

Behaviour was monitored on a daily basis, whilst records were combined for a given month to examine monthly variation in their performance. In instances where comparisons were made between different seasons, data were combined for all months in that season. All observations were made from a stationary vehicle at distances of less than 300 m. An ideal watching distance was considered to be approximately 75 m. The study involved following focal animals for a duration of one hour, the same individual being watched at different times on different days if possible. By carefully co-ordinating the watch times, individuals were never watched more than once at a particular time of the day over the course of a month. Both ewes and non-territorial males were randomly chosen from the population for observation, using random numbers generated by the vehicle's odometer to determine which animal was followed. Observations were made from sunrise to sunset, thus observation periods varied from a maximum of 14 to a minimum of 10 hours per day over the course of the year, as day length varied.

A territory was considered as the area in which a male was consistently dominant over all other males. However males did not necessarily have to express this dominance overtly, such that other males could be tolerated on a territory despite their subordinate status.

Nocturnal activity of territorial males was also recorded towards the end of the study period from April-September 1993. These watches were made over the period of the full moon, when individuals could generally be followed with the use of binoculars. Up to the period of the full moon watches were made from sunset until the middle of the night. After full moon watches were started in the middle of the night and continued until dawn. In doing so full use could be made of the available light, which was restricted by the times of moonrise and moonset. When an animal was lost to sight a spotlight was used to relocate the individual. A single animal was watched for the duration of these observation periods because of the difficulties in locating further individuals at night.

Different categories of behaviour were recorded using instantaneous and continuous sampling techniques (see Martin & Bateson 1986). Those behaviours of a more general nature (*e.g.* grazing, ruminating) as well as less frequently observed activities (*e.g.* linked urination-defecation) were recorded by instantaneous sampling at three minute intervals over the course of a one hour observational period. Rare but important actions such as sexual and aggressive interactions were also continuously sampled. Thus every time a particular behaviour was observed or performed to a different individual, such as a sexual advance, this was noted.

During the first year of study territorial rams, non-territorial rams and ewes were all followed. These observations were made from June 1990 to April 1991. Over this period 1024 h of observations were completed, 456 h on territorial rams, 304 h on non-territorial rams and 264 h on ewes. These data were used to compare the behaviour of territorial males with that of non-territorial males and females. The data on territorial males were subsequently extended over the course of the next two years to provide information on the behaviour of territorial male springbok from June 1990 until July 1993. A total of 1134 h of observations on territorial males were made outside rutting periods, of which 85 h were nocturnal observations. A further 243 h of observations were made during the rut. In all 35 marked males were watched outside rutting periods, with a further 30 h of information being collected from unmarked territorial males. These data were supplemented during the rut by watches on an additional 12 identified individuals and 37 h of information collected from unmarked males. The behaviour of 12 marked non-territorial males was recorded, of whom nine were also territorial at some stage during the course of the study. In addition 130 h of observations were made of unmarked non-territorial males. Behaviour was divided into the following categories for the purpose of the study:

1. Sexual behaviour

Neck Stretch: in which a male springbok will approach a ewe with head held high and neck stretched forward. Ears are directed forward with the tail often held vertically and the approach is accompanied by a series of nasal grunts. The approach may either be at a walk or a gambolling trot.

Urine sniffing: the act in which an animal sniffs a ewe's urine either by immersing it's nose in the stream of urine as a female urinates or by sniffing the ground on which a female has just urinated.

Vulva sniffing: in which the male's nostrils make contact with the ewes vulva.

Flehmen: The act in which the upper lip is drawn up and the shape of the nasal passages modified in order to increase gaseous flow over the vomeronasal organ in order to assess the state of a ewe's urine.

Together the above activities have been categorised as *primary* (investigatory*) sexual activities.* This was done in order to prevent overcomplicating the results, which would otherwise have included too many similar variables.

Laufschlag: The act in which a ram will approach a ewe with the front legs held straight and moved in a stiff fashion. An animal may also stand still whilst laufschlag is performed, in which case the front legs are again held stiffly and raised in such a manner.

Mount: in which a ram will attempt to mount and mate with a ewe. The ewe however does not permit intromission by walking off as the ram attempts to penetrate.

Ejaculation: follows a successful mount in which penetration is achieved. This act is accompanied by a single violent pelvic thrust which lifts the male's body almost vertically into the air.

In order to simplify the results for the purpose of the present study, the preceding behaviours were considered together as *secondary* (mating) *sexual activities.* Rutting was defined as a period of significantly increased sexual activity, evidenced by the higher frequency of primary and secondary sexual behaviours. This represents an ethological definition, whilst the functional importance of rutting behaviour is considered in chapter twelve. For the purpose of this thesis periods of increased sexual activity during which actual mating was seen are termed *ruts*, whilst periods of increased sexual activity which were not accompanied by mating activity are termed *false ruts.*

2. Aggressive behaviour

Chasing: All chases made by territorial males against males intruding onto their territories were recorded, together with the duration of the chase. Rams would normally walk or trot towards an intruder and break into a run when nearing the intruder. The intruder would thus be displaced from a male's territory or forced to leave the herd with which it had been associating.

Fighting: Incidents of fighting and the duration of actual physical contact (horn clashes) were recorded. The social status of the fighting males was also recorded; territorial or non-territorial.

3. Marking behaviour

Linked urination-defecation: Restricted to males, a characteristic urination posture is adopted, with the back legs being stretched backwards whilst urinating, such that the groin is brought closer to the ground. If a linked sequence is to occur the ram will then immediately squat on its haunches and defecate before moving off. Linked urination-defecation in sometimes preceded by scraping of the ground and sniffing.

Object aggression: The base of the horns are rubbed in vegetation, or sometimes even on the ground. This can become quite violent, with the horns being thrashed around in the vegetation, sometimes leaving them covered in plant material.

4. General behaviour

Grazing: Feeding on grass or herbs, with the mouth held close to the ground.

Browsing: Feeding on bushes and trees, generally with the mouth held above ground level.

Ruminating: Distinct lateral movements of the jaws were observed, together with movement of food boluses from the rumen to the mouth.

Resting: No obvious motivational behaviour apparent. Ears relaxed, giving an idea of the individual's low state of arousal. Also included sleeping animals, which rested their heads on the ground, usually with the neck curled round and the head tucked in next to the body. Alternatively the neck was stretched forward in front of the body with the head resting on the ground in line with the neck. Eyes were closed and ears relaxed.

Watching: Head with ears held up and pointing forward. Body posture relaxed with attention not necessarily focused in any particular direction.

Alert watching: Head held up with ears erect and pointing forward. Body orientated in direction in which springbok looking. Body posture rigid, gaze being fixed at a particular point. Often accompanied by nasal alarm whistle if a predator is seen.

Self-grooming

Drinking

Urinating or defecating

As well as recording an individual's behaviour notes were made of the number of animals with which it was associated. These were made in terms of the sex of mature individuals *i.e.* those which posed a potential threat to territorial rams and those ewes old enough to be mated. In cases where a herd extended over the border of a ram's territory only those individuals on his territory were noted as being in the company of a male. Territory occupancy or temporary vacancy was noted for territorial males. Additional information was collected concerning whether an animal was in the sun or shade and standing or lying.

DATA MANAGEMENT

All data were collected directly onto paper in the form of data sheets, lists and tables. These were later transcribed to computer in the form of database files. Transcription was made both directly onto files or through a Psion 'Organiser'™ pocket computer, programmed to accept the data. The 'Organiser'™ was also used in the field for the collection of information concerning herd structure (see chapter seven). Extensive use was made of Dbase III+™ and Statgraphics™ programmes in data analysis.

As behavioural data normally violate many of the assumptions of parametric statistical tests (Martin & Bateson 1986), all analyses were done using non-parametric methods as detailed in Siegel (1956) and Siegel & Castellan (1988). The most commonly used statistical techniques were the Mann Whitney U, Wilcoxon matched-pairs, Kruskal Wallis one-way ANOVA, Spearman rank correlation and chi-squared tests. Parametric tests were only used in relation to environmental and population variables according to the procedures of Sokal & Rohlf (1981). Unless otherwise stated all tests were two-tailed.

Chapter 4

Environmental conditions

A brief description on the prevailing environmental conditions in the area are given in chapter two. As conditions varied considerably during the three years of fieldwork a more detailed account for that period are presented in this chapter.

1. Temperature

Average monthly maximum and minimum temperatures on the riverbed are shown in Figure 4. Highest mean maximum temperatures were recorded from November-January in different years, when they exceeded 36°C. The highest recorded temperature was 42.5°C in January 1993, whilst the lowest maximum, measured in June 1992, was only 9°C. In all years the lowest mean minimum temperature was recorded in July, in which month the mean was always below freezing. The lowest recorded temperature over the study period was -9.0°C in July 1990. The highest noted minimum temperature was 25.5°C in January 1992. Whilst mean minimum temperatures fell below 5°C from May until August, they were always above 5°C in the other months. Mean minimum temperatures were important in defining the seasons

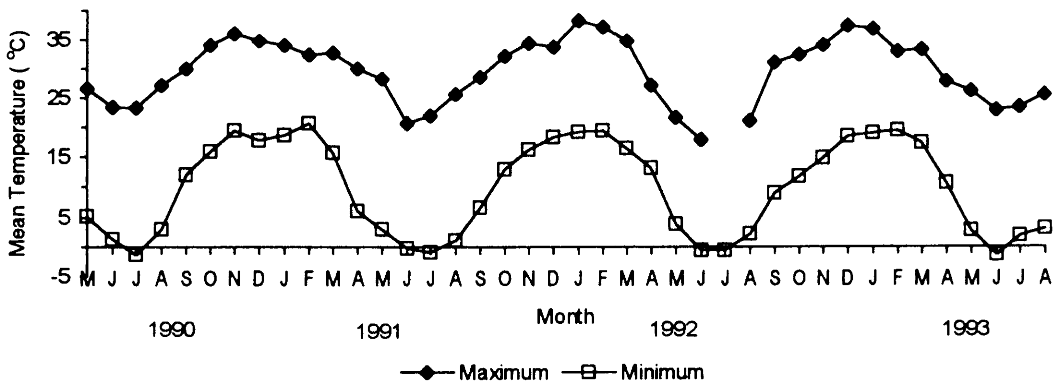

Figure 4 The variation in mean monthly maximum and minimum temperatures on the Nossob riverbed (no data were available for maximum temperatures during July 1992)

that were recognised for data analysis. The transition from cold to hot periods of the year is less well defined by mean maximum temperatures which show some degree of overlap over this period.

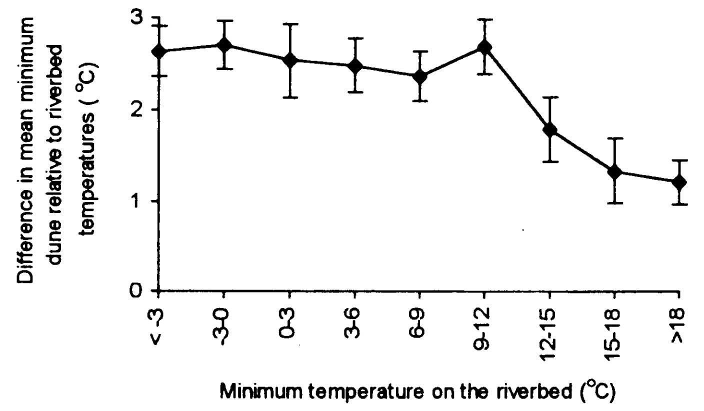

Figure 5 Differences in the minimum temperatures between the riverbed and surrounding dunes, showing the effect of minimum temperature on the degree of difference between dune and riverbed temperature

Minimum temperatures were recorded on both the riverbed and the surrounding dunes. From this it was apparent that the dunes were significantly warmer than the riverbed at night (Wilcoxon matched-pairs, $Z=12.78$, $n=247$, $p<0.001$; Figure 5). It was also found that as the minimum temperature on the riverbed increased, so the temperature gradient between the riverbed and dunes decreased (ANOVA; $F=3.32$, $df=245$, $p<0.005$).

2. *Precipitation*

The monthly rainfall over the study period is illustrated in Figure 6. The pattern of rainfall over the three wet periods differed significantly. Rainfall for the 1990/1991 and 1992/1993 seasons fell predominately from January until March. This is in contrast to the 1991/1992 pattern in which rainfall occurred intermittently, with dry spells between the wet periods. During the 1990/1991 season 380mm of rain fell, making it a relatively wet year for the area. The total rainfall for the 1991/1992 season was 160mm; a comparatively dry year. The 1992/1993 season was intermediate, with 222mm of rain falling.

3. *Vegetation biomass*

The vegetation levels on the riverbed differed markedly over the study period. These differences could be attributed to the rainfall pattern in a given year. In response to the rains in both the 1990/1991 and 1992/1993 seasons there was active plant growth on the riverbed (Figure 6). Wet vegetation biomass reached 250 gm^{-2} in March 1991 and 98 gm^{-2} in February 1993. However following the 1991/1992 rains there was no marked increase in vegetation biomass on the riverbed. Over this period the wet vegetation biomass reached a peak level of 13 gm^{-2} in December 1991. Vegetation biomass declined to its lowest level immediately prior to the onset of the next rains. Thus the lowest vegetation biomass on the riverbed was recorded in November 1990 and January 1993 during those years. Despite some observed vegetative growth during December 1991, this was offset by the rate of vegetation removal, and so no net increase in wet biomass levels were recorded for the year.

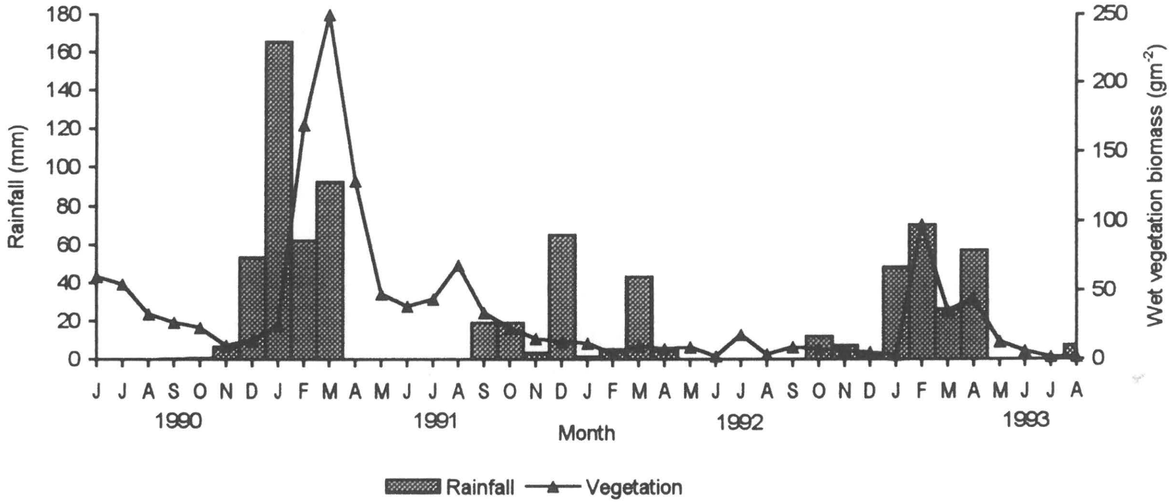

Figure 6 Monthly variation in vegetation biomass and rainfall on the Nossob riverbed

Based on the broad pattern of changes in rainfall, vegetation and temperature patterns the year could be divided into three seasons. These are used for examining the behavioural adaptivity of springbok in relation to their fluctuating ecological environment. The seasons are defined below:

Hot-dry season: Average minimum temperature for the month exceeding 5°C. Average maximum temperature of approximately 25°C or above. Little or no monthly rainfall. This period falls between September and November for 1990 and 1991. In

1992 only 2 mm of rain fell in December and so the 1992 hot-dry season extended through from September until December.

Hot-wet season: Average minimum temperature for the month exceeding 5°C. Average maximum temperature of approximately 25°C or above. The start of the hot-wet season was characterised by 40 mm of rain or more during the month, the first substantial rains of the year. The hot-wet season was taken to end when monthly minimum night-time temperatures fell below 5°C in May. Thus the hot-wet season fell between December and April in 1990/1991 and 1991/1992. Due to the extended dry period preceding it, the 1993 hot-wet season began a month later in January.

Cold-dry season: Average minimum temperature for the month less than 5°C. Average maximum temperature of approximately 25°C or below. Little or no monthly rainfall. In all years the cold-dry season fell between May and August.

Chapter 5

General activity

INTRODUCTION

This chapter examines both the effect of individuals' sex and the social status of males, either territorial or non-territorial, on their general maintenance activities, as well as temporal variation in these activity levels. Davie's *et al.* (1986) recorded a difference in the plant species selected by male and female springbok in the Karoo (South Africa) as well as a difference in their utilisation of vegetation types. These findings are in common with other studies where both the sex and social status of an individual have been shown to affect its general maintenance activities. Amongst other species, sexual differences in diet have been recorded in red deer (Clutton-Brock *et al.* 1982, Staines *et al.* 1982) and muskoxen (Oakes *et al.* 1992). Beier (1987) found that female white-tailed deer fed on a higher quality diet than males. A sexual disparity in habitat utilisation was also found for the white-tailed deer (Mc Cullough *et al.* 1982), as well as being recorded in the red lechwe (Williamson 1990) and impala (Murray 1981), which presumably relates to a dichotomy in the feeding habits between the two sexes in these species.

It is also possible that differences in the diet of individuals are not only determined by their sex, but also by their social status. Tomlinson (1981) observed that non-territorial waterbuck males avoided areas occupied by territorial individuals. By monopolising certain areas, territorial males could exclude other males from important resources, such that the non-territorial individuals are disadvantaged. Alternatively, the mobility of territorial males may be limited by their association with a territory. It is well established in ungulates that animals move to certain preferred habitats in different seasons. Territorial affinity may limit males' ability to respond to temporal variation in habitat quality relative to non-territorial males, effectively diminishing their feeding ability.

Whilst important differences in the maintenance activities of individuals are probably related to their sex and social status, they should also vary temporally. Such differences could occur at different time scales, be they hourly, daily, seasonally, annually or over the course of an individual's life span.

In common with other species (Kutilek 1979), springbok showed a seasonal change in their foraging behaviour in the Transvaal (Novellie 1978). Mountain gazelles (Baharav 1981, 1983*a*), dorcas gazelles (Baharav 1982), Grant's gazelles (Spinage *et al.* 1980) and impalas (Jarman 1971, Rodgers 1976, Jarman & Sinclair 1979) all show an increase in the proportion of browse in their diet as the dry season progresses. Both the crude protein content and digestibility of plant material have been shown to decrease through the dry season (Afolayan & Fafunsho 1978, Skarpe & Bergstrom 1986, Owen-Smith & Cooper 1989). Whilst sprouting grasses have relatively high protein and carbohydrate levels, these decrease sharply following maturity and seed production. Crude protein levels show more marked seasonal changes in grasses than browse species, falling with maturation and onset of drought, when they are lower than browse species (Field 1975), and increasing again with rain (Field & Blakenship 1973). Browse species, which were previously of lower nutritional value, become of greater importance as the dry season progresses as they maintain higher crude protein and carbohydrate levels than grasses.

General activity patterns are almost certainly affected by temperature, which fluctuates by over 50°C from the highest maximum to the lowest minimum in the Kalahari. Over such a temperature range springbok may be expected to minimise heat loss at low temperatures and minimise heat gain at high temperatures by behavioural means. These include orientating with the sun or wind as has been shown by Hofmeyr & Louw (1987). The availability of shade trees is probably also important at high ambient temperatures. As trees are generally larger on the riverbeds than the dunes (pers. obs.), the inclusion of shade-bearing trees on a territory could increase its attractiveness to females. Springbok may also gear their feeding to those times when the water content of their food plants is potentially highest, during the night and in the early morning (Taylor 1968).

A difference was recorded in the minimum nighttime temperatures between the riverbed and dune areas (chapter four). When nighttime temperatures were extremely low, individuals frequenting the dune areas would not be subject to temperatures as low as on the riverbed. Springbok may show day/night variation in their habitat utilisation and subsequently in their maintenance activities over cold periods.

Variation in the general activity pattern of springbok is important when considering their mating system, as this appears to be the sit-and-wait method of resource defence polygyny. The success of a breeding male may well be affected by the influence of prevailing ecological conditions on the activity and movements of both potential breeding partners and rivals.

The effect of an individuals sex and the social status of males were therefore examined in this chapter. General maintenance activities of springbok were investigated on a daily and seasonal basis, as well as considering the effect of temperature on behaviour and the importance of shade as a resource. A comparison was made between the activity of territorial males in years of both high and low annual rainfall. The implications of variation in the general activity patterns of individuals, both because of differences in their sex and status or because of seasonal variations, are discussed with particular reference to territorial males and the breeding system of springbok.

METHODS

Data collection concerning the comparison of the general activity budgets of different social classes were conducted over the first year of research from May 1990 until April 1991. Due to practical limitations all other results on differences in the general maintenance activities refer only to territorial males as other individuals could not be watched on a monthly basis after April 1991. No data presented in this chapter include behaviour measured over rutting periods. The effect of the rut on the activities of individuals is examined in chapter eleven. Some results are presented on a monthly and others on a seasonal basis. These seasons correspond to the hot-wet, hot-dry and cold-dry periods defined in chapter four.

Work on the nocturnal activity of territorial males was conducted from April-July 1993. For analytical purposes, data collected during the night was divided into two categories. Data collected in early April and May were considered as *warm nights*, with the exception of two particularly cool evenings when temperatures fell below 4°C. All data collected in June and July, when the nightime minimum consistently fell to 4°C or less are referred to as *cold nights* in the data analysis. Additional information was collected by radio-telemetry techniques. On relatively moon-less nights, when focal watches were impossible, individuals were tracked at night to determine whether they were on the riverbed or dune habitats.

Any relationship between diurnal and nocturnal activity patterns are made relative to diurnal behaviour recorded over the same period and are therefore directly comparable. It was not possible to consistently distinguish between resting and ruminating behaviour at night so these data have been pooled; comparisons can therefore only be made between these summed rest and ruminating times and not for just resting or ruminating times alone.

RESULTS

1. General diurnal activity

Feeding was the most important activity of all springbok, accounting for 45.1% of their daytime activity. Springbok were both seen to graze and browse. Resting accounted for 15.2% of their activities, ruminating for 19.5% and locomotory behaviour 10.9%. Vigilant behaviour (watching or alert) consumed 5.7% of time, grooming only 1.7% and the other 1.9% was divided between various activities including the sexual and aggressive behaviour of males, drinking, urinating and defecating.

Considering territorial males specifically, the social group for whom the most data were collected, their daily time budgets were compared on a seasonal basis (Figure 7). Only the major components of behaviour (feeding, resting and ruminating), which comprised an average 79.8% of animals' daily activities, were considered. Activity levels of territorial males varied over the course of the day in different seasons and statistical results are summarised in Table 1. Territorial males showed a definite feeding peak in the early morning and late afternoon, with most resting and ruminating occurring in the mid-morning and mid-afternoon periods.

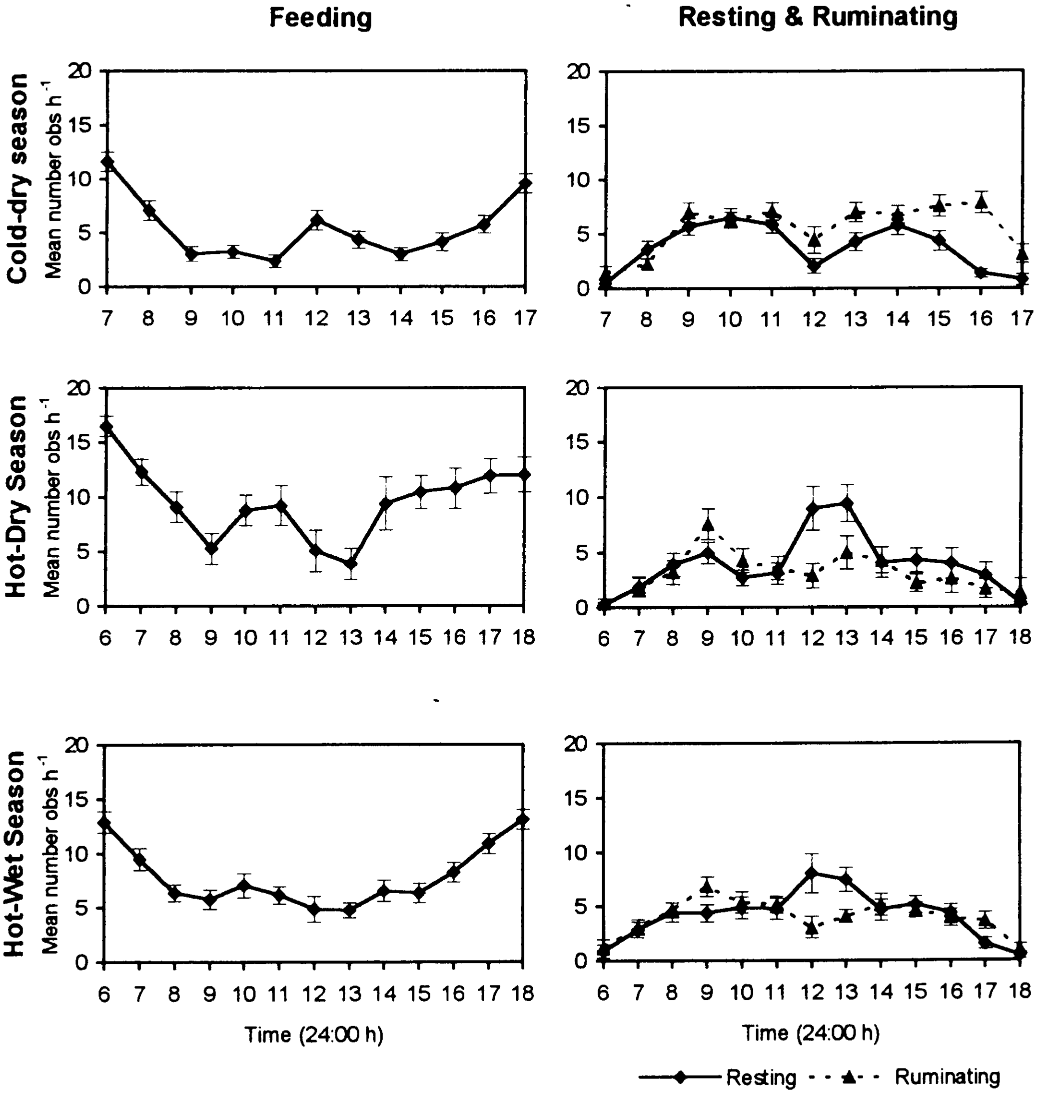

Figure 7 The diurnal time budgets of territorial males (± standard error of the mean S.E.M.) in different seasons, showing the distribution of feeding, ruminating and resting behaviour through the course of the day

Activity	Season		
	Cold-dry	Hot-dry	Hot-wet
Feeding	<0.001	<0.001	<0.001
Ruminating	<0.001	<0.005	<0.001
Resting	<0.001	<0.001	<0.001

Table 1 Showing statistical summary of daily variation in different activities through the course of the day in different seasons (KW ANOVA)

The proportion of time involved in different activities in the different seasons are shown in Table 2. Feeding activity was highest in the hot-dry season and lowest in the cold-dry season. The opposite was true for ruminating which was found to be highest in the cold-dry season and lowest in the hot-dry season. Resting did not vary significantly between seasons.

Activity	Season		
	Cold-dry	Hot-dry	Hot-wet
Feeding (%)	26.2±1.3	48.7±2.4	39.6±1.4
Ruminating(%)	30.2±1.4	15.8±1.6	20.7±1.1
Resting (%)	19.9±1.3	19.0±1.8	20.5±1.3

Table 2 The overall proportion of time spent in different activities by territorial males in different seasons

2. *Diurnal activity in relation to temperature*

The daily activity patterns were considered in relation to maximum daytime temperature, across the different seasons. The results of this comparison are illustrated in Table 3 and Figure 8. As maximum daily temperatures increased so too did the amount of time animals spent resting (KW ANOVA, H=21.48, n=1049, p<0.0001). At the highest temperatures resting peaked at 60.0% of all recorded behaviour by 15:00 h but only 24.5% of activity at its highest point at intermediate temperatures. Resting was the dominant activity from 11:00-16:00 h at high temperatures but was

Activity	Maximum daily temperature		
	<27°C	27-36°C	>36°C
Feeding (%)	29.7±1.5	40.9±1.4	35.9±2.2
Ruminating (%)	26.9±1.5	20.9±1.1	19.3±1.6
Resting (%)	18.2±1.3	17.2±1.0	28.0±2.1

Table 3 The proportion of time spent by territorial males in different activities in relation to the maximum daily temperature

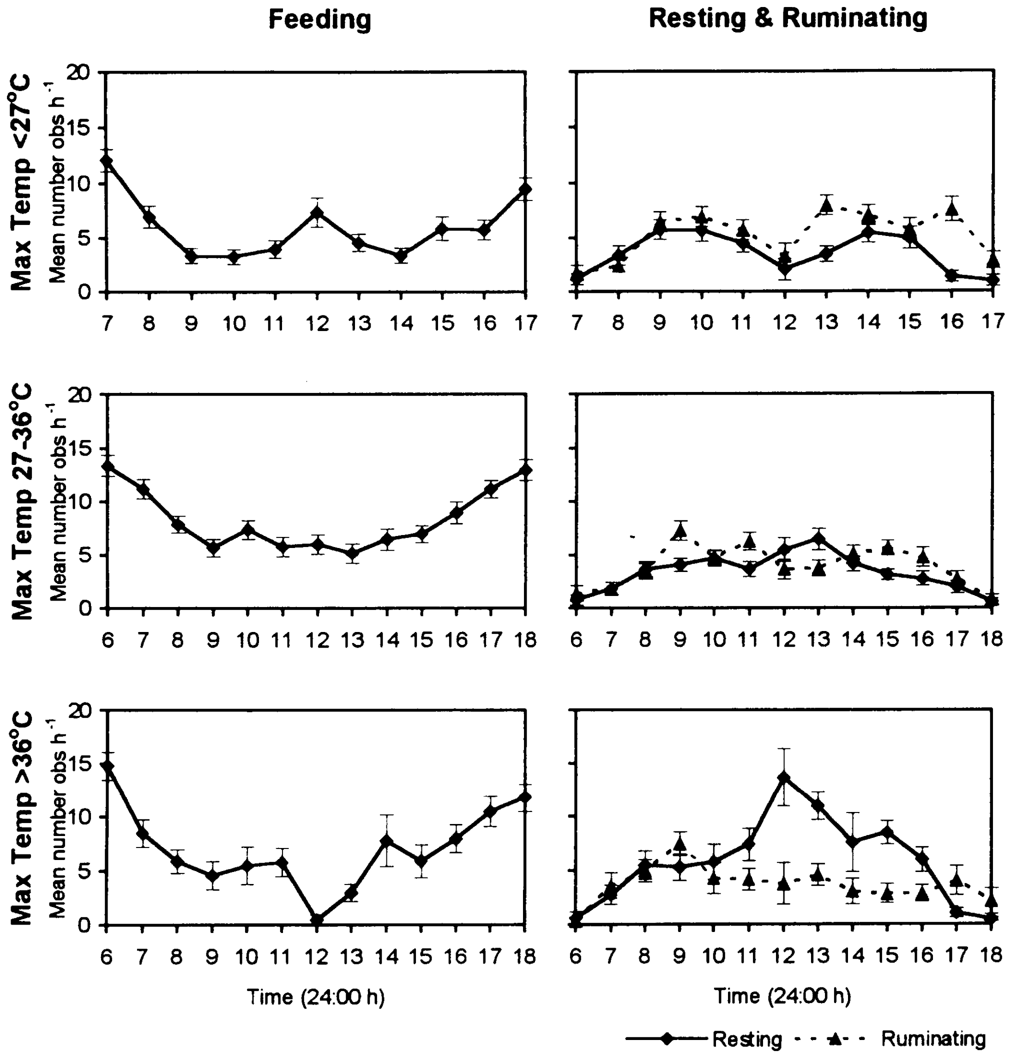

Figure 8 The diurnal time budgets of territorial males at different daily maximum temperatures (±S.E.M), showing the distribution of feeding, ruminating and resting behaviour through the course of the day

never the dominant activity at temperatures less than 36°C, when feeding or ruminating always predominated.

Ruminating times were also found to vary significantly with temperature (KW ANOVA, H=16.40, n=1049, p<0.001), being highest at temperatures less than 27°C and lowest at intermediate temperatures. Feeding activity was also lowest in the hottest conditions (KW ANOVA, *H*=25.03, n=1049, p<0.0001), with the highest feeding activity occurring at intermediate temperatures. The implication of relatively low diurnal feeding activity and high ruminating activity at lower temperatures is considered later in relation to the nocturnal activity patterns.

3. Activity patterns in relation to social status

Comparing only those months in which animals of different social status were simultaneously observed, territorial male springbok spent 42.1±1.4% (n=466) of the day feeding, whilst non-territorial males fed for 40.1±1.8% (n=315) of the time. This difference in the feeding time of adult male springbok is not significant (Mann Whitney U, *z*=0.33, n=781, NS). Adult female springbok were found to feed for 56.0±2.0% (n=275) of the day, representing a greater proportion of their activity budgets than that of territorial or non-territorial males (KW ANOVA, *H*=41.76, n=1056, p<0.0001).

Territorial rams ruminated for 20.1±1.2% and non-territorial males for 21.8±1.6% of the day. The difference in time these two types of males spent ruminating did not differ to any measurable degree (Mann Whitney U, *z*=0.19, n=781, NS). In contrast ewes ruminated for only 16.0±1.5% of the day, significantly less than the rams (KW ANOVA, *H* =9.32, n=1056, p<0.01). Female springbok fed more and ruminated less than males.

In the same way territorial and non-territorial rams rested and were involved in locomotory activity for a similar proportion of their time (Resting; Mann Whitney U, *z*=0.39, n=781, NS. Locomotory; Mann Whitney U, *z*=0.74, n=781, NS). Territorial males spent 15.6±1.1% of their time resting compared to the 18.0±1.5% of time for which non-territorial males were observed resting. Females spent only 11.1±1.3% of their day resting, much lower than either territorial or non-territorial males (KW ANOVA, *H*=16.30, n=1056, p<0.001). Territorial males spent 10.4±0.6%, non-territorial males 12.2±0.9% and females 10.2±0.8% of their time engaged in locomotory activity. Locomotory behaviour did not vary between individuals of different sex or social status (KW ANOVA, *H*=0.50, n=1056, NS).

4. General activity of males in relation to status and season

Whilst the general activity of territorial and non-territorial males did not appear to vary significantly over the whole year, this did not exclude potential seasonal variation in their activities which evened themselves out over such a long time span. Therefore the general activity patterns of territorial and non-territorial males were compared in different seasons (Table 4).

	Season			
	Hot-Wet	Cold-Dry	Hot-Dry	Probability of seasonal variation
Feeding (%):				
Territorial	40.5±1.9	36.4±3.1	48.7±3.1	*
Non-territorial	46.4±2.8	33.4±3.4	37.4±3.1	*
Resting (%):				
Territorial	15.8±1.6	10.1±2.2	19.3±2.2	***
Non-territorial	11.5±1.8	20.7±3.3	23.2±2.8	*
Ruminating (%):				
Territorial	21.2±1.5	25.2±3.1	14.6±2.0	***
Non-territorial	21.0±2.6	24.6±3.1	21.0±2.6	NS

*Table 4 Seasonal variation in the activity budgets of adult males in relation to their social status. (Statistical results based on KW ANOVAs. Probability levels: $0.01<p<0.05$= * ; $0.005<p<0.01$= ** ; $p<0.005$= ***)*

Considering the differences between males, it appears that the largest variation occurred between the resting and ruminating times of territorial and non-territorial males over the cold-dry and hot-dry seasons; whilst the proportion of time spent resting increased for both types of male, with a concurrent drop in ruminating times, this was only significant in the case of the territorial males. This was paralleled by the feeding behaviour of territorial males which peaked at this time, whilst that of non-territorial males was at an intermediate level.

Presuming that feeding and ruminating levels are an indicator of feeding efficiency, the ratio of feeding : ruminating increased substantially from 1.44 to 3.33 for territorial males between the cold-dry and hot-dry seasons. Over the same period the feeding : ruminating increased from 1.36 to 1.78 for non-territorial males. Thus non-territorial males appear to forage far more efficiently over the hot-dry season than territorial males.

5. General nocturnal activity of territorial males

During warm nights, territorial males remained on the riverbed and a definite activity rhythm was recorded (Figure 9). Feeding levels decreased shortly after sunset, with two feeding bouts in the late evening and early morning. Rates of feeding activity varied through the night (KW ANOVA, H=25.65, n=46, p<0.05). Periods of resting and ruminating occurred in the early evening, the middle of the night and later in the morning, varying significantly over the course of the night (KW ANOVA, H=22.18, n=46, p<0.05).

On warm nights grazing accounted for 98.8% of feeding activity and browsing for only 0.2%. Over the same period diurnal grazing made up 98.1% of feeding time. Thus there was no significant difference in the relative proportion of graze and browse material in the diet between day and night at this time (Mann Whitney U, z=0.73, n=54, NS).

Over cold nights males spent on average 68.8±10.0% (n=9) of their time off their territories. Again, two feeding bouts were observed (Figure 10), feeding rates varying over the course of the night (KW ANOVA, H=22.3, n=40, p<0.05) as did resting and ruminating periods (KW ANOVA, H=22.9, n=40, p<0.05). On such nights grazing constituted only 28.0% of feeding time and browsing 72.0%, whilst during the colder

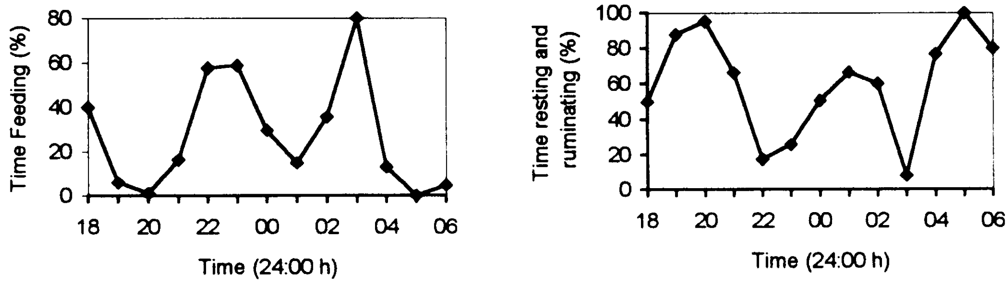

Figure 9 The nocturnal time budgets of territorial males on warm nights, showing the distribution of feeding and resting and ruminating behaviour over the course of the night

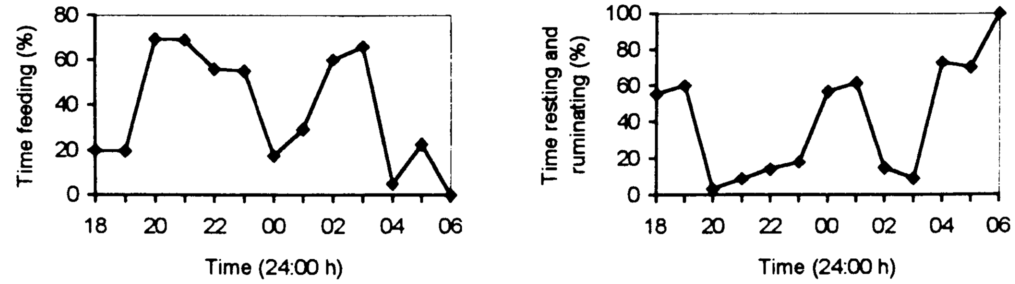

Figure 11 The nocturnal time budgets of territorial males on cold nights, showing the distribution of feeding and resting and ruminating behaviour over the course of the night

days grazing made up 87.1% of feeding time. Thus, unlike the warm period, there was a significant shift in feeding behaviour from day to night (Mann Whitney U, z=5.14, n=65, p<0.0001).

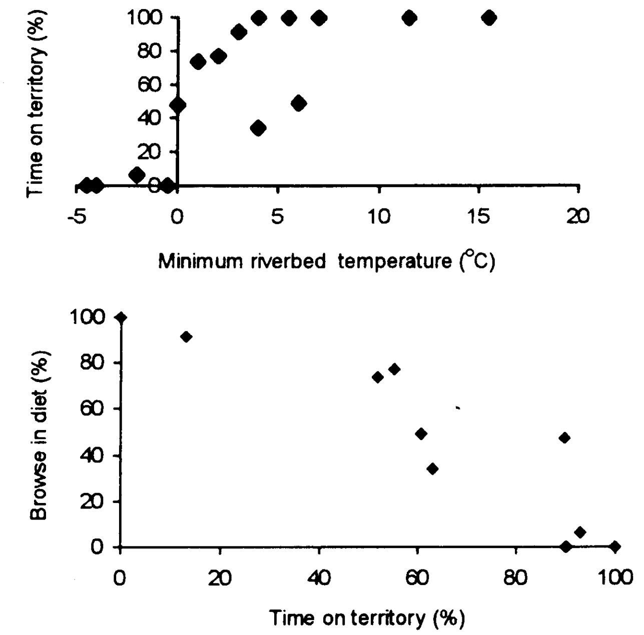

Figure 10 The effect of minimum nightime temperature on the amount of time individuals were observed on their territories during the night (above) and the relative proportion of browse material taken by rams when feeding at night in relation to the percentage of time spent on their territories (below)

The effect of minimum overnight temperature on both the amount of time males spent on their territories and thus the amount of browse in their diet are clearly shown in Figure 11. The time males spent on their territories decreased at lower nightime temperatures (r_s=-0.88, n=16, p<0.001), whilst the proportion of browse in their diet decreased as time off their territories increased (r_s=-0.95, n=16, p<0.001).

Feeding time made up 29.6% of a males diurnal activity and 27.4% of nocturnal activity over the warmer period. There was no significant difference in the amount of time males spent feeding during the day or night over warm periods (Mann Whitney U, z=1.29, n=69, NS). However over the colder period there was a significant increase in the amount of time spent feeding from 17.2% in the day to 45.1% at night (Mann Whitney U, z=4.85, n=98, p<0.001). Conversely resting or ruminating constituted only 32.5% of their activity at night over cold periods, but 61.6% of their time during the day. Males spent significantly more time resting or ruminating during the day than the night over cold periods (Mann Whitney U, z=3.87,n=98, p<0.001). Over the warm period males spent 42.1% of the day resting or ruminating and 59.9% of the night. Thus, in contrast to cold periods, males rested more during the night than the day over warm periods (Mann Whitney U, z=2.19, n=69, p<0.05).

Specific sexual, agonistic and marking behaviours of males were also examined to determine if there was any variation between day and nightime over both warm and cold periods (Table 5). None of these activities showed any apparent variation between day and night over warm periods. The rate of sexual activity varied between day and night over the colder period. The absence of any apparent sexual activity at night was synonymous with an increase in the amount of time males spent both alone and off their territories.

	Warm			Cold		
	Day	p	Night	Day	p	Night
Time alone	14.9±1.6	NS	17.0±1.0	12.3±1.2	<0.001	18.7±0.7
On territory	18.6±0.9	NS	19.8±0.2	18.4±0.6	<0.001	7.8±1.4
Primary sexual	2.1±0.9	NS	0.9±0.5	1.6±0.5	<0.001	0
Linked U-D	0.2±0.1	NS	0.3±0.1	0.5±0.1	NS	0.2±0.1
Horn-rubbing	0	NS	0	0.1±0.0	NS	0
Chasing	0	NS	0.5±0.3	0.1±0.0	NS	0

Table 5 The mean recorded occurrence of particular types of behaviour over a one hour watch period, as well as the time males were either alone or on their territories (maximum=20), comparing day/night differences over warm and cold periods

6. *Influence of temperature on habitat utilisation*

The use of the riverbed habitat during the day and at night is shown in Figure 12. Data were collected by radio-telemetry techniques and not by watches on focal individuals. This has been subdivided to show the influence of minimum temperature. When animals were not on the riverbed they were in the dune habitat. It was found that the

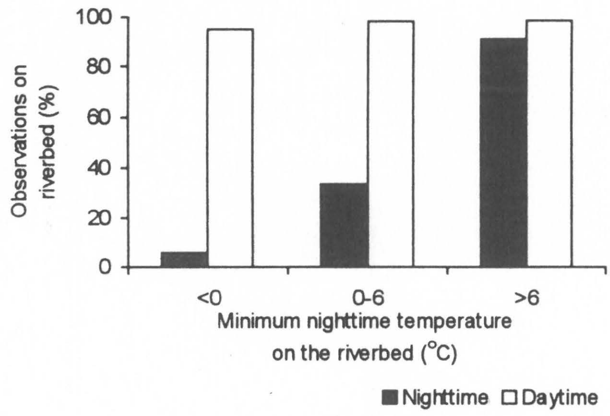

Figure 13 The effect of minimum nightime temperature on the riverbed on habitat utilisation by territorial males

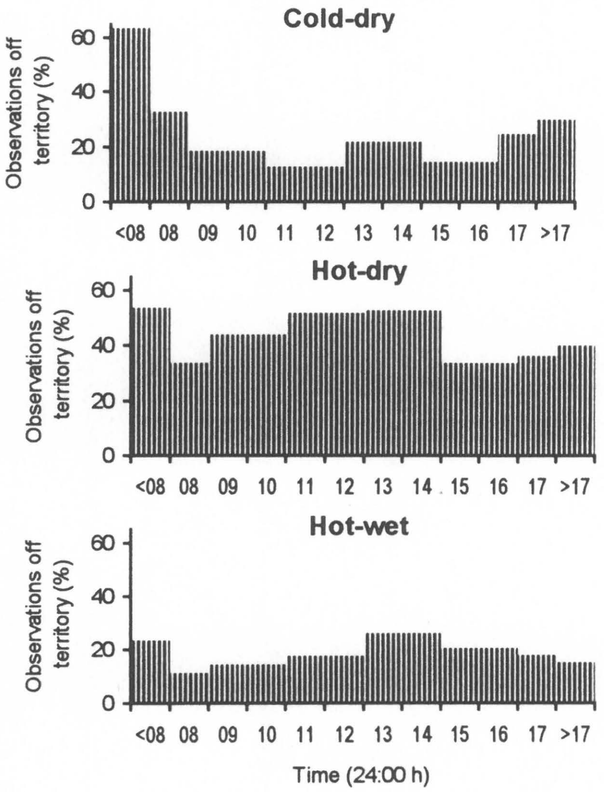

Figure 12 The proportion of time males were absent from their territories at different times of the day in different seasons

diurnal use of the riverbed habitat did not vary with the minimum temperature (χ^2=0.08, df=2, NS). However springbok made less use of the riverbed on colder nights (χ^2=16.97, df=2, p<0.001). Minimum temperatures in the range of 0-6°C appear to be critical in determining whether springbok would remain on the riverbed at night or move off into the surrounding dunes (see also figure 11). As daytime feeding habits did not change between warm and cold days (see above) and as there is a significant temperature difference between the riverbed and dunes at night it was concluded that the springbok moved into the dunes at night because this area was warmer.

7. *Temporal occupancy of territories in different seasons*

The temporal occupancy of territories in different seasons is illustrated in Figure 13. During both the hot-wet and hot-dry seasons there was no significant variation in the proportion of time a male spent on his territory at different times of the day (hot-wet; $\chi^2=7.87$, df=7, NS. Hot-dry; $\chi^2=5.85$, df=7, NS). During the cold-dry season, the proportion of time males spent on their territory did vary significantly at different times of the day ($\chi^2=50.30$, df=7, $p<0.001$). Males spent more time off their territories in the early mornings in the cold-dry season.

8. *Seasonal changes in feeding habits*

Territorial males spent 4.6±0.9% (n=258) of feeding time browsing during the hot-wet season, when feeding conditions on the riverbed favoured grazing. As the availability and quality of food material diminished in the cold-dry season so browsing increased to account for 24.6±2.3% (n=258) of feeding activity and by the hot-dry season this had increased to 34.9±3.1% (n=174) of feeding activity. Thus browsing accounted for a significantly higher proportion of diurnal feeding activity in drier conditions (KW ANOVA, H=127.32, n=786, $p<0.0001$).

The amount of graze material in the diet of territorial males was examined relative to rainfall in that and previous months. The results (Table 6) indicate that the amount of graze in the diet could be correlated to rainfall levels in a given month and also for the rainfall up to two months previously. Beyond that there was no correlation between the amount of graze material in the diet and monthly rainfall. The effect of rainfall on the proportion of browse in the diet is clearly shown in Figure 14.

Rainfall	Grazing	
	r	p
In month	0.41	0.02
1 month previously	0.54	0.002
2 months previously	0.37	0.04
3 months previously	0.30	0.1
4 months previously	0.14	0.46

Table 6 The correlation between rainfall and the proportion of time individuals were seen grazing, relative to browsing, both during a given month and over the preceding months

Acacia mellifera bushes were a particularly important source of browse material to the springbok. The flowers of this bush were heavily browsed when it bloomed in August

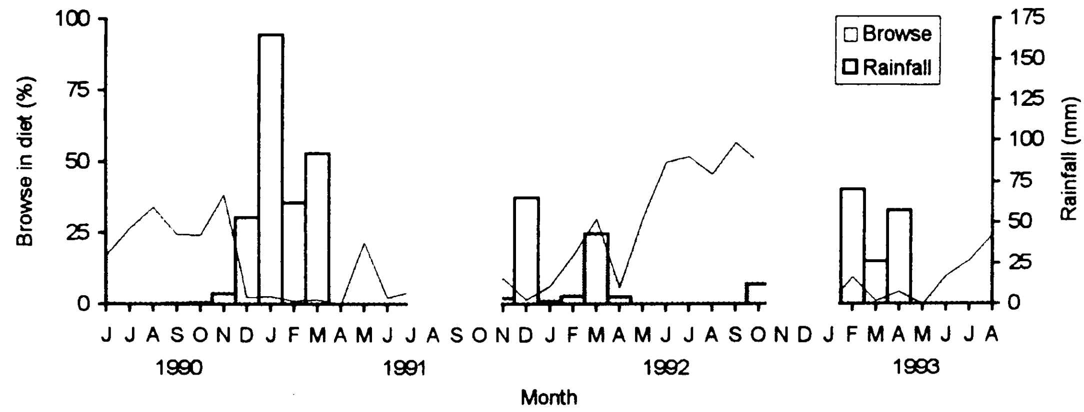

Figure 14 The proportion of time territorial males spent browsing, relative to grazing, in relation to rainfall in different months. (Months in which no observations on feeding activity recorded left blank)

or September at the start of the hot-dry season. *Acacia erioloba* trees also came into bloom at the same time of the year and these were heavily browsed too, where they could be reached.

9. Annual variation in the general activity of territorial males

Table 7 details the allocation of time to different activities during the years 1991 and 1992. These represent the two years in which data were collected in every season. Rainfall was above average for the area in 1991 and below average in 1992, with

Season	Year		
	1991	1992	p
Cold-dry (n=207):			
Feeding (%)	31.7±3.0	20.3±1.9	<0.001
Resting (%)	18.4±2.7	20.9±2.0	NS
Ruminating (%)	23.4±3.2	33.3±5.5	<0.01
Hot-dry (n=76):			
Feeding (%)	60.4±6.5	42.7±4.7	<0.05
Resting (%)	8.1±2.9	23.8±3.9	<0.02
Ruminating (%)	24.0±5.5	15.0±3.0	NS
Hot-wet (n=390):			
Feeding (%)	40.9±2.0	38.8±2.5	NS
Resting (%)	16.8±1.7	25.1±2.3	<0.005
Ruminating (%)	22.1±1.6	19.4±1.9	NS

Table 7 Comparison of the amount of time territorial males were occupied in various activities in different seasons in two contrasting years (probability levels based on differences between the two years for a given activity in a given season; Mann Whitney U test)

subsequent effects on vegetation growth (see chapter four). The proportion of time animals were observed to feed was higher in the 1991 than the 1992 hot-dry season and cold-dry season, though it did not vary between the two wet seasons. Resting times were also higher in the two hot seasons of the 'dry' 1992 year than the 'wet' 1992 year, though they did not vary significantly in the cold-dry seasons. Ruminating time was higher in the cold-dry season in 1992 than 1991 but did not vary significantly in the two hot seasons. Males in 1992, when veld conditions were poorer, took a consistently higher proportion of browse in their diet in all seasons than in 1991 (Table 8).

Season	Year			
	1991	1992	n	p
Cold-dry (%)	5.2±1.7	8.1±1.3	207	<0.02
Hot-dry (%)	5.6±4.2	21.8±4.1	76	<0.005
Hot-wet (%)	0.7±0.3	4.0±1.1	390	<0.005

Table 8 The proportion of time territorial males were seen to browse, relative to grazing in two contrasting years, showing increased browsing in the poorer year (1992). Statistical analysis using Mann Whitney U test

*10. **Utilisation of shade***

The amount of time individuals were found to rest or ruminate in the shade of trees or bushes was closely correlated to the daily maximum temperature, considering only those records in which animals spent at least 50% of their time either resting or ruminating (r_s=0.46, n=418, p<0.0001); on hotter days springbok spent a greater proportion of their time in the shade.

As the use of shade is related to temperature, it was expected that shade cover would be utilised less in the cold-dry season than the two hot seasons. Springbok spent 23.8±2.5% of their time in the shade in the hot-dry season, 32.7±1.7% in the hot-wet season and only 17.8±1.9% in the cold-dry season. Animals spent more time in the shade in the hot seasons than in the cold season, this difference being significant (KW ANOVA, H=33.42, n=927, p<0.001).

DISCUSSION

The greatest difference in the general maintenance behaviour of springbok was found to be between males and females. The higher period of time ewes allocated to feeding activity, with less time spent ruminating suggests that they might be more selective in their feeding habits than males, spending a longer time in selection and less time in the digestion of their food. Lower rumination rates have been noted amongst female Chanler's mountain reedbuck compared to males (Roberts & Dunbar 1991). Sex-based differences in the diets of a number of species have also been recorded (*e.g.* red deer; Clutton-Brock *et al.* 1982). Typically females feed on a higher quality of food as evidenced by the greater levels of nitrogen recorded in the rumens of female red deer (Staines *et al.* 1982) and the faecal nitrogen levels of white-tailed deer (Beier 1987), though Loggers (1991) found no significant difference in the faecal nitrogen between male and female dorcas gazelles. It would appear for springbok too that males and females may have been selecting different food items or ingesting food at a different rate, based on observations of their feeding and ruminating rates. Interestingly though, van Rooyen & Skinner (1989) found a significant dietary difference between territorial and non-territorial male impalas, but not between non-territorial males and females.

Clutton-Brock & Harvey (1978) noted that gross nutritional requirements increased with [body weight]$^{0.75}$. Therefore absolute energetic requirements increase with body size, but relative requirements decrease per unit body weight. Using this principle Beier (1987) concluded that the sex related differences in the quality of white-tailed deer were related to the difference in their body size; as males were larger than females, so they could afford to subsist on a lower quality diet than females but taken in greater quantity. In common with other antelope, springbok males are larger than females (Skinner & Smithers 1990) and it is thus probable that they too are selecting for lower quality vegetation than ewes.

The general maintenance activities of territorial and non-territorial males were similar over the course of the year. It is probable that males attained their best condition two to three months after rainfall, as was found for Thomson's and Grant's gazelles (Stelfox & Hudson 1986). However, considering seasonal differences in the activities of males, it appears that territorial males feed less efficiently over the nutritionally-demanding hot-dry season than non-territorial males. Skinner *et al.* (1995) found that the kidney fat index, an indicator of body condition, of springbok rams in the southern Kalahari was invariably lowest in the hot-dry season. The results of these two studies suggest that not only are males in their poorest condition during the hot-dry season but also that territory possession may detrimentally affect the feeding behaviour of territorial males relative to non-territorial individuals when they are in their poorest condition. Whilst this chapter deals with general activity, the specific effect of the rut on a male's feeding behaviour relative to pre-rut periods is considered in chapter eleven, whilst differences in the demography of territorial and non-territorial males are examined in chapter six.

Considering temporal differences in the activity of springbok, these show the same basic trends as other medium-sized antelopes, most of which exhibit a bimodal feeding peak at dawn and dusk. These include species such as the dorcas gazelle (Ghobrial 1974, Baharav 1982), impala (Jarman & Jarman 1973*a*) and red lechwe (Lent 1969). Nocturnal activity patterns are less fully documented. Jarman & Jarman (1973*a*) found that impala lay down predominantly at night, with a limited feeding bout in the middle of this period.

Territorial males altered their feeding habits on a seasonal basis, with increasing levels of browse in their diets as the dry season progressed. Direct comparisons between the two hot seasons show an increase in feeding time between the hot-wet and hot-dry seasons, whilst ruminating times diminished, as has been recorded amongst browsers (Owen-Smith 1992). An increase in feeding times probably reflects both an increase in the time necessary to ingest browse material relative to grass and the reduced availability of food material at this time of year, necessitating higher search times. This is ultimately reflected in the shorter ruminating times associated with the hot-dry season relative to the hot-wet season.

During the cold-dry season feeding rates were significantly higher at night than during the day. This represents a fundamental difference in animals' feeding habits relative to the hot period; diurnal and nocturnal feeding rates were similar at this time. Hofmeyr & Louw (1987) found that the pelage thickness of the springboks was thinner than expected for an animal of its size. Whilst this may facilitate rapid heat loss by springbok after running, they may be expected to come under temperature stress under cold conditions. Given this and the fact that the dunes are significantly warmer than the riverbeds on cold nights it is perhaps not surprising that males moved off into the dunes at such times, where feeding rates were higher than on the riverbed. Similarly Williamson (1985), working in the central Kalahari noted that springbok tended to move from valleys into the surrounding dunes at night, returning to the valleys in the morning. This would represent a form of behavioural thermoregulation. Similar vertical movement patterns have been observed in a number of species and attributed to environmental factors (Simpson 1968, Clutton-Brock *et al.* 1982).

Whilst this thermal regulatory activity is important in determining the activities of individuals it has particular implications for the territorial males. Not only do these males leave the riverbeds at night over cold periods but personal observations suggest that ewes do so too. Females were often seen returning to the riverbeds from the surrounding dunes sometime after sunrise on colder mornings. If there was to be a rut over such periods, as was observed, it would be of no benefit for territorial males to remain on the riverbed at night as this is not an attractive area to females at this time. Thus whilst the riverbed may be an important resource to which females are attracted most of the time, it is of little importance on colder nights.

At one extreme temperature may be important in reducing the number of animals present on the riverbed, whilst at the other it may be important in increasing their numbers. Animals spent more time resting or ruminating in the shade at higher temperatures. The availability of shade cover was identified as a variable which may increase the attractiveness of a male's territory to ewes; males with more shade cover on their territories may have greater access to ewes. This possibility is examined in chapter eleven.

The proportion of graze material in the springbok's diet could be correlated to rainfall. Browse material must therefore be negatively correlated to rainfall; as the period following rain increased so browse became more important in the animals' diets. It was also found that browse was more important in years of lower rainfall. It was perhaps surprising to find that diurnal feeding rates were higher during the hot-dry season of the relatively wet 1991 year than the drier 1992 year, even though ruminating times did not vary significantly, suggesting that overall ingestion rates were similar in these two contrasting years.

Whilst the grasses associated with the riverbeds may be of importance after rainfall, most browse species were found in the surrounding dunes. If animals were to shift their feeding technique from grazing to browsing this would also mean a shift from the riverbeds to the dune areas. This represents a movement from areas in which males hold territories, to a habitat in which territoriality was not observed. Whilst habitat selection is detailed in chapter seven, monitoring of the springboks feeding behaviour suggests that any change in habitat utilisation is probably related to feeding preferences.

SUMMARY

- Female springbok fed more and ruminated less than males, suggesting they may have been selecting a better quality of diet than males.
- The feeding efficiency of territorial males decreased dramatically during the hot-dry season, whilst that of non-territorial males only decreased slightly.
- General maintenance activity varied over the course of the day as well as being subject to seasonal variation.
- Temperature was important in determining general activity levels, shade being more heavily utilised at higher temperatures.
- Over warm periods territorial males showed similar diurnal and nocturnal activity patterns.
- Over cold periods territorial males moved off their territories into the surrounding dune areas, where there was a shift in food selection with more browse material in their diet.
- An increase in nocturnal feeding over cold periods was offset by decreased feeding and increased ruminating rates over the course of the day.
- The proportion of graze in animals' diets was related to rainfall patterns; conversely the amount of browse material in the diet was found to be higher both in drier years and as the dry seasons progressed.

Chapter 6

Population and the environment

INTRODUCTION

This chapter explores those key ecological resources which are important to the springbok, how these may support resource defence polygyny as a mating system and how their utilisation could differ between females, non-territorial and territorial males.

Within an area certain habitats may be favoured at particular times of the year. The distribution of species such as the Dorcas gazelle (Baharav 1982), mountain gazelle (Baharav 1983*a*), Grant's gazelle (Walther 1972b) tsessebe (Child *et al.* 1972) and white-eared kob (Fryxell 1987*a*) in different habitats have been shown to change seasonally. Such movements have been attributed to nutritional differences in the food available in particular areas (Fryxell & Sinclair 1988, McNaughton 1988, 1990). In chapter five it was found that springbok grazed preferentially following rain. Thus those areas providing the best grazing would be of particular value at this time of the year. As the soils of the fossil riverbeds are not as mineral deficient as the dunes (van Rooyen 1984) it was expected that they would be more heavily grazed following rainfall. As grasses lignify later in the year and browse species become more attractive a gradual movement away from the riverbeds into the surrounding dune system was expected.

Whilst the riverbeds could maintain some attraction through most of the year, other resources may only be attractive to springbok at particular times of the year. Water sources have been found to be used predominantly at particular times of the year (Ayeni 1975, McNaughton 1990). Similarly in areas including riverine habitats a movement from surrounding areas towards this habitat in the dry season is a common phenomenon (Jarman 1971, Ghobrial 1974, Leuthold 1978*b*). Under captive conditions other arid-adapted animals drank readily; Dorcas gazelles were found to take up to 23% of their body weight in water daily (Ghobrial 1974), whilst both mountain and sand gazelles increased water intake during hotter months (Williamson & Delima 1991). Though springbok are able to survive conditions in which the water content of the available vegetation may drop as low as 10%, they will readily drink (Child *et al.* 1971, Knight *et al.* 1988), particularly over hot and dry periods of the year (Davies & Skinner 1986*a*). As the dry season progressed springbok were expected to concentrate their movements more around the waterholes in the area.

Springbok have been observed at higher densities on calcareous pans than on the surrounding dune areas (Parris & Child 1973). The pans differ from the fossil riverbeds as they lack any trees and are therefore devoid of shade cover. In the two hot seasons shade is a resource which springbok readily utilised (chapter five). The pans support a different plant community from the riverbeds and it was noted that the vegetative growth was not as substantial as on the riverbeds. Springbok were therefore expected to utilise the pans differently from the riverbeds.

These three resources, the riverbeds, water sources and pans, were identified as areas which may be attractive to springbok. If they were not only attractive, but attractive during rutting periods and energetically defendable by individuals, conditions would be suitable to support resource defence polygyny.

The nature of resource defence polygyny, or territoriality, necessitates that individuals are confined to the area in which they have established their territory. Male springbok have been observed to maintain territories throughout the year (David 1978*b*, Williamson 1985). This is in contrast to some other territorial ungulates which may maintain territories only at specific times of the year (*e.g.* pronghorn: Gilbert 1973; impala: Jarman & Jarman 1973*b*; red deer: Carranza *et al.* 1990). Springbok are highly mobile, capable of moving large distances in search of food or water, responding rapidly to rainfall and the subsequent growth of herbaceous plants (Mills & Retief 1984*b*, Williamson 1985, Knight *et al.* 1988). The ability of the population to respond rapidly to changing environmental conditions is contrasted by the constraints males may impose upon themselves by being territorial. It would not be surprising therefore if territorial males were using the environment differently from the rest of the population and that this represented some nutritional cost to them.

The aim of this chapter is to quantify habitat utilisation by the springbok, to determine which habitats are favoured at particular times of the year. It also aims to quantify any differences in habitat utilisation between females, non-territorial and territorial males to determine both whether females and non-territorial males respond similarly to their changing environment and also whether the response of territorial males differs from that of non-territorial males.

METHODS

Three important environmental variables were examined to determine their possible influence on the springbok population density and that of the territorial males. These were the availability of vegetation on the riverbed, the effect of rainfall and the distribution of springbok relative to the waterholes. The density of the population and of territorial males was examined to investigate whether it was influenced by monthly rainfall and wet vegetation biomass. This was done both for the current month and in relation to rainfall and vegetation levels during previous months.

As both the number of territorial males and of other males could vary independently on the riverbed, it was presumed that neither would reach their highest numbers at the same time. Therefore in order to calculate the maximum proportion of males which were territorial within a given year the maximum density of territorial males and of all adult males in the population were used.

In order to relate the distribution of territorial males and the rest of the population to waterholes, the number of territorial males and of the rest of the population excluding territorial males ≤1km from water were calculated. Months in which less than fifty springbok herds or fifty territorial males were recorded in the monthly riverbed count have been ignored from the final analysis because of the high variation in results this produced. These months were October, November and December 1992.

Calculation of animal home ranges was based on versions of the programmes detailed in Kenward (1987). These were modified for use in the present study by H.M. Dott[†]. The home ranges calculated from this programme were multinuclear probability polygons derived by two-dimensional cluster analysis. The advantage of this method in the present study is that it allows clusters to chain along line features such as rivers (Kenward 1987). Both 100 % and 90 % minimum convex polygons have been calculated. However because of the considerable time, distance and cost involved in collecting information from individuals which had wandered from the main study area between Marie's loop and Kwang waterhole on the riverbed, there is a reduction in the number of sightings of outliers. Thus whilst the results show the underlying trends, they must be treated as a conservative estimate of an individual's home range.

RESULTS

1. Fossil riverbeds

a) Population trends

The density of springbok on the riverbed in different months is shown in Figure 15. The number of springbok present on the Nossob riverbed did not remain constant between different months but showed strong monthly variation. Springbok appeared to use the riverbeds most extensively during the hot-wet season. Springbok density on the riverbed peaked in either March or April in all years. Their density on the riverbed reached 58.3 km^{-1} in 1991, 36.7km^{-1} in 1992 and 33.6 km^{-1} in 1993. From this time onwards numbers utilising the riverbed reached a low at the end of the hot-dry season.

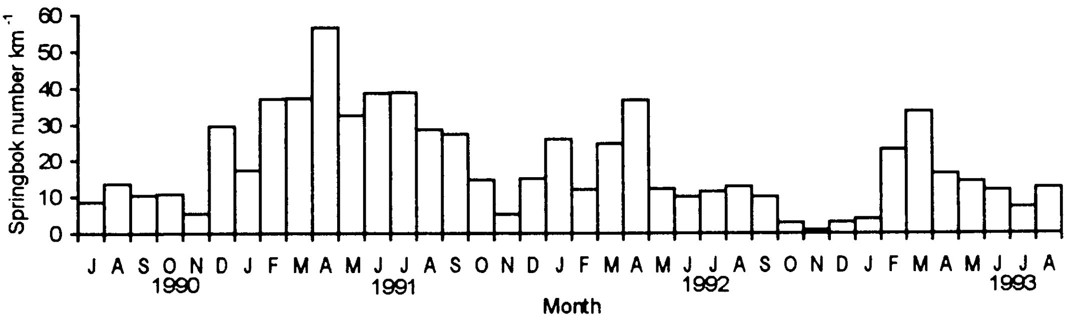

Figure 15 Monthly variation in the density of the springbok population on the Nossob riverbed

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The lowest density of springbok on the riverbeds occurred in November during the study period. Springbok density fell to 5.4 km^{-1} in 1990, 5.2km^{-1} in 1991 and 0.9km^{-1} in 1992. The change is springbok density between its lowest at the end of the previous hot-dry season and its peak at the end of the hot-wet season was thus 37 fold between 1992 and 1993.

The average size of springbok herds utilising the riverbed is shown in Figure 16. Herd size varied significantly over the course of the year. Springbok aggregated on the riverbeds in large herds towards the end of the hot-wet season. Herd size peaked in March 1991 (x=86.7±20.0, n=69), April 1992 (x=60.5±16.1, n=77) and March 1993 (x=44.9±11.3, n=96). The size of herds appears to be related to the density of springbok in the riverbed in a given month, and the two are closely correlated (r=0.84, n=35, $p<0.001$).

The riverbed population was compared in different months to examine whether there was a differential movement of male and female springbok from the riverbeds. The proportion of non-territorial and territorial males relative to female numbers was examined each month, and the results are shown in Figure 17.

It was found that the proportion of non-territorial males relative to females was independent of the density of female springbok on the riverbed (r_S=-0.07, n=33, NS). The proportion of territorial male springbok relative to female springbok however increased with decreasing female numbers (r_S=-0.93, n=32, $p<0.001$). This would suggest that those factors affecting female springbok density on the riverbed could be

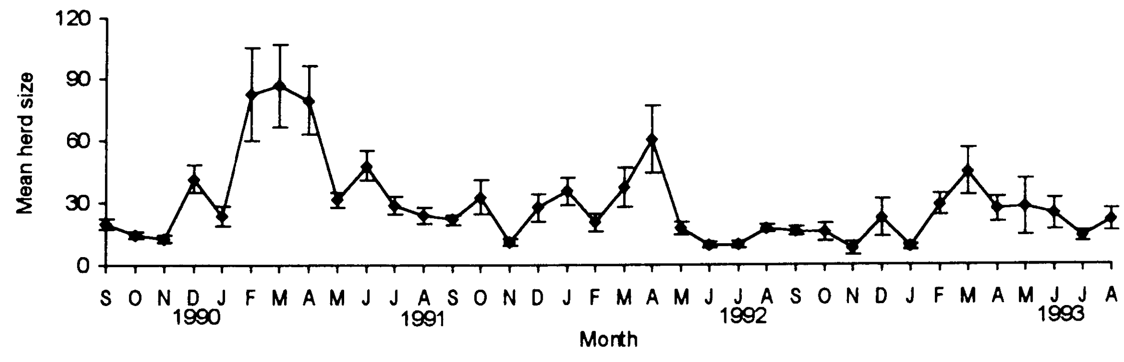


Figure 16 Monthly variation in mean herd size of springbok groups on the Nossob riverbed

affecting non-territorial males in the same way, but not territorial males.

b) Territorial males

The density of territorial male springbok on the riverbed is illustrated in Figure 18. The relative density of the population and of territorial males was compared over different months. The density of territorial males could not be predicted from the population density that month (χ^2=2569.39, df=35, p<0.001). Variation in the density of territorial males and of the population appear to be controlled by different factors.

The density of territorial males peaked in March 1991, July 1992 and February 1993. Maximum density reached 2.17 territorial males km^{-1} (TM km^{-1}) in 1991, 2.54 TM km^{-1} in 1992 and 2.13 TM km^{-1} in 1993. The maximum density of territorial males on the riverbed did not differ significantly between years (χ^2=5.5, df=2, 0.1>p>0.05). Timing of peak territorial male density corresponded to times of rutting activity. Smaller peaks were recorded in March of 1991 and 1992 at the time of the 'false rut' (see chapter twelve). Thus, whilst territorial males were always recorded on the riverbed, an increase in their density over the rut would suggest that some males are taking up territories specifically for the rut. Whilst 1991 and 1992 showed a similar trend, the density of territorial males did not reach the same levels in July 1993. Instead, territorial numbers remained high from the February rut through to the April rut.

The lowest density of territorial males was recorded at the end of the hot-dry season, in common with the rest of the population. Their density fell to 1.09 TM km^{-1} in December 1990 and

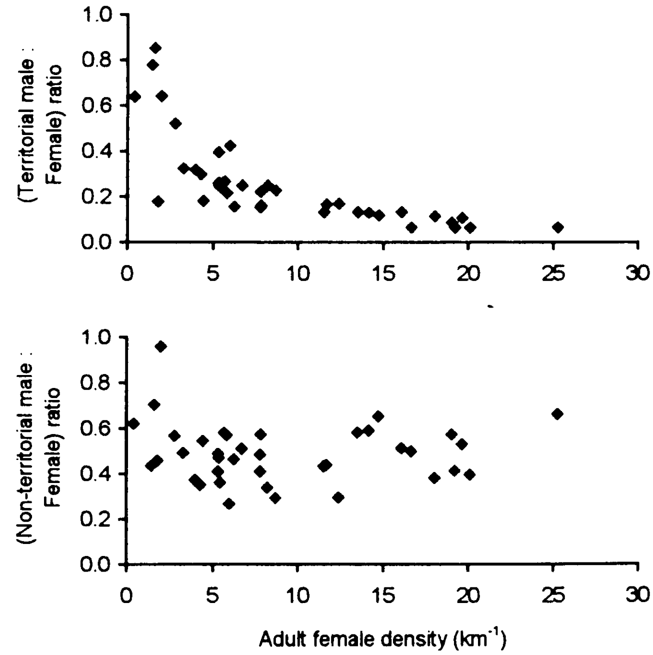


Figure 17 The relationship between male (territorial and non-territorial) and female numbers in relation to the density of female springbok present on the riverbed

1.21 TM km^{-1} in October 1991. In November and December 1992 the territorial network on the riverbed completely disintegrated, with the number of territorial males falling to 0.26 TM km^{-1} and 0.32 TM km^{-1} in these two months. Thus the lowest recorded density of territorial males on the riverbed differed significantly in different years (χ^2=74.4, df=2, p<0.001).

c) *Proportion of adult males which were territorial*

The proportion of adult males in the population which were believed to be territorial in different years are shown in Table 9. Taking the average for the three years, the mean number of adult males which were territorial was estimated at 21.2%. As the maximum number of territorial males coincided with the rut in all years, on average one in five of all adult males were territorial during the rut.

	1991	1992	1993
Territorial (maximum)	273	325	274
All adult males (maximum)	2355	1167	1134
Estimated proportion of territorial males	11.6 %	27.8 %	24.2 %

Table 9 Calculation of the proportion of adult males which held territories in different years, based on maximum territorial and adult male numbers in those years.

d) *Rainfall*

The correlations between the density of the springbok population and of territorial males on the riverbed with rainfall are shown in Table10. The population density did not appear to be related to rainfall during the same month, though numbers on the riverbed did relate significantly to the previous month's rainfall. In fact the density of

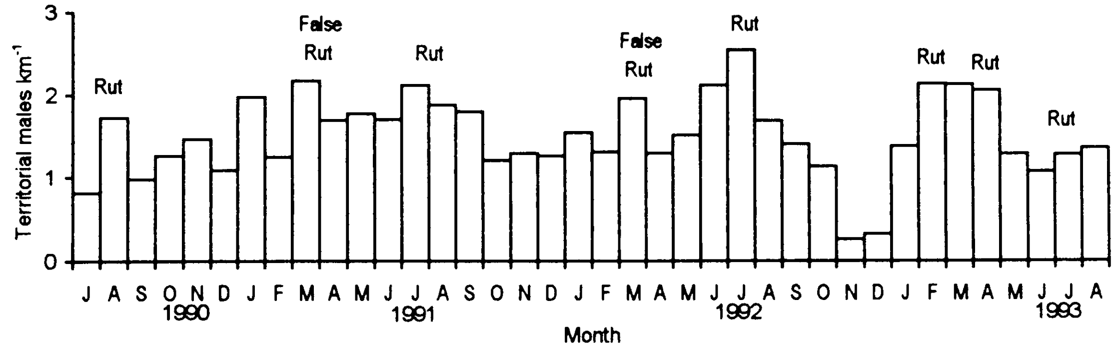


Figure 18 Monthly variation in the density of territorial males on the Nossob riverbed

the springbok population on the riverbed could be related to rain which fell up to four months previously. As the last substantial rain fell in March in both 1991, 1992 and April in 1993, rainfall was correlated to springbok density on the riverbed until July or August of these years. It was only in August and September that the springbok density on the riverbed became independent of rainfall or factors related to rainfall. The same was not true for territorial males. The density of territorial males was not related to rainfall over the previous six months.

Time after rainfall	Population		Territorial males	
	Correlation (r)	p	Correlation (r)	p
Rainfall	0.16	NS	0.19	NS
1 month post rain	0.60	<0.005	0.03	NS
2 months post rain	0.40	<0.05	0.21	NS
3 months post rain	0.64	<0.0001	0.30	NS
4 months post rain	0.48	<0.01	0.32	NS
5 months post rain	0.14	NS	0.23	NS
6 months post rain	0.21	NS	0.33	NS

Table 10 The effect of rainfall during a month, and in previous months, on the density of the springbok population and territorial males on the Nossob riverbed

e) Vegetation biomass

The vegetation levels on the riverbed and rainfall are obviously related. In fact vegetation biomass was related to rainfall for up to two months following the rain, when the highest degree of correlation was recorded between vegetation and rainfall. The density of the springbok population and territorial males relative to vegetation on the riverbed are also illustrated in Table 11.

	Population		Territorial males	
	Correlation (r)	p	Correlation (r)	p
Vegn level in month	0.60	<0.005	0.23	NS
1 month previous	0.69	<0.001	0.25	NS
2 months previous	0.53	<0.01	0.14	NS
3 months previous	0.36	NS	0.17	NS
4 months previous	0.59	NS	0.24	NS

Table 11 The correlation between wet vegetation biomass on the Nossob riverbed and the density of the springbok population and of territorial males counted on the riverbed.

The density of the springbok on the riverbed could be related to vegetation levels on the riverbed during a particular month and for two months afterwards. Whilst the population density on the riverbed could be related to vegetation levels, this was not true for territorial males during a particular month or over the four previous months.

f) Utilisation of waterholes

The proportion of the springbok population and of territorial males within one kilometre of water were compared in different months. The percentage of animals ≤1km from water are shown in Figure 19. It was found that the distribution of the population relative to waterholes varied significantly between seasons (χ^2=2344.00, df=7, $p<0.001$) over the study period.

The proportion of springbok found in the proximity of waterholes reached a peak in July and August over the study period. This also corresponds to the time at which the density of the springbok population on the riverbed could no longer be related to monthly rainfall. The two full years which were studied showed the same distribution pattern of springbok relative to the waterholes. A greater proportion of springbok were found close to water in the cool-dry than the hot dry than the hot-wet season

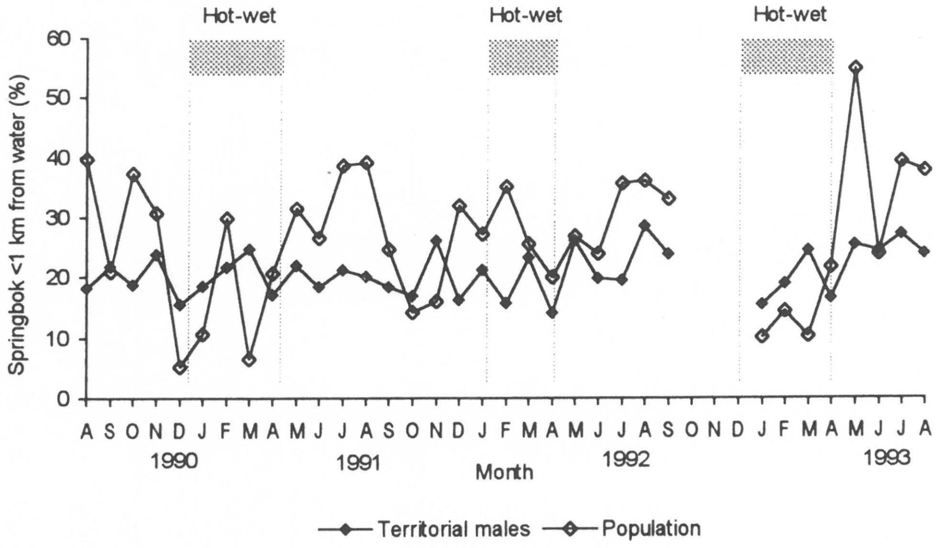


Figure 19 The relative numbers of territorial male springbok and of other individuals ≤ 1 km from waterholes in different months (hot-wet season shaded)

(Table12). However during 1992, following poor rainfall, this trend was not pronounced and individuals made greater use of the waterholes in the hot-wet season of this year than in any other year.

Year	Season		
	Hot-wet	Cool-dry	Hot-dry
1991	16.1%	33.7%	20.5%
1992	26.0%	31.0%	29.7%
1993	13.9%	40.2%	N/A

Table 12 The proportion of all springbok, excluding territorial males, seen $\leq$ 1 km from waterholes in different seasons.

The proportion of territorial males within one kilometre of water showed no such fluctuation but remained constant between seasons (χ^2=5.09, df=7, NS). A comparison between the proportion of territorial males and females within one kilometre of water in different months showed that the two varied independently of each other (Figure 20; r_s=0.13, n=34, NS). In comparison, the distribution of non-territorial males and females relative to water were not independent of each other and the two were closely related (Figure 20; r_s=0.87, n=34, p<0.001). Similarly the proportion of territorial males within one kilometre of water was independent of the proportion of non-territorial males within one kilometre of water in a given month (r_s=0.12, n=34, NS). Though the distribution of territorial males did not vary seasonally relative to the waterholes, more territorial males were found within one kilometre of water than would be expected if they were distributed evenly along the course of the riverbed

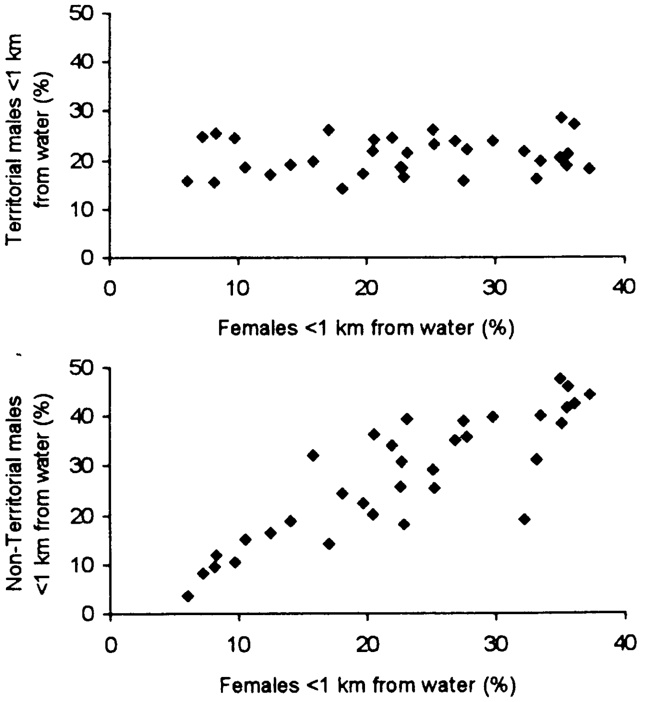


Figure 20 Variation in the number of territorial and non-territorial males within 1 km of water, in relation to the number of adult females within 1 km of water in different months

(χ^2=169.89, df=1, $p<0.001$) *i.e.* territorial males were clumped around areas close to waterholes.

2. *Calcareous pans*

Springbok made regular use of the pans in the area. Whilst records of springbok numbers were frequently recorded at Kwang pan, they were only recorded once a month at the Sewe Panne complex. The average total monthly density of springbok on Kwang pan did not differ significantly from the monthly density of springbok at Sewe Panne (Wilcoxon matched-pairs; Z=1.31, n=22, NS). As the number of springbok counted on the pans showed considerable daily variation, Kwang pan has been used to illustrate the underlying principles.

The density of springbok on Kwang pan is shown in Figure 21. The way in which springbok used the pans differed markedly from their use of the riverbeds. The density of springbok on the pan peaked at 22.3km^{-2} in February 1991 and 192.5km^{-2} in April 1993. The difference between these densities was attributed to the difference in rainfall between these two years; in 1992 no vegetation was obvious on the pan, whilst in 1993 a green flush was seen. Though no quantitative data were being collected at the time a more substantial green flush was observed in March 1991 following that year's good rain. Whilst the density of springbok on the riverbeds could be related to rainfall for one to four months following rain, on Kwang pan the density of springbok could only be related to rainfall two months previously (r=0.63, n=22, $p<0.005$). This shows the 'all or nothing' utilisation of the pans. For the Sewe Panne complex a similar trend

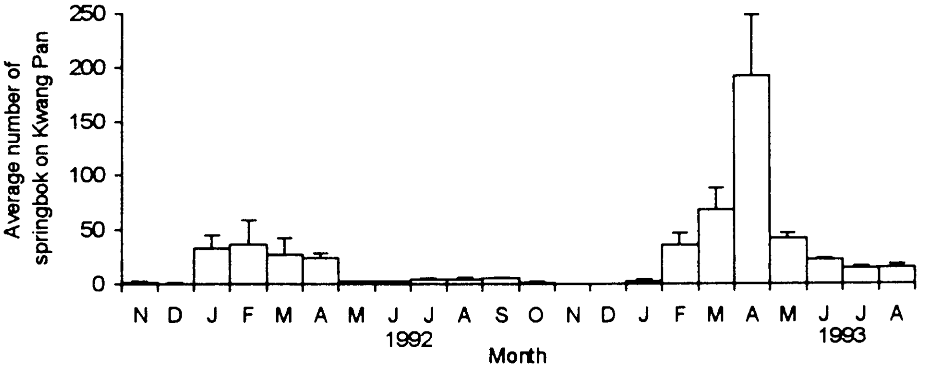


Figure 21 Monthly variation in the mean number of springbok on Kwang Pan

was found though with the high variation in the numbers counted this was not found to be a significant relationship.

The relationship between pan size and the mean number of springbok found on the Sewe Panne complex, together with Ratel pan was also examined; as pan size increased so did the mean number of springbok on the pan (Figure 22; r=0.86, n=8, p<0.01).

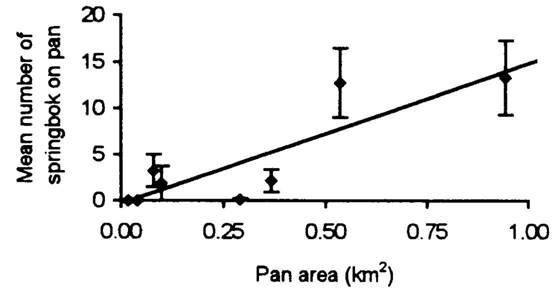


Figure 22 The relationship between pan size and the mean number of springbok observed on the pan

3. Habitat selection: riverbed, pans and dunes

The relative density of springbok using the three habitat types each month are shown in Figure 23. Springbok density was significantly higher on the riverbed than the pan habitat (Wilcoxon matched-pairs Z=3.99, n=22, p<0.001). Only in April 1993 did the density of springbok on Kwang pan exceed that of the riverbed. It was concluded that whilst there may have been selection for this habitat during this month, springbok show

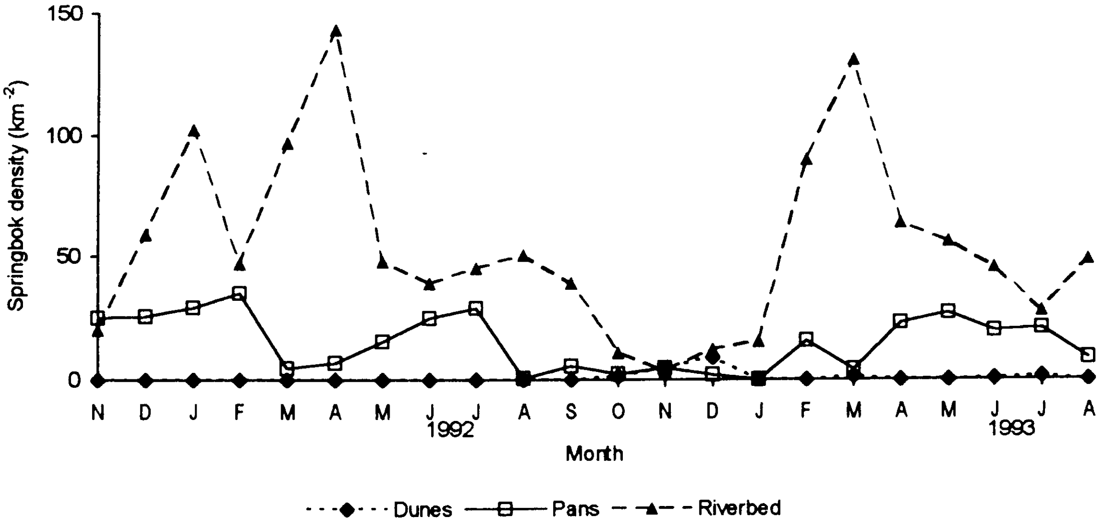


Figure 23 Monthly variation in the density of springbok on the Nossob riverbed, calcareous pans and the dune system

a strong preference for the riverbed habitat through the year.

Comparing the utilisation of the pan and dune habitats, springbok were found in higher densities on the pans than in the dunes (Wilcoxon matched-pairs Z=3.78, n=22, p<0.001). Thus whilst springbok mainly prefer the riverbed to the pan habitat, there is a strong preference to utilise the pan relative to the dune habitat. Only at the end of the 1992 hot-dry season, following the relatively dry year, did springbok move into the dunes in any numbers. This was the only time during which the density of springbok on the dunes exceeded that on the riverbed or pans.

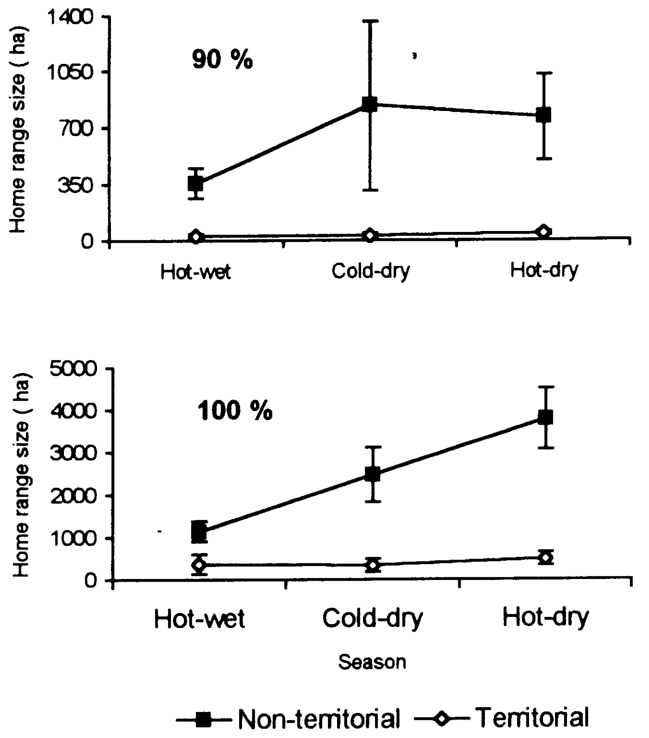


Figure 24 The home ranges of adult male springbok, showing both the effect of their status and the season

Males were observed holding territories on both the riverbeds and pans. Though solitary males were observed in the dunes there was no evidence that they were holding territories in this habitat. It was more likely that they held territories elsewhere and were simply feeding in the dunes, as was observed amongst males which were being closely followed (chapter five).

4. *The effect of season on the home ranges of adult males*

The 100 % and 90 % home range areas of territorial and non-territorial males recorded in different seasons are shown in Table 13 and Figure 24. From this it can be seen that the home range areas of territorial males did not vary substantially over the

Season	Territorial male range (ha)		Non-territorial male range (ha)	
	100 %	90 %	100 %	90 %
Hot-wet	370±235	29±13	1140±240	360±95
Cold-dry	342±155	29±15	2470±635	835±530
Hot-dry	490±147	44±13	3790±720	765±265

Table 13 Comparison of the 100 % and 90 % MCP home ranges of territorial and non-territorial males, showing the effect of both a male's status and the season on rangeing behaviour

different seasons (100 % MCP: KW ANOVA, Z=3.96, n=84, NS; 90 % MCP: KW ANOVA, Z=1.98, n=84, NS).

This contrasted to the home range use of non-territorial males. These males appeared to increase the size of their home ranges from the wet season to the dry seasons as conditions on the riverbed deteriorated (Table13; 100 % MCP: KW ANOVA, Z=8.42, n=42, p<0.02; 90 % MCP: KW ANOVA, Z=1.20, n=42, NS). This was true when considering the 100 % MCP data, whilst the 90 % MCP is probably too conservative an estimate because of the problems associated with tracking these animals over large distances in the dry seasons.

5. *The effect of social status on the home ranges of adult males*

The status of a male, as well as season (Table 13) were important in determing rangeing behaviour of males. In all seasons the home ranges of territorial males were substantially smaller than those of non-territorial males (Figure 25; 100 % MCP; Hot-wet: Mann Whitney U, Z=3.79, n=42, p<0.0001; Cold-dry: Mann Whitney U, Z=4.34, n=48, p<0.0001; Hot-Dry: Mann Whitney U, Z=4.29, n=36, p<0.0001).

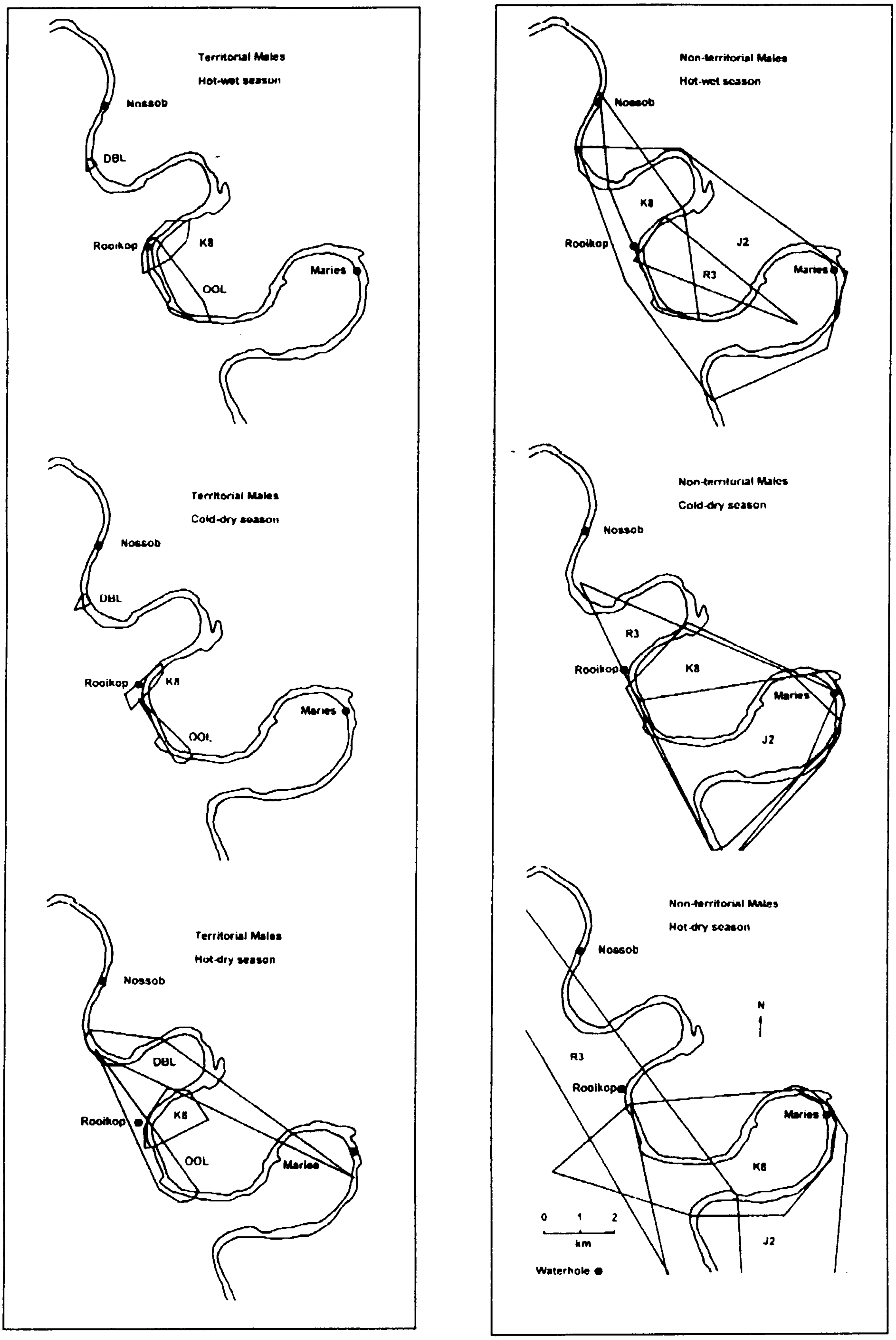


Figure 25 The relative home-ranges of three territorial (DBL, K8, OOL) and non-territorial (J2, R3, K8) males in different seasons. N.B. Home range of male K8 shown both when a territorial and non-territorial male

DISCUSSION

It is clear that the demography of non-territorial males differed from that of territorial individuals. Non-territorial males, lacking the spatial constraints imposed on themselves by territorial boundaries moved more freely in their environment. Thus changes in their habitat utilisation were based upon proximate environmental factors such as rainfall, vegetation biomass on the riverbed and the availability of drinking water.

Males which occupied territories, many of them perennially, were unable to respond as effectively to these environmental fluctuations as non-territorial individuals. This is reflected in their movements, as their density on the riverbed could not be shown to fluctuate in response to changing conditions. Instead their utilisation of the riverbed habitat remained more constant throughout the year and their density appeared to be controlled more by rutting periods and the first substantial rainfall of the year than anything else (see chapter ten for details of territory acquisition and turnover). Further, the home ranges of territorial males did not change over the course of the year, whilst those of non-territorial males increased with deteriorating environmental conditions. The rangeing movements of territorial and non-territorial male springbok follow the generalised findings of Grant *et al.* (1992) that male ungulates not restricted by a defended area range more extensively than those which choose to defend a territory. However it should be noted that the home ranges of territorial males are undefended areas, the only defended area being their territory itself.

In contrast to territorial males, non-territorial rams and ewes appeared to respond similarly to fluctuations in habitat quality. The proportion of non-territorial males on the riverbed relative to females did not alter as female densities changed in different months. So too the proximity of non-territorial males to waterholes did not fluctuate differently to that of females.

It is significant that springbok will concentrate around waterholes at particular times as they can survive long periods without water (Child *et al.* 1972). It was concluded that the demography of both females and non-territorial males were largely influenced by environmental conditions. The demography of territorial males appears to be determined by other factors, particularly the breeding periods, which override their ability to respond as effectively to environmental variables as other individuals.

The proportion of adult male springbok which were territorial in the population is similar to that found in other studies. Jarman & Jarman (1973*b*) reported 33% of impala males were territorial at any one time. For wildebeest 10-20% of the total population were territorial (Estes 1969), as were 10% of male waterbuck (Wirtz 1981). As territorial status appears to be a pre-requisite to achieve mating success in springbok (chapter eleven), it appears as though only about 20% of males are in a position to breed in any one year.

Whilst the riverbeds make up less than five percent of the available habitat, they contain far higher springbok densities than the surrounding dune areas. Springbok used the riverbeds to a varying extent throughout the year. Thus the riverbed would appear to be the most attractive area in which males could establish territories. This is reflected in the activity of males which maintained territories on the riverbeds at all times of the year.

Territories were also observed on the calcareous pans. No tagged individuals were present on the pans, but it appeared that males only held territories on the pans when environmental conditions allowed, from the start of the rains through until the cold-dry season. The 'all or nothing' utilisation of the pans by the springbok population is in accordance with Eloff's (1959, 1961, 1962) findings, who reported seeing large concentrations of springbok on Mabua Sehubi and Kang pan, Botswana, during March and April. During years of poor rainfall, such as 1992, herbaceous annuals are virtually absent (van Rooyen *et al.* 1984). Correspondingly no substantial numbers of springbok were observed on the pans in this year and no marked increase in the number of territorial males was seen.

At no time were males observed holding territories on the dunes, though solitary males were observed in the dune habitat. Focal watches of some of these individuals identified them as males which had left their riverbed territories to feed in the surrounding dunes. During August *Acacia melifera* bushes, which are found predominantly on the dune habitat, came into flower. It has been found in other antelope species (*e.g.* impala, Jarman 1971, Rodgers 1976; mountain gazelle, Baharav 1983; greater kudu, Owen-Smith & Cooper 1989) that individuals are particularly attracted to the flowers of certain plants. Similarly the springbok will heavily browse the flowers of *Acacia melifera* bushes. It is probably a combination of the flowering of such plants at this time and a deterioration in the condition of the vegetation available on the riverbeds that prompts the springbok to move away from the river habitat in the hot-dry season, when the dune habitat is most extensively utilised (Williamson 1985). Browsing is preferred to grazing on the lignified grasses available on the riverbed at this time (Davies 1985). The dunes can therefore be seen as a food 'reservoir' during the dry periods.

Although animals remaining on the riverbeds tended to keep close to permanent waterholes, particularly during the cold-dry season, but distributed themselves more evenly along the course of the riverbed during the wet period. Thus whilst the majority of the population gained nutritional and drinking advantages by their seasonal movements, territorial males gave up these opportunities by being more sedentary, showing no seasonal movement towards waterholes and using the dunes to a much lesser extent.

The sedentary nature of certain individuals has also been implicated in an increased risk of predation (Fryxell & Sinclair 1988). Fryxell *et al.* (1988) found that whilst 10% of the sedentary Ngorongoro wildebeest population was killed annually by lions, lion predation only accounted for one percent of individuals in the neighbouring migratory Serengeti population. Not only may territorial males be unable to capitalise on the nutritional advantages of seasonal movements, but they may also be exposed to an increased predation threat.

In conclusion then, males only maintained territories on the riverbeds and pan areas, where the density of springbok was generally far higher than in the surrounding dune areas. Their territories appeared to be resource-based, though this possibility is examined more thoroughly in chapter eleven. Whilst holding a territory could improve a male's reproductive success, some of the costs could be related to their restricted rangeing behaviour and limited response to changing environmental conditions relative to non-territorial males and females.

SUMMARY

- In a given year approximately 20% of males achieved territorial status.
- Fossil riverbeds appeared to be the favoured habitat type, whilst calcareous pans were used in preference to dune areas.
- Utilisation of the riverbed by the springbok population showed seasonal variation, being used most extensively in the hot-wet and most sparsely in the hot-dry seasons.
- Springbok appeared to use pans on an 'all or nothing' basis, utilising them extensively in March and April, but little at other times of the year.
- Springbok moved into the dunes as the dry season progressed, with a corresponding increase in browsing activity, but their density on the dune habitat was always relatively low.
- Springbok used the riverbed in response to rainfall patterns and the subsequent plant growth, grazing extensively after rain.
- Territorial males differed from other individuals in that their density was independent of fluctuating environmental variables, numbers peaking during rutting periods.
- The proportion of non-territorial males, relative to females remained constant at differing female densities on the riverbed, whilst that of territorial males increased at lower female density, indicating a similar response by females and non-territorial males to environmental variables which was not synonymous to the response of territorial males.
- The home ranges of non-territorial males were larger than those of territorial males in all seasons, indicating a greater response to fluctuating environmental variables.
- Utilisation of the areas surrounding waterholes was similar for female and non-territorial but not for territorial males. These individuals aggregated around waterholes most in the cold-dry and least in the hot-wet seasons. Territorial males showed no such seasonal variation.

Chapter 7

Social organisation and predation risks

INTRODUCTION

The social organisation for many antelope species is widely documented. Walther (1972*b*) discusses a variety of social groups amongst Grant's gazelles including female herds, 'harem' herds, solitary males and bachelor herds. Similar descriptions of social organisation are discussed in the literature for a number of species, including gerenuk (Leuthold 1978), bontebok (David 1975), impala (Jarman & Jarman 1973*b*), topi (Jewell 1972) and blue wildebeest (Estes 1969). Whilst these give a basic understanding of a species' social organisation, most fail to describe any dynamic fluctuations in group organisation or the factors controlling such variation (but see Murray 1981).

In chapter six it was found that springbok responded to rainfall by accumulating in larger herds on the fossil riverbeds. Whilst this is different from the more commonly recorded pattern of dispersal over wet periods and aggregation during the dry season, it demonstrates an adaptive response to the available physical resources. Such variation of population demography has been documented in a number of species. Whilst *environmental* factors have been considered which may affect populations, the *social* affects of individuals on group structuring have received far less attention.

One of the prerequisites of territoriality is that such individuals are dominant over other individuals on their territories *i.e.* males may exhibit dominance over all other rams on their territory. As a consequence other males may be excluded from a territory, particularly during the breeding season; Murray (1981) noted that non-territorial impala rams were found in areas of comparatively dense herbaceous material avoided by female herds.

Following the rut the collapse of territoriality amongst impala populations leads to a free mingling of all age and sex classes (Jarman & Jarman 1973*b*, Rodgers 1977). Similarly, du Plessis (1972) reported that territorial male blesbok did not tolerate non-territorial males during the rut, but that large mixed-sex herds occurred after the rutting period. These results suggest that territoriality has an organising effect on both impala and blesbok society. Likewise, bachelor groups of waterbuck, which had avoided areas occupied by territorial males during the rainy season were found feeding in the same areas during the dry season (Tomlinson 1981). Underwood (1982*a*) compared the companionship indices, during the peak of conception, of 'average' males and males with at least one female for several species, corresponding probably to bachelor and territorial males. 'Average' males were found to associate significantly more with other males and less with females in impala, tsessebe, wildebeest, kudu, and zebra than males with at least one female. Changes in the behaviour of territorial males could therefore have an effect on the social structure of the population.

Gregariousness has been attributed to a number of factors including predation risk and forage quality (Fryxell 1991). Both theoretical (Hamilton 1971, Vine 1971, Treisman 1975) and field studies (Schaller 1972, Kenward 1978) have demonstrated that group formation reduces vulnerability to predation. Predation risk to individuals should decrease with increasing group size (Dehn 1990). Gregariousness both reduces individual vigilance times whilst increasing overall group vigilance (Berger 1978, Siegfried 1980, Lipetz & Bekoff 1982, Underwood 1982*c*, Brown & Brown 1987) and reduces the probability that a particular individual within a group is predated. However individuals found towards the periphery of groups (Milinski 1977, Rayor & Uetz 1990) and lekking grounds (Balmford & Turyaho 1992) as well as less vigilant individuals (Fitzgibbon 1988) are selected by predators more frequently than other individuals.

In many ungulate species there is a tendency for solitary individuals to be male, presumably as a consequence of territorial behaviour. It is also true that males tend to occupy more peripheral positions within a herd than females, as well as occurring in smaller herds and showing decreased vigilance levels than females (Fitzgibbon 1990). Thus it was expected that predation rates should be higher amongst male than female springbok.

This chapter investigates the social structure of springbok and has two principal aims. First, to see if the aggressive behaviour of territorial males has an effect on social grouping amongst springbok. Second, to see if the behaviour of males and particularly of territorial individuals increases their predation risk, leading to intersexual variation in mortality rates and thus contributing to a female biased sex ratio in the adult population.

METHODS

The level of intraspecific aggression was monitored in territorial springbok rams, and its possible consequences analysed on a monthly basis. In parallel to this work data were collected on the association of individual springbok to determine whether any variation could be attributed, amongst other factors, to the rut or females with young dissociating from other individuals.

Interherd group structure Data were collected in the course of routine monthly population counts (see chapter three for details). The data for adult springbok extended between August 1990 and July 1991, covering every month of a two year period. Specific data on lambs were collected during the first two months of the year's lamb crop. These periods cover January and February of both 1991 and 1992. Any comparisons made between individuals of different statuses are made within these periods. Thus lambs are compared with other individuals only for the January and February counts, whilst comparisons between adults are made over the two year period. This includes the adult sex ratio. The sex ratio of lambs was calculated when individuals could first be reliably sexed during population counts at 2-3 months of age. Infant mortality figures are based on the number of immature animals (less than one year old) counted in a particular month in relation to the number of adult females counted. As springbok only produced one major lamb crop a year, and as most lambs were born within a few weeks of one another, these did not provide complicating variables.

Intraherd group structure Each month between November 1991 and October 1992 specific details were collected on each individual within a group. Where possible these were made at the same time as the population counts. However where additional data were required these were collected by systematically analysing every herd encountered over the data collection period, rather than haphazardly collecting data from herds as this may have led to a bias in the data set.

Animals were observed at ranges of less than 150 m from a stationary vehicle using a pair of 10 x 50 binoculars. Information was punched directly into a database file on a Psion "Organiser" pocket computer. Variables that were recorded included an animals sex and age, the sex and age of its nearest neighbour, the distance between the focal animal and its neighbour, its position within the herd (centre or edge) and the size of the herd in which it was observed. The nearest neighbour was defined as the individual the focal animal's head was closest to. The distance between individuals was recorded from the focal animals head to the nearest part of its neighbours body. As the ability to estimate inter-animal distances decreases as the distance increases the following discreet distances were used in the estimate; 0, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 12, 15, 18, 20, 25, 30, 40, 50, 60, 70, 80 and 90 metres. The ability to estimate distances was regularly checked against objects at known distances.

A measure of the tendency for individuals to associate with other individuals of a particular status was devised; the neighbour preference ratio (*NPR*). For an individual of status x and neighbour of status y the $NPR = \frac{xy(\text{expected})}{xy(\text{observed})}$ from the population.

Thus an *NPR* of 1 should be obtained if the association between x and y is random and the frequency of their proximity is a result of the total frequency of x and y within the population. However if the frequency with which x and y are associated is not random then we would not expect the *NPR* to equal 1. For individuals showing a positive association then $NPR>1$ and those showing a negative association $NPR<1$.

Time budgets Details of individuals' time budgets (see chapter three for details) were used to determine the vigilance levels maintained by adult springbok of different status. They were also used to calculate the level of aggression (chasing behaviour) territorial males displayed to other males during different months and the rut.

Vegetation height The height of the predominant vegetation present in the riverbed was recorded every kilometre during the population census in March 1991. The height of the vegetation in which springbok were encountered was also recorded. Both heights were measured using a steel tape held perpendicularly to the ground. Vegetation height was divided into three sub-sets; <35cm (short), 35-69cm (medium), ≥70cm (tall).

Vigilance Vigilance levels (watching or alert behaviour) were recorded for focal individuals. Data were collected every three minutes by instantaneous sampling. In order to control for the possible effect of group size on vigilance, a comparison was made between focal individuals in groups of different sizes. Group size ranges of 0-1, 1-2, 2-5, 5-10, 10-17, 17-30 and >30 were used in the data analysis.

Injury and predation In the course of other fieldwork notes were taken on the age/sex of any injured animals as well as the nature of their injuries. Data were collected in the same manner for any springbok kills that were seen. Note was made on predator species. In cases where a predator had left a kill it was sometimes possible to determine the species from proximate cues such as spoor or, for leopard, a carcass hanging in a tree.

Mills (1984) witnessed lions consuming a springbok lamb in less than five minutes whilst Eloff (1973) observed that small sized prey such as springbok lambs were consumed almost entirely by lions. In the light of these findings, no attempt has been made to compare the rate of predation on lambs with sub-adult and adult springbok.

RESULTS

1. Social organisation

a) Group structure

Of all the springbok counted 97.6% (n=69714) were found within a group (2 or more animals) and 2.4 % were solitary. Of the solitary animals that were counted 1623 (95.6%) were adult males, 57 (3.4%) were adult females and 17 (1.0%) were non-adult males and females. Thus, significantly, 7.4% of all adult males were solitary whilst only 0.2% of the total female population were solitary (χ^2=2402.00, df=1, p<0.001). The proportion of male springbok in a group decreased with increasing group size (ANOVA, F=114.2, df=2247, p<0.001; Figure 26), whilst the proportion of ewes increased (ANOVA, F=67.3, df=2247, p<0.001; Figure 26). Thus small groups contained a disproportionately high number of males and large groups of females. Only 6.4% of males were found in herds in which no adult female was present.

Considered in terms of group frequency, and not the frequency of the individual within the group, 41.1% (n=3945) of 'groups' were of a solitary male, 43.0% mixed sex groups (containing one or more males and females), 10.2% were groups containing no adult female and 2.5% were groups containing no adult male. All other groupings made up only 3.2% of sightings.

A total of 2828 sightings of collared or ear-marked rams were made whose status as a territorial or non-territorial individual was known. Their occurrence with other adult springbok is recorded in Table 14. Territorial individuals accounted for 82.4% of sightings of solitary males. The relative frequencies with

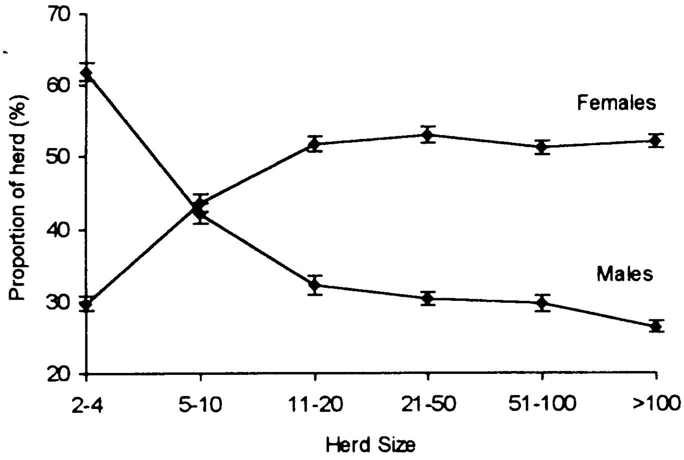


Figure 26 The effect of herd size on the proportion of adult male and female springbok present in the herd

which territorial and non-territorial males were sighted with other individuals differed significantly ($\chi^2=568.9$, df=3, $p<0.001$); territorial males were found far more frequently on their own or exclusively with females than non-territorial males. Non-territorial males were found more often in mixed herds and all-male groups than territorial rams. Interestingly, non-territorial males were seen more often together with adult females than territorial males were.

	Solitary	Females only	Males & Females	Males only	(n)
Territorial males:					
Overall	45.9	21.4	26.3	6.3	2163
On territory	49.3	24.1	21.5	5.1	1799
Off territory	29.1	8.2	50.3	12.4	364
Non-territorial males:	10.5	4.4	66.0	19.1	665

Table 14 Re-sightings of marked animals of known status, showing the proportion of times they were seen with other adult springbok

The association of males changed significantly when on or off their territories ($\chi^2=182.4$, df=3, $p<0.001$); the proportion of time they spent with mixed-sex groups and male-only groups increased and consequently they spent less time by themselves or exclusively with females.

b) Position of individuals within a herd

Overall, a greater proportion of adult male springbok (82.1%, n=3747) were found on the periphery of herds than adult females (76.5%, n=5987; $\chi^2=43.09$, df=1, $p<0.001$). However as group size increased so the proportion of female springbok increases and that of males decreases. This may account for more males being found at the edge of groups. To investigate this possibility herds were grouped into a number of size classes and the position of animals within those classes was examined (Table15). More males were found at the periphery of herds, within individual herd classes, than expected from the population ($\chi^2=26.66$, df=4, $p<0.001$). The position of females within group classes did not differ from that expected for the population ($\chi^2=2.23$, df=4, NS).

Herd size	Centre		Edge	
	Male (%)	Female (%)	Male (%)	Female (%)
2-12	94.8	95.5	5.2	4.5
13-25	88.0	84.7	12.0	15.3
26-40	82.5	74.5	17.5	25.5
41-70	70.3	70.0	29.7	30.0
>70	64.5	60.1	35.5	39.9

Table 15 The proportion of adult male and female springbok observed at the edge and centre of herds of differing size

c) Nearest neighbour distance

The distances between adult springbok of both sexes and their nearest neighbour, relative to their position in the herd, are shown in Table 16. For animals positioned in the centre of a herd the distance to their nearest neighbour did not differ between the sexes (t=-0.03, df=2073, NS). Males at the edge of herds were found, on average, to be 11.8±0.3m (n=3074) from their nearest neighbour and females to be 7.5±0.2m (n=4576) from their nearest neighbour; males at the edge of herds were found at greater distances from their nearest neighbour than females (t=13.82, df=7648, p<0.001). Both male and female springbok at the edge of herds were found at greater distances to their nearest neighbour than centrally positioned individuals of the same sex (males; t=13.11, df=3742, p<0.001, females; t=11.96, df=4870, p<0.001).

The distances between adult springbok of both sexes and their nearest neighbour, relative to the sex of the neighbour, are shown in Table 17. The average distance of males from their neighbour could not be attributed to the sex of that animal (t=1.52, df=3270, 0.05<p<0.1). Female springbok were found to be closer to female than male neighbours (t=-5.65, df=4870, p<0.001). Male springbok were found to maintain a greater

Sex	Distance to neighbour	
	Centre	Edge
Male	3.65±0.23 m	11.84±0.29 m
Female	3.65±0.17 m	7.50±0.17 m

Table 16 Nearest neighbour distances of adult springbok, in relation to their position in a herd.

Sex	Distance to neighbour	
	Male	Female
Male	11.01±0.35 m	10.19±0.42m
Female	8.43±0.39 m	6.33±0.17 m

Table 17 The relative distance of adult male and female springbok to their nearest neighbour, relative to the sex of the neighbour

neighbour distance than females for both animals of the same sex ($t=13.59$, $df=5619$, $p<0.001$) and of the opposite sex ($t=3.08$, $df=2521$, $p<0.005$).

d) Neighbour preference

Male springbok were generally found to be positioned closer to other males more often than expected, correcting for the adult sex ratio, within a given month ($\chi^2=618.4$, $df=11$, $p<0.001$). Conversely they were found adjacent to females less often than expected ($\chi^2=162.0$, $df=11$, $p<0.001$). In the same way female springbok were found to have another female as their nearest neighbour more frequently than expected from the population ($\chi^2=257.02$, $df=11$, $p<0.001$) and a male less frequently ($\chi^2=276.91$, $df=11$, $p<0.001$).

Overall males were found adjacent to other males 51.4% and females 36.0% of the time. Females were found adjacent to other females 61.8% and males 19.6% of the time. The degree to which animals associated with each other was examined to determine whether this difference was constant throughout the year or varied from month to month. Changes in the neighbour preference ratio are shown in Figure 27. For males there is both seasonal variation in their association with other males ($\chi^2=51.66$, $df=11$, $p<0.001$) and females ($\chi^2=67.24$, $df=11$, $p<0.001$). Males were found to associate most closely in January, when the springbok lambed, and the rutting periods in March and July when the aggressive behaviour of territorial males was at its

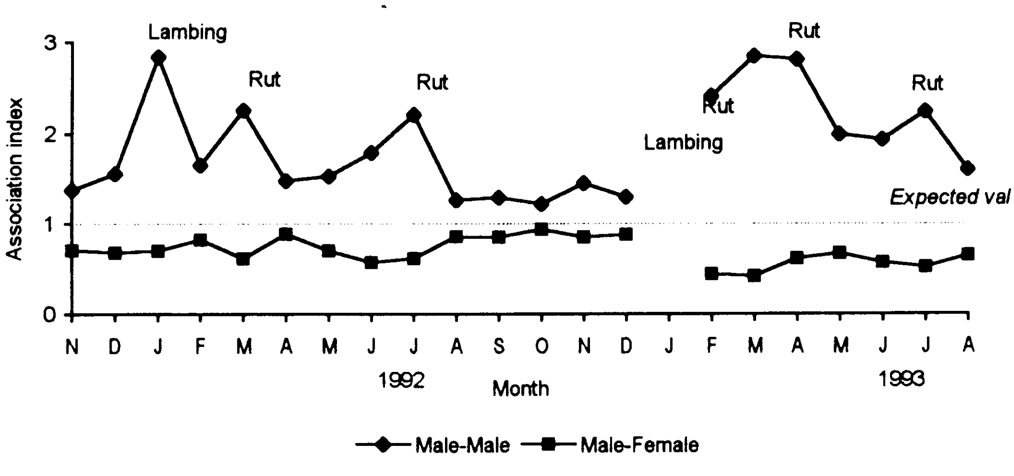


Figure 27 Monthly variation in the association of male springbok with other males and females

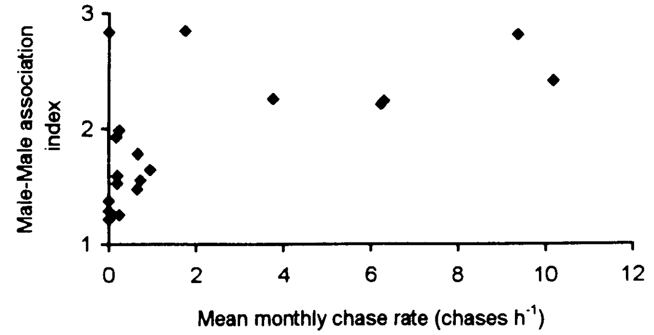


Figure 28 The effect of chasing behaviour by territorial males on the level of association between male springbok

highest. The period during which males were found together the least followed the rut. This is the period in which males were found to associate most with females. Springbok ewes were also found to show seasonal variation in their association with other females and males. The extent to which females associated with each other was lowest between the two ruts and following the July rut. These were the times at which female springbok were found to associate most with males.

e) Influence of the territorial male

Territorial male springbok, outside the peak lambing month, influence the degree to which male springbok associate with each other. It was found that the degree to which adult males associated could be directly correlated to the rate at which they were chased by territorial males in a given month ($r=0.73$, $n=20$, $p<0.001$; Figure 28). As intruding males were chased more frequently by territorial males, there was a tendency for males to associate more with each other.

Observations were also made on the rate at which territorial males chased other males when only males were present on their territory and when both males and females were present. When the two were compared on a monthly basis it was found that territorial males chased other males at a higher rate when females were also present (Wilcoxon matched-pairs; $T=0$, $N=9$, $p<0.005$). This should provide some pressure for males to associate together in single sex herds, particularly during the rut when the rate at which non-territorial males were chased was greatest.

f) Population sex ratio

Analysis of springbok counts over a two year period gave a sex ratio amongst adult springbok of 1:1.60 towards ewes. Males made up 38.4% of the adult population and females (61.6%, n=56935). This differs markedly from the sex ratio expected within the population if the sex ratio of springbok at birth is unbiased and mortality rates are equal between adult male and female springbok.

An examination was made of the sex ratio of individuals as soon as the sexes could be reliably identified (approximately 2 months) after birth. In 1991 a sex ratio of 1:1.01 towards females was calculated, based on a count of 1063 lambs, suggesting no selection acting on the sexes at this stage of development (χ^2=0.05, df=1, NS). Similarly an insignificant bias of 1:1.20 towards females (χ^2=1.08, df=1, n=134, NS) was made on a much smaller sample of lambs in 1992, and 1:1.16 towards females (χ^2=0.58, df=1, n=110 NS) in 1993, also showing no significant shift from parity. As the sex ratio of young lambs did not differ from parity, the shift in the adult sex ratio must be attributed to differential mortality rates between the sexes in sub-adult or adult springbok.

The sex ratio was subsequently analysed amongst sub-adult springbok. The sub-adult female:adult female ratio peaked 15 months after the lambing peak before declining, whilst the sub-adult male:adult male ratio did not decline until an age of 21 months. These indicate the maximum ages at which sub-adults of both sexes could be accurately identified in the field. Consequently any differences in the sex ratio of sub-adults was made at 15 months to prevent any unnatural bias towards males. In 1991 a sub-adult sex ratio of 1:1.10 (n=323) towards males was found, showing no significant bias (χ^2=0.70, df=1, NS). For the 264 sub-adults which were observed in 1992, the calculated sex ratio of 1:1.05 towards females did not differ significantly from parity (χ^2=0.13, df=1, NS), which was also true in 1993 when a sex ratio of 1:1.06 towards males was calculated (χ^2=0.15, df=1, NS). Therefore the only bias recorded was in adult male and adult female mortality.

2. *Predation risk*

a) Debilitating injuries

Those debilitating injuries that were seen amongst adult springbok are summarised in Table 18. Of these 76.9% could be accounted for by damaged leg joints. There did not appear to be any bias in damage to the front or back legs (χ^2=0.75, df=1, NS), although the sample size is small. Such damage varied from a pronounced limp by animals, through animals whose leg joints were swollen to the approximate size of a snooker ball, to an animal whose wound was so severe the underlying bone and cartilage structure was clearly visible. All were considered to have impaired flight speeds. The next most common injury, though only accounting for 13.5% of injuries seen, was a missing eye. These were observed both from the absence of the eye and from the stream of vitreous humor left on the face when an eyeball had been punctured.

SEX	Leg: Front	Leg: Back	Leg: Unclassified	Eye	Hip (limp)	Punctured rumen	Total
Female	1	0	3	0	1	0	5
Male	18	14	4	7	0	4	47
Total	19	14	7	7	1	4	52

Table 18 Occurrence of debilitating injuries to both adult male and female springbok

Of those injuries incurred by adults, 89.7% (n=29) were to males and only 10.3% to females. Males were significantly more prone to receiving debilitating injuries than females (χ^2=57.76, df=1, $p<0.001$). Of the injuries that adult male springbok did receive 84.8% (n=26) were inflicted during the course of the ruts and 15.2% at other times of the year.

b) Cover

When the height of the vegetation along the Nossob riverbed was recorded during March 1991, at the end of the hot-wet season, all springbok showed a marked preference for areas of low cover, <35cm high (χ^2=1430.5, df=2, $p<0.001$) in which herbaceous plants were dominant (Figure 29). Given that springbok prefer areas of low cover, the distribution of different population sub-sets was examined to see if they differ from that of the overall population. In the areas of the shortest cover the occurrence of territorial rams, non-territorial rams and ewes was similar (Figure 30; χ^2=1.25, df=2, NS). In areas of intermediate vegetation height fewer territorial and more non-territorial males were found than one would predict (Figure 30; χ^2=7.84. df=2, $p<0.05$). More territorial rams were seen than expected in the areas with the tallest vegetation cover (Figure 30;$\chi^2=103.6$, df=2, $p<0.001$). These areas were dominated by dense stands of the annual grass *Shmidtia kalahariensis* and the shrub *Galenia africana*. It is the distribution of the territorial rams which deviates most significantly from that of the overall population, in areas characterised by their high vegetation cover.

In March 1991, a month in which males would be expected to remain on their territories, a decline in territory occupancy was observed (see chapter ten). This occurred at the time when vegetation levels peaked on the riverbed. Though it was not possible to document events quantitatively, marked territorial rams were seen to aggregate together with other males, some of which were also marked territorial individuals. These groups were made up of between two and four animals. Some of these males were territorial neighbours and were found to interact aggressively with each other in the month preceding as well as that following their temporary aggregation. All marked territorial animals were found to interact with cheetahs in this month. It is suggested that there may have been a partial breakdown in territoriality as males grouped together in small anti-predator

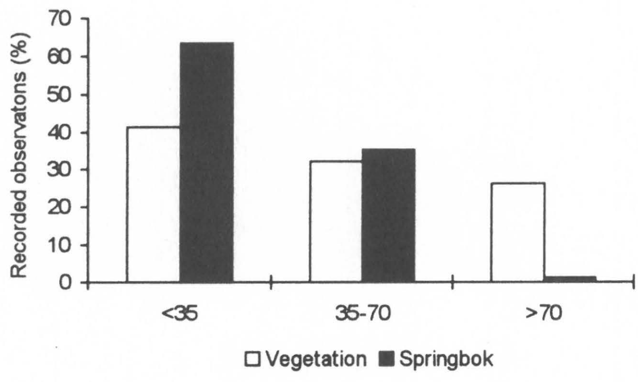


Figure 29 The relative distribution of springbok and vegetation of different heights on the Nossob riverbed

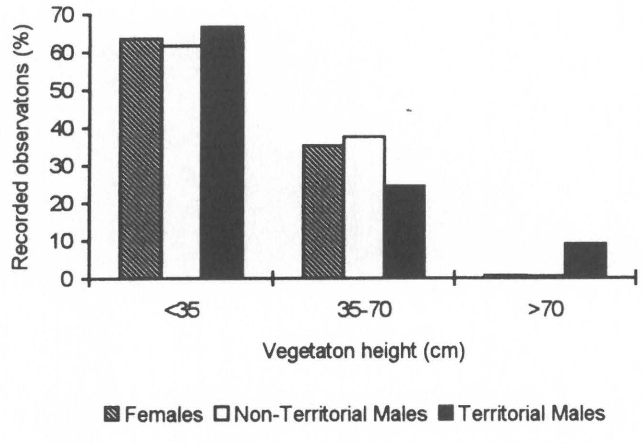


Figure 30 The relative distribution of adult female, non-territorial and territorial male springbok in relation to vegetation height on the riverbed

coalitions before returning to a more territorial existence.

c) Vigilance

Territorial males were found to be alert or simply watching for 7.0±0.6% of observation periods. This compared with 4.8±0.4% of the time for ewes and 4.8±0.4% of the time for non-territorial rams. Vigilance levels differed significantly between individuals of different status (KW ANOVA Z=10.6, n=1056, $p<0.005$), territorial males being significantly more vigilant than other individuals. No appreciable differences could be detected in the vigilance levels of non-territorial and female springbok (Mann Whitney U, Z=0.35, n=590, NS).

The higher vigilance levels of territorial males over other individuals may have been accounted for by the greater proportion of time they spent alone. Figure 31 compares variation in vigilance levels of territorial and non-territorial males when associating with different numbers of other adult springbok. Statistical analysis of the data showed no significant difference between the vigilance levels of territorial and non-territorial males, when present in a group of a given size (*e.g.* for 0-1 other group members; Mann-Whitney U, Z=0.17, n=183, NS).

As no significant difference between vigilance levels of the two male classes could be detected the data were pooled and analysed to determine whether vigilance levels were independent of group size. However a difference in vigilance levels was detected for differing group size (KW ANOVA; Z=19.95, n=719, $p<0.005$), individuals in larger groups spending less time

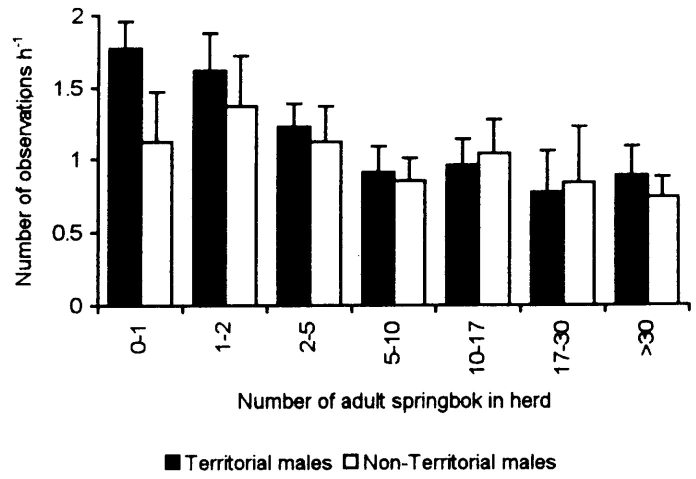


Figure 31 The effect of herd size (other adults in the herd) on the vigilance behaviour of territorial and non-territorial males; max=20

watching than those in smaller groups.

3. *Predation*

a) Prey analysis

Given the adult sex ratio it was expected that 38.4% of kills would be of males and 61.6% of females due to the preponderance of females in the adult population. However, significantly more adult male kills (64.1%, n=64) were observed than female kills (35.9%; χ^2=17.76, df=1, $p<0.001$). Considering cheetahs specifically, 56.7% of kills were of males (n=30) and 43.3% females; again a significant selection for males (χ^2=4.27, df=1, $0.02<p<0.05$). Excluding springbok lambs of 0-2 months of age, immature and sub-adult springbok accounted for 22.0% of all kills (n=82). These springbok make up 14.7% of the population (excluding lambs) and predation was not found to be significantly different on immature and sub-adult springbok than adults (χ^2=3.51, df=1, NS). Springbok lambs accounted for 17.2% (n=99) of all springbok kills observed.

b) Predators

The major diurnal predator of the springbok on the riverbeds appears to be the cheetah, accounting for 66.7% (n=69) of all springbok kills. Other predators observed include leopards (17.4% of kills), lions (5.8% of kills), jackals (8.7% of kills) and martial eagles (1.4% of kills). It would be of little meaning to go into further detail concerning these kill data. A number of variables were likely to add considerable bias to this data set.

4. *Natural mortality*

Recorded instances of non-violent mortality were low. This was due to the speed with which scavengers were able to utilise the carcasses. Those carcasses on which scavengers were found, but for which predation could not be determined were neither classified as non-violent mortalities nor predated. For this reason only six cases of non-violent mortality were recorded; two adult rams and four adult ewes. One of the rams was a confirmed anthrax case whilst the other was found, in a semi-conscious state, being brought down by jackal. Of the ewes one died during parturition and the others from old age or disease. Apart from the ewe which died in labour all were watched as they died. Three individuals were found which had become blinded because of a parasitic larva invading the eyeball.

DISCUSSION

The association between adult springbok of different sexes was found to be dynamic, changing over the course of the year. The rut and lambing were both important events affecting the social organisation of springbok herds. During the rut territorial males were less tolerant of other males, leading to other males being evicted from their territories, who then aggregated in non-territorial groups. During the lambing period females tended to associate together in maternal groups, such that males aggregated together by default. Following the rut there was a subsequent decline in the aggressive behaviour of territorial males. As lambs were now older the mother-young bond was presumably also weaker at that time. Thus there was little motivation for specific age/sex groups to either attract or repel one another and the population mixed much more freely than at any other time of year.

Most authors have previously differentiated between particular herd types (*e.g.* Estes 1967, Leuthold & Leuthold 1975, Walther 1981, Loggers 1992). For instance Bigalke (1970) considered mixed herds, solitary males and bachelor groups of springbok in the Kalahari Gemsbok and Etosha National Parks. Intersexual variation in the feeding habits have been suggested as a mechanism whereby males and females occupy different habitats outside breeding periods. Jarman & Jarman (1973*b*) noted that the collapse of territoriality in a population of impala during the dry season was concurrent with a free mingling of all age and sex classes. At this time territorial males are tolerant of and will freely mix with non-territorial males (Jarman, M 1979). Similarly, an increased tolerance of males after the rut was associated with the formation of mixed-sex winter herds in pronghorns (Gilbert 1973). Considering specifically the effects of adult male aggression on other members of the population Wahlstrom (1994) showed the significance of agonism as the proximate factor underlying yearling male dispersal amongst roe deer. The present study is one of the first accounts to suggest that the social behaviour of a wild ungulate population, rather than environmental variables, may directly influencing individuals' associations with conspecifics.

In almost all ungulate species which have been monitored a female biased adult sex ratio has been recorded (*e.g.* wildebeest: Estes 1969; topi: Jewell 1972; Grant's gazelle: Walther 1972*b*; tsessebe: Child *et al.* 1972; impala: Jarman & Jarman 1973*b*; gerenuk: Leuthold 1978; mountain gazelle: Baharav 1983; dorcas gazelle: Grettenberger 1987; greater kudu: Owen-Smith 1990, 1993). However Robinette & Child (1964) reported a male biased sex ratio amongst Kafue lechwe, which they attributed to a greater number of females being killed by locals for meat. Only in the equids is there substantial evidence for male biased adult sex ratios (Berger 1983). The ratio of male to female springbok lambs showed no bias when it was measured, as soon as individuals could easily be sexed in the field. Thus presuming no sex-based bias in neonate mortality rates the birth sex ratio for springbok should not differ from parity, in accordance with Brand's (1963) and Van Zyl & Skinners' (1970) findings. Unbiased sex ratios at birth have been recorded in other ungulates (tsessebe: Child *et al.* 1972; mule deer: Robinette *et al.* 1957; topi: Jewell 1972). Thus any bias in the adult sex ratio must be the result of a higher mortality rate amongst mature individuals of one sex and not a consequence of any imbalance at parturition, providing that there is no differential emigration of one sex from the area.

Some predators actively select young animals (Hornocker 1970, Fitzgibbon & Fanshawe 1989). In some species higher infant mortality has been reported for males than females. Jarman & Jarman (1973*b*) found a higher rate of survival to one year (40%) of female impala than males (20-35%), probably because of the eviction of young males from their natal herds. No such differential mortality was observed in springbok (though see Crowe & Liversidge 1977). This implies that the differential mortality rate between the sexes is occurring amongst adult animals, more than 15 months of age.

Disease, nutrition, injury, and predation are all factors which have been shown to increase mortality rates in males relative to females. Males have been shown to be more susceptible to disease in some species. Schaller (1972) noted that male Thomson's gazelles were more prone to sarcoptic mange than females and he found a greater proportion of males dying or dead from disease. Males may also be less able to withstand severe climatic conditions, either as a result of their higher metabolic costs or reduced body condition relative to females. Male-skewed mortality rates have been reported in a number of species due to nutritional and environmental stresses (mule deer: Robinette *et al.* 1957; reindeer: Klein 1968; nyala: Anderson 1980; wildebeest: Child 1972; pronghorns: Barret 1982, Byers 1989; Soay sheep: Grenfell *et al.* 1992). Springbok rams decrease their feeding rate during the rut (chapter eleven) and are possibly less selective in their food choice than ewes. Territorial rams also showed a greater tenacity to a particular area than other individuals (chapter six). One would therefore expect springbok males, and particularly territorial rams, to show a lower tolerance to adverse conditions than ewes, leading to a higher rate of natural mortality.

Whilst Skogland (1991) emphasises the importance of food limitation, rather than predation in limiting large ungulate populations, there was little evidence to support the idea that poor condition and disease were important factors in biased male mortality in springbok. Likewise Owen-Smith (1993) found that almost all kudu mortality occurred through predation. However it was not possible to determine the condition of individuals selected by predators, which may have been poorer than that expected from the population as a whole. Fitzgibbon & Fanshawe (1988) showed that Thomson's gazelles that stotted at lower rates, and were presumably weaker individuals, were more likely to be selected by wild dogs; certainly those individuals which were captured had lower bone marrow fat and were therefore in worse condition than other individuals (Fitzgibbon & Fanshawe 1989). Similarly Kenward (1978) found that goshawks singled out defective woodpigeons when hunting. The reproductive effort of springbok rams has other more immediate consequences for their survival than that through periods of food deprivation. Their increased injury risk, particularly during the rut, should increase predation pressure. Both spotted hyaenas and cheetahs were seen on occasion running through springbok herds, probably in search of injured animals.

The results of this study do clearly show the differential predation rates on adults males over females. Similarly studies of large carnivore predation on ungulates show this to be a common phenomenon (*e.g.* mountain lions: Hornocker 1970; cheetahs: Mills 1984; wild dogs: Estes 1967; lions: Schaller 1972, Owen-Smith 1993). Interestingly wild dogs appear to be equally successful in catching adult male and female Thomson's gazelles, but are twice as likely to hunt rams (Fanshawe & Fitzgibbon 1993) which suggests that flight ability *per* se was not a major factor contributing to biased mortality rates by wild dogs.

Ungulate social organisation certainly predisposes males to a higher predation risk. In other studies individuals in smaller groups, at greater distances from their nearest neighbour, more peripheral in groups, or in areas of taller vegetation (van Orsdol 1984) were found to be more heavily predated than other individuals. Fitzgibbon (1990) found all these attributes to increase predation rate amongst cheetahs hunting Thomson's gazelles, which predisposed males to higher predation pressure. Male springbok exhibit all the above criteria at higher frequencies than expected relative to females and are therefore also presumably at a higher predation risk than females. In relatively closed habitats individuals may compensate for poorer visibility by increasing vigilance levels (Underwood 1982*c*). This possibility was not explored, though individuals in smaller groups appeared to increase vigilance activity relative to those in large groups. The higher vigilance levels of territorial over non-territorial males could be attributed to such group-size effects.

The amount of time territorial males spent alone (see also Estes 1969) must increase their vulnerability to predation. Schaller (1972) found that the success rate of lions increased when hunting solitary members of social ungulates. Similarly cheetahs selected for solitary Thomson's gazelles (Fitzgibbon 1990). In experiments on fish (Milinski 1977, Landeau & Terbogh 1986, Parrish 1989) and birds (Kenward 1978) attacks on solitary individuals and stragglers were more successful than those on group members. This provides some strong support for the idea that singletons are more prone to predation than group members. Therefore one would expect the preponderance of solitary males which have been reported in a number of species (*e.g.* gerenuk: Leuthold 1978; Grant's gazelles: Walther 1972*b*; Thomson's gazelle: Fitzgibbon 1990) to contribute to their higher predation rates and consequently female biased adult sex ratios. Few accounts actually distinguish solitary males of different status, though in one population territorial impalas males spent about 30% of their time alone (M. Jarman 1979), and territorial male Grevy's zebras spent 42% of their time alone when on their territories and only 7% when off their territories as they tended to join groups of other males (Ginsberg 1988).

Finally, the importance of the cheetah as a major predator of adult gazelles was re-emphasised by the present results of cheetah predation in the Kalahari. They confirm Mills' (1984) findings. In Etosha N.P. 96.8% of cheetah kills were reported to be of springbok. In all cheetah accounted for 81% of springbok kills in the park (Berry 1981). Cheetahs only accounted for an estimated 9.6% of Thomson's gazelle kills in the Serengeti (Caro 1994). However this is due to their low densities in the area, and kill rate per individual was higher for cheetahs than any other predator species; Thomson's gazelles made up 66% of cheetah kills.

This chapter has shown the dynamic nature of springboks' social organisation, which fluctuated over the course of the year, and appeared to be influenced by the agonistic behaviour of territorial males and female lambing periods. Their social structure probably enhanced predation risk amongst males, and particularly territorial males, such that mortality was greater amongst adult male than adult female springbok.

SUMMARY

- Almost all solitary animals were adult males; of these over 80% were territorial.
- Disproportionately more adult males were observed in small groups relative to females.
- Males were positioned more peripherally in herds than females.
- For animals in the centre of herds, nearest neighbour distance was independent of sex. However males at the edge of herds were found at greater distances from their nearest neighbours than females.

- Male springbok tended to associate more with other males, and females with females within a given herd.
- The monthly rate of agonistic behaviour by territorial males was directly related to the degree of association between males; association was maximum during the rut, when agonistic behaviour peaked.
- Lambing also appeared to affect the degree of association between males; there was a high rate of male-male association over lambing periods, probably by default as a consequence of increased female-female association at this time.
- The adult sex ratio was female biased, though the sex ratio of lambs did not differ from parity.
- Almost 90% of debilitating injuries observed were amongst males, most occurring over the rutting periods.
- Though springbok generally favoured areas of low vegetation cover, more non-territorial males were found in areas of intermediate vegetation height and territorial males in areas of tall vegetation than were expected.
- When the herd size in which individuals were observed was taken into account, there was no difference in vigilance levels between individuals of different status.
- Individual vigilance levels decreased with increasing group size.
- Predation levels were higher for male than female springbok, specifically so for the cheetah.
- Cheetahs did not appear to select for immature or sub-adult springbok over adults.
- Cheetahs accounted for two thirds of all springbok killed.
- Natural mortality rates were low; sick and injured animals were probably removed by predators before natural death could occur.

Chapter 8

Territorial Advertisement

INTRODUCTION

Marking behaviour may serve as a form of territorial advertisement in the springbok. This chapter considers the methods and function of territorial advertisement in the springbok by identifying both the type of signals used, as well as the possible social and spatial motivation for their occurrence.

Johnson (1973), specifically discussing olfactory communication, detailed the following possible functions of marking behaviour which may be relevant to the present study:

1. As a deterrent or substitute for aggression, to warn conspecifics away from occupied territory.

2. As a sex attractant or stimulant.

3. As an indicator of individual identity, perhaps including data on sexual status, age, dominance *etc.*

Several types of marking behaviour have been documented amongst the ungulates. These may have olfactory, visual or auditory components. Such types of behaviour have been extensively recorded, and a role in territorial advertising implicated:

Linked urination-defecation. This is particularly common amongst medium-sized antelopes such as the Grant's gazelle (Estes 1967), mountain gazelle (Grau & Walther 1976), gerenuk (Leuthold 1978*a*), Thomson's gazelle (Walther 1978a), blackbuck (Dubost & Feer 1981), sand gazelle (Habibi *et al.* 1993) and pronghorn (Gilbert 1973, Byers 1989). It has also been recorded in the springbok (Bigalke 1972). The deposition of urine and/or faeces could serve an olfactory role, whilst the distinctive posture of a male performing this sequence could act as a strong visual image. This has been associated with territoriality amongst the gazelles (Walther *et al.* 1983). The linked urination-defecation sequence is commonly repeated at the same site, leading to the formation of dung-piles or middens.

Pre-orbital gland marking. These glands are widespread amongst antelope species (Gosling 1985), from the diminutive dik-dik (Brotherton 1994) to much larger species such as the blue wildebeest (Estes 1969) and topi (Gosling 1987). The secretion from these glands is used to anoint objects. In many cases these are grass stems or the twigs of common food plants and bushes (Gosling 1981, Gosling 1987). However the glands may be used to mark other individuals (Lichtenstein's hartebeest; Dowsett, 1966) and in the case of the gerenuk (Leuthold 1978*a*) territorial males will actually mark females, whilst puku appear to develop a neck patch as a result of pre-orbital gland marking (Rosser 1987,1990). The frequency of pre-orbital gland marking was found to be higher amongst territorial than non-territorial Thomson's gazelles (Walther 1978*c*).

Object aggression. Thrashing of vegetation with the horns acts as a strong visual display. It is believed to have territorial connotations *e.g.* in mountain gazelles (Grau & Walther 1976), gerenuk (Leuthold 1978*a*), blackbuck (Dubost & Feer 1981), impala (Jarman, M. 1979), mountain goats (Geist 1964) and pronghorns (Gilbert 1973).

Vocalisation. This may also be used to advertise an individual's presence (*e.g.* blackbuck: Dubost & Feer 1981; sand gazelle: Habibi *et al.* 1993; springbok: Walther 1981; impala: Jarman, M. 1979; pronghorn: Gilbert 1973, Byers 1989). In impala territorial individuals accounted for 86% of incidents of roaring (Jarman, M. 1979), whilst 81% of roe deer barking calls were made by territorial stags (Bramley 1970) and pukus' whistling bouts were restricted to territorial males (Rosser 1990).

Static optic marking. In some species certain individuals appear to take up a characteristic body posture which makes them stand out clearly from others, even to a human observer. These include the gerenuk (Walther *et al.* 1983), tsessebe (Joubert

1972) and impala (Jarman, M. 1979). Their characteristic postures have been associated with territorial individuals.

Scent-urination. During the rutting period males may urinate on their pelage. However, for arid-adapted species such as the springbok and the gazelles there are no records of scent-urination occurring. This behaviour appears to be restricted to those species where dehydration is not an important survival consideration, such as the waterbuck and species found in temperate areas (*e.g.* feral goats: Coblentz 1976; reindeer: Mossing & Dambar 1981; elk: Bowyer & Kitchen 1987).

Accounts of the spatial aspects of scent marking amongst ungulates remain patchy and is further complicated by the fact that they are sub-divided between species which breed polygynously and monogamously. However it is logical that individuals could position their marks most effectively by choosing a site which will maximise its encounter rate by other individuals. This may be achieved in several ways (Richardson 1993):

1. Concentrating marks along territory borders.

2. Concentrating marks along paths and conspicuous landmarks used by conspecifics.

3. Marking at a lower rate in those areas of a territory unlikely to be subject to intrusions.

By positioning marks along territorial borders an animal is better able to advertise its presence to another individual, which crosses into its territory. This pattern of marking has been documented for the dung piles of mountain gazelles (Walther *et al.* 1983), Thomson's gazelles (Walther 1978*b*), blackbuck (Walther *et al.* 1983), topi (Gosling 1987) and dik-dik (Hendrichs 1975, Brotherton 1994), whilst M. Jarman (1979) reported that impala tended to mark more in the periphery of their territories. The spatial distribution of dung piles on a territory appears to differ from that of pre-orbital gland marks (Walther 1978*b*, Brotherton 1994, Roberts 1994). Gerenuks appear to mark their territories using a concentric circle of pre-orbital gland marks, set in from the perimeter, with a number of branches extending outwards towards the territory boundary (Gosling 1981). These findings have recently been confirmed for the klipspringer (Roberts 1994). Gilbert (1973) found increased evidence of object aggression and linked urination-defecation along the borders, relative to the middle, of a pronghorn territory.

Spatial use within a territory is not homogenous; marking more frequently visited areas within a territory will enhance a male's ability to signal his status to others. Specific instances of object marking have been reported for a number of species. Hartebeest will often mark next to termite mounds, something commonly used as a raised platform for vigilance or territory advertisement activities. The association of dung piles with termite mounds was also noted for blesbok by Coe & Carr (1978). A preponderance of dung piles or pre-orbital marks on or adjacent to game trails have been recorded for the Thomson's gazelle (Walther 1978*b*) dik-dik (Brotherton 1994) and gerenuk (Gosling 1981). Similarly white-tailed deer rubs were concentrated at trail junctions along old roadbeds and in woods adjacent to areas of open understory (Kile & Marchinton 1977, Benner & Bowyer 1988).

Certain territorial borders may be infringed upon more frequently than others. This has been found amongst territories which are bounded on one side by a less favourable habitat. Walther (1978*b*) found that a Thomson's gazelle marked the border of his territory more sparsely on the side which was not bordered by another male.

The use of behaviour patterns believed to be utilised by males in territorial advertisement were examined for the springbok. Specifically linked urination-defecation and object aggression were considered in detail. Neither pre-orbital gland marking nor scent urination have been recorded amongst springbok (see accounts by Bigalke 1970, 1972, Mason 1976, Walther 1981). The chapter aims to determine whether these behaviours are used in a territorial context and how they may function. First, by examining the relative use of these behaviours by territorial and non-territorial males. Second, to assess the social context in which the different behaviours were used, together with the temporal distribution of marking rates at different times of the year. Third, to examine the spatial distribution of the urination-defecation sequence.

METHODS

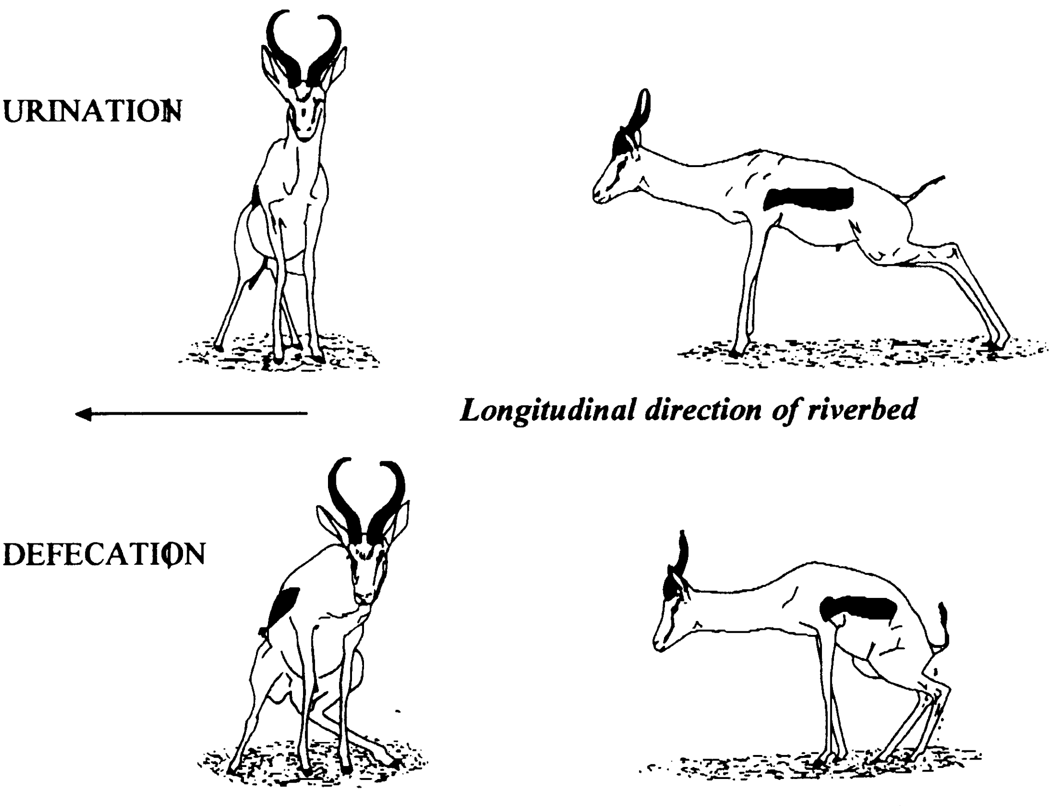
Over the first year of the study, when focal watches were being conducted on animals of different sex and social status, data were collected on the rate at which individuals (territorial males, non-territorial males, females) performed object aggression, whilst linked urination-defecation was considered amongst males. The location of territorial males, either occupying or absent from their territories, together with the number and sex of other individuals in their presence was recorded. As non-territorial males wandered freely no record was kept as to whether they performed the above behaviours on or off a male's territory. The context in which linked urination-defecation occurred was also recorded (*e.g.* a territorial dispute).

Territorial boundaries were known from prior knowledge of the focal individuals which were watched. Boundaries were considered to follow the locations in which males had been seen to engage in territorial disputes with their neighbours and where they failed to follow females and intruding males as they left their territories. Based on this information territory maps were produced by plotting the bearing and distance (using a rangefinder) of trees integral to males' territories on paper and superimposing the territory boundaries, together with the edges of the riverbed, on them.

The position of linked urination-defecation sequences were recorded on these males' territories during individual focal watches. These positions were fixed relative to their distance and orientation from nearby landmarks (particularly trees) and are considered to be accurate within 20 m. Data were collected only in periods during which the territorial boundaries remained stable.

Middens were defined as roughly circular patches of ground recognisable by both an accumulation of springbok faeces and by a loosening of the soil through scraping by springbok. The use of a midden, tree or open ground as a linked urination-defecation site was recorded.

The territories of springbok in the southern Kalahari often follow a course along the fossil riverbeds in a linear fashion, a territory stretching across the width of the riverbed. If linked urination-defecation sequences have a visual component, their orientation could be related to that of the territory; a lateral orientation relative to another individual would create a more dramatic display than a frontal orientation. Therefore the orientation in which a male performed the sequence relative to the orientation of the riverbed was noted; parallel to the length of the river, perpendicular to it or at an intermediate angle (see Figure 32). As a control the orientation of males was recorded during the course of focal watches, but only on those instantaneous observation periods when they were both standing and active *i.e.* they were not resting or ruminating.



Orientation perpendicular to that of the riverbed

Orientation parallel to that of the riverbed

Figure 32 The recorded orientation in which males performed linked urination-defecation in relation to that of the riverbed, showing parallel and perpendicular stances. A diagonal position was also recorded, when linked urination-defecation was intermediate between these extremes

In comparing the frequencies at which particular behaviour patterns were used by territorial and non-territorial males, data were used from the period over which both groups were watched during the first year of fieldwork (see chapter three). Results concerning only territorial males are presented with data collected over the entire study period. Territorial males were followed irrespective of whether they were on or off their territories, so any differences in marking rate are real and not biased by collection methods.

RESULTS

1. Status and marking; territorial vs. non-territorial males

a) Linked urination-defecation

A comparison of the frequency at which territorial and non-territorial males performed either the linked-urination defecation sequence and object aggression, over the period in which both groups were watched, is shown in Table 19. For territorial males these rates are shown for individuals both on and off their territories. The rate at which territorial males performed this sequence on their territories was much higher than linked urination-defecation by non-territorial males ($\chi^2=64.9$, df=1, $p<0.001$). However, both territorial and non-territorial males were seen to perform linked urination-defecation and no significant difference was found in its frequency between territorial males off their territories and non-territorial males ($\chi^2=3.32$, df=1, $0.05<p<0.1$).

Status of male	Linked U-D		Object aggression		Hours obs.
	Total obs.	Rate h^{-1}	Total obs.	Rate h^{-1}	
Territorial: on territory	118	0.33	75	0.21	356
Territorial: off territory	9	0.10	11	0.13	87
Non-territorial	15	0.06	13	0.04	304

Table 19 Comparative occurrence and rate of linked urination-defecation (linked U-D) and object aggression by territorial males, both on and off their territories, and by non-territorial males.

The total number and the rate of linked urination-defecation and object aggression events by territorial males, over the whole study period, are shown in Table 20. By far the highest proportion of linked urination-defecations, 95.5% (n=602), were performed by males on their territories. This confirms that males marked at higher frequencies when present on their territories (χ^2=68.9, df=1, p<0.001) than during periods of absenteeism.

Territorial male:	Linked U-D Total obs.	Linked U-D Rate h^{-1}	Object aggression Total obs.	Object aggression Rate h^{-1}	Hours obs.
On territory	575	0.54	265	0.25	1060
Off territory	27	0.12	40	0.18	222

Table 20 The occurrence and rate of linked urination-defecation by territorial males, both on and off their territories, over the entire study period.

b) Object aggression

Both territorial and non-territorial males were observed showing object aggression towards vegetation (Table 19). The rate at which territorial males performed object aggression was significantly higher than that of non-territorial males when comparing periods in which territorial males were both absent from (χ^2=7.9, df=1, p<0.01) and present on (χ^2=34.8, df=1, p<0.001) their territories.

The total number and rate of object aggression by territorial males, over the whole study period, are shown in Table 20. Eighty seven percent of incidences of object aggression were recorded for males on their territories. Their frequency was also slightly higher on than off their territories (χ^2=3.86, df=1, p<0.05).

Females were also seen to show object aggression on occasion. This was however a rare event and was only recorded twice in watches of focal individuals. Casual observation suggested that it appeared to be commonest during the rut, particularly amongst females which had been mated.

c) Scent-urination, pre-orbital gland and static optic marking

Scent-urination was never observed in springbok; urination was almost always associated with the linked urination-defecation sequence when performed by territorial males. On no occasion were male springbok seen to use their pre-orbital glands, either to anoint inanimate objects, females or themselves. Though the presence of territorial males may have been apparent to the observer when they took up prominent central positions within their territories, at no time did they adopt a resting posture which distinguished them in any way from non-territorial males. However the dramatic pose adopted during ritualised urination-defecation sequences could be considered as a visual signal in itself as it was very striking, even to a field observer.

d) Vocalisation

Unfortunately no quantitative measurements were made of vocalisation by springbok. However it does appear that vocalisation was important as a means of advertisement. Whilst vocalisation was significant in mother-lamb contact and in response to predators, it was also important in a territorial context. Territorial males appeared to be far more vocal than non-territorial males, but only while present on their territories. The frequency and intensity of vocalisation increased considerably over rutting periods. Calls were directed both towards adult males and females present on a territory. Territorial males evicting intruders from their territories would call after them during the chase. The nasal vocalisations of springbok were also predominant during males' approach towards a female on their territory, and formed part of the neck-stretch display (chapter three).

2. Social context of marking behaviour

a) Territory density and marking rate

Both the density of territorial males (chapter six) and their rates of linked-urination defecation and object aggression varied on a monthly basis. It was found that a weak but positive relationship existed between the density of territorial males in the riverbed and linked urination-defecation frequency (Figure 33; $r_s=0.42$, $n=29$, $p<0.05$).

Though the same was true for object aggression, this relationship was however weaker. A comparison of the rate of object aggression at differing territorial male densities revealed that the correlation had to be rejected at the five percent probability level (r_s=0.34, n=29, 0.05<p<0.1).

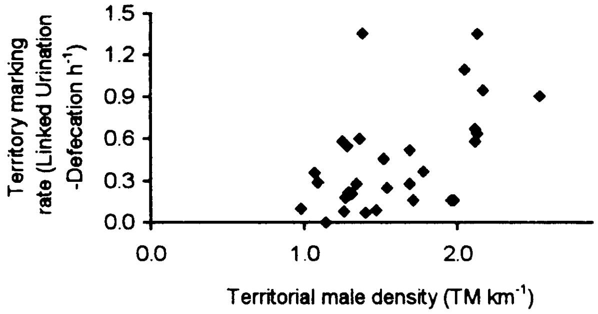


Figure 33 The effect of territorial male density on the marking rate of males in different months

b) The influence of conspecifics on marking rate

The frequency of linked urination-defecation by territorial males in different months was found to be significantly higher in the presence of other individuals than when males were alone on their territories (Wilcoxon MP; Z=4.20, n=36, p<0.001). The same was true for object aggression, which was performed at a higher rate when other individuals were present than when a male was alone on his territory (Wilcoxon MP; Z=4.37, n=37, p<0.001).

The rates of linked urination-defecation and object aggression were analysed in relation to the number of ewes and rams on a male's territory. The linked urination-defecation rate increased with a higher number of ewes on a territory both outside (r_s=0.10, n=1049, p<0.001) and during (r_s=0.17, n=285, p<0.005) rutting periods. However, the number of rams on a territory did not appear to influence the rate of linked urination-defecation either outside (r_s=-0.01, n=1049, NS) or during (r_s=0.10, n=285, NS) rutting periods.

The same was true for the rate of object aggression at different female densities; at higher ewe numbers on a territory, the rate at which rams performed object aggression both outside (r_s=0.19, n=1049, p<0.001) and during (r_s=0.26, n=285, p<0.001) rutting periods increased. Also, as the density of rams on a male's territory increased, the rate of horn rubbing by territorial males also increased both outside (rs=0.16, n=1049,

$p<0.001$) and during ($rs=0.21$, $n=285$, $p<0.001$) rutting periods, in contrast to their rates of linked urination-defecation.

c) Situational motivation of linked urination-defecation

Table 21 shows the situations which were believed to elicit a linked urination-defecation by territorial males. Periods of sexual activity were found to evoke more instances of linked urination-defecation than any other situation.

Situational motivation	Obs. (n)	Occurrence (%)	Total occurrence (%)
Increase in ewe numbers on territory	73	13.3	
Decrease in ewe numbers on territory	65	11.8	
Change in ewes numbers on territory	**138**		**25.1**
Increase in male numbers on territory	39	7.1	
Decrease in male numbers on territory	57	10.4	
Change in male numbers on territory	**96**		**17.5**
Period of sexual activity only	142	25.8	
Period of mixed sexual and chasing activity	59	10.7	
All periods of sexual and chasing activity	**201**		**36.5**
Displacement activity with neighbour	59		10.7
Territorial male leaving his territory	27	4.9	
Territorial male returning to his territory	30	5.5	
Territorial male moving on/off territory	**57**		**10.4**
Walking or chasing intruder away	20		3.6
Change in general activity (e.g. feed→rest)	75		13.6
Other	3		0.5

Table 21 Situational motivation in which territorial males were seen to perform the linked urination-defecation sequence (summary data in bold type).

The movement of other animals on or off a male's territory was also important. Considering changes in female numbers on a territory, 52.3% of marking was associated with an increase in the number of ewes on a territory and 47.7% with a decrease in the number of ewes. Thus the incidence of linked urination-defecation was not biased towards an increasing or decreasing number of ewes on a territory ($\chi^2=0.46$, df=1, NS). In the case of male numbers on a territory, 59.4% of linked urination-defecation was associated with a reduction in their numbers, and again there was no preponderance of marking for increasing relative to decreasing numbers of males on a territory ($\chi^2=3.38$, df=1 $0.05<p<0.1$). Thus whilst it would appear that marking is associated with changing numbers of males or females on a territory, the direction of the change was not important.

3. Spatial and temporal distribution of marking

a) Monthly variation in marking rate

Figure 34 shows the monthly variation in the rates at which territorial males performed linked urination-defecation and object aggression on their territories. It is apparent that the rate at which males performed these two acts varied on a monthly basis (linked urination-defecation: KW ANOVA, H=282.85, df=39, p<0.001; object aggression: KW ANOVA, H=168.85, df=39, p<0.001). Their rates were highest during rutting periods and lowest during the hot-dry season. The rates of these two types of

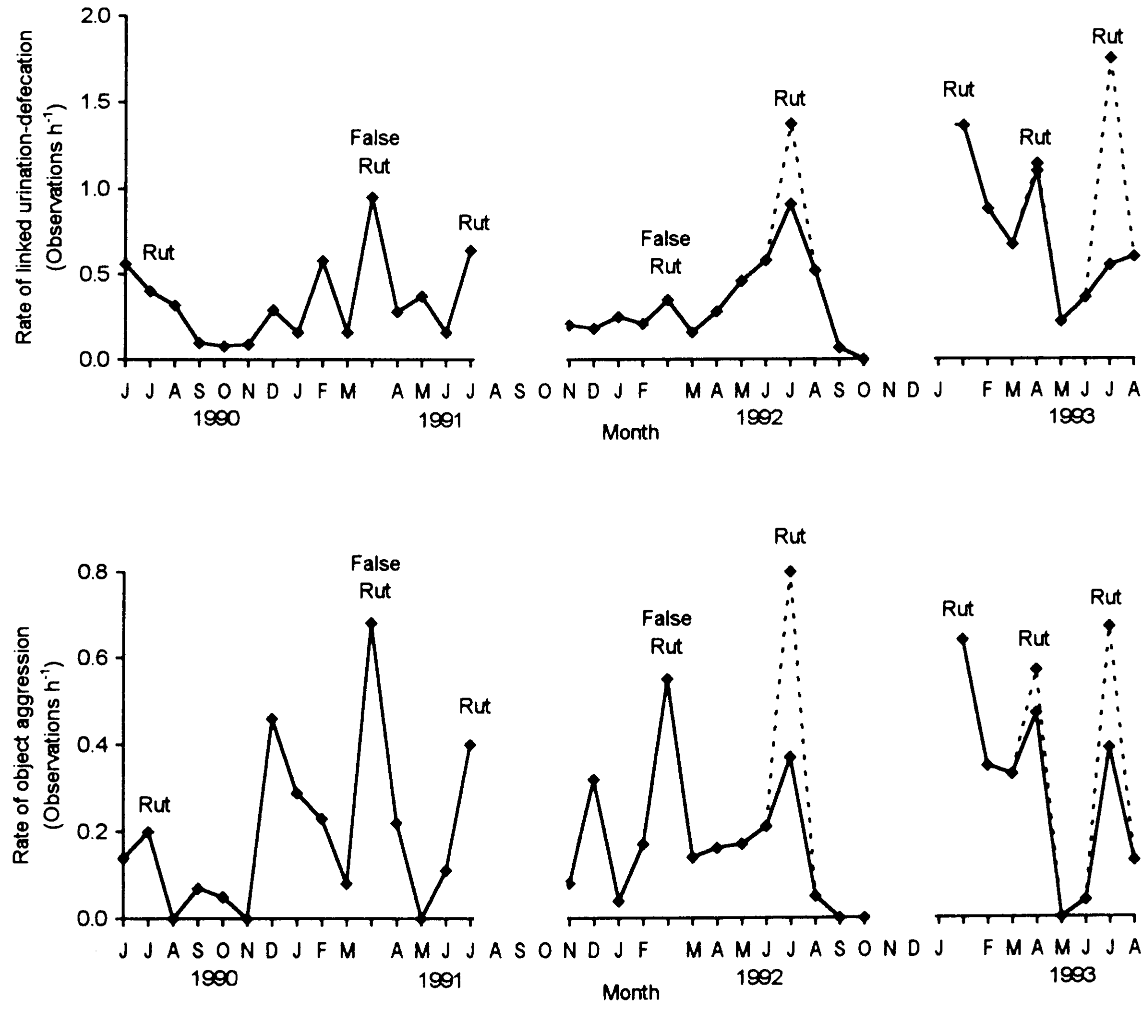


Figure 34 Monthly variation in the rate of linked urination-defecation (top) and object aggression (bottom) by territorial males

behaviour fluctuated in similar ways and are closely correlated on a monthly basis (r_s=0.62, n=29, p<0.001).

b) Orientation of linked urination-defecation

It was found that the orientation of males performing the linked urination-defecation sequence was not evenly distributed relative to the direction of the riverbed. A bias towards an orientation parallel to the riverbed was observed (Table 22; χ^2=13.6, df=2, p<0.01). This was compared to the general orientation males adopted whilst active on their territories, which also showed a bias parallel to the direction of the riverbed. No significant difference was found between the orientation of males performing linked urination-defecation and their normal orientation on the riverbed (χ^2=4.70, df=2, 0.05<p<0.1).

Orientation of ram	Time in given orientation (%)	
	Linked U-D	General activity
Parallel	40.9	39.7
Diagonal	29.9	26.9
Perpendicular	29.2	33.3

Table 22 The orientation, relative to the length of the riverbed, in which territorial males were seen to perform linked urination-defecation and its position in comparison to their body orientation at other times.

c) Mark sites for linked urination-defecation

The use of middens in open ground, under trees and sites where no midden was seen were considered. The frequency at which linked urination-defecation occurred were compared for these three sites. A position under trees made up 47.1%, open ground middens 37.4% and open areas 15.5% (n=380) of marking sites. The proportion of marking on middens relative to trees was compared for both low (≤15) and high (>15) tree numbers on a territory, Figure 35. At low tree numbers, it was found that the proportion of marking performed under trees relative to middens increased as the number of trees on a territory increased (r_s=0.89, n=9, p<0.02). However at high tree numbers there was no correlation between the proportion of marking under trees relative to middens (r_s=-0.19, n=9, NS).

Continual marking in the same spot was apparent during the period of territory establishment. Whilst no middens may have been apparent at the start of a rut, their position was obvious towards its end. The development of middens was probably enhanced by rams pawing the ground before marking. This was the only time in which males were seen to show object aggression towards the ground. All such instances of object aggression were made on territories void of vegetation and were performed on middens, further increasing the disturbance of the soil at midden sites.

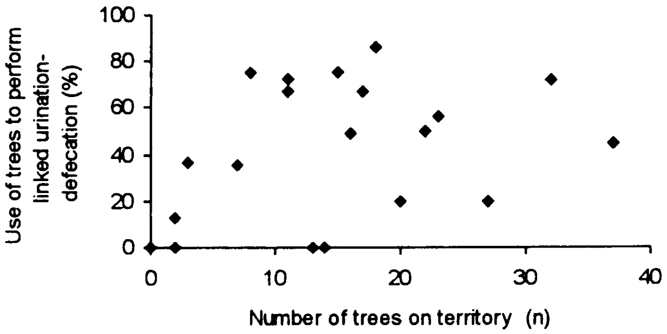


Figure 35 The effect of tree numbers on the use of trees to perform linked urination-defecation by rams on their territories

d) Distribution of marks

The distribution of linked urination-defecation sites by different territorial males are shown in Figure 36. These sites were observed during focal watches and are thus not necessarily exhaustive. These data are summarised in Table 23. A significantly higher number of marking sites were found in the outer than the inner half of all territories (Wilcoxon MP; Z=2.45, n=8, p<0.02). Considering the outer 25 % area of territories,

Territorial male	25 % Edge Area				50 % Edge Area			
	Site		Frequency		Site		Frequency	
	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside
H4	4	5	6	8	1	8	1	13
M7	2	3	2	3	0	5	0	5
D9	5	5	15	11	3	7	10	16
R3	3	8	6	18	1	10	1	23
AB	8	6	11	9	4	10	9	11
K8	2	5	2	6	1	6	1	7
(1992) DBL	5	7	7	9	3	9	4	12
(1993) DBL	5	3	9	4	2	6	4	9
Total	34	42	58	68	15	61	30	96

Table 23 Distribution of observed marking sites and marking frequencies for specific territorial males. Results shown for both a 25:75 % division and 50:50 % division of the territories into outer and inner areas.

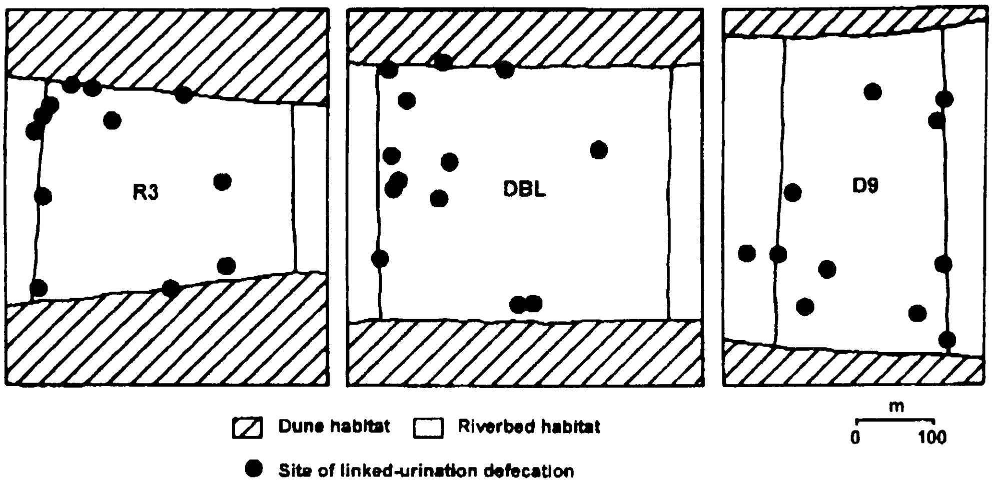


Figure 37 The locations at which three different territorial males (R3, DBL and D9) were seen to perform linked urination-defecation on and around their territories

the number of marking sites was greater than expected in this boundary region (χ^2=42.65, df=7, $p<0.001$).

e) Frequency of marking

The frequency of use of marking sites was analysed in the same way as their distribution (Table 23 and Figure 37). For each territory that was analysed, the frequency of linked urination-defecation was significantly higher in their outer half

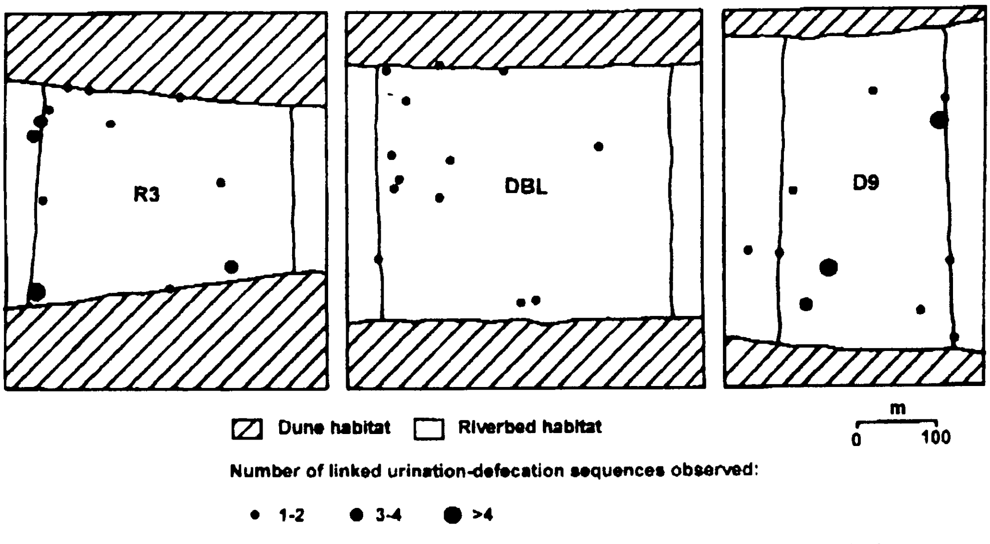


Figure 36 The number of observed instances of linked urination-defecation for three different territorial males (R3, DBL and D9) on and around their territories

(Wilcoxon MP; Z=2.45, n=8, p<0.02). Considering the outer 25 % area of territories, the frequency of use of these sites was greater than expected in this boundary region (χ^2=70.88, df=7, p<0.001).

DISCUSSION

The marking behaviour of the springbok is relatively simple compared to other gazelle species. There was no evidence to suggest that individuals used their pre-orbital glands, though their presence points to a possible ancestral importance. In some other gazelle species too pre-orbital glands are present but unused (*e.g.* Grant's gazelles: Estes 1967; Sömmering's gazelles; dama gazelles; dorcas gazelles; mountain gazelles: Walther *et al.* 1983). Similarly, scent-urination was not recorded. Also, whilst territorial male springbok regularly used middens, they did not always sniff or scrape them before use. This is in marked contrast to blackbuck males which often sniff and perform flehmen at middens (Walther *et al.* 1983). This would suggest that whilst olfactory cues are important to species such as the blackbuck, they are of limited importance to the springbok. The primary importance of linked the urination-defecation sequence was probably as a type of static-optic display, and was very apparent even to the human observer. Unfortunately the rates and loudness of vocalisations of males were not recorded in this study as they are a relatively important form of territory advertisement for springbok (Walther 1981).

A comparison of linked urination-defecation and object aggression between territorial and non-territorial males showed that territorial males used these behaviour patterns more frequently than non-territorial males. The distribution of territorial males' performance of object aggression and linked urination-defecation was also important, being much higher on than off their territories. Likewise, territorial blue wildebeest (Estes 1969) and blackbuck (Dubost & Feer 1981) ceased similar activities when off their territories and behaved in the same way as non-territorial individuals. It was concluded that both linked urination-defecation and object aggression were used to advertise the presence of a territorial male springbok on his territory.

Spatially, both the distribution and frequency of linked urination-defecations were biased towards the edges of a male's territory. However it is unclear to what degree this may be affected by those situations naturally leading rams to perform linked urination-defecation towards the periphery of their territories. Marking was associated with rams moving on and off their territories, following other individuals to the edge of their territory or interacting with their neighbours. In all of these circumstances rams would naturally drawn to the edge of their territories anyway. Similarly boundary encounters between topi were usually focused on dung piles (Gosling 1987). In contrast though, territorial blue wildebeest (Estes 1969) and blesbok (Lynch 1974) were found to concentrate activities around one large dung pile situated centrally on their territories.

In common with species such as the otter (Erlinge 1968) and beaver (Muller-Schwarze & Heckman 1980) the marking rate of springbok was higher at greater territory densities. A similar increase in marking rate has not previously been recorded for other ungulates. This increase probably reflects a greater number of interactions between territorial neighbours or higher intruder pressure, which often elicited performance of linked urination-defecation. The overall marking rate could also be bolstered by those rams which had just taken up a territory at this time. Walther (1978*b*) noted that male Thomson's gazelles took one to two weeks to fully mark a territory and that marking activity decreased after a period of three to five months of occupancy.

In some instances marking was performed whilst territorial males were alone. However it is clear that both linked urination-defecation and object aggression increased when more females were present on a territory, and object aggression increased with more males on a territory. Thus both linked urination-defecation and object aggression appear to be important in communicating a ram's territorial status in the presence of other individuals.

Marking could be directed either to potential mates, potential rivals or both. Considering females, as only 10-20% of males are territorial at any one time (chapter six), and as only territorial males were found to breed (chapter eleven), signalling their territorial status to ewes could demonstrate these males' potential as a mating partner. If this was effective, males which marked more frequently might be expected to breed with more females. Certainly Deutsch & Nefdt (1992), studying both lekking Uganda kob and Kafue lechwe, found that females were attracted to areas in which the topsoil was more heavily used by other females, suggesting that females may be attracted by this olfactory cue.

However, the number of female springbok using individual males' territories did not vary between pre-rut and rut periods, suggesting that they were visiting territories primarily for their resources and not for breeding purposes (chapter eleven). Therefore marking by males may not influence territory utilisation by females. Also, there was no significant difference in habitat usage between female and non-territorial male springbok (chapter six). These facts suggest that non-territorial male and females will try and make use of the same resources, and that marking does not effect territory use by females. They also suggest that when more females are present on a territory there are presumably more non-territorial males present in the vicinity of the territory. Alternatively then, increased rates of linked urination-defecation and object aggression when more females are present may be used as a signal to non-territorial males in the immediate vicinity. These displays act to show that a territory was already occupied. Knowing that a territorial male was already present should discourage other males from entering a territory, particularly during the rut when they would be chased off by the territory owner. The only circumstance in which a non-territorial male should deliberately intrude at such times would be to challenge for territory ownership.

Whilst rams were often chased off territories during periods of increased sexual activity, advertising their territorial status may serve to reduce chases, as non-territorial males are intimidated from entering a territory. Territorial males reduce their feeding activity in rut relative to pre-rut periods (chapter eleven). The advantage marking could give in signalling their presence, particularly over the rut when territorial males are energetically stressed, is in conserving energy which would otherwise be expended in chasing off rival males. This is in accordance with Gosling (1990), who suggested that the function of scent marking in male intrasexual competition is primarily in advertisement of territory ownership. However, unlike Gosling who emphasised the importance of close-range scent-matching between a male and his territory (Gosling 1982, Gosling & McKay 1990), territory advertisement by male springbok appears to operate primarily as a long-range visual signal to intimidate rival males from entering his territory.

SUMMARY

- Territorial males performed linked urination-defecation at higher rates than non-territorial individuals, though this difference was only significant whilst males were on their territories.
- Rates of vegetation object aggression were higher amongst territorial males than non-territorial males, both on and off their territories.
- The rate of performance of the above behaviours varied on a monthly basis, being highest during the rutting periods and lowest at the end of the dry season.
- At higher territory densities, individuals marked their territories at higher rates.
- The rate of object aggression was unrelated to territorial male density.
- Linked urination-defecation rate increased with a higher number of ewes on a territory, but not with a higher number of rams.
- Object aggression increased with both a higher number of ewes and rams on a territory.
- Linked urination-defecation was associated with periods of sexual and agonistic activity, an influx or efflux of individuals from a territory and a male leaving or returning to his territory.
- Both trees and middens were important areas at which linked urination-defecation occurred.
- Both the site and frequency of occurrence of linked urination-defecation was biased towards the periphery of territories.

Chapter 9

Agonistic Behaviour

INTRODUCTION

In maintaining a territory male springbok are exposed to territorial intrusions by other adult males. The response of territorial males to these individuals is likely to depend on their status; whether intruding males are non-territorial or territorial neighbours, as well as the presence and reproductive state of any females on the territory. Furthermore the magnitude of a males' response could well be density dependent and increase with both the number of potential rivals and mating partners on his territory.

Considering the first of these factors, the status of an intruding male. When a territorial male fights an intruding male the stakes are a switch in ownership between the two individuals, whilst in a clash between two neighbouring territorial males there will not necessarily be a winner or a loser. Selection should favour short conflicts between individuals when the costs are high relative to resource value (Parker & Rubenstein 1981). There is obviously a bigger differential in the resource value of a territory to the two individuals in a confrontation between a territory holder and non-territorial male trying to take over the territory than between two neighbouring territorial males. Thus when fights do occur, their severity should be dependent on the nature of the two aggressors; an encounter between a territorial and non-territorial male should logically be more intense than that between two territorial individuals, as the difference in the resource value to the two males would be greater.

More often though conflicts situations are resolved without recourse to physical contact between opponents. Ritualised displays between territorial males have frequently been recorded amongst the Antilopinae (Grau & Walther 1976, Walther 1978c, Dubost & Feer 1981). These may be characterised by a series of displacement activities such as parallel marching, displacement grazing and grooming. The linked urination-defecation sequence and object aggression, discussed in detail in chapter eight, are also associated with these displays (Gilbert 1973, Walther 1978*a*). Similarly, agonistic encounters between territorial and non-territorial males are more commonly terminated by the intruder being chased from the territory than actual fights (Bromley 1969, Walther 1972, Grau & Walther 1976, Rosser 1990).

Another potentially important aspect when considering the nature of agonistic encounters is the number of individuals on a territory, be they potential rivals or potential mates. As female numbers on a territory increase, so the value of the resources (potential mating partners) held by a territorial male relative to other males will increase, and so too will the type or magnitude of a males response to intruders. Certainly Fryxell (1987) found that the frequency of aggressive interactions on white-eared kob lek territories was positively related to the number of females present.

However, outside rutting periods these males are unlikely to gain access to oestrous females and the breeding threat posed by non-territorial males may be negligible. At this time the only threat they would pose would be an actual territory take-over. This situation would change dramatically over the rut, as potential mating opportunities increase and any male intruding onto a territory would pose a take-over threat. Consequently, it is predicted that the reaction of territorial males to intruders should differ between rutting and non-rutting periods because of the reproductive condition of females.

Finally, the reaction of males may be related to the age of intruding rams. Males lambs would obviously pose no take-over threat. However there is a transitional period when males who have reached sexual maturity are still to attain full physical maturity. Whilst they presumably pose little threat to a males' territorial status they do represent a potential breeding threat and should therefore be excluded from a territory.

This chapter therefore examines the agonistic behaviour of territorial male springbok. In doing so those parameters which are predicted to influence aggressive interactions between males are examined. These are the status of a rival (territorial neighbour or non-territorial intruder), the number of adult females or intruding males on a territory, the influence of the rut and the sexual and physical maturity of males.

METHODS

Two major types of agonistic behaviour were recognised during the course of focal watches; fighting and chasing of other individuals. Additionally information was collected on the status of the conflicting individuals (neighbour or intruder) as well as the mean number of adult males and females recorded on a territory over the one hour focal watch period. Further details concerning the collection of these data are presented in chapter five.

RESULTS

1. Chasing behaviour

a) Description of chasing behaviour

The degree to which territorial rams tolerated other males on their territories varied at different times of the year, and so too did the extent to which they were chased and the intensity of chases. At one extreme an intruding ram would simply be walked off a territory by the resident male. At the other extreme males would run after intruding rams, vocalising loudly as they did so. Strong vocalisation could therefore be used as a form of territorial advertisement or threat, directed towards non-territorial males. If they got close enough they would sprint after the offending male in an attempt to horn it from behind. The chase normally ended when the intruding ram had been chased off a territory or when the territorial male decided to return to chase off another ram or court the females on his territory.

b) Monthly variation in chasing behaviour

The frequency with which territorial males chased other males (Figure 38) did not remain constant, but varied significantly in different months (KW ANOVA, H=414.92, df=39, p<0.001). Males were seen to chase other males at the highest rates during

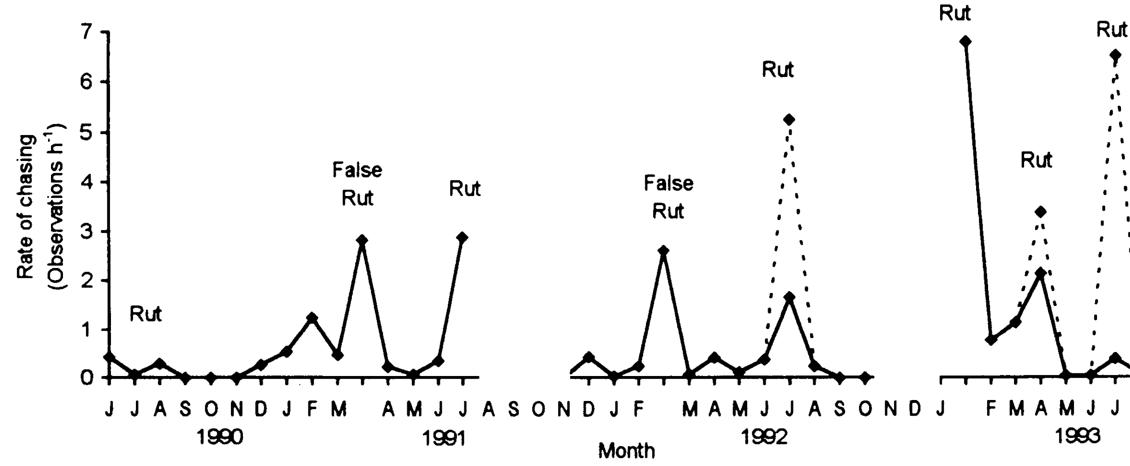


Figure 38 Monthly variation in the rate of chasing behaviour by territorial males. Observations made at a second locality, outside the main study area (at Kaspersdraai in July 1992, Kwang in April 1993 and Ditbardskolk in July 1993), are indicated by dotted line. Months when no data were collected are excluded.

rutting periods, whilst chasing was performed at its lowest rates following the July ruts when all other territorially orientated activity also declined.

c) The influence of conspecifics on chase rate

The rate at which territorial individuals chased other males was found to be influenced by both the number of conspecific males and females on their territories. A significant positive correlation was found between the number of females on a territory and the rate at which males were chased both during the rut (r_s= 0.55, n=285, p<0.0001) and outside the rut (r_s=0.29, n=1049, p<0.0001). Thus as the number of females on a territory increased, so did the frequency with which intruding males were chased off.

The same was true for males on a territory; as male numbers increased, both during and outside the rut, so did the frequency at which they were chased by territorial males (rut r_s=0.42, n=285, p<0.0001. Non-rut; r_s=0.19, n=1049, p<0.0001).

d) The influence on conspecifics on chase duration

The duration for which territorial males chased intruders both during and outside the rutting periods was found to differ significantly. Mean chase time outside the rut was 5.5±0.3secs (n=275) and 10.3±0.5s (n=838) during the rutting periods. The duration of chases was therefore higher during the rut (Mann Whitney U; $Z=-9.41$, $n=1113$, $p<0.0001$).

The duration of chases was also found to be dependent on the number of animals on a territory. As the number of rams on a territory increased, so there was a slight but significant tendency for the duration of chases to decrease (rut; $r_s=-0.16$, $n=838$, $p<0.0001$. Non-rut; $r_s=-0.17$, $n=275$, $p<0.005$). Thus with more rams present on a male's territory the frequency of chases increased, whilst individual chase times decreased.

This is in contrast to the effect that an increasing number of ewes on a territory has on the response of territorial males to intruding rams. Outside the rut the number of ewes present on a territory had no effect on the duration for which rams were chased ($r_s=0.01$, $n=275$, NS). However, during the rut the number of ewes present on a territory did affect the duration for which non-territorial males were chased. As the number of ewes on a territory increased there was a slight but significant tendency for rams to be chased for longer ($r_s=0.11$, $n=838$, $p<0.002$). Thus rams were both chased at higher frequencies by territorial males as female numbers increased on their territories and they were also chased for longer periods during the rut, though not outside the rut.

e) Chasing of adult, sub-adult and juvenile males

Territorial males were observed to chase both adult and sexually mature sub-adult males from their territories. Males below the age of approximately 15 months were not seen to be chased by territorial rams. The tolerance of juvenile, sexually immature individuals was so strong that males would allow lambs a few months of age to attempt to mount oestrous females. In doing so these lambs actively interfered with a male's mating attempts, as they prevented him from attempting to mount the oestrous female himself.

Table 24 shows both the duration and relative frequencies at which males chased adult and sub-adult individuals from their territories in two different areas during the July

1992 rut. In both cases sub-adult males were chased for shorter periods than adult males (Main study area; Mann Whitney U, Z=3.18, n=116, p<0.001. Kaspersdraai; Mann Whitney U, Z=3.18, n=262, p<0.001). During this month sub-adult males made up 12.7% (n=510) of the sub-adult and adult male population counted during the population census. However, only 7.9% of chases were directed towards sub-adult males; sub-adult males were chased less often than expected, relative to adult males during the rut (χ^2=7.73, df=1, p<0.01).

	Number of chases observed		Mean duration of chases (secs)	
	Adult	Sub-adult	Adult	Sub-adult
Main study site	106	10	14.3±1.1	5.3±0.9
Kaspersdraai	242	20	6.5±0.3	4.0±0.6

Table 24 Comparison of both the relative number and duration of chases directed towards adult and sub-adult males at two different areas during the July 1992 rut.

2. Fighting behaviour

a) Description of fighting behaviour

Fighting between neighbouring territorial rams could easily be distinguished from that between a territorial male and intruder. Fights between neighbours were normally accompanied by characteristic displacement activities. The commonest of these was the adoption of the grazing posture, whilst facing up head to head with the opposing ram (Figure 39). During many of these grazing rituals males were seen to groom themselves. This was often complemented by champing, an action in which a male would shake his head to the side together with quick lateral movements of the lower jaw. Other activities seen at such times were the linked urination-defecation sequence and horn-rubbing, actions inherently associated with territoriality in the springbok (see chapter eight). Such encounters did not necessarily end with a physical confrontation.

Territorial males may lunge towards each other, without actually making physical contact, or more rarely clashing or locking their horns together in a frontal presentation. Such confrontations took place on the shared border of the males' territories. They commonly ended with both males grazing away from each other in the directions of their territories. Alternatively males may have become distracted by

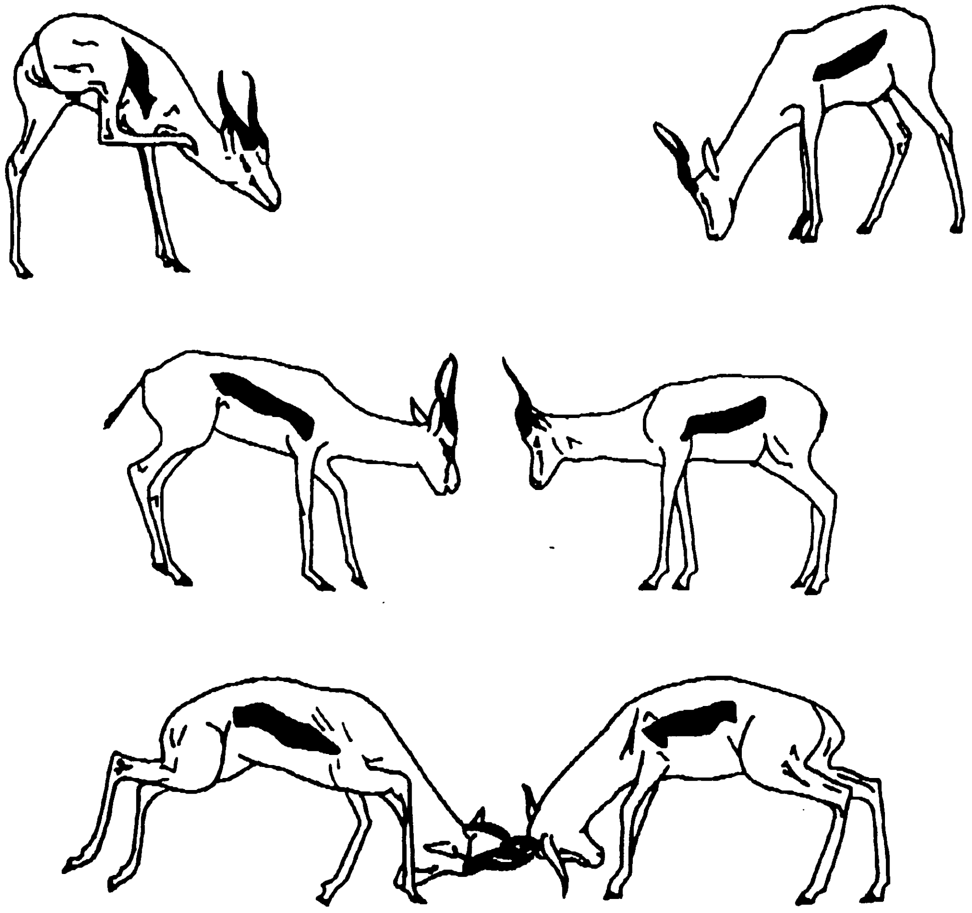


Figure 39 Postures associated with the fighting behaviour of territorial males at their common territory border; displacement grazing and grooming activity (top), champing (left, middle) and an actual fight (bottom) consisting of a brief frontal clash of horns.

other activities on their territories, such as an intruding male or an influx of ewes, which would cause them to terminate the confrontation.

In contrast fights between a territorial male and intruder were not characterised by any ritualised activity. They often started when a male which was chased by a territorial male stood his ground. In such cases displacement activities were rarely seen and fighting was almost always inevitable and immediate. Serious fighting included neck wrestling whilst the two rams' horns were locked. Fights terminated with the winner chasing the other ram off, often trying to horn the loser from behind in the process.

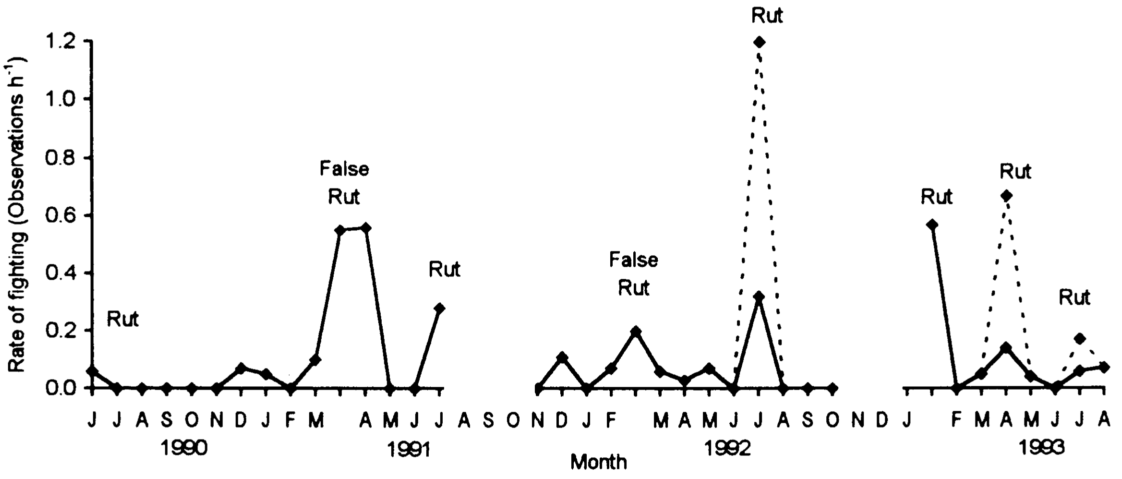


Figure 40 Monthly variation in the rate of fighting behaviour by territorial males. Observations made at a second locality, outside the main study area, indicated by dotted line. Months when no data collected are excluded.

b) Monthly variation in fighting behaviour

Variation in fighting showed the same monthly trends as chasing behaviour. The relative frequency with which fights were observed in different months is illustrated in Figure 40. Fighting was most pronounced during the rutting periods, but virtually absent from the territorial males' behaviour from the end of the July rut until the following rainy season. This represents a significant variation in the rate of fighting behaviour between different months (KW ANOVA, H=266.78, df=39, $p<0.001$).

c) Fighting behaviour; intruding and territorial males

The duration of physical clashes in fights between neighbouring territorial males and between territorial and intruding males both in and out of the rut are shown in Table 25. Both during and outside of the rut fights were of longer duration in territorial-intruder disputes than in territorial-neighbour disputes (Non-rut; Mann Whitney U,

	Territorial neighbour			*Intruding Male*			Ratio of fights (neighbour : intruder)
	Incidence of fighting	% of fights	Duration (secs)	Incidence of fighting	% of fights	Duration (secs)	
Rut	59	79.7	2.9 ±0.6	15	20.3	30.4 ±12.5	3.9:1
Non-rut	14	60.9	4.9±1.2	9	39.1	16.9±7.3	1.6:1

Table 25 Total number and duration and relative proportion of fights between a territorial male and a) *territorial neighbour or* b) *intruding male, both during and outside rutting periods.*

Z=2.09, n=33, P<0.05. Rut; Mann Whitney U, Z=5.92, n=131, P<0.0001).

The duration of neighbour-intruder fights did not vary significantly between rutting and non-rutting periods (Mann Whitney U, Z=-0.56, n=35, NS). In contrast the duration of fights between territorial neighbours decreased in the rut, relative to non-rutting periods (Mann Whitney U, Z=3.66, n=129, p<0.0001).

The proportion of fights between neighbours increased relative to the proportion with an intruder during the rut. This was however only a weak trend (Table 25; $\chi^2=3.33$, df=1, $0.05<p<0.1$) and not conclusive.

DISCUSSION

The fighting behaviour of springbok is similar to that of the other gazelles. The intensity and frequency of chasing and fighting is influenced by both the density of animals on a territory, the social status of the intruding male and the rut. Considering the chasing of other rams by territorial males; as the number of males on a territory increased, so the duration for which individuals were chased decreased. In contrast the rate at which intruding males were chased increased with an increasing number of intruding males. This trend was common to both rut and non-rut periods. This shows that as the density of intruding males increases on a territory so males react by increasing their overall chase rate, but are probably unable to chase individual rams as effectively, as evidenced by their decreased chase time.

Similarly the rate at which males chased intruding rams from their territories increased with an increasing number of ewes, both during and outside rutting periods. However the time for which intruding males were chased did not show the same trend with increasing female numbers on a territory as for increasing male numbers. In fact outside the rut, the time for which males were chased was independent of the number of females on a territory. During the rut however the time that males were chased increased with an increasing number of ewes on a territory. Thus the way in which territorial males responded to intruding rams varies in and out of the rut relative to female but not male numbers on a territory.

The frequency of fights increased during the rut, whilst the proportion of territorial-neighbour fights rose relative to territorial-intruder fights. This suggests that neighbouring males may represent a greater breeding threat to a territorial male than a non-territorial ram. This is supported by results from the present study showing that whilst all observed matings were by territorial males, occasionally both a male and his territorial neighbour would mate with the same female (see chapter eleven). However an increase in fighting activity between bordering males is probably also affected by the frequency at which rams moved to their territorial boundaries. Two factors almost certainly increased territory boundary visitation. First, the herding behaviour of rams towards females attempting to leave their territories increased dramatically during the rut, which consequently drew rams to the edge of their territories. Second, intruding males may be chased to or beyond their territorial boundaries, again bringing males more frequently to the edge of their territories than during non-rutting periods.

When fights between individuals occurred, the duration of physical contacts, and presumably therefore the risk of injury to individuals, was higher in territorial-intruder than in territorial-territorial male conflict. 'Clash fighting' between territorial males, with horn contacts of only 1-2 seconds, would appear to be very common amongst male antilopinae (Walther *et al.* 1983, Grau & Walther 1976). However the incidence of territorial-intruder fights was far lower than that between territorial neighbours, though their duration and presumably therefore the risk of injury to individuals was higher. Grau & Walther (1976) also found that whilst 28% of encounters between territorial males ended in fights, only 4% did between territorial and non-territorial males. In addition, the frequency of fights was far higher between territorial neighbours than between a territorial and intruding male. The low incidence of fights with an intruding male adds support to the idea that males avoid such conflict situations because of their potentially high costs.

These differences are probably a consequence of the asymmetry of pay-offs for territorial and non-territorial individuals in a take-over situation (see Maynard-Smith & Parker 1976). Maynard-Smith & Price (1973) showed that individual selection can explain why potentially dangerous offensive weapons are rarely used in contests (*cf.*

territorial-neighbour conflicts), but that individuals must respond to an escalating contest by escalating it themselves. This accurately reflects the increased fight times, relative to territorial-neighbour fights, recorded when intruding males stood and fought rather than allowed themselves to be chased off by a territorial male.

Only sexually mature rams were chased by territorial males. These included physically immature, sub-adult males. Territorial males commonly become intolerant of young males at 1-2 years of age (*e.g.* impala; Jarman 1979, blackbuck; Dubost & Feer 1981, pronghorn; Bromley 1969) though Baharav (1982) reports that young dorcas gazelle males were excluded from groups as young as 5-6 months old. More specifically Wahlstrom (1994) found that agonism by adult male roe deer was directed not just towards yearling males, but also that it was directed mainly towards the sexually more mature yearlings. Sexual maturity in male springbok does not accelerate until they are over 60 weeks old (Skinner *et al.* 1971). This may indicate that all sexually mature animals were considered as rivals by territorial animals, even though the sub-adult animals were not well enough developed physically to hold a territory themselves. No sub-adult males were ever seen engaged in serious fights or in possession of a territory. The diminished threat immature males presented is reflected in the shorter chase durations and frequencies they elicited from territorial males. However the reproductive threat posed by physically immature but sexually mature animals has been demonstrated in a population of white-tailed deer; male fawns were able to breed due to the absence of physically mature males (Schultz & Johnson 1992).

SUMMARY

- Both fighting and chasing activity were greatest over rutting periods.
- Chasing rates increased with greater female and male numbers on a territory.
- Individual chase times decreased with male numbers, but increased with female numbers on a territory over the rut.
- Sub-adult males were chased less frequently and for shorter times than adult males, whilst males under 15 months were never chased.
- Fighting behaviour directed towards territorial neighbours was highly ritualised, and of short duration.
- Fighting behaviour directed towards intruding males was not ritualised and fiercely contested.

- **The proportion of fights directed towards neighbours, relative to intruders, tended to increase during the rut.**

Chapter 10

Acquisition and turnover of territories

INTRODUCTION

In all antelope tribes, except those in the subfamily Bovinae, males are territorial (Estes 1991). Territory acquisition and maintenance would therefore appear to be of fundamental importance to such males. Territories may be maintained by a monogamous pair of individuals, as has commonly been observed in small antelope species such as the dik-dik (Hendrichs 1975, Brotherton 1994). Amongst the larger species males may defend large, presumably resource-based, territories (*e.g.* sand gazelle; Habibi *et al.* 1993, waterbuck; Spinage 1982, black lechwe; Thirgood *et al.* 1992. red lechwe; Williamson 1994, puku; Rosser 1987,1990, topi; Gosling 1991, Gosling *et al.* 1987) or small lek-based territories (*e.g.* topi; Gosling 1987, Balmford & Blakeman 1991, Uganda kob; Balmford 1990, Kafue lechwe; Schuster 1976, Nefdt 1992).

Considering specifically resource-defence polygyny (Emlen & Oring 1977), it is thought that by establishing territories and defending resources of importance to adult females, males are able to monopolise mating opportunities. Indeed it has been reported in many antelope species that territoriality is a prerequisite for mating (Owen-Smith 1977, Gosling 1986, chapter 11). Given the functional link between territorial status and a male's breeding success, territory tenure may well be dependent on the availability of reproductively active females. Thus in populations whose breeding is synchronised to a specific time, males may only be expected to hold territories over the same period. Similarly in those populations which breed throughout the year, some males could be expected to maintain territories at all times. Both of these situations have been reported for wild ungulate populations (summarised in Table 26). Paradoxically, in some ungulate populations breeding appears to be synchronised within the year, as evidenced by synchronised lambing periods, yet males still maintain perennial territories (Table 26).

Species	*Seasonal breeder*	*Synchronised Parturition*	*Males Hold Perennial Territories*
Seasonal breeders, males territorial over breeding period			
Topi [1,2]	✓	✓	✗
Impala [3]	✓	✓	✗
Pronghorn [4,5]	✓	✓	✗
Red deer [6]	✓	✓	✗
Roe deer [7]	✓	✓	✗
Seasonal breeders, males territorial throughout year			
Blue wildebeest [13]	✓	✓	✓
Puku [14]	✓	✓	✓
Bontebok [15]	✓	✓	✓
Red lechwe [16]	✓	✓	✓
Aseasonal breeders, males territorial throughout year, unsynchronised parturition			
Thomson's gazelle [9]	✗	✗	✓
Grant's gazelle [9]	✗	✗	✓
Gerenuk [10,11]	✗	✗	✓
Mountain gazelle [8]	✗	✗	✓
Aseasonal breeders, males territorial throughout year, synchronised parturition			
Springbok [12]	✗	✓	✓

Table 26 Comparison of the territory-holding status of male ungulates in relation to their observed breeding pattern.

References: 1; Gosling 1986, 2; Gosling & Petrie 1990, 3; Murray 1982 b, 4; Byers 1989, 5; Maher 1991, 6; Carranza et al. *1990, 7; Bramley 1970, 8; Habibi* et al. *1993, 9; Walther* et al. *1983, 10; Leuthold 1978 ab 11; Leuthold & Leuthold 1975b, 12; Jackson* et al. *1993, 13; Estes 1969, 14; Rosser 1987, 15; David 1975 ab, 16; Williamson 1994.*

This would suggest that, even in species with a synchronised breeding season, it is to the males' advantage to maintain a perennial territory in order to maximise their breeding success. Gosling (1986) argued that the costs of remaining territorial through the year are probably outweighed by the benefits of being in territorial residence at the start of the mating season. Furthermore males may maintain perennial territories because of the possibility of obtaining extra copulations outside of the main breeding periods (Rosser 1987, Jackson *et al.* 1993). Finally, once a male has relinquished his territory it may be difficult to re-gain it or another territory (Rosser 1987).

This chapter explores the potential breeding benefits to the springbok, in maintaining a territory for longer periods than the rut, when almost all conceptions take place. In order to do so the timing of territory establishment and abandonment of rams is considered together with its motivation, as well as the tenacity of males to their territories both within and between different seasons.

METHODS

A number of behavioural cues were used to determine when a ram had established a territory. A non-territorial ram would show a sudden and marked change in its behaviour towards other springbok, becoming dominant to other males and showing sexual interest in females. This was accompanied by a tendency to remain in a particular area, even when the accompanying herds moved on, and an increase in marking behaviour. Territory establishment was an active process and thus generally easy to determine.

A ram was considered to abandon his territory when he was not observed on the former territory for a number of consecutive days. This is in contrast to other rams which may have been sighted sporadically on their territories, but would return to them at infrequent but regular intervals. Territory abandonment was not as easy to assess as establishment because the tenacity of a male to a particular area could decline gradually, though increased tenacity was dramatic on establishment. The time of abandonment was recorded as the first day on which no further records were made for an individual on his former territory.

Territory establishment was investigated relative both to rutting periods and the first significant rainfall of the year, which is itself related to plant growth (chapter 4). In arid and semi-arid regions showers of less than 10-15 mm are considered ineffective in promoting plant growth (Bothma 1972, Caughley & Gunn 1993, Knight pers.

comm.[‡]). Thus the incidence of territory establishment was recorded in relation to the first rainfall of ≥15 mm for the year.

Results estimating the duration of territory occupancy relate to known individuals in the main study area on Haagner's and Marie's loops. To examine the possible effect of prior residency on territory turnover rates over the rut, nine territories were monitored in this area, whilst four were monitored in the immediate vicinity of Kaspersdraai waterhole during the July 1992 rut. It was established from an examination of population counts that probably only one territorial male was present at the Kaspersdraai site in the month prior to this rut.

RESULTS

1. Timing of territory establishment

The proportion of marked animals observed to establish territories in different months of the year is illustrated in Figure 41. This shows that most territories were established early in the year, at times corresponding to the start of the rains and rutting periods. A closer examination of territory establishment was made relative to these two factors Table 27, Figure 42). Together the first significant rainfall of the year, of 15mm or more, and the rutting period coincided with 84.4% (n=45) of territory establishment. Only in February 1993, following a prolonged period with no rainfall, did territory establishment coincide with both the first significant rainfall of the year and a rut.

	(%)
Rain only (first shower ≥15 mm)	27.9
Rut and preceding 30 days	44.4
Rut and rain together (all records from February 1993)	13.3
Total take-up at time of rut and/or rain (n=45)	84.4

Table 27 The incidence of territory establishment of known males in relation to: i) the first significant rainfall of the year ii) the rut and preceding period iii) simultaneous rainfall and rutting activity iv) all periods involving either the first rains and/or rutting periods

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[‡] Dr. M.H. Knight, National Parks Board, PO Box 110040, Hadison Park, Kimberley 8306

This is reflected in data collected during the monthly riverbed census. Figure 43 shows the change in density of territorial males between different months. The largest changes in territorial male densities corresponded to rutting periods and the first good rains of the season. The exception to this was the start of the 1992 hot-wet season, with below average rainfall. Consequently there was no large change in the density of territorial males on the riverbed at this time.

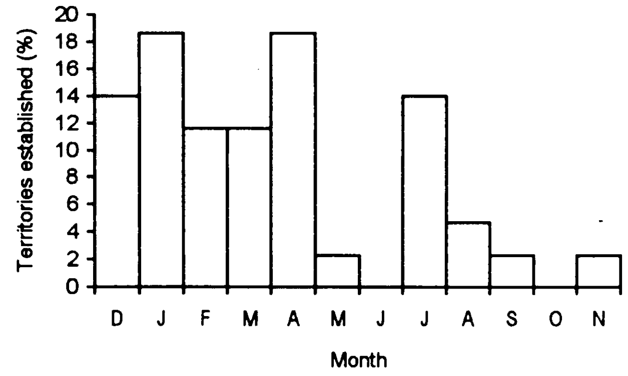

Figure 41 The relative frequency of territory establishment by males in different months of the year

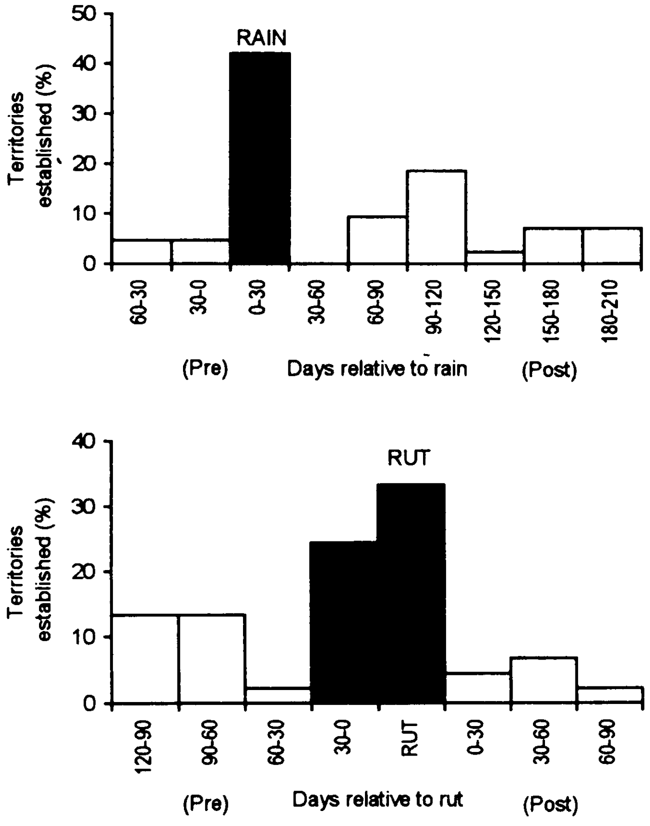

Figure 42 Timing of territory take-up by males in relation to rainfall (above) and the rut (below)

2. Method of territory establishment

Males established their territories in a variety of different ways. The relative frequencies with which these were observed are illustrated in Table 28. Males were most often observed returning to previously held territories, which became the basis for their new territory. Alternatively males were seen to displace other rams from their territories or to establish a territory in an area unoccupied by a territorial male. This may be because the previous male had abandoned his territory or because he had been killed by a predator. Finally males were recorded to displace other rams from a segment of their territories and so create a new territory between two established

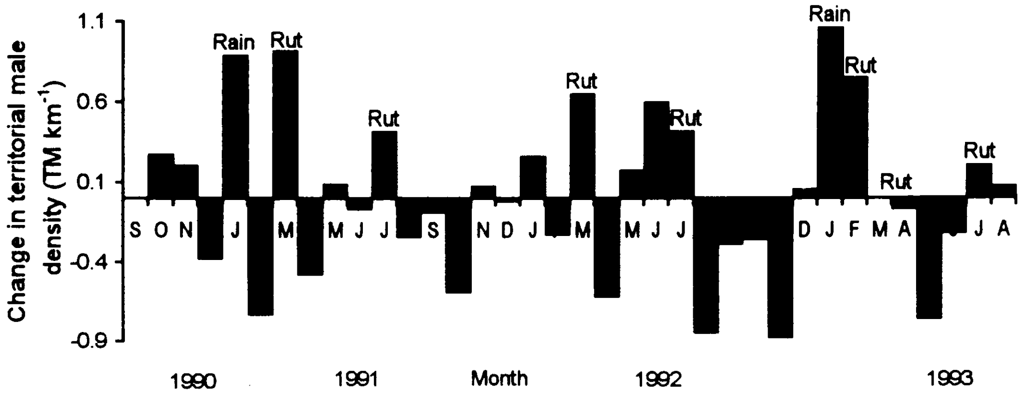

Figure 43 The change in territorial male density on the riverbed between different months, reflecting the relative increase or decrease in numbers between months in relation to the first significant rainfall of the year (≥15 mm) and ruts or false ruts

territories. As data on the territorial borders of unmarked rams were not available, it was almost impossible to record how frequently this type of territory take up occurred. An example was male D9 who lost half his territory to an unmarked ram.

Method of territory establishment	*(n)*	(%)
Displace owner	11	26.2 %
Squeeze between two established territories	2	4.8 %
Return to old territory	20	47.6 %
No territorial male / territorial male killed	9	21.4%

Table 28 The relative frequencies at which males either actively or passively established themselves on a territory.

3. Method of territory abandonment

By far the commonest way in which rams relinquished their territories was by passively leaving them (Table 29). This was particularly so as the dry season progressed; rams would simply leave their territories and make no attempt to return to them, mark or defend them against other males. Approximately equal numbers were killed whilst they were actively territorial or were forcefully evicted from their territories by a rival male.

Reason for territory relinquishment	*(n)*	(%)
Actively displaced	7	11.7 %
Passively abandoned	47	78.3 %
Killed by predator	6	10.0 %

Table 29 The relative frequencies at which territory owners either actively or passively relinquished their territories

4. Timing of territory abandonment

The proportion of marked rams abandoning their territories at different times of the year is shown in Figure 44. It was found that 62.7% (n=59) of rams abandoned their territories in the second half of the year between June and November, though this trend did not represent significantly more territories being abandoned than expected over this period ($\chi^2=3.81$, df=1, $0.05<p<0.1$). A number of territories were abandoned in July following the rut, though the largest number were relinquished in August after the rut the previous month.

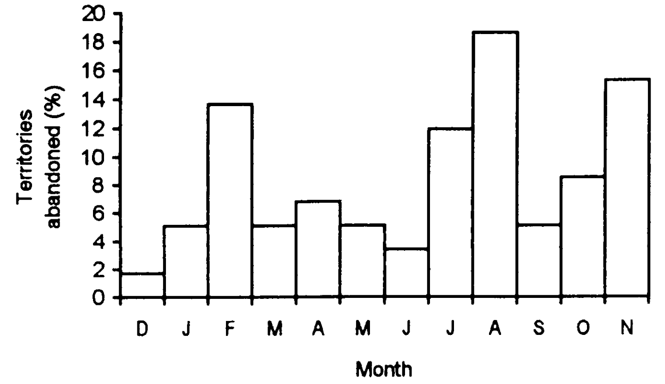

Figure 44 The relative frequency of territory abandonment by males in different months of the year

5. Monthly variation in the time spent on a territory in relation to vegetation biomass

The proportion of time that males spent on their territories was related to vegetation biomass on the riverbed in a given month (Figure 45; r=0.55, n=37, $p<0.02$). Males occupied their territories for a greater proportion of the time when vegetation biomass was higher on the riverbed. The actual density of territorial males on the riverbed was however independent of vegetation biomass (see Chapter 5).

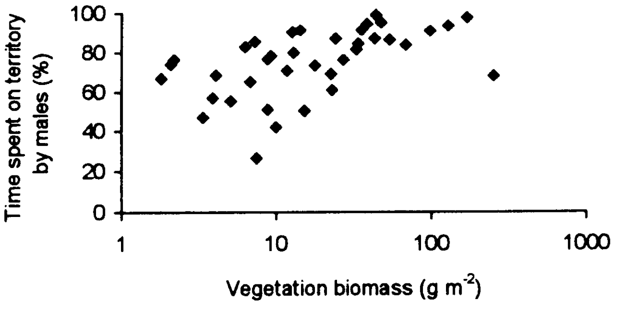

Figure 45 The effect of vegetation biomass on the riverbed on the amount of time territorial males spent on their territories. N.B. The reduction in time males' spent on their territories when the vegetation was too thick

6. Tenacity to territories and territory shifting

Of those rams which abandoned their territories during one year and re-established territories the following year, 91.3% (n=23) initially showed fidelity to their old territories, whilst only 8.7% set up territories at a completely new site; the majority of rams remained loyal to their old territories in consecutive years.

On the other hand, in several instances rams were recorded to shift their territories during the course of the year (Figure 46). Thus whilst a ram may have initially returned to his old territory, this was abandoned and a new territory established during the same year. Such a shift was recorded for 17.1% (n=41) of territorial males, 82.9% not changing their territory site all year. This does not however represent a significant difference in the proportion of males shifting territories between years, relative to those moving within a year (χ^2=1.04, df=1, NS).

7. *Motivation to shift territories within a year*

Table 30 shows some details relating to a male's territory both before and after a territory shift. In one case the ram established a territory which was obscured from view, such that it was impossible to count the number of ewes present. In all other cases a shift in territory site was accompanied by a significant increase in the mean number of females recorded on the ram's territory (one-tailed signs test; n=5, p=0.031).

New territories were generally established in the vicinity of a male's old territory. The furthest recorded distance between these territories was 6.5km along the course of the

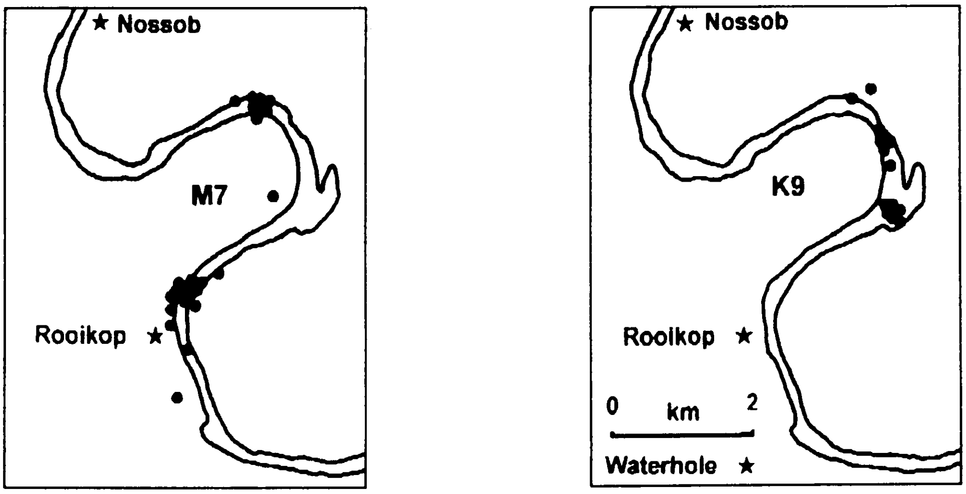

Figure 46 The territories of males (M7 and K9) who were observed to shift their territories within the course of a year. Individual sightings shown by black dots

Territorial male	*Mean number of ewes on territory*		*Territory size (ha)*		*Distance between territories*	*Days between ownership*
	Pre-shift	Post-shift	Pre-shift	Post-shift		
K9	0.6±0.4	1.2±0.6	5.0	1.7	0.6 km	40
F8	0.4±0.3	0.7±0.6	8.4	5.6	1.0 km	21
M7	0.2±0.1	2.5±1.5	8.0	5.6	3.0 km	18
J2	1.2±0.6	8.8±6.0	8.0	N/A	6.5 km	57
K8	10.0±5.2	N/A	8.0	7.5	1.5 km	136
R3	3.2±2.2	9.3±4.6	8.0	3.1	0.1 km	2

Table 30 Summary of some of the important aspects concerning the shifting of territory sites by a male within a given year.

riverbed. Though few such observations were made, territory shifts did not appear to be constrained to any particular time of the year. In only one case (R3) was the ram actively evicted from his territory, for the rest of the observations the shift was a passive one.

8. *Duration of territorial periods*

The duration of territory occupancy for marked individuals, for whom both the time of establishment and abandonment were known, was on average for 88 days (n=31); approximately 3 months. The longest complete period of territory occupancy recorded was 340 days, though one ram first marked when he was already territorial, remained territorial for the next 380 days.

For most males either the time of territory establishment or abandonment was unknown and these results are almost certainly an underestimate of occupancy periods because of the higher probability of recording whole periods of tenure when territories were held for a shorter duration. As results suggest that most territories were established either with the first good rains of the year or at the time of the rut, a very rough estimate was made of the duration of territory occupancy by extrapolating back from the date they were first recorded on their territory to the preceding rut and the start of the rains. As rams established territories at either time in approximately equal numbers the average duration of occupancy was taken as the average of both the time of occupancy back to the rut and to rainfall. Whilst this figure is not a realistic estimate for an individual ram, it is the only way in which an estimate could be made of mean territorial occupancy. Using this method the average duration of territory occupancy was estimated at 137 days (n=57); approximately 4.5 months.

9. Territory turnover during rutting periods

The number of different males which held territories at both the main study site and the Kaspersdraai site, together with their turnover rate are shown in Table 31. Significantly more males occupied the Kaspersdraai territories, where only one male had been resident prior to the rut, than at the main study area where males had been territorial for extended periods. The rate of territory turnover was lower in the area where males had held territories for extended periods relative to the area where males only took up territories over the rut (χ^2=8.18, df=1, p<0.01).

	Observation area	
	Main study site	Kaspersdraai site
Number of territories observed	9	4
Observed number of males occupying territories	9	13
Expected number of males occupying territories	15.2	6.8

Table 31 The relative turnover of territories in an area where males had been territorial for periods prior to the rut (main study site) and an area where males were not observed to hold territories prior to the rut (waterhole site).

DISCUSSION

Males were observed to hold territories at all times of the year. Two key events, the start of the rains and of the rut, were important in both the establishment of new territories and males re-establishing their old territories. An increase in territoriality has been recorded for a number of species with increased rainfall (wildebeest; Estes 1969, blesbok; Lynch 1974, impala; Jarman, M. 1979, Thomson's gazelle; Walther *et al.* 1983). Conversely, males have also been observed to spend more time off their territories as the dry season progressed (blesbok; Lynch 1974). Thus both nutritional factors, and the mating benefits over breeding periods (chapter 11), are important elements influencing territoriality.

It is plausible that nutritional factors are in fact more important than mate access in determining territory dynamics amongst ungulates. It is apparent from Table 26 that those species which do not occupy perennial territories could do so for nutritional reasons alone. Certainly this would be true for temperate species, which often move between exclusive summer and winter feeding areas. As for warmer areas, most of those species which limit their periods of territoriality to breeding periods may be forced to by prevailing environmental conditions. Hence impala, which remain territorial throughout the year in East Africa (Jarman, M. 1979), are seasonally territorial in southern Africa (Murray 1982*b*) despite birth peaks being observed in both populations, and white-eared kob are forced by food limitation into making an annual migration from savannah grassland to swamped grassland in the dry season (Fryxell 1987*ab*), precluding any form of perennial territory occupancy.

Alternatively, year-round territoriality could serve to increase individuals' mating opportunities. Whilst this is true for species such as Thomson's and Grant's gazelles which breed continuously, it is not necessarily true for synchronised breeders. Despite the fact that wildebeest maintain perennial territories in the Ngorongoro (Estes 1969) breeding is highly synchronised to specific times of the year (Estes 1976, Estes & Estes 1979). Similarly, of all the springbok matings which were observed in the present study, none were seen outside the brief rutting periods (chapter 11). This is reflected in the lambing periods, which were highly clumped, with very few neonates recorded outside these periods (chapter 12). Also it appears that the survivorship of such lambs is much lower than those which were conceived during the rut (chapter 12), so even if males were able to gain extra mating opportunities, the chances of their offspring surviving to sexual maturity would be considerably diminished. Thus it seems unlikely that males need to remain territorial throughout the year to maximise their breeding opportunities outside the period of the rut in the Kalahari.

Whilst the temporal aspects of territory acquisition are obviously significant, the results of this study also emphasise the importance of their spatial properties. It is significant that males which were territorial in consecutive years normally returned to their former, rather than occupying new territories. Observations on the fidelity of individuals to their old territories are common for ungulate species (*e.g.* blue wildebeest; Estes 1969, hartebeest; Gosling 1974, impala; M. Jarman 1979, roe deer;

Bramley 1970, sika deer; Miura 1984, pronghorn; Bromley 1991). Familiarity with an area, may therefore have a number of social or ecological advantages to an individual.

If a number of territorial males were to re-establish territories in the same area one benefit could be a reduction in aggression between individuals; the 'dear enemy' phenomenon (Fisher 1954, page 73). The benefit of having a known individual occupying an adjacent territory is that owners avoid the costs of having to regenerate boundaries with a new and unfamiliar neighbour (Getty 1987, Picman 1987, Temeles 1994). Though this phenomenon has not been investigated methodically amongst ungulate species, field observations certainly suggest that territorial males respond differently to territorial neighbours than to less familiar individuals (chapter 9, Walther *et al.* 1983, Rosser 1990). The possible importance of familiarity with other individuals in reducing aggressive behaviour is apparent from a study of fallow deer. Apollonio *et al.* (1989) found that the removal of successful males from a lek increased the incidence of fighting between males, which they attributed to the disruption to the stags' social hierarchy. Thus familiarity with territory neighbours may be advantageous to males in decreasing the level of aggression between them.

The benefits of site-specific advantage in enhancing future reproductive success, with no immediate benefits, are well illustrated in avian studies. For instance red-winged blackbirds may defend a breeding territory at the end of the breeding season, as the previous owner departs, when their is little chance in reproducing that year. However, this appears to invoke a delayed long-term, site-specific advantage to these new males the following year (Yasukawa 1979); levels of overt aggression with neighbouring birds are reduced and consequently the likelihood of successfully occupying the territory are improved. Certainly males react less vigorously to the song of neighbouring males than to strange calls, and are discouraged more from trespassing into neighbouring territories when they recognise the song as that of an established neighbour (Yasukawa *et al.* 1982).

Applying this to an understanding of territory dynamics in ungulates, Wirtz (1981, 1982) reported the presence of satellite males in a waterbuck population; though they remained subordinate to a territorial male, their satellite behaviour increased their chances of succeeding the dominant male in territory ownership (Wirtz 1981). Thus whilst their pseudo-territorial behaviour may not offer them any immediate territorial advantage, it would improve their probability of becoming territorial, and potentially their future breeding success.

Males' fidelity to a particular territory is not universal amongst ungulates. Festa-Bianchet *et al.* (1990) found that fallow deer did not return to the same lek territories in consecutive years. Interestingly they reported that stags increased their access to females by defending lek territories which had previously attracted more hinds (Apollonio *et al.* 1990). Thus stags shifted to more successful territories in successive years. Similarly Floody & Arnold (1975) reported incidents in which Uganda kob males shifted from lek territories with little reproductive activity to more desirable territories.

Observations from other species also suggest that territory-shifting is a calculated decision, designed to increase individuals reproductive success. This has been shown for red squirrels (Wauters *et al.* 1995) and sage sparrows (Petersen & Best 1987). Within a given year, territory shifting by springbok rams was associated with an increase in the number of females seen on their new relative to their old territories. It appears that territory shifting by springbok, as with other species, is a mechanism males use to try and increase their access to potential mates.

In territorial conflicts it has often been recorded that residents almost always win aggressive interactions (Davies 1978, Stamps 1987, Krebs & Davies 1987). The advantage prior residency can have may clearly be shown by experimental manipulation of individuals. Dominance reversal has been demonstrated by the early introduction into a locality of individuals which are normally subordinate; the effect of introducing young birds into an area before adults is to reverse their dominance, the subordinate young birds becoming dominant due to their prior residency (Cristol *et al.* 1990, Sandell & Smith 1991). Further, when two contestants are tricked experimentally into simultaneous ownership of a territory such that both believe they have the advantage of prior residence, an escalated contest can arise (hamadrayas baboon; Kummer 1971, speckled wood butterfly; Davies 1978, damselfly; Waage 1988).

Not only is prior residency of importance in determining the outcome of contests, but the duration of territory occupancy is also significant. As new owners spend more time on a territory, and former holders more time away, so the probability of the newcomer winning a contest increases (Krebs 1982). Together these facts suggest that, regardless of any differences in two individuals' resource holding potential, an asymmetry in pay offs exists due to both prior residency *per se* and to the duration of this residency by one individual.

As the advantages males may gain by the length of territory occupancy are reduced aggression, and a greater asymmetry in resource holding potential relative to intruders, this should be reflected in the length of their territory tenure over rutting periods. In other words these males should be able to maintain their territorial status for longer periods than those that only establish their territories at the time of the rut. An indication of this is that springbok which established territories during the rut, such as those observed at Kaspersdraai, were found to relinquish their territories at a higher rate than those which had held territories for extended territories prior to the rut in the main study area.

For those territorial ungulate species which have been studied, possession of a territory is a pre-requisite to gain mating opportunities (Owen-Smith 1977). Applied to the present study this would indicate that springbok males could improve their reproductive success by remaining in possession of a territory for as long as possible during the rut. Males could enhance this period of possession, and ultimately their reproductive success, both by returning to their former territories in different years and by maintaining these for as long a period as possible over both rutting and non-rutting periods, which were often only relinquished as ecological conditions deteriorated. Evidence to support the idea that the duration of territory occupancy is important comes from those individuals which only established territories during the rut and whose rate of territory turnover was higher than individuals which established territories prior to the rut.

These factors do not apply only to the springbok, but could be important for all ungulate species holding resource-based territories. It is proposed that it is beneficial for male ungulates to maintain their territories for as long a period as is permitted by pervading ecological conditions in order to maximise territory tenure over the rut and thus maximise their potential reproductive success. This would explain why both year-round breeders such as Thomson's gazelles, and year round but potentially synchronised breeders such as the springbok, maintain territories at all times of the year and not just over the breeding season.

SUMMARY

- Territory establishment could largely be attributed to the rut and the first good rainfall of the year.
- Most territories were established by males returning to a previous territory, whilst displacing a previous owner and moving onto vacated territories were also important.
- By far the greatest proportion of territories were relinquished passively.
- Males sometimes shifted their territories within a season, though significantly, new territories always had higher numbers of ewes on them than their old territories.
- Territorial males were observed in all months of the year, though mean territory occupancy was only for a period of approximately 4.5 months.
- As vegetation biomass decreased towards the end of the dry season males spent less time actually resident on their territories and more time in the surrounding areas.
- These factors indicate that males may hold year round territories in order to increase their ability to hold a territory over the rut and ultimately to maximise their reproductive success.

Chapter 11

Resource-defence polygyny

INTRODUCTION

Current research on ungulate mating systems has focused on lek breeding (Gosling & Petrie1990, Balmford 1991, Balmford *et al.* 1993, Clutton-Brock *et al.* 1993). This breeding system has however only been confirmed for four antelope species (Uganda kob: Buechner & Roth 1974, Floody & Arnold 1975, Balmford 1990, 1992, Deutsch 1994; white-eared kob: Fryxell 1987; Kafue lechwe; Nefdt 1992; topi: Gosling 1991) and possibly two cervids (fallow deer: Pemberton & Balmford 1987, Clutton-Brock *et al.* 1988; sika deer: Clutton-Brock *et al.* 1993).

Whilst lek-breeding is of important academic interest, there is relatively little known about resource-defence polygyny in relation to our current understanding of ungulate mating system theory. Its fundamental importance is evident from the fact that resource-defence has been recorded as a pure reproductive strategy in ungulates, whereas lekking always appears as a specialist mixed response (Gosling & Petrie 1990, Alvarez *et al.* 1990). It is also the most common mating system amongst antelopes (Gosling 1986) and has been inferred for a number of medium-sized species (*e.g.* sand gazelle: Habibi *et al.* 1993; waterbuck: Spinage 1982; black lechwe: Thirgood *et al.* 1992; red lechwe: Williamson 1994; puku: Rosser 1987, 1990; topi: Gosling 1991, Balmford *et al.* 1992, Gosling *et al.* 1987). In still more species the presence of solitary or territorial males has been recorded (*e.g.* Grant's gazelle; Walther 1972*ab*, gerenuk; Leuthold 1978*a*, Thomson's gazelle; Walther 1978ac, dorcas gazelle; Grettenberger 1987, Habibi *et al.* 1993, mountain gazelle; Baharav 1983*a*, blackbuck; Dubost & Feer 1981, pronghorn; Bromley 1969). Yet only in a few species (puku: Rosser 1987, 1992; impala: Murray 1982; pronghorn: Byers & Kitchen 1988, Byers *et al.* 1994; red deer: Carranza *et al.* 1990) has any attempt been made to quantify territoriality in relation to resource-defence polygyny. This chapter therefore explores the mating system of the springbok in respect to current theory. It aims to improve our current understanding of resource-defence polygyny amongst ungulates and to provide some parallels between the prevailing ideas regarding lek and resource-based territoriality.

In almost all records of copulatory activity amongst ungulates, a prerequisite of success has been the establishment of male dominance over other individuals, either in a territorial or harem-holding respect. Observed copulatory activity has been restricted to dominant males in all but a few recorded instances (but see Byers & Kitchen 1988, Byers 1989). It was therefore expected that territorial male springbok would achieve higher rates of copulation than their non-territorial counterparts.

One apparent difference between a lek breeding situation and resource-defence polygyny is the apparent lack of ecological resources on lek territories which may serve to attract females. Some leks are primarily visited by females in oestrous, whilst other leks are regularly visited by females, many of whom are not in oestrous (Clutton-Brock *et al.* 1988). Thus on some leks a disproportionate number of females observed on lek territories are in oestrus, relative to the proportion of oestrous females off leks. Males defending important resources to females would expect to attract both oestrous and non-oestrous females to their territories in equal proportions. Furthermore, if the resources *per se* are an important factor attracting females to a male's territory it was predicted that the number of females visiting particular territories would not vary between pre-breeding and breeding periods. This does not however imply that the number of ewes visiting different territories does not differ significantly as the apparent quality of different territories to females is probably governed by a variety of ecological factors.

Female harassment appears to be an important factor affecting breeding ungulate populations. Similarly the removal of dominant males from a fallow deer lek coincided with an increase in aggression between males and a reduced copulation rate (Apollonio *et al.* 1989). Clutton-Brock *et al.* (1992) showed that female harassment was lower on lek territories than elsewhere and that harassment rate per female decreased with an increasing number of females on a territory. Whilst the effect of harassment has been documented on lek territories, the effect of female numbers on the rate of attention by males has not been properly investigated on resource-based territories. However in a population of pronghorns, increased intrusion pressure by non-territorial males appeared to cause the complete disintegration of territoriality, with a subsequent high copulation rate achieved by non-territorial males (Byers & Kitchen 1988). If female harassment is an important consideration, it was expected that oestrous ewes would chose to associate with other females in larger herds where presumably the rate of harassment was lower.

In some ungulates multiple mating of females have been recorded by either one or several males (blackbuck; Dubost & Feer 1981, topi; Gosling & Petrie 1990, Uganda kob; Balmford 1990, red deer; Pemberton *et al.* 1992, puku; Balmford *et al.* 1992, tsessbe; Child *et al.* 1972, domestic sheep; Gibson & Jewell 1982). In other species multiple matings of a particular female are very uncommon (impala; Jarman, M. 1979, reindeer; Espmark 1964, fallow deer; Asher 1986, pronghorn; Byers *et al.* 1994). As the reproductive success of a particular male is dependent on the number of females he fertilises, it is in a male's interest to try and maximise the probability that he is successful when mating with a female. In the case of females that only mate once in a breeding season, paternity is guaranteed. However as females often mate more than once a male must try and determine his optimum investment time with a given female; whether to stay with one female or search for another in order to maximise fertilisation rate (Parker 1973). By staying with one female a male would be showing pre-copulatory mate guarding. This type of male investment is apparent from accounts on elk, reindeer (Espmark 1964), greater kudu (Owen-Smith 1984) and nyala (Anderson1980), and these males are thus almost guaranteed of siring a female's offspring.

However when a female may be repeatedly mated, a particular male's paternity is no longer guaranteed. In such cases a period of both post-copulatory mate guarding (Hogg 1984, Owen-Smith 1984) and 'retaliatory' matings, related to sperm competition, as males regain control of females (Hogg 1988) have been recorded. In a study of the territorial Grevy's zebra, in which multiple mating of females is common, Ginsberg (1988) found that the intercopulation intervals of females mated by single males was longer than that of females mated by more than one male. This he attributed to sperm competition between males. In a more complex scenario, there is evidence to suggest that feral goats adjust their willingness to join and leave female groups in response to both oestrous female numbers and the number of competing males in a group (Dunbar *et al.* 1990).

The importance of post-copulatory mate guarding is dependent on the point of conception in relation to oestrus. If a female is likely to conceive after first mating then the function of mate guarding is defunct. However if a female may conceive at some other point during oestrus, mate guarding will have the benefit of reducing the number of matings by rival males and therefore increase a male's paternity certainty. The siring success of male sheep has been shown to vary at different periods of oestrus, when ewes were mated with more than one male (Jewell *et al.* 1986).

Rutting behaviour by territorial males has been shown to have a disruptive affect on their general activity budgets, representing an energetic cost. Feeding by such males is greatly reduced in many species and in some there is an almost complete cessation in feeding behaviour together with associated ruminating activities. Conversely locomotory activity has been shown to increase, both of which act as an energetic cost of reproduction to males. The effect of rutting behaviour on springbok rams was monitored in to determine what influence this may have on their food intake, resting and locomotory rates. Further, as the number of females on a territory fluctuates throughout the rut, it was expected that this would have an influence on males' activities; with more females present on a territory it was predicted that feeding, ruminating and resting levels would decline, whilst locomotory activity together with sexually orientated behaviour would increase.

The aim of the chapter is to examine some aspects of the breeding behaviour of springbok rams. First, to describe the sexual behaviour of the springbok and to examine whether springbok restricted their breeding periods to specific periods in the Kalahari, or whether there is little variation in their sexual activity throughout the year. Second, to determine whether the ultimate benefit of territoriality is to increase a male's mating opportunities. Third, to establish whether territories are visited by females primarily for feeding or breeding purposes by comparing individual territory use both over rut and during pre-rut periods; *i.e.* whether resource-defence polygyny is the fundamental mating system in this population of springbok. Fourth, to examine those ways in which males may maximise their probability of siring a ewe's offspring, either through frequent insemination or female guarding. Finally to determine the cost of the rut on the daily maintenance activity of territorial males by analysing any changes in their general activity between pre-rut and rut periods, as well as the impact of female numbers on their maintenance activity over the rut.

METHODS

In order to establish whether female numbers on a territory altered during the period of a rut the number of females on the territories of known rams were recorded. The minimum period between records was a day. From this the average number of ewes present on a particular territory could be calculated prior to the rut and during the rutting period. As the length of individual ruts was not constant, the pre-rut period was taken as the same duration as the rut itself *i.e.* if a rut was 11 days long, a pre-rut period of 11 days was used to calculate the average number of females on a territory.

Once a springbok was observed to be mated by a ram she was subsequently followed as a focal animal. A ewe was identified as such either during a focal watch on a particular male or by observing the precopulatory and copulatory behaviour of males in the vicinity of observations. Focal ewes could only be identified by natural markings. Horn size, shape and abnormalities, together with a combination of other identifying features including scars, coat colour on the nose, lactation, body condition and unusual patterns of hair eruption (twirls) were used. Even so ewes showed very little phenotypic variation and despite constant watching were sometimes lost within a herd. In such cases the lack of mating of any of the ewes in a herd was indicative of the fact that a ewe had not been remated. Data were collected on the number of females found together with the oestrous ewe at the time of intromission, together with any subsequent changes in female numbers. The status of males mating with a ewe was recorded (territorial\non-territorial) and the identity of the male, whether the original male or a subsequent mating partner. Movements of the ewe from one territory into another or to an area not defended by a territorial male were also recorded. The number of unsuccessful mounts a ram made before intromission and the inter-mating period between consecutive matings was recorded. The duration of courtship activity was considered from when a male began 'touching laufschlag' (see below) until ejaculation. Ejaculation consisted of a single rapid pelvic thrust by the male, in common with other gazelles. Mated females were followed for as long a period as possible. Any watch periods of less than one hour were ignored in the final analysis. The longest focal watch extended over 400 minutes. Observations terminated when an individual was lost in a herd or at dusk.

Males were considered to show a continued interest in a female after mating when they remained in the immediate proximity of the female. Such males ignored all other ewes on their territories and would perform laufschlag to the ewe and may have tried to remate the ewe. Males were considered to ignore the ewe when they returned to regularly courting all the females on their territory, such that their interest in a mated ewe did not differ significantly from that displayed to other females.

RESULTS

1. General observations on breeding behaviour

The courtship and mating behaviour of springbok are illustrated in Figure 47. Males' laufschlag behaviour in a courtship sequence preceding intromission typically differed from that in which mating did not occur. Laufschlag consisting of slow stiff-legged movements, actually rubbing the female's hind legs, raising the forelegs to the height of the ewe's belly, generally preceded copulation (touching laufschlag). In a situation which was not terminated by mating, the male's laufschlag appeared to be more half-hearted; the forelegs were thrust more rapidly forwards, not normally lifting more than

30 cm above the ground and not making physical contact with the females back legs (non-touching laufschlag). The difference in this laufschlag behaviour was a good predictor of whether or not mating would occur.

In all observed instances of copulatory behaviour males appeared to solicit females, rather than vice versa. However, males were sometimes distracted from a ewe by intruding males or even another female on their territory. In such instances a male would leave the female he had been interested in. It appeared that at this stage females may actively solicit the male which had left them. In one instance a ewe traversed the entire length of a territory to join the male who had broken off his courtship with her earlier. When he again re-crossed his territory she followed again and was eventually mated by him.

It appears therefore that males always initiated pre-copulatory and copulatory activity, but that oestrous females would also solicit males who had left them prior to copulation. Non-territorial males showed very limited

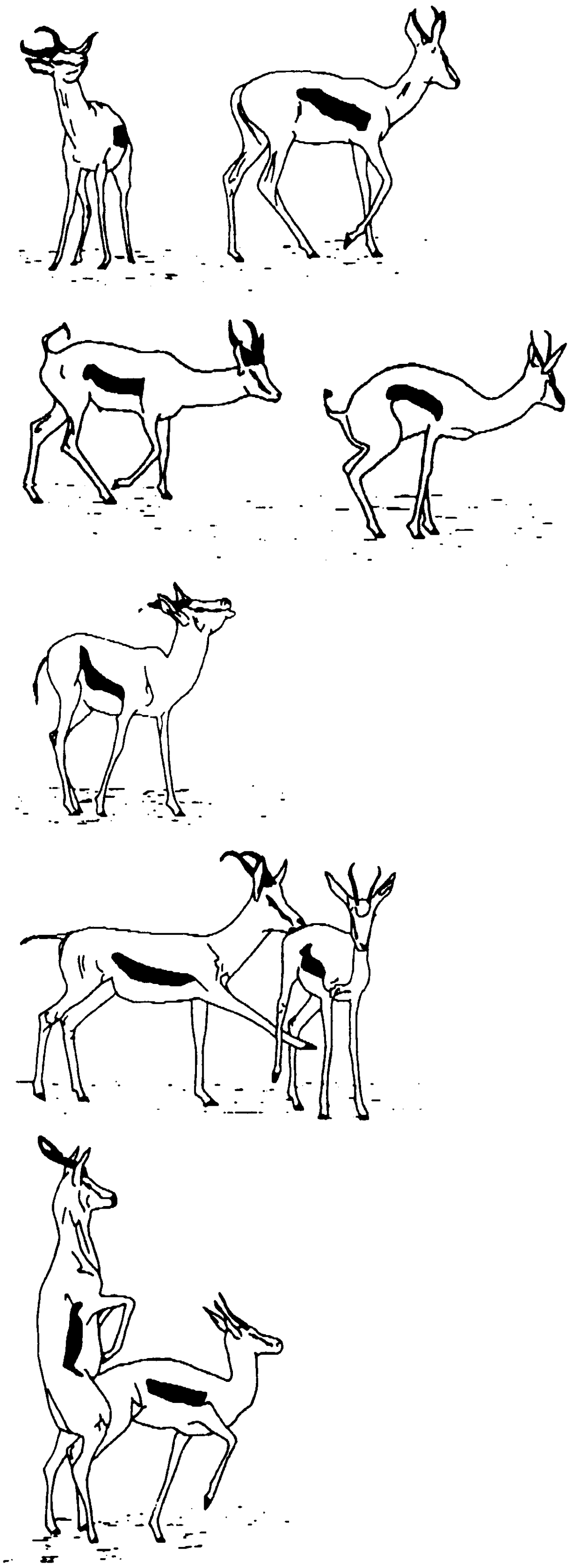

Figure 47 Sexual activity of springbok. From top to bottom: neck stretch, urine sniffing, flehmen, laufschlag and copulation.

interest in oestrous females. They would however sometimes sniff the vulva of an oestrous female, as well as showing the flehmen response to their urine.

2. Sexual activity through the year

Both primary (investigatory) and secondary (precopulatory) sexual activity were found to vary significantly between different months (primary sexual activity: KW ANOVA, H=494.98, df=39, p<0.001; secondary sexual activity: KW ANOVA, H=452.20, df=39, p<0.001; Figure 48). Both were found to be consistently high in July each year, with a secondary peak in March/April. As the March/April peaks did not generally coincide with any observed mating activity these have been termed 'false ruts'. The one exception being the April 1993 rut in which a number of copulations were observed. The effectiveness of these different rutting periods is examined in

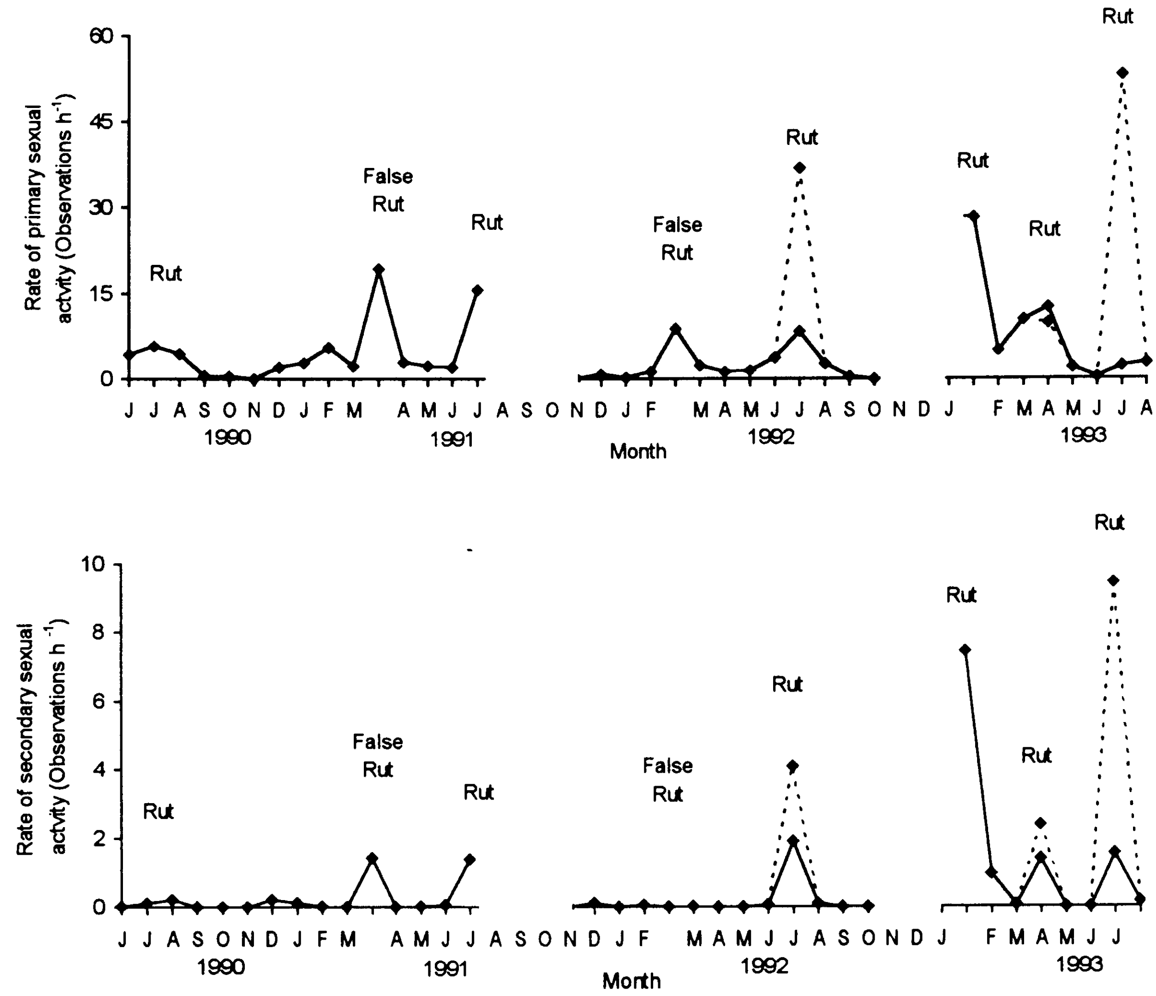

Figure 48 Monthly variation in the primary (above) and secondary (below) sexual activity of territorial males. Dotted lines show second observation site within a month where females numbers and sexual activity were both higher.

further detail in chapter twelve. Additionally a rut was observed in February 1993. This coincided with both the end of a very dry period (chapter four), the time at which males re-established their territories and other springbok returned to the riverbed (chapter six).

3. The status of breeding males

Table 32 shows the number of individual males observed to mate with a focal ewe. All females were mated initially by a territorial male. Whilst females were often mated more than once, few were actually seen to mate with more than one ram. Those which did so mated with a second territorial ram, which in all instances was the neighbour of the first male.

On no occasion were females seen to be mated by non-territorial rams, either initially or subsequent to first mating. This was despite the fact that some ewes were observed to wander off territories into undefended areas. Of the observed matings 82.1% (n=39) of matings subsequent to first mating were accountable to the male which initially mated with a female.

Number of territorial males mating with ewe	*n*	%
1	28	87.5
2	4	12.5
>2	0	0.0
Non-territorial	0	0.0

Table 32 The status and number of males seen to mate with a ewe which was followed prior to the first observed mating, including first-mating males.

4. Resource-defence polygyny

a) The number females on a territory: rut vs. pre-rut periods

The average number of females on a particular territory prior to the rut was found to be 5.97±1.20 (n=33). During the course of the rut the average number of females on the same territories was 4.17±0.78 (n=33). Individual males were tested to see whether the average number of females on an individual male's territory differed in pre-rut and rutting periods. It was found that the number of females on a territory did not vary significantly between these two periods (Wilcoxon M.P.; Z=1.14, n=33, NS).

b) The effect of territory size on female numbers

It was found that there was a weak but significant correlation between male territory size and the mean number of females observed on the territory over the rut ($r_s=0.33$, n=37, $p<0.05$; Figure 49); as territory size increased so too did female numbers.

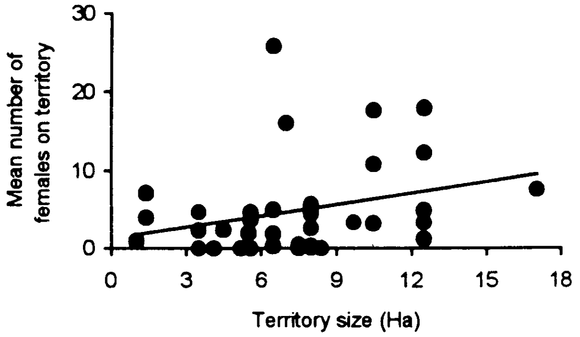

Figure 49 The effect of territory size on the mean number of ewes present over the rut.

c) Female group size: mated vs. population

During the July 1993 rut, the mean number of adult females in a group was found to be 7.1±0.7 (n=76). The mean number of females in a group which included a female which had been observed mating was 12.9±2.5 (n=14). Comparing these group sizes, it was found that the mean number of adult females in groups including mated females was significantly larger than that found for females in general (Mann Whitney U; Z=2.30, $p<0.05$, n=76). However this difference could simply be related to the fact that as herd size increased, there was a greater chance of finding a mated female in a herd anyway. Thus the distribution of mated females was compared to the distribution of all females in herds of different sizes. This was done by comparing their cumulative distribution curves (Figure 50).

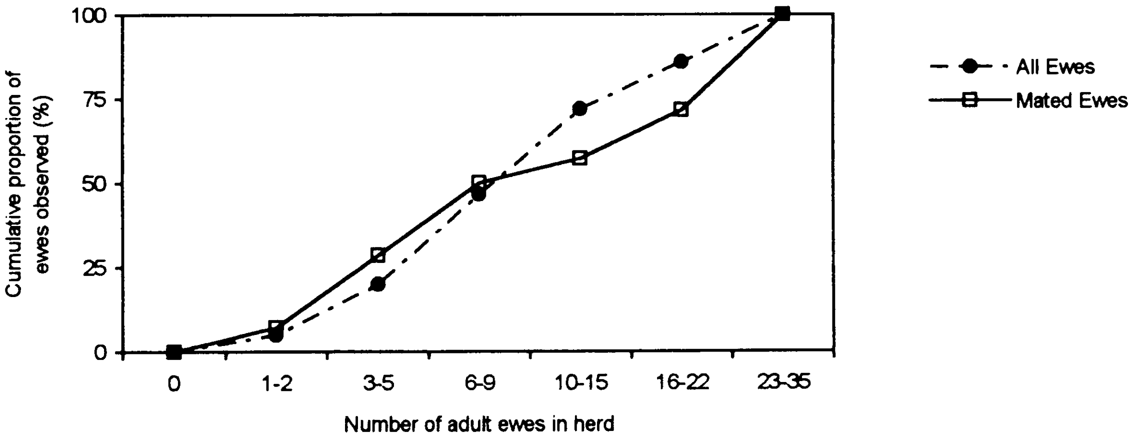

Figure 50 Comparison of the cumulative distribution within herds of mated females and all adult females during the rut (July 1994).

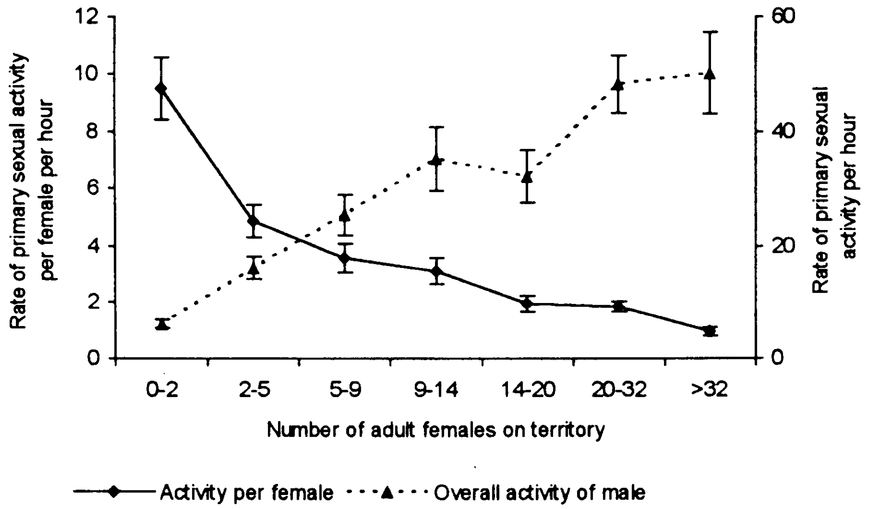

Figure 51 The affect of the number of females on males' territories on i) the overall *rate of primary sexual activity by the territory holder and ii) the rate of sexual activity* per female *on the territory*

It was found that the two distributions did not differ significantly (Kolmogorov-Smirnov one sample test: D=0.14, n=14, NS) *i.e.* mated females were not found to associate more in smaller or larger herds than expected, but were randomly distributed with other females in herds.

d) The effect of female numbers on the sexual activity of territorial males during the rut

The rate at which males were seen to engage in sexual activity with females was directly related to the number of females on a territory. As female numbers increased there was a strongly correlated increase in both primary (r_s=0.84, n=285, p<0.0001) and secondary (r_s=0.60, n=285, p<0.0001) sexual activity.

Whilst both the rates of primary and secondary sexual activity by territorial males increased with increasing numbers of females on a territory, the rate of sexual activity per female decreased significantly with more females present on a territory (KW ANOVA, Z=47.69, n=213, p<0.0001; Figure 51).

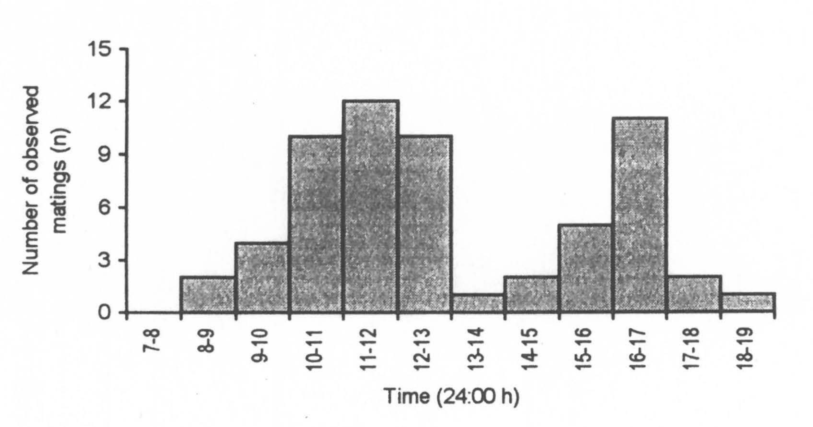

Figure 52 Variation in the number of observed matings at different times of the day

5. Mating, post-copulatory activity and mate guarding

a) Timing of mating

The time at which females were mated was not distributed evenly through the course of the day (Figure 52). Nor was it entirely coincident with the general springbok activity peaks in the early morning, midday and late afternoon periods (chapter five). In fact the pattern of matings differed markedly from parity ($\chi^2=44.0$, df=11, $p<0.001$), showing a bimodal peak. These occurred in the late morning and late afternoon. The late morning peak would correspond to the times at which ewes tended to either rest or ruminate.

b) Mating frequency of females

A total of 32 ewes were watched intensively subsequent to their first observed mating. Of these females 59.4% were seen to be mated on only one occasion, whilst 40.6% were mated more than once. Thus, multiple-mating is common amongst springbok ewes. The maximum number of matings observed for a single female was six, performed by two different territorial males.

c) Intermating interval

The average time interval between first and second matings or between second and subsequent matings did not vary significantly (Mann-Whitney U; Z=1.12, n=21, NS; Table 33). The distribution of time intervals between multiple matings is shown in

Figure 53. Overall, the mean inter-mating interval was found to be 44.8±16.4 min (n=21). Similarly, the average number of times a male mounted a female before mating successfully did not vary significantly between their first or subsequent matings (Mann-Whitney U; Z=0.21, n=42, NS). On average males mounted a female 14.7±2.1 times before achieving intromission.

	Observed mating	
	First	Second or subsequent
Mating interval (min)	60.6±19.1 (n=13)	19.1±6.7 (n=22)
Number of mounts prior to intromission	12.6±1.5 (n=8)	17.1±4.0 (n=20)

Table 33 Mating intervals between first observed and subsequent matings of a ewe and the number of mounting attempts by a male prior to achieving intromission.

d) Pre-copulatory interest in females and mate guarding

On no occasion were males seen in constant attendance of oestrous females prior to the first observed mating. An example of this is a male (R3) who spent the half hour before mating with a ewe in feeding on the far side of his territory, but came over and mated with her immediately after he joined the group of females on his territory.

e) Post-copulatory interest in females and mate guarding

The number of males still showing interest in ewes subsequent to their first been mated is shown in Figure 54. Of these 38.1% showed an immediate loss of interest in ewes with which they had mated. On average males lost interest in a female 12.7±4.1 min after initial mating (excluding one anomalous case where a male maintained interest for 332 min and mated six times with a female).

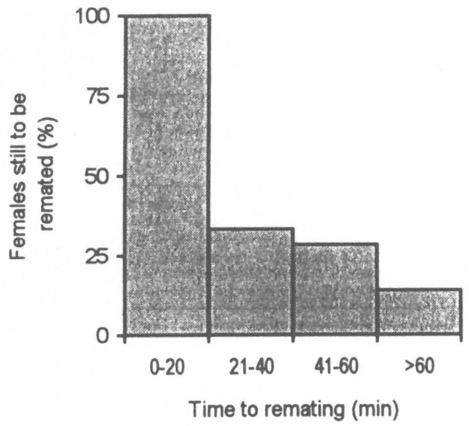

Figure 53 The proportion of springbok ewes still to be remated at different time intervals following their initial mating

The time for which males maintained an interest in a mated ewe was not related to the total number of ewes present on their territories; r_s=-0.17, n=21, NS). Thus the period of continued interest in a mated ewe was independent of female numbers on a territory.

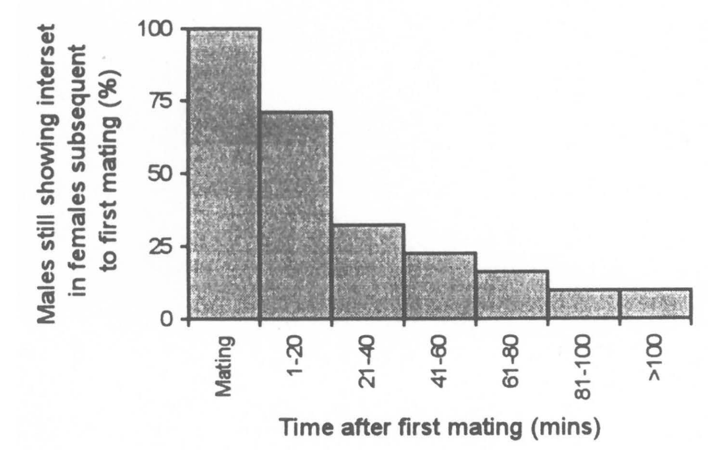

Figure 54 The number of males maintaining interest in a female subsequent to first observed mating

6. General maintenance activity of territorial males: rut vs. pre-rut periods

a) The effect of female numbers on a territory

The number of females present on a territory was found to influence rams' general maintenance activities during the rut (Figure 55). As female numbers increased the proportion of time rams spent both resting and ruminating decreased (resting; KW ANOVA, Z=32.54, n=285, p<0.0001. Ruminating; KW ANOVA, Z=42.19, n=285, p<0.0001). With more than 25 ewes on a territory resting was reduced to 19.9% and ruminating to 27.5% of that recorded when no females were present on a territory.

In contrast the time males spent walking or running on their territories increased with increasing ewe numbers (KW ANOVA, Z=81.68, n=285, p<0.001), rising 3.73 times with more than 25 ewes present on a territory relative to the situation when no ewes were present. Feeding was the only behaviour which did not appear to be affected significantly by the number of ewes present on a territory (KW ANOVA, Z=5.07, n=285, NS).

During the pre-rut period, the number of ewes present on males' territories had no bearing on their general maintenance activity (Figure 55). In all instances the differences in the recorded levels of particular activities was independent of ewe numbers (Feeding; KW ANOVA, Z=0.78, n=124, NS. Resting; KW ANOVA, Z=0.52, n=124, NS. Ruminating; KW ANOVA, Z=0.73, n=124, NS. Moving; KW ANOVA, Z=7.81, n=124, NS). This is in contrast to the activities of territorial males during the rut.

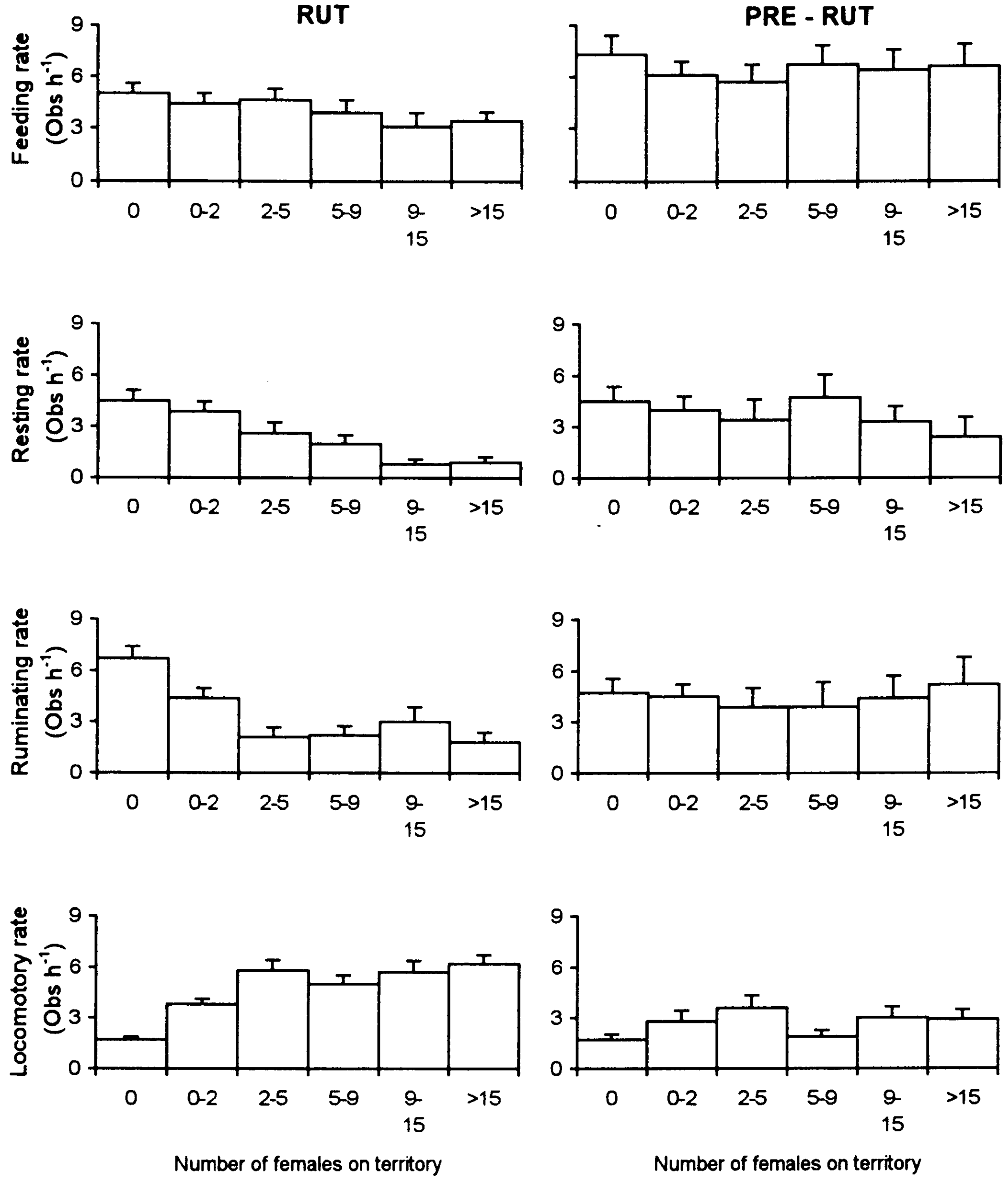

Figure 55 The effect of both the rut and female numbers on males' territories on the rate of general maintenance activities

b) Rut vs. pre-rut periods

Overall, the proportion of time territorial males spent in particular activities did vary between the rut and pre-rut situations. Feeding levels declined significantly from 32.3±2.3% of pre-rut activity to 21.1±1.3% of activity time during the rut (Mann-Whitney U; Z=4.37, n=409, p<0.0001). Similarly the amount of time territorial males spent both ruminating and resting decreased from the pre-rut to rutting periods. These differences were only slight, though significant, in comparison to the decline in feeding time. Ruminating declined from 22.5±2.1% to 18.8±1.5% of activity time (Mann Whitney U, Z=2.03, n=409, $p<0.05$), whilst resting time fell from 19.0±2.1 to 14.1±1.2% of all activity (Mann Whitney U, Z=2.25, n=409, $p<0.05$) from the pre-rut to rut period. Conversely, locomotory behaviour increased significantly from 12.9±1.3% to 21.3±1.0% of activity time (Mann Whitney U, Z=5.23, n=409, $p<0.0001$). It appeared that, during the rut, males may have been compensating for the reduced levels of ruminating when ewes were present on their territories by increasing rumination time when alone. The time they spent ruminating when alone was not however any higher than during the pre-rut period, as may have been expected in such circumstances (Mann Whitney U, Z=1.53, n=107, NS).

DISCUSSION

Previous chapters have highlighted some of the costs of being territorial; an increased threat of predation, higher risk of debilitating injuries during the rut and the limited rangeing abilities of territorial compared to non-territorial individuals. Another cost is energetic, brought on by an increase in the sexual, agonistic and marking activities of territorial males during the rut relative to pre-rut periods. Most notably there was a reduction in the amount of time territorial males spent feeding, with a concurrent increase in locomotory activity, as recorded in other species (*e.g.* pronghorn; Maher 1991). Many males of polygynous mammal species lose weight over the breeding period (Clutton-Brock 1991). However, unlike a number of cervids (*e.g.* red-deer: Clutton-Brock *et al.* 1982, Bobek *et al.* 1990; reindeer: Espmark 1964, Mossing & Damber 1981, Suttie *et al.* 1992; moose: Miquelle 1990) there was no complete, or near complete cessation of feeding behaviour by springbok. This suggests that the underlying physiological factors controlling breeding in African antelope species may be different from those acting on those cervid species which have been studied in areas of increased latitude. Certainly for the moose, appetite suppression over the period of the rut could be a by-product of the physiological processes associated with scent-urination (Miquelle 1990).

Nagy & Knight (1994) calculated that rutting males needed to increase their energy intake from 20g/kg/day to approximately 90g/kg/day to maintain their body mass. However as the results of this study show, males' food intake decreased during the rut as one might expect, such that their body condition probably also deteriorated. Similarly (Murray 1982*b*) recorded a decrease in both femur marrow and kidney fat amongst impala rams during the rut, indicating the decline in body condition males suffer at this time. Resting and ruminating were also reduced during the rut, though not as markedly as feeding behaviour. Springbok (Skinner *et al.* 1995), in common with other ungulate species (reindeer; Espmark 1964, red deer; Gibson & Guinness 1980), may show a decline in body condition and body weight during the course of the rut. Female numbers also affected the general behaviour of territorial springbok rams during the rut. As female numbers increased on a territory, males devoted more of their time to sexual, aggressive, marking and locomotory activities which consequently reduced the amount of time spent resting and ruminating. Surprisingly levels of feeding activity remained independent of female numbers. However this extra cost is presumably balanced by some extent to the increased mating opportunities males may gain.

The level of sexual activity amongst territorial springbok rams was found to vary significantly between different months. Peaks of sexual activity occurred in July of each year under study and are referred to as rutting periods; mating was observed in all ruts (chapter 12). Similarly ruts were recorded in February and April 1993. A second set of sexual activity peaks were recorded in March/April 1990, 1991 and 1992. Concurrently the density of territorial males on the riverbed (chapter eleven), together with agonistic (chapter ten) and marking activity (chapter nine) increased at this time. However these periods were not accompanied by mating activity. As they do not appear to vary from a rut in any other way, they could be considered as 'false ruts'. This phenomenon is discussed in more detail in the concluding chapters.

A springbok ram's territorial status would appear to be a prerequisite to mating success. Similarly breeding has been recorded exclusively amongst territorial males in a number of other species (mountain gazelle: Baharav 1983; red lechwe: Williamson

1994), whilst in others territory holders accounted for a disproportionate number of matings (impala: Jarman & Jarman 1973*b*, Murray 1982; Uganda kob: Floody & Arnold 1975; waterbuck: Wirtz 1981; pronghorn: Kitchen 1974; fallow deer: Thirgood 1990, Clutton-Brock *et al.* 1989, 1992; sika deer: Miura 1984). Thus territoriality itself, on both resource and lek-based territories has been shown to increase males' access to reproductive females.

Territorial males did not appear to guard mated females for extended periods either before or after the first known intromission was observed, despite the fact that oestrous activity could extend for 12-48 hours as it does in other ungulates (Uganda kob 12 h: Balmford 1990; red deer 12-24 h: Gibson & Guinness 1980, Clutton-Brock *et al.* 1982; fallow deer 24 h: Asher *et al.* 1990; reindeer 48 h: Espmark 1964; nyala 48 h: Anderson 1980). Presumably though males do not guard their mated females as it would not benefit them to do so.

For many lek-breeding ungulates oestrous ewes actively seek out territorial males (Clutton-Brock *et al.* 1988, 1992, Balmford *et al.* 1993, Stillman *et al.* 1993). It was predicted that if this were so for the springbok, female numbers on territories should increase over the rut, with the concurrent increase in mating activity. However the average number of females on individual territories showed no noticeable change between pre-rut and rut periods. Females did not increase their visits to territories over the period of the rut; territories appear equally attractive to females over both periods. Similarly Carranza *et al.* (1990) reasoned that the correlation between the number of females in red deer harems and female density in an area both before and during the rut implied that females were using the area primarily for foraging and not for reproductive purposes. In addition the density of springbok on the fossil riverbeds was much higher than in the surrounding dune areas (chapter six), and this was the area in which males were observed to hold territories, together with the pans. From these observations it is concluded that males maximised their reproductive success through the defence of resources on the riverbeds attractive to females.

Amongst ungulate populations individual females' mate choice may not be independent of each other. Recent studies have concluded that females could in fact be copying each others decisions, rather than choosing to mate with a particular male. A reduction in female harassment is one of the hypotheses put forward to suggest why oestrous females may join others on lekking grounds (Balmford 1991, Nefdt 1992, Clutton-Brock *et al.* 1992, 1993). Certainly the reduced copulatory rates on a fallow deer lek appear to be related to an increase in the frequency of fights (Apollonio *et al.* 1989). Oestrous fallow deer does tended to join males that already had females on their territories, being attracted to female groups rather than the presence of a stag (Clutton-Brock & McComb 1993). These authors reasoned that females may be attracted to other females on a lek as an adaptation to avoiding harassment in mixed sex herds rather than through choice for a particular mating partner (McComb & Clutton-Brock 1993). Likewise, female bighorn sheep resisted the advances of coursing rams, which tried to force copulations, choosing to mate with tending rams (Hogg 1987).

Despite the results of other workers, the findings of the present study suggest that mated female springbok were located randomly amongst herds, neither choosing to join larger or smaller herds. This was despite the fact that the rate of sexual activity per individual female decreased with increasing female numbers, which may have prompted oestrous females to join larger herds. Thus unlike lek-based territoriality, oestrous female springbok did not appear to try and reduce any sexual harassment from males by choosing to associate in larger herds. These females appeared to be attracted to a territory primarily for its resources, such that all males but the territorial owner will have been excluded from the area. Therefore any chance of being harassed by intruding males should be relatively small, and harassment does not appear to be important in influencing resource-defence polygyny as a mating system for the springbok.

There is evidence to show that the phenotypes of breeding (territorial) and non-breeding (non-territorial) males can be distinguished. This appears to be true for the springbok as parallel observations on the same study population found that the neck girth of territorial males was greater than that of non-territorial individuals (Skinner *et al.* 1995).. A similar difference has been recorded for neck girth between territorial and non-territorial puku (Rosser 1990). However no such correlation was recorded between territorial and non-territorial impalas (Jarman, M. 1979). Indeed impala males in poor condition still maintained territories over non-territorial males in better condition to a certain threshold. However it is not known to what extent an individual's ability to establish a territory is related to phenotype and to what extent phenotypic differences are related to underlying physiological factors once a male has established a territory; certainly testosterone secretion by male Grevy's zebras is higher when on than off their territories, at which time it does not differ significantly from that of non-territorial males (Chaduri & Ginsberg 1990). As testosterone promotes muscle growth, this suggests that thicker necks may be a consequence rather than a cause of such differences between territorial and non-territorial males.

Specifically considering territorial males, there is still very little evidence to suggest that differences in the reproductive success of different male antelope defending resource territories is directly related to their phenotype (though see Balmford *et al.* 1992). Considering territorial male pronghorns, despite the high skew in individual male mating success, the relative success of different territorial males could not be related to differences in body size, horn size, age *etc.* (Byers *et al.* 1994). As Gosling (1986) has pointed out the competitive ability of ungulates in relation to morphological and physiological features are still poorly documented amongst ungulates. Certainly for such medium-sized ungulates as the springbok, male body size reaches an asymptote at approximately 18-22 months (Rautenbach 1971). As a maximum of 20% of springbok rams are territorial at any one time (chapter six), by choosing to mate with territorial rams springbok ewes are already creating a high skew in male reproductive success within a rutting period, with or without selection for phenotypic differences between territorial males. Possibly what is more important in determining reproductive success for medium-sized, resource-defending ungulates is their ability to maintain territories for long periods (chapter ten). Whilst this itself may be related to male phenotype, it would override the importance of obvious phenotypic differences between territorial males during breeding periods. Similarly Deutsch (1992) and Deutsch & Weeks (1992) suggested that mate choice may play a smaller role in determining reproductive success on Uganda kob leks than previously argued, females rather choosing to visit areas already used extensively by other females and a tendency for females to aggregate at high visibility sights.

The physical properties of a particular territory probably affect mate access. Larger territories were associated with greater female numbers over the rut. Females also avoided areas of the riverbed covered by tall vegetation (chapter seven) and showed a movement towards areas of the riverbed closer to water sources in the dry seasons (chapter six). These indicate that characteristics of a male's territory are probably of greater importance in female choice than the phenotypic characteristics of the males themselves. However, no detailed observations of the attributes of different males' territories were made and so these differences were not quantified. Balmford *et al.* (1992) found that forage quality and predation risk were both significant, independent predictors of female choice in both puku and topi holding resource-based territories. Even on lek territories both grass height, and the olfactory cues left by previous female visits contributed significantly to differences in female territory preference (Deutsch 1992, Nefdt 1992, Deutsch & Nefdt 1992).

In conclusion, springbok held resource-based territories. In doing so the dispersion of females and non-breeding males was related to the available resources, whilst that of breeding males was related to female dispersion. Females appeared to move freely over males' territories and mated females were distributed randomly amongst herds. The effect of male phenotype on individual success has not been clearly shown for such a mating system. What may be more important is the ability of individuals to hold territories outside rutting periods in order to maintain them for as long as possible during the rut, rather than obvious phenotypic differences between males during the rut. Thus the major benefit of holding a perennial territory is in improving breeding success during the rut.

SUMMARY

- Sexual activity varied on a monthly basis, being highest over the rut and 'false rut'.
- Only territorial males were seen to mate with females
- Males held resource-based territories.
- Mated females were distributed randomly within herds, such that female copying or harassment models were not important in modifying resource-defence polygyny for springbok.
- Males quickly lost interest in a female following copulation, and no prolonged mate-guarding activity was seen, suggesting that the first successful mating may guaranteed paternity.
- Differences in males' phenotype may not be as important as their ability to hold a territory prior to the rut and thus to their potential reproductive success.
- A major cost of the rut to territorial males was a reduction in feeding, resting and ruminating rates

Chapter 12

Breeding Synchrony

INTRODUCTION

Whilst reproductive synchrony has been reported for a large number of species, the underlying mechanisms are far more complicated than were first believed (Ims 1990). Reproductive synchrony may be mediated by a number of underlying 'proximate' ecological processes (Baker 1938, Sadleir 1969), whilst more recently a number of sociobiological influences have also been recognised (Ims 1990). It is however important to remember that these proximate factors are distinct from the ultimate evolutionary processes responsible for synchrony.

Three mechanisms are thought to be responsible for breeding synchrony; environmental, social and internal cues (Campbell & Turek 1981, Bronson 1988, Turek & Cauter 1988). Environmental cues have received the most attention, partly because they are the most obvious cues and partly because the majority of work has been undertaken in temperate areas where climate plays an important role. Climatic variables which appear to influence reproductive seasonality include daylength (Goss & Rosen 1973, Lincoln & Davidson 1977, Lincoln & Short 1980), temperature and lunar cycle (Sinclair 1977). Ecological factors include food availability and the possible influence of plant chemicals (Sadleir 1969, Berger *et al.* 1977, Negus & Berger 1977, Sanders *et al.* 1981) which may mediate female receptivity under unpredictable conditions.

In equatorial systems it may be expected that a species will breed throughout the year. This is certainly true for sheep which have been translocated from temperate localities to equatorial Kenya (Sadleir 1969) and those cervid species which are believed to have extended their distribution to equatorial areas (Goss & Rosen 1973, Bronson 1988) as well as certain antelope species which appear to breed at all times of the year. However even under equatorial conditions certain species may show considerable synchrony of breeding events (wildebeest; Estes 1969, Sinclair 1977, Estes & Estes 1979), such that environmental seasonality alone is insufficient to explain the degree of reproductive synchrony occurring. In such instances Ims (1990) defined reproductive synchrony as a phenomenon caused by biological interactions operating to produce a tighter clustering of reproductive events than would have been imposed by environmental seasonality alone. This could be a consequence of animals' endogenous rhythms; a natural periodicity such as the circanual rhythm reported for sika deer kept under controlled conditions (Goss & Rosen 1973). Alternatively the proximate cues inducing reproductive synchrony may be by some form of social stimulation, be it pheromonally, acoustically or optically induced (see Watson & Radford 1960).

Amongst ungulates reproductive synchrony is common, with uneven annual birth rates being reported for many different species (Skinner *et al.* 1974, Leuthold & Leuthold 1975, Skinner & van Jaarsveld 1987, Rosser 1989). With increasing latitude daylength is most commonly accepted as the proximate cause of such synchrony, as well as in some equatorial species (Spinage 1973). There is however evidence to support the view that social influences are also important in determining reproductive activity at specific times in wild ungulates, which contributes to breeding being more highly synchronised than if only environmental factors were of importance (McComb 1987, Skinner *et al.* 1992). The differing reproductive pattern of a species in two geographically separated areas supports the idea that a number of factors are contributing towards its breeding periodicity (*e.g.* dik-dik: Brotherton 1994, Hendrichs 1975; impala: Jarman & Jarman 1973*b*, Jarman, M. 1979, Murray 1982*b*; sable: Sekulic 1978). Whilst these examples are taken from widely separated populations, the reproductive pattern of two neighbouring populations of mountain gazelle have also been found to differ substantially despite a separation of only 80 km (Baharav 1983).

The ultimate factor driving reproductive synchrony is presumably an increase in individual reproductive success. The two most important factors influencing offspring survivorship and therefore annual reproductive success in ungulates are food availability and reduced predation risk to individuals (Rutberg 1987). Restricted breeding periods may reduce predation on young and particularly vulnerable animals in three ways. First by increasing the probability of predator detection and repulsion (*e.g.* muskoxen). Second by predator swamping (Estes 1976, Estes & Estes 1979, Rutberg 1987) and lastly by predator confusion (Sadleir 1969, Ims 1990).

Within the southern Kalahari the breeding behaviour of the springbok is largely restricted to rutting periods (chapter eleven). The purpose of this chapter is to examine those factors which may influence the timing of the rut and parturition, to investigate the extent to which the sequence of events during the rut may be affected by the behaviour of territorial males and to determine how the occurrence of a rut may affect male and female reproductive success.

METHODS

Data spanning identical time intervals were collected to compare the activity of individuals during both the rut and pre-rut periods. Thus for a 15 day rut, the pre-rut period was considered to be 15 days, whilst for a seven day rut a seven day pre-rut period was considered. Data from all ruts over the course of the study were pooled in order to simplify analysis and present a single set of results. Due to their density-dependence, all data are considered in relation to female numbers on a territory.

In order to compare the distribution of various activities over the course of the rut, cumulative frequency curves were constructed. Data were collected from several ruts of varying intensity. To a large extent this was related to the number of females in an area at the time of the rut. To compensate for these differences in female numbers when calculating these cumulative frequency curves, the rate at which activities were performed were corrected for the number of females on a territory over an observation period. In addition the amount of data collected varied with the time of the rut; more data were collected during the second half of the rut. Allowance was made for this, such that the final data set was not biased by differing female densities or data collection rates. In order to simplify the findings object aggression and linked urination-defecation were combined as marking data for this analysis. The distributions of particular types of behaviour over the course of the rut were then compared using a Kolmogorov-Smirnoff goodness-of-fit test (Siegel 1956). This compares two cumulative curves to determine whether they are drawn from the same distributions.

Survivorship of lambs was determined by first counting the number of lambs observed in a given month relative to females (lamb:female ratio). Then a comparison of the proportion of lambs observed in consecutive months was made to give an estimate of the proportion of lambs surviving from one month to the next. Unfortunately this method would be complicated by any births in the second month artificially increasing survivorship estimates, but it does provide an indication of the effect of lamb numbers on their survival.

RESULTS

1. The effect of the rutting activity of territorial males on breeding

a) Pre-rut versus rut differences in activity

Figure 56 considers the levels of sexual and agonistic activities of territorial males in both the rut and pre-rut periods. Two things are apparent from these data. First, the level of all sexual and agonistic activity increased dramatically from pre-rut to rut periods (Mann-Whitney U: primary sexual; $Z=10.12$, $n=409$, $p<0.0001$: secondary sexual; $Z=6.30$, $n=409$, $p<0.0001$: herding $Z=4.32$, $n=409$, $p<0.0001$: chasing; $Z=7.14$, $n=409$, $p<0.0001$: fighting; $Z=5.31$, $n=409$, $p<0.0001$). Second, the presence of more females on a territory increased the rate of all these activities during the rut (KW ANOVA: primary sexual: $H=197.26$, $n=285$, $p<0.0001$; secondary sexual: $H=102.44$, $n=285$, $p<0.0001$; herding: $H=48.03$, $n=285$, $p<0.0001$; chasing: $H=90.56$, $n=285$, $p<0.0001$; fighting: $H=16.04$, $n=285$, $p<0.01$). However, the observed difference in fighting behaviour was only significant when comparing the presence or absence of females on a territory. Considering only those instances in which ewes were present on a territory, fighting rate was independent of the number of ewes (KW ANOVA; $H=6.04$, $n=213$, NS).

b) Timing of different activities over the rut

The cumulative totals of various activities through the course of a rut, corrected for both the number of females on a territory and uneven collection rates over the course of the rut, are shown in Figure 57. In all instances specific activities were compared to primary (investigatory) sexual activity. It was found that the distribution of all activities under consideration were different from that of primary sexual activity. Both secondary (precopulatory and copulatory) sexual activity and herding behaviour lagged behind primary sexual activity in their occurrence. Thus it appears that activities associated with primary sexual activity may act as a primer to actual pre-copulatory and copulatory (secondary sexual) activity. A close temporal link is suggested between copulation-related activities and herding behaviour. However, further analysis showed that their distribution through the rut was not coincidental (Kolmogorov-Smirnov goodness of fit: $n_1=285$, $n_2=285$, $D=0.126$, $p<0.025$), though the magnitude of the

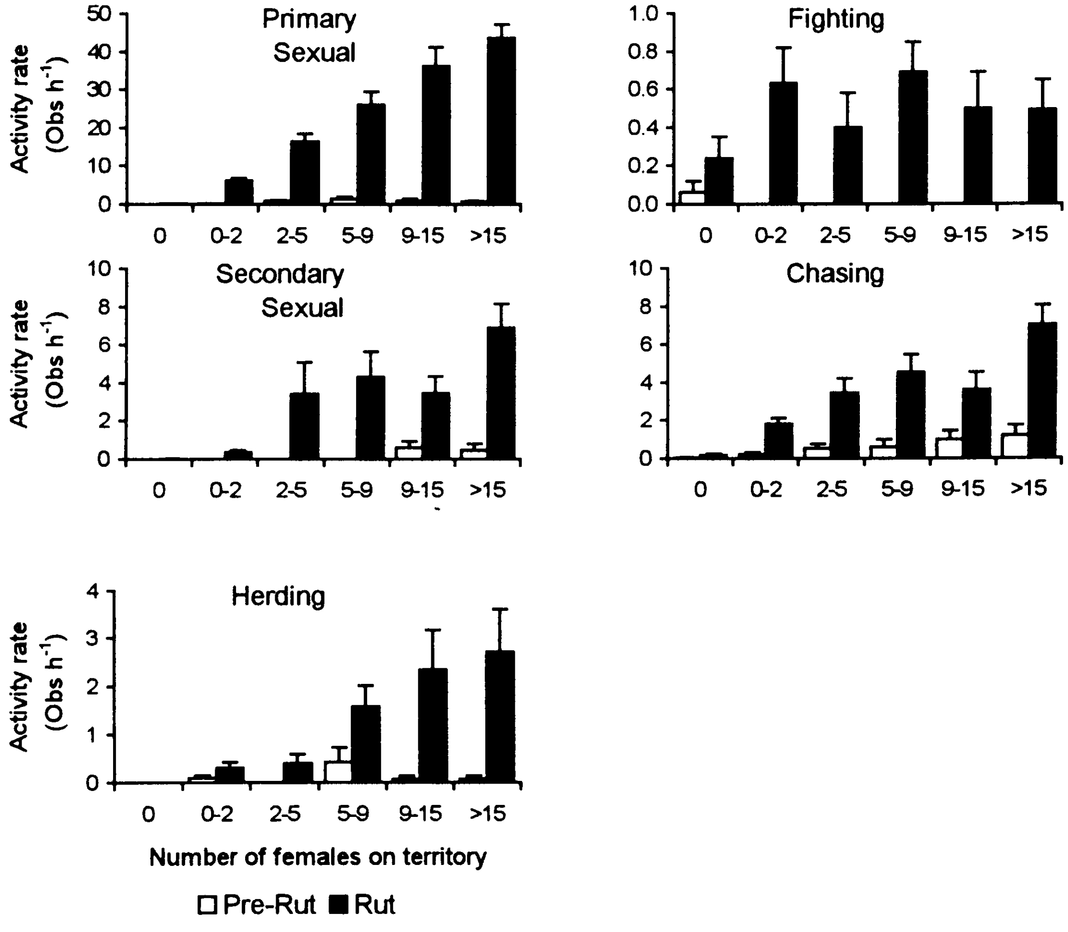

Figure 56 Comparison of the sexual and agonistic behaviour of territorial males, showing both the effect of the rut vs. pre-rut period and the number of females on a territory

difference was not as great as that for primary sexual activity.

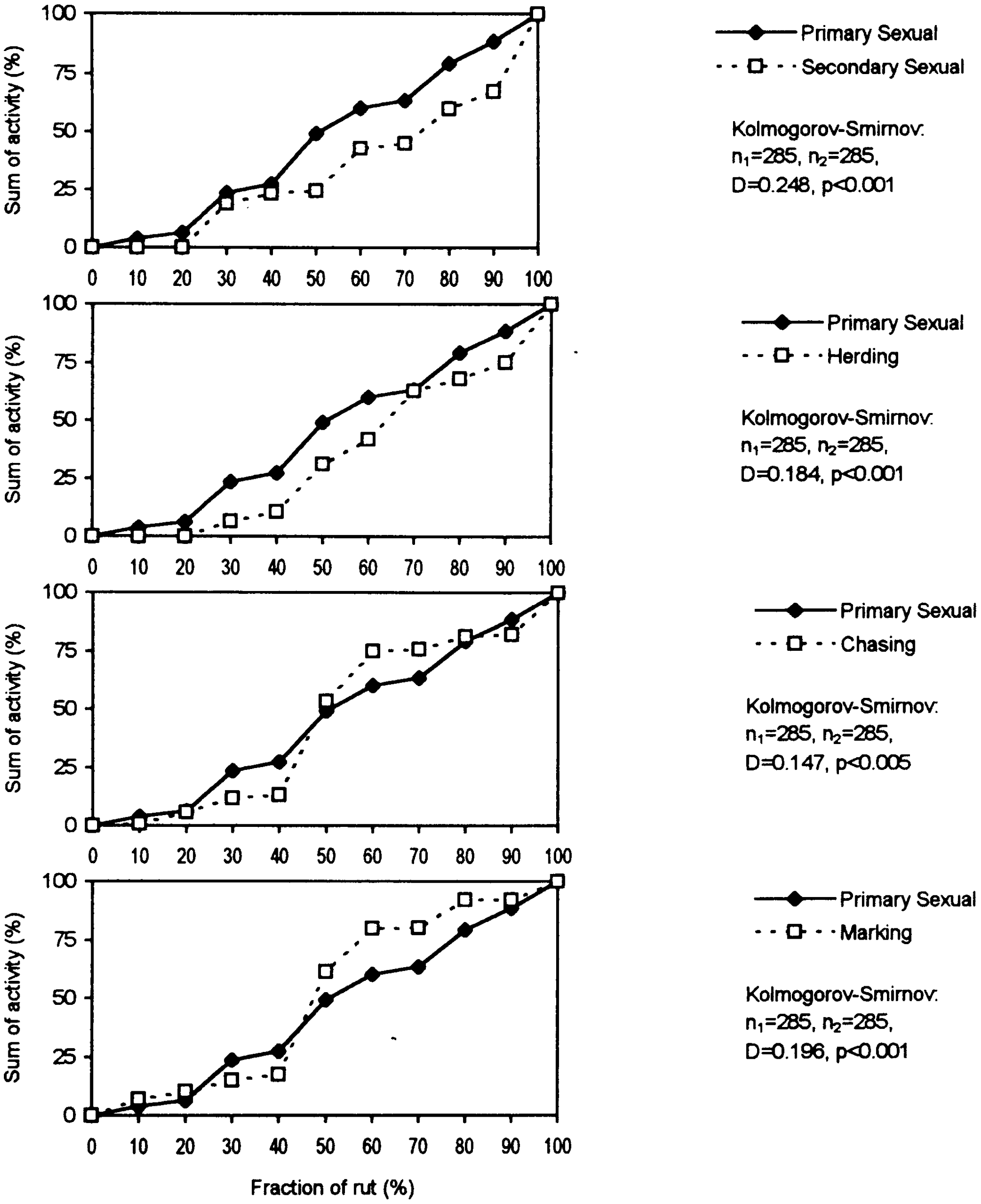

Figure 57 Cumulative distribution of sexual, agonistic and marking behaviour of territorial males over the course of the rut, showing dissimilar distribution of different activities relative to primary sexual activity

Marking activities and chasing by territorial males appeared to be most prevalent through the middle period of the rut. The distribution of these two activities did not differ significantly from each other (Kolmogorov-Smirnov goodness of fit: n_1=285, n_2=285, D=0.108, NS).

c) Timing of ejaculation, relative to other activities

The cumulative distribution of copulations, relative to secondary sexual activity and herding activity is shown in Figure 58. Data are analysed from 37 individually mated females. Both herding and mating activities were distributed similarly through the rut, whilst lagging behind the distribution of primary sexual activity. It is hardly surprising that the cumulative distribution of mated females through the rut was similar to that of secondary sexual activity. More significantly the parallel distribution of copulations and herding behaviour shows that males maximised herding activity to the time when mating was most likely, and that it was not distributed indiscriminately through the rut.

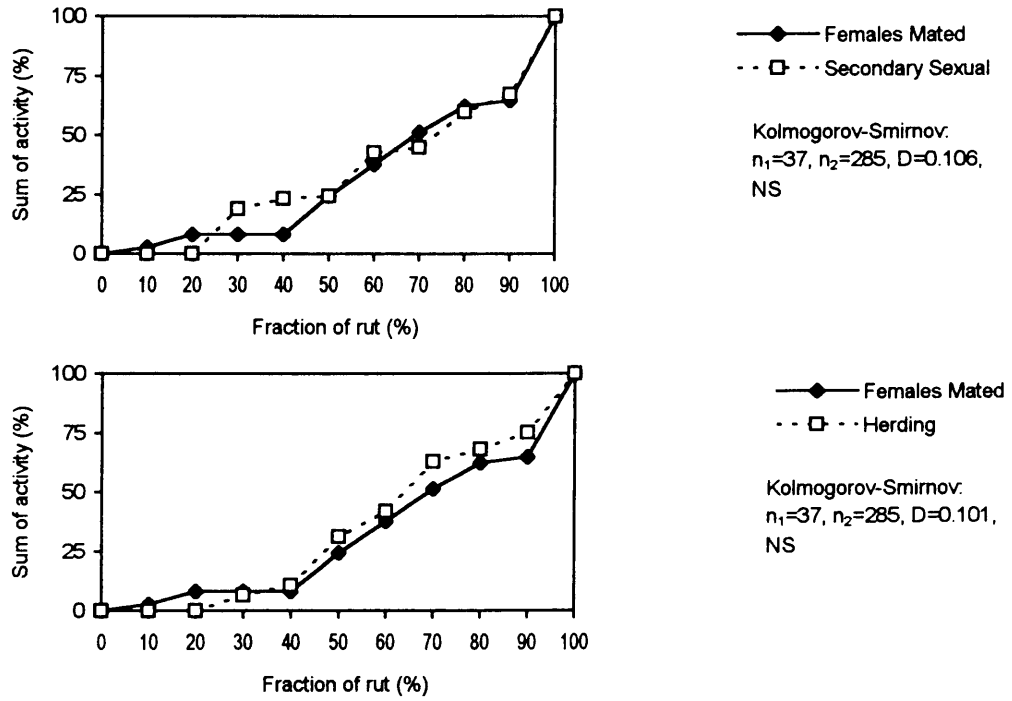

Figure 58 The cumulative distribution of mated females over the rut in relation to both secondary sexual and herding activities.

2. Timing of parturition

a) Monthly variation in parturition rate

New-born lambs were observed in every month of the year except June and November (Figure 59). However, the proportion of lambs observed, relative to the number of adult females, varied considerably in different months (Figure 60). Lambing was restricted to particular months, especially when considering that counts did not discriminate between neonates and lambs up to the age of a month, which would tend

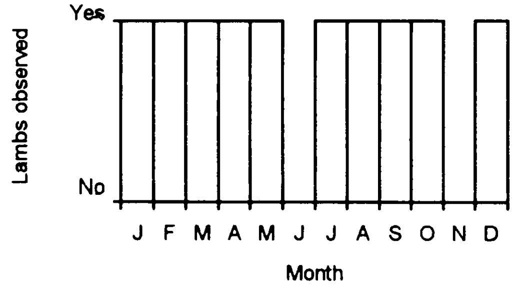

Figure 59 Months in which new-born lambs were observed

to broaden the estimated lambing period. The highest lambing rates were recorded in January 1991 and 1992 and February 1993, corresponding to the July rutting periods in the previous year. Thus all of the July ruts appeared to lead to high conception rates amongst ewes, with lambs being born six months later.

There was also a lambing event in October 1993, following the April 1993 rut. This was the only April rut which led to lambing being recorded, all other April ruts failing to produce a significant lamb crop.

b) The effect of rainfall on parturition

With the exception of the October 1993 lambing period, all lambing peaks occurred during the middle of the hot-wet season. Comparing monthly lamb numbers (lamb:female ratio) with rainfall, a strong relationship was found both in a given month as well as rainfall in the subsequent month (Figure 61).

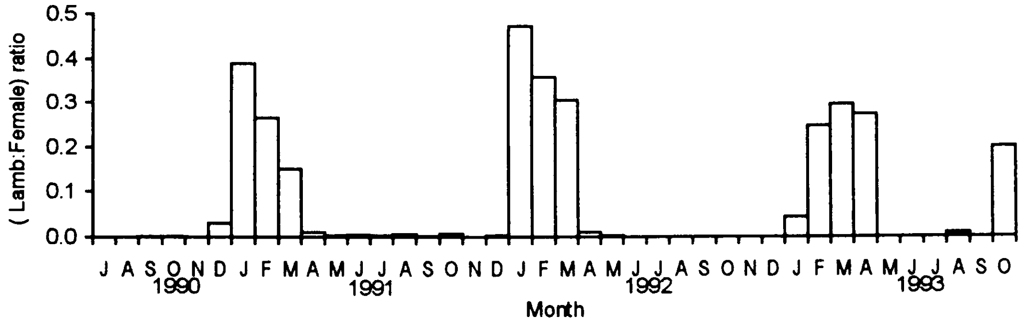

Figure 60. Variation in the proportion of lambs observed relative to adult females in different months of the study.

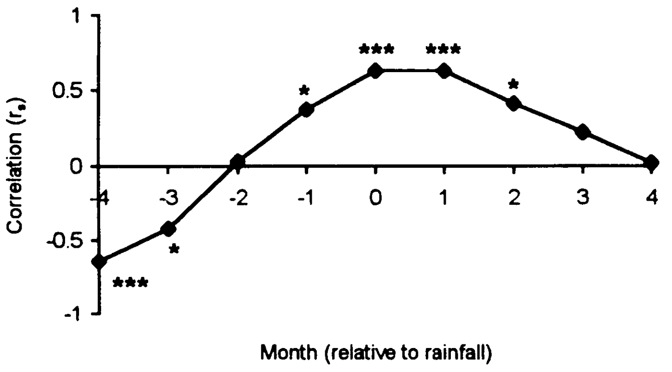

Figure 61. Correlation between the relative number of lambs observed and rainfall in a month, and rainfall in both the preceding and following months. [Probability levels: $p<0.001$(***), $p<0.01$(**), $p<0.05$(*)]

c) The effect of vegetation biomass on parturition

The proportion of lambs observed on the riverbed could not be related to vegetation biomass, either during a particular month or over the following six month period (Figure 62).

d) Lamb survivorship

The survivorship of lambs, as measured by the decrease in the proportion of lambs counted relative to adult females in consecutive months is illustrated in Figure 63. The survivorship of lambs is not linear, but increases at higher lamb:female ratios.

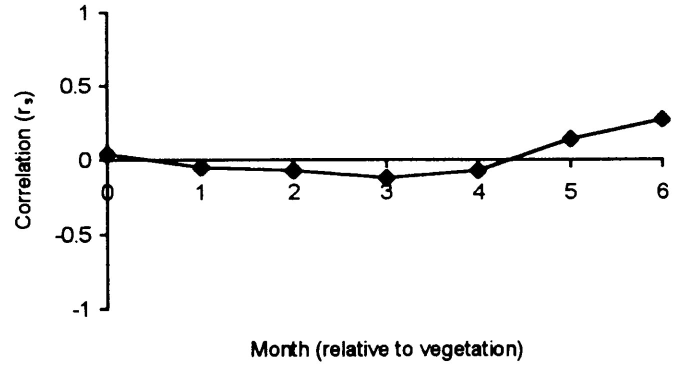

Figure 62. Correlation between the relative number of lambs observed and vegetation biomass in a month, and in following months

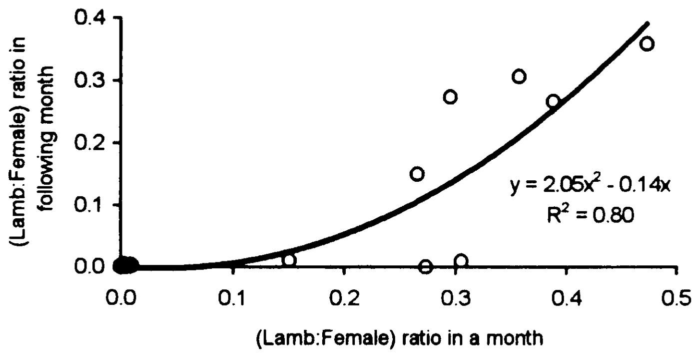

Figure 63 The survivorship of lambs in consecutive months, based on changes in the (lamb:female) ratio between months.

DISCUSSION

The concept of the rut is one which is commonly accepted in describing the breeding behaviour of ungulates and has been applied when sexual activity reaches high levels over a restricted period of time. Despite its widespread recognition, it is not well understood. A few definitions of a rut are given below:

- The period in which master bulls possessed and defended harems of cows (elk; Bowyer 1981).
- A period of especially intense sexual activity, directly controlled by males' testosterone levels (red deer; Lincoln *et al.* 1970).
- The time between first and last observed copulation (fallow deer; Apollonio *et al.* 1990).
- The period of overt sexual activity of the buck (fallow deer; Asher 1985).
- Peak of rut defined as period in which 95% of the observed breeding behaviour seen (moose; Miquelle 1990).

These definitions of rutting activity are confined to particular field situations, without providing an adequate general functional explanation. For instance the sexual activity of springbok rams is elevated well before the first copulations were observed and Murray (1982*b*) found that agonistic activity amongst rutting impala was most frequent prior to the first matings. Even territory defence on fallow deer leks begins one or two days prior to the first observed copulation (Apollonio *et al.* 1990), such that a definition based on mating *per se* is inadequate. The results of this thesis also show a temporal separation of rutting activities for the springbok. The period of primary sexual activity tends to occur before that of secondary sexual activity, herding and ultimately mating.

Evidence concerning which of the sexes is responsible for initiating the rut is ambiguous. Sexual activity in red deer stags in response to rising testosterone secretion escalates well before mating and ovulation occurred amongst the hinds (Lincoln *et al.* 1970, Lincoln & Short 1980). However rutting male fallow deer are influenced by pheromonal cues emitted by pro-oestrous females, possibly as a result of 'silent' ovulations, in which the short life span of the corpora lutea may be an endogenous factor in the synchronisation of the first oestrus (Asher 1986).

An understanding of rutting activity may be extended by reports in the literature of 'false ruts' *i.e.* periods of increased male sexual activity which do not lead to copulations or subsequent births (Lynch 1974, Anderson 1975, reviewed by Anderson 1979). These support the hypothesis that rutting activity is initiated by males. In the case of a 'false rut', periods of increased male sexual activity are not accompanied by a parallel increase in female receptivity. If rutting behaviour was initiated by females, such that males respond by increasing their sexual activity, one would expect all instances of rutting activity by males to be coincident with increased sexual activity amongst females.

It is probable that the rutting activity of males increases reproductive synchrony amongst females. The effect of vocalisation, a significant factor in the springbok rut, has been shown to advance the timing of oestrous in red deer hinds (McComb 1987). The 'ram effect', in which the oestrous cycle of domestic sheep and goats is influenced by the introduction of a ram is well known (Skinner & Hofmeyr 1969, Watson & Radford 1960, Oldham *et al.* 1978, Ott *et al.* 1980), and used to manipulate their breeding behaviour. Similarly Parsons & Hunter (1967) found that the duration of oestrus in Merino sheep was reduced by 30-50% when females were kept continuously with males through oestrus. Verme *et al.* (1987) attributed the earlier breeding dates of penned relative to free-ranging female white-tailed deer to the stimulation generated by close confinement with a stag. Thus the natural tendency of females to breed over any particular time span is further compressed by a socially mediated means; the rutting behaviour of territorial males acting on ovarian cyclicity.

This raises the question as to why males should increase their sexual activity without any reward? It suggests that males are unable to predict when females may be induced to reinitiate oestrous activity. The rutting behaviour of males is certainly associated with a number of costs. Both increased fighting and chasing activity over the rut are allied to an increase in debilitating injuries amongst males (chapter seven). There is a concurrent decrease in feeding, resting and ruminating activity (chapter eleven), whilst locomotory activity and subsequently energy expenditure increases (Nagy & Knight 1994). Rutting activity must therefore be considered to incur some cost to males. An unsuccessful rut has no direct benefit to territorial males, as it provides no mating opportunities, and can must be seen as a period of intense male-male competition with no immediate pay-offs. The evolution of such behaviour suggests it may be advantageous in some way, perhaps because the mating benefits of initiating a full-blown rut outweigh the costs of such a failure.

If we assume that rutting activity is initiated by the males, it is also necessary to explain why in some instances rutting should lead to successful copulations and in others why no increase in conception rate was observed. For females to conceive they must be capable in going from an anoestrus to an oestrus state. It is known that white-tailed deer kept on a lower plane of nutrition bred later and with a reduced fecundity than individuals kept on a higher nutritional plane (Verme 1965). Similarly Guinness *et al.* (1971) found that their captive population of red deer came into oestrus in their first year, unlike the surrounding wild population; one major difference between these two populations was their weight, the captive population being heavier, lending support to the idea that a female's plane of nutrition effects her ability to come into oestrus. Interestingly though Dauphiné & Mc Clure (1974) could not attribute variation in the conception dates of caribou to differences in age, body weight or fat measurements. The number of receptive females on Uganda kob leks increased with grass greenness on the lek leading Deutsch & Ofezu (1994) to suggest that oestrus may be condition-dependent. Lactation is known to represent a high nutritional costs to females (Clutton-Brock *et al.* 1989) and age can also affect fecundity (Alados & Escos 1991). At certain times females may be capable of conceiving whilst at others they may be forced to remain in an anoestrous state dependent on their condition. This would explain why in certain instances an increase in sexual activity by males may lead to a breeding peak, whilst at others females will be incapable of coming into oestrus despite the social stimulus provided by the males.

Whilst the springbok rut may be male-led, the results of this study, together with those of Skinner *et al.* (1995) indicate a number of different factors which could trigger rutting activity. Over the current study period ruts were initiated at three times of the year, within the southern Kalahari population; in February, late March/early April and July. The fact that these ruts led to lambing events at times of widely varying ecological conditions suggests that they may be opportunistic events determined by the immediate reproductive state of individuals with no consideration of future ecological conditions, though it is true births were generally correlated to rainfall patterns. March/April was the time when vegetation biomass was generally greatest and males were possibly in prime physical condition. Similarly in east Africa Thomson's and Grant's gazelle males attain their best body condition two or three months after rainfall (Stelfox & Hudson 1986). For males this period of peak physical condition presumably constitutes the least costly time to rut, so that the benefits of trying to initiate a successful rut may outweigh the costs.

The physical condition of females through March/April remains uncertain; for any females which had given birth in December or January, this period three to four months later must come at a time of maximum lactational stress (Liversidge & de Jager 1984) and possibly therefore lactational anoestrus. Thus the physical condition of lactating females would be relatively poor, in contrast to that of males. Only after a further two to three month period, during July, may female condition have improved sufficiently that a rut could possibly reinitiate female ovarian activity. The majority of successful ruts occurred in July, during which time environmental conditions, and presumably male condition too, were deteriorating. What factors should initiate a rut at such a time remains a matter of conjecture. Unlike wildebeest (Sinclair 1977) or impala (Murray 1982*b*) lunar cycle appears to play no role in fine-tuning the rut (Skinner *et al.* 1995). Territory establishment by males often occurred in a period up to 30 days prior to the July rut (chapter ten), such that males pre-empted the forthcoming event. Again this suggests that it was the males who were important in instigating the rut, though with worsening ecological conditions, relatively small changes in daylength and their own condition also deteriorating it is difficult to see what factors could stimulate them apart from a possible improvement in female condition as their lambs were weaned. Indeed it may have been an improvement in the ewes' condition, possibly with a few starting to re-cycle, which finally triggered the males to rut. Similarly the rut which took place in February 1993, with the rains ending a particularly barren period, could have occurred as ewes were finally capable of coming into condition-dependent oestrus.

The effect of the rut was to produce a pulse of lambings at a specific time. Estes (1976) found calf survivorship was significantly lower amongst early-born wildebeest calves, with virtually total mortality of calves born before the birth peak. The survivorship of springbok lambs increased disproportionately with a higher proportion of lambs in the population, relative to females. By rutting springbok are able to maximise their degree of breeding synchrony and in doing so reduce predation pressure on neonates. Predation is not the only factor which can affect juvenile mortality; environmental variables may be of considerable importance too. Clutton-Brock *et al.* (1987) found that survivorship of red deer calves in a predator-free environment was affected by birth date; survival being lower in late born calves. Similarly, the survival of juvenile greater kudus was significantly correlated with the preceding rainfall (Owen-Smith 1990). Significantly there was a correlation between springbok births and rainfall, suggesting that not only a lambing event *per se* is important as an anti-predator ploy, but that the timing of lambing with favourable environmental conditions, will also act to enhance juvenile survival.

It is plausible that males could synchronise the oestrous activity of females through the 'ram effect', which will enhance both their mating opportunities and offspring survival.

Whilst rutting activity is influenced by a number of important ecological factors acting on the males, the success or failure of any rut is ultimately dependent on females' underlying physiological state and their ability to be respond to the males' increased sexual activity.

SUMMARY

- The sexual and agonistic activity of territorial males increased dramatically from pre-rut to rutting periods.
- Temporally, the distribution of primary sexual activity preceded that of secondary sexual activity, herding and ultimately mating.
- The breeding biology of the springbok suggests condition dependent oestrus in females, fine-tuned by the rutting activity of territorial males. This should allow reproductive activity to occur at any time, with synchronisation achieved by the rut.
- Lambing periods were restricted, but not seasonal, even though they could be related to environmental variables.
- Lamb survivorship appeared to increase when more females lambed at a given time.

Chapter 13

Conclusions

THE MATING SYSTEM OF THE SPRINGBOK

The role of the rutting activity by territorial males is probably to shorten and thus synchronise female oestrous activity. Certainly the timing of primary sexual activity by territorial males precedes both secondary sexual activity, herding behaviour and ultimately copulation. Thus the primary sexual activity of territorial males, which is accompanied by much vocalisation (Walther 1981, pers. obs.) may act as the cue to reactivate cycling by ewes. The direct advantage this would proffer to individual males is to maximise the number of ewes coming into oestrus whilst they maintain their territorial status, and therefore to maximise their own reproductive success for a given rut. This has been suggested as a reason for the high roaring rates in red deer stags, which is known to advance the date of oestrous in females (Mc Comb 1987), females preferring to mate with stags who roar at higher rates (Mc Comb 1991). The indirect advantage such synchronicity infers would be in predator swamping as both the conception period of ewes and consequently their lambing periods are synchronised. Thus the breeding behaviour of the springbok is dependent on the ability of ewes to conceive at any given time, which is finely tuned by their interaction with territorial males.

Quite what factors trigger territorial males' rutting behaviour remain obscure. The result however is to induce oestrous activity amongst females (Skinner *et al.* 1992). Further, Skinner *et al.* (1992) postulated that ewes show a silent heat as they came out of anoestrus and mate at their second ovulation some 14-17 days later (Liversidge & de Jager 1984). It is interesting that males appeared to increase their sexual and agonistic activity at times, with additional males acquiring territories, but with no subsequent lambing peak occurring. These are the periods referred to as 'false ruts' throughout this study (Figure 64). Yet at other times the same changes in the activity of males did induce a full blown rut, for which both a peak in conception and consequently lambing were recorded.

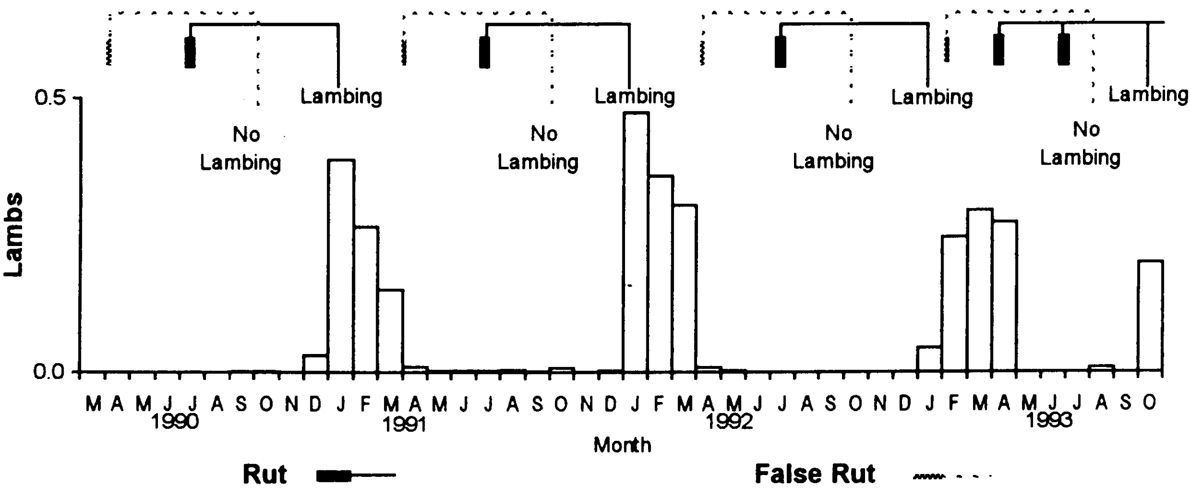

Figure 64 Incidence of rutting activity by territorial male springbok showing ruts and their subsequent lambing peaks, together with false ruts for which no lambing peaks were recorded.

This suggests that males are unable to asses females' physiological status and time their rutting activity accordingly. From this it can be inferred that those factors triggering rutting behaviour in the rams are different from the factors to which ewes respond. Certainly the underlying reproductive physiology of male and female springbok differ. Male spermatogenesis continues throughout the year (Skinner & van Zyl 1970*b*) such that males are always capable of breeding. This is in contrast to species whose breeding periods are restricted to particular times of the year, for whom spermatogenesis is also restricted (Robinson *et al.* 1965, Skinner 1971*ab)*. Given a pregnancy of approximately six months (van Zyl & Skinner 1970) and a period of lactation extending up to four months (Liversidge & de Jager 1984), which may inhibit oestrus cycling (Skinner pers. comm.), females may be precluded from mating for periods of up to approximately ten months at a time. It is presumably these differences which have led to the apparent male-female conflict over the timing of successful rutting periods.

Multiple breeding peaks within a year could result when a species satisfies two criteria; a gestation period of less than half a year and the ability to come into post-partum oestrus. Such conditions are satisfied by several gazelle populations (Thomson's gazelle: Hvidberg-Hansen 1970, Robinette & Archer 1971, Hvidberg-Hansen & de Vos 1971; mountain gazelle: Baharav 1983*b*; Cuvier's gazelle: Olmedo *et al.* 1985; dorcas gazelle: Loggers 1992) and consequently two lambing peaks have been recorded, separated by a six month interval. Unfortunately this does not fit the pattern observed for the springbok, as neither the males breeding efforts or the females parturition peaks show this six month cyclicity.

Information concerning the time of lambing and the consequent mating peaks in areas other than the southern Kalahari is summarised in Table 34. The peak lambing periods for springbok in the southern, central and northern Kalahari, together with southern Angola and Etosha N.P. in northern Namibia are similar, falling in December/January. Assuming a gestation period of almost six months this suggests that a rut during June or July is common in these northern areas.

Within the southern extent of their range springbok lamb predominantly in September and October, which would correspond to a conception peak in March and April (Table 34). However on the west coast of South Africa, which receives predominantly winter rainfall, January was the modal lambing month. For all of these records the modal lambing periods follow the rainfall pattern within the area, as David (1978*a*) suggested. Thus the unsuccessful rutting periods which were observed in March and April (with an exception during April 1993) in the southern Kalahari coincide with successful breeding in more southerly areas where the summer rains occur earlier. From this it may be inferred that males respond to the same cues in different geographical areas.

The lambing period in October 1993 shows that springbok are not strictly seasonal breeders, as lambing peaks which do occur are not necessarily coincident in consecutive years *i.e.* whilst springbok may show *synchronised* lambing they are not *seasonal* lambers. The October lambs in the present study followed a year of low rainfall. The repercussions of such an unsettling effect are reinforced by findings that lamb crops and survival rates are lower in dry relative to wet years (Penzhorn 1974, Bigalke *et al.* 1975). Thus the poor rainfall year broke up the cycle of lambing activity which had occurred in 1992 and 1993 in the southern Kalahari population.

Other factors have also been reported to disrupt the lambing periods of springbok. Skinner & van Zyl (1970*a*) recorded that the early death of springbok lambs in a population through culling may have influenced breeding; together with the exceptional rainfall in those years this apparently advanced oestrous activity, allowing ewes to lamb twice in one year. In order to do so springbok have to be in particularly good condition (Bigalke *et al.* 1975) as a result of very good environmental conditions; this could also be induced through predation on lambs. Skinner *et al.* (1971) found that cropping 25-75 % of springbok lambs in successive years, led to yearly lambing percentages exceeding 100 % *i.e.* some ewes must have lambed twice. Skinner (1984)

Area	Lambing peaks	Conception peaks	References
Early summer rainfall areas			
Pretoria	Oct	Apr	Brand 1963
Kimberley	Sept/Oct	Mar/Apr	Bigalke (1970), Bigalke et al. (1975)
Central Karoo	Sept/Oct	Mar/Apr	Skinner et al. (1986)
Western Transvaal	Sept/Oct	Mar/Apr	Skinner et al. (1974)
Pilansberg N.P.	Sept/Oct	Mar/Apr	van Dyk (pers. comm.[§]), pers obs.
Bontebok N.P.	Sept	Mar	David (1978ab)
Mountain Zebra N.P.	Sept/Oct	Mar/Apr	Penzhorn (1974)
Mid summer rainfall areas			
Angola	Dec/Jan	Jun/Jul	Penrice (in Shortridge 1934)
Northern Namibia	Dec/Jan	Jun/Jul	Bigalke (1970), Brotherton (pers. comm.[**])
Northern Kalahari	Jan	Jul	Ritter (pers. comm.[††])
Central Kalahari	Dec/Jan	Jun/Jul	Williamson (1985)
Southern Kalahari	Dec/Jan	Jun/Jul	Present study
Winter rainfall areas			
Hester Malan N.R.	Jul	Jan	Skinner et al. (1977)

Table 34. Data summarising the lambing and conception peaks of springbok in different areas of southern Africa, based on the modal lambing months.

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concluded that cropping removes lactational stress and consequently lactational anoestrus in springbok, such that females can come into oestrus for a second time.

Based on the theoretical function of the rut in ungulates, together with the field observations made in this thesis on the rutting and lambing activity of springbok in the southern Kalahari and a literature review of springbok lambing periods, a functional model for the breeding biology of the springbok is presented below. This is based on a regime of condition-dependent oestrus by female springbok, which is fine-tuned by the rutting activity of males. This model allows females to recommence oestrous activity under a number of alternative conditions.

1. Annual lambing cycle

In Figure 65 a regular 12 month cycle is shown. Given a gestation length of approximately six months and a lactation period of four months, a further two months are necessary to complete the annual cycle. If we assume that the high energetic cost of lactation induces lactational anoestrus, and reduces female body condition, this suggests that it takes females approximately two months post-weaning before cycling recovers; the trigger for this being the rutting activity of territorial males. The significance of such a cycle is that once a ewe falls into it there may be a natural tendency to lamb on an annual basis.

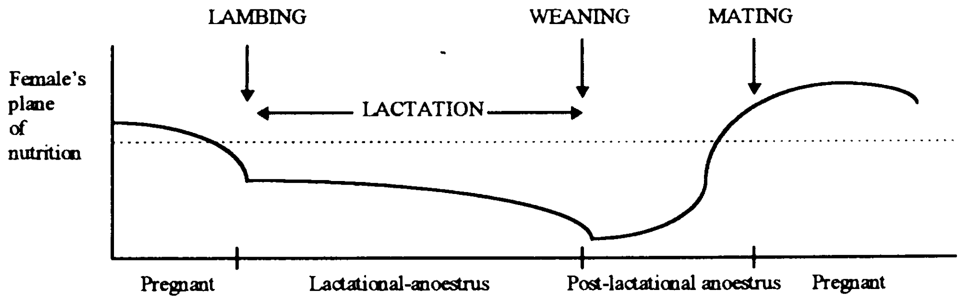

Figure 65 Typical breeding cycle of springbok ewes. Threshold for oestrus shown by dotted line. A six month pregnancy is followed by four months of lactational

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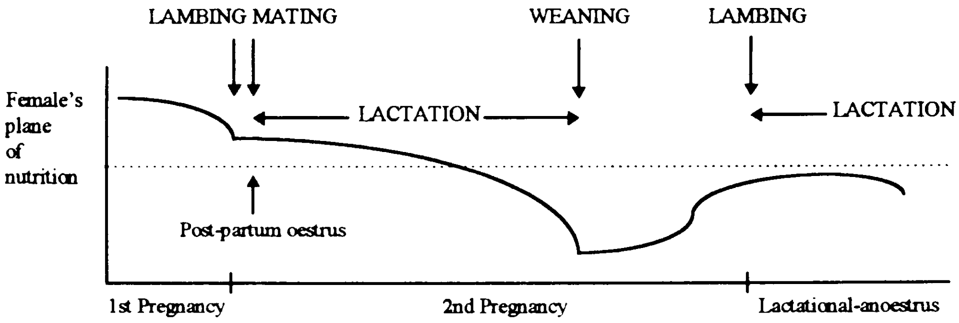

anoestrus. The condition of the female recovers sufficiently after approximately two months after weaning to allow cycling to recommence.

Figure 66 Breeding cycle of ewe under very good environmental conditions. Female's plane of nutrition high enough to allow post-partum oestrus (dotted line). Lambing twice in a year, with suckling of first lamb overlapping foetal development of second.

2. Post-partum oestrus

Springbok ewes are capable of coming into post-partum oestrus 9-15 days after parturition (Liversidge & de Jager 1984). Only when conditions are particularly favourable will females be in good enough physical condition for this to occur (Figure 66). Shortly after lambing the ewe will conceive again, and will undergo the concurrent burden of lactation and pregnancy. This would explain why the springbok rutted in February 1993, as not only had many females just given birth at this time, but environmental conditions improved substantially.

3. Lamb removal

Finally removal of a lamb, either by cropping or through natural predation, will relieve the lactational burden on females. Provided environmental conditions are good enough this should allow females to cycle again within a given year (Figure 67), allowing ewes to lamb twice over the course of the year. Alternatively during particularly good years females may regain condition sufficiently quickly that lactational anoestrus has ended by the time males rut in March/April, allowing them to mate successfully at this time.

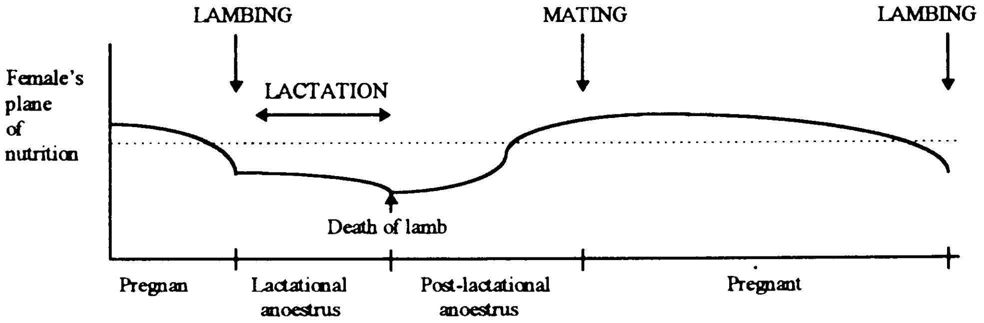

Figure 67 Breeding cycle of ewe modified by death of lamb. Female's condition recovers more quickly than when lamb suckled to weaning age allowing termination of anoestrus earlier in the year, early conception, and second lambing

In conclusion then this thesis has shown that male springbok are indeed resource-defence polygynists, who maintain perennial territories. Rather than confining observations to a particular aspect of male territoriality it has attempted to synthesise a holistic view of the territorial system of a male antelope. In doing so it has been able to answer some of the questions regarding territorial dynamics and territory maintenance, the costs to males in holding a territory, the importance of resource-defence polygyny as a mating system and therefore the benefits of territoriality and finally some of the causes and functions of rutting behaviour.

SUMMARY

The breeding biology of the springbok was examined in the southern Kalahari, with particular reference to the costs and benefits to males in being territorial. Males defended their territories on the fossil riverbeds and calcareous pans. Whilst these accounted for less than five percent of the land area, the density of springbok on these areas was far higher than the surrounding dune environment. Also, the number of females visiting these territories did not vary between rut and pre-rut periods suggesting that territorial male springbok are resource-defence polygynists.

Their territorial status imposed a heavy cost on males, due to both the ecological and social pressures males place upon themselves. The springbok is an animal traditionally known to respond rapidly to changing ecological conditions. Territorial individuals were not found to adjust their rangeing patterns to the prevailing environmental conditions. Thus whilst the density and movement of non-territorial males and females could be related to vegetation biomass and rainfall on the dry riverbeds, as well as the availability of surface water, this was not true for territorial males. The home ranges of territorial males were also found to be significantly smaller than those of non-territorial males in any given season. Comparing the maintenance activities of these three groups, that of females was substantially different to males. Territorial males fed less efficiently than non-territorial males over the hot-dry season, when environmental conditions were most severe. During the rut itself territorial males reduced their feeding, resting and ruminating activities, relative to pre-rut periods, with a reciprocal increase in locomotory activity.

As well as these ecological constraints, the social organisation of males and territorial males in particular, exposed them to a higher predation risk. In general males were found in smaller herds, more towards the periphery of herds and at greater distances from their nearest neighbour. Also, territorial males were more solitary than other individuals and tended to be found in areas of taller vegetation cover. The occurrence of disabilitating physical injuries was higher amongst males than females. As all these factors have been associated with higher predation risk in similar species, it was predicted this would be true for the springbok too.

An evaluation of actual predation showed that this was indeed higher amongst males than females. Cheetahs, the major predator of adult springbok in the Kalahari, killed twice as many adult males as adult females. However it was impossible to determine the status of those males which had been killed. The higher male mortality rate was reflected in the population sex ratio. Amongst adults this was heavily female biased, though no such bias was found amongst lambs when they could first be sexed.

Despite these immediate costs, males held territories throughout the year. Both environmental and breeding criteria determined territory establishment patterns by males; these being the rut and the first significant rains of the year. Males would often return to their former territories. Some shifted territory site, but only when this was accompanied by an increase in the number of females on their new, relative to their old, territories. Most territories were abandoned passively, again as environmental conditions deteriorated or after the rut. Evaluating the evidence available from other ungulate species and the current theoretical understanding of territory dynamics it is proposed that males held their territories for extended periods despite the shortness of the rut to maximise their chances of maintaining their territories, and ultimately breeding success through the rut.

Aggression by territorial males was directed predominantly towards intruding non-territorial males. These males were normally chased off a territory. However when fights did occur they were long and violent clashes. Conversely, the agonistic interactions of neighbouring territorial males were highly ritualised. Whilst accompanied by much displacement activity any fights were brief, with no obvious winner. Males tolerated non-territorial individuals on their territories outside the rut. The agonistic behaviour of territorial males was found to reflect the association of males and females in herds. Non-territorial males tended to affiliate more with each other during the rut as a direct consequence of being evicted more from the mixed sex herds at this time. During the periods of low agonistic activity, male and female springbok associated more freely in mixed-sex herds.

Males advertised their territorial status by marking activities. Linked urination-defecation provided an optical marking system, together with the deposition of dung, predominantly under trees or on middens in open areas. This they did more frequently towards the boundary of their territories. Males would also rub their horns in any available vegetation. These actions were performed at higher rates by territorial than non-territorial males, and more frequently on than off their territories. Vocalisation, both towards females and intruding males provided an acoustical signal of a male's territorial status. The main function of this marking was probably to advertise their presence both to intruding males, and females who were observed to mate exclusively with territorial individuals.

Thus the ultimate benefit to males of achieving territorial status was in enhancing their breeding success. However ewes were often mated on more than one occasion; in some instances this was with a second territorial male, but never with a non-territorial male. Males did not appear to guard oestrous ewes with whom they had mated for any extended period, suggesting that the first insemination was often successful.

In the southern Kalahari springbok synchronised their breeding periods, though not necessarily at the same time in different years, through the rutting behaviour of territorial males. Ruts were initiated by males, though females did not always respond to this increase in male sexual activity. Thus only some rutting periods culminated in a period of mating, A schematic model was developed to show how the observed pattern of breeding could be achieved by both the social cue provided by rutting males and condition-dependent oestrous in females; the rut itself could act to terminate the period of anoestrous in females and synchronise the conception period of females through the 'ram effect'.

Quite what factors are important in triggering the males to rut remain obscure. Interestingly the false ruts observed in this population occurred at a time when springbok bred successfully in other areas, suggesting that the cues acting in both areas are the same, whilst the difference in female response occurred as a result of variation in the rainfall patterns and therefore ecological variables between the two areas.

The benefit to males of a synchronised breeding period would be to maximise their own mating opportunities, whilst restricting the lambing period. This could both reduce the effect of predation pressure and, if timed correctly, lead to a maximal lambing rate when environmental conditions for survival were most optimal. Certainly the survival of springbok lambs was greater when a larger lamb crop was born at a given time, and would ultimately maximise males' reproductive success.

OPSOMMING

Teling in die springbok, met spesiale verwysing na kostes en voordele vir territoriale ramme is in die suidelike Kalahari ondersoek. Op fossiele rivierbeddings en kalkpanne verdedig ramme hul territoria. Terwyl hierdie gebiede slegs vyf persent van die totale grondoppervlakte verteenwoordig is die digtheid van springbokke hier baie hoër as op droë omliggende sandduine. Omdat dieselfde aantal ooie hierdie territoria gedurende die pre-brons en bronstigheidstydperke besoek is springbokramme waarskylik bronsverdedigend poligamies.

Die territoriale status van ramme het 'n hoë koste weens selfopgelegde ekologiese en sosiale druk. Tradisioneel word die springbok beskou as 'n diersoort wat vinnig op veranderende ekologiese toestande kan reageer. Territoriale ramme kon egter nie hul loopgebiede vinnig by heersende omgewingstoestande aanpas nie. Alhoewel die digtheid en bewegingspatrone van nie-territoriale ramme en ooie in verband met plantbiomassa, reënval op droë rivierbeddings en die beskikbaarheid van bogrondse water gebring kon word, was dit nie die geval vir territoriale ramme nie. Gedurende 'n spesifieke seisoen was die tuisgebiede van territoriale ramme ook betekenisvol kleiner as die van nie-territoriale ramme. Die onderhoudsaktiwiteite van ooie het ook opvallend verskil van die van ramme. Gedurende die warm-droë seisoen wanneer omgewingstoestande op die slegste was, het territoriale ramme minder effektief as nie-territoriale ramme gevoed. Gedurende die bronstigheidstydperk het territoriale ramme minder gevreet, gerus en geherkou as gedurende die pre-bronstigheidstydperk, met 'n omgekeerde vemeerdering in bewegingsaktiwiteite.

Bogenoemde ekologiese beperkinge sowel as die sosiale organisaie van ramme, veral dié van territoriale ramme, stel hulle aan 'n hoër predasie risiko bloot. Gewoonlik is ramme in kleiner troppe, aan die buitekant van troppe en op groter afstande vanaf die naaste buurram, gevind. Territoriale ramme is ook meer solitêr as ander individue en is gewoonlik in gebiede met 'n hoër plantegroei gevind. Fisiese beserings was ook meer algemeen onder ramme as onder ooie. In soortgelyke spesies word al hierdie faktore met 'n hoë predasie risiko geassosieer en dit word voorspel dat dit ook die geval sal wees in springbokke.

'n Ondersoek van werklike predasie het getoon dat die predasie risiko vir ramme wel hoër was as vir ooie. Jagluiperds wat die mees belangrike roofdier van volwasse springbokke in die Kalahari is, het twee keer meer ramme as ooie gevang. Die sosiale status van die ramme kon nie bepaal word nie. Hierdie geslagsselektiewe predasie word in die geslagsverhouding van die bevolking weerspieël. Die volwasse geslagsverhouding was ten gunste van ooie maar by lammers was dit nie die geval nie.

Ten spyte van hierdie onmiddellike kostes was ramme regdeur die jaar territoriaal. Beide omgewings- en telingskriteria, naamlik bronstigheid en die eerste noemenswaardige reën het die patrone van territoriale vestiging beïnvloed. Ramme het dikwels na hul vorige territoria teruggekeer. Sommige ramme se territoria het slegs verskuif wanneer daar 'n toename in die aantal ooie relatief tot die aantal op hul vorige territoria was. Meeste territoria is passief verlaat wanneer omgewingstoestande na bronstigheid versleg het. Gebaseer op bestaande inligting vir hoefdiersoorte en die huidige teoretiese interpretasie van territoriale dinamika, word voorgestel dat ten spyte van die kort bronstigheidsperiodes, ramme territoria vir solank as moontlik beset om sodoende hul geleentheid vir die besetting van hul territoria te maksimaliseer, en uiteindelik hul teelsukses regdeur die bronstigheidstydperk.

Territoriale aggressie was hoofsaaklik teenoor nie-territoriale, indringer ramme getoon. Hierdie ramme is gewoonlik weggejaag vanaf territoria. Gevegte wat egter wel voorgekom het, was hewig en het lank geduur. Hierteenoor was agonistiese interaksies tussen aangrensende territoriale ramme baie geritualiseerd. In hierdie gevalle was gevegte altyd kort en dit het met 'n groot hoeveelheid verplasingsaksies gepaard gegaan. Daar was ook geen ooglopende wenner gedurende sulke interaksies nie. Territoriale ramme het egter die teenwoordigheid van nie-territoriale ramme op hul territoria buite die bronstigheidstydperk verdra.

Die agonistiese gedrag van territoriale ramme het die assosiasie tussen ramme en ooie in troppe weerspieël. Nie-territoriale ramme het geneig om meer met mekaar gedurende die bronstigheidstydperke te assosieer as gevolg van die feit dat hulle dan verstoot is uit gemengde-geslag troppe. Ramme en ooie in troppe het meer dikwels met mekaar gedurende tye van min agonisties interaksies geassosieer.

Ramme het hul territoriale status deur merkaktiwiteite adverteer. Tesame met ontlasting, gewoonlik onder bome of op mishope in oop gebiede, het urinering met ontlasting gekoppel, as 'n optiese merksisteem gedien. Dit is meer dikwels naby die grense van territoria gedoen. Ramme het ook hul horings teen enige beskikbare plantegroei gevryf. Hierdie aksies is meer dikwels deur territoriale as nie-territoriale ramme uitgevoer en ook meer dikwels op as weg van hul territoria. Vokalisasie teenoor beide ooie en nie-territoriale ramme het as akoestiese sein van 'n territoriale ram se status gedien. Die hooffunksie van merking deur territoriale ramme was waarskynlik om hul teenwoordigheid aan indringer ramme en ooie, wat hoofsaaklik met territoriale ramme gepaar het, te adverteer.

Die uiteindelike voordele wat 'n ram deur territorialiteit verkry het was die bevoordeling van hul teelsukses. Ooie het dikwels meer as een keer met 'n ram gepaar, soms ook met 'n ander territoriale ram, maar nooit met 'n nie-territoriale ram nie. Ramme het ook nie vir lang tydperke oor ooie in oestrus gewaak nie, wat daarop dui dat die eerste inseminasie dikwels suksesvol was.

In die suidelike Kalahari het springbokke hul telingsperiodes deur bronstigheid by ramme gesinkroniseer. Die het nie noodwendig op dieselfde tyd gedurende verskillende jare geskied nie. Bronstigheid is deur die ramme begin maar ooie het nie altyd gereageer op die toename in die seksuele aktiwiteit van ramme nie. Gevolglik het slegs sommige bronstigheidstydperke in 'n paringstydperk geëindig. 'n Skematiese model is ontwikkel om aan te toon hoe die waargeneemde patrone van teling bereik kon word deur sosiale seine verskaf deur bronstigheid onder die ramme en deur kondisie-afhanklike oestrus in ooie; bronstigheid self kan die tydperk van anoestrus laat eindig en konsepsie deur die "ram-effek" sinkroniseer.

Die faktore van belang vir die aanvang van bronstigheid onder ramme is nog nie bekend nie. Dit is interessant dat die vals-brostighede in dié bevolking in 'n tydperk voorkom wanneer springbokke in ander gebiede suksesvol teel. Dit wil dus voorkom asof die seine in die verskillende gebiede dieselfde is en asof die verskille in die reaksie van die ooie die gevolg is van variasies in reënvalpatrone, en dus as gevolg van verskille in ekologiese veranderlikes in die twee gebiede.

Die voordeel vir ramme in die sinkronisering van die teeltydperk is in die maksimisering van hul geleenthede om te paar gesetel, terwyl die lamtydperk beperk word. Hierdeur kan die invloed van predasie druk beperk word en, indien die tydsberekening korrek is, die maksimale hoeveelheid geboortes plaasvind wanneer geleenthede vir die oorlewing van lammers optimaal is. Die oorlewing van springbok lammers was gewis beter wanneer 'n groot hoèveelheid lammers op 'n bepaalde tyd gebore was. Dit sal uiteindelik die ram se voortplantingsukses bevoordeel.

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APPENDIX I

Common and scientific names of animals cited in the text

Mammals

Order Artiodactyla

Cephalophini

grey duiker	*Sylvicapra grimmia*
suni	*Neotragus moschatus*

Neotragini

dik-dik	*Madoqua kirkii*
klipspringer	*Oreotragus oreotragus*
steenbok	*Raphicerus campestris*

Antilopini

blackbuck	*Antilope cervicapra*
Cuvier's gazelle	*Gazella cuvieri*
dorcas gazelle	*Gazella dorcas*
gerenuk	*Litocranius walleri*
Grant's gazelle	*Gazella granti*
mountain gazelle	*Gazella gazella*
sand gazelle	*Gazella subgutturosa*
Sömmering's gazelle	*Gazella sommeringii*
springbok	*Antidorcas marsupialis*
Thomson's gazelle	*Gazella thomsoni*

Reduncini

black lechwe	*Kobus leche smithemani*
Chanler's mountain reedbuck	*Redunca fulvorufula fulvorufula*
Kafue lechwe	*Kobus leche kafuensis*
puku	*Kobus vardoni*
red lechwe	*Kobus leche leche*
Uganda kob	*Kobus kob thomasi*
waterbuck	*Kobus ellipsiprymnus*
white-eared kob	*Kobus kob leucotis*

Alcelaphini

black wildebeest	*Connochaetes gnou*
blue wildebeest	*Connochaetes taurinus*
blesbok	*Damaliscus dorcas phillipsi*
bontebok	*Damaliscus dorcas dorcas*
Coke's hartebeest	*Alcelaphus buselaphus cokei*
Liechtenstein's hartebeest	*Alcelaphus lichtensteini*

	red hartebeest	*Alcelaphus buselaphus*
	topi	*Damaliscus lunatus jimela*
	tsessebe	*Damaliscus lunatus lunatus*
Aepycerotini		
	impala	*Aepyceros melampus*
Tragelaphini		
	eland	*Taurotragus oryx*
	greater kudu	*Tragelaphus strepsiceros*
	nyala	*Tragelaphus angasii*
Hippotragini		
	gemsbok	*Oryx gazella gazella*
	sable	*Hippotragus niger*
Antilocapridae		
	pronghorn antelope	*Antilocapra americana*
Bovidae		
	muskoxen	*Ovibos moschatus*
Cervidae		
	caribou	*Rangifer tarandus groenlandians*
	elk	*Cervus canadensis*
	fallow deer	*Dama dama*
	moose	*Alces alces*
	mule deer	*Odocoileus hemionus*
	red deer	*Cervus elaphus*
	reindeer	*Rangifer tarandus*
	roe deer	*Capreolus capreolus*
	sika deer	*Cervus nippon*
	white-tailed deer	*Odocoileus virginianus*
Caprinae		
	feral goats	*Capra hircus*
	mountain goat	*Oreamnos americanus*
Ovinae		
	big-horn sheep	*Ovis canadensis*
	sheep spp.	*Ovis aries*
Equidae		
	Grevy's zebra	*Equus grevyi*

Order Carnivora	
Hyaenidae	
aardwolf	*Proteles cristatus*
brown hyaena	*Hyaena brunnea*
spotted hyaena	*Crocuta crocuta*
Canidae	
black-backed jackal	*Canis mesomelas*
wild dog	*Lycaon pictus*
Felidae	
caracal	*Felis caracal*
cheetah	*Acinonyx jubatus*
leopard	*Panthera pardus*
lion	*Panthera leo*
mountain lion	*Felis concolor*
Mustelidae	
otter	*Lutra lutra*
Order Primata	
hamadryas baboon	*Papio hamadryas*
Order rodentia	
beaver	*Castor canadensis*
red squirrel	*Sciurus vulgaris*
Birds	
Order Columbiformes	
woodpigeon	*Columba palumbus*
Order Falconiiformes	
goshawk	*Accipter gentilis*
martial eagle	*Polemaetus bellicosus*
Order Passeriformes	
red-winged blackbird	*Agelaius phoeniceus*
sage sparrow	*Amphispiza belli*
Insects	
Order Lepidoptera	
speckled wood butterfly	*Pararge aegeria*
Order Odonata	
damselfly	*Calopteryx maculata*

APPENDIX II

Future research priorities

1. Female reproductive state

Female springbok provide an ideal opportunity to work on those factors which affect oestrous activity. Based on the model which has been developed, three principle types of manipulation are envisaged. First, using differential feeding techniques the importance of their plane of nutrition could be examined. Second, early removal of lambs from females should affect their breeding activity relative to ewes who are allowed to keep their lambs through to weaning. Again this should affect the plane of nutrition amongst females. Third, the rutting behaviour of territorial males could be reconstructed either by using specific stimuli (*e.g.* vocalisation, urine samples) or by controlling the presence of males in contact with females. If the conclusions of this thesis are correct, all three of these factors should affect female oestrous activity. Towards this end T. Richter, in collaboration with J.D. Skinner are presently hand-rearing female springbok lambs, with the aim of monitoring their reproductive behaviour and the underlying physiological state.

2. Female breeding behaviour; the importance of resource quality and male phenotype

The present thesis concentrated on the territorial behaviour of springbok males over a three and a half year period. In doing so a relatively small numbers of rams were monitored at any one time. Whilst this was able to address many of the problems associated with territoriality, it was unable to monitor the activity of a large number of known rams over a single rut. To answer questions relating to the influence of male phenotype and resource quality in determining male reproductive success, this short term, high intensity approach would be necessary. Working on a springbok population such as that of relatively tame individuals found in the KGNP, it would be possible to make substantial progress in answering this problem.

3. Female breeding behaviour; comparison of pre-rut and rut periods

Whilst oestrous ewes were monitored during the rut, it was not possible to compare this with their pre-rut behaviour. Pronghorn females are known to sample various territorial males before choosing the territory on which they breed (Byers *et al.* 1994). Perhaps the same is true for the springbok. Also, if female harassment is an integral part of springbok breeding behaviour, individual females may choose to associate with larger groups when in oestrous. Rather than considering events from the males' viewpoint, a comparison of the behaviour of individual females both before and during oestrus would add a new perspective to their breeding biology.

4. The timing of male rutting behaviour

Quite what factors are important in determining the rutting time of males remain obscure. Proximate factors such as daylength, lunar cycle and nutrition cannot explain the observed variation in rutting time. However it is interesting that the March/April rutting period, which was normally unsuccessful in this study, coincided with successful ruts in other areas. A comparison between the breeding biology within its northern and southern distribution, between which environmental conditions differ temporally, might highlight the common factors which are of fundamental importance in triggering the rut.

So far though behavioural and ecological based studies have not provided a definitive answer. Presently D. Skinner & J. Robinson are undertaking research on the function of the pituitary gland in mediating breeding behaviour in both seasonal and aseasonal breeders, the impala and the springbok. It is hoped that this will go some way towards understanding the physiological mechanisms responsible for underlying the synchronised male rutting activity in an aseasonal breeder like the springbok.

5. Comparison of riverbed and pan territories

Whilst males were observed to maintain perennial territories on the fossil riverbeds, observations suggest males only held territories at particular times of the year on the pans. As this was observed within the same population, it allows further exploration of territory dynamics amongst ungulates. As in some areas pans border riverbeds, the only difference between the these resource territories would be ecological. Presumably rainfall patterns would be similar, and the springbok would all be from the same study population. Thus any difference in males' territory dynamics or their utilisation by females could be related to ecological factors.

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Some costs of maintaining a perennial territory in the springbok, *Antidorcas marsupialis*

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Summary

The territorial behaviour of male springbok was investigated over a period of 12 months along the Nossob riverbed in the southern Kalahari. Springbok males maintain perennial territories and as such are constrained into being sedentary and unable to respond to changing environmental conditions by migrating to more favourable areas with the other members of the population. During the dry seasons many territorial males have to subsist in areas with vegetation of low nutritional value and water content. Being solitary, territorial males are at a higher predation risk than the rest of the population. Furthermore, during the rains they may be limited to areas of tall vegetation cover and be even more susceptible to predation. In response to these costs only 46% of territories were maintained when veld condition was poorest, despite the potential breeding advantages of continued maintenance.

Key words: breeding, costs, perennial territory, predation, springbok

Résumé

Pendant 12 mois, on a étudié le comportement territorial du springbok mâle, le long du lit de la rivière Nossob, dans le sud du Kalahari. Les springboks mâles gardent un territoire toute l'année et sont donc obligatoirement sédentaires et incapables de répondre aux changements de conditions climatiques en migrant vers des régions plus favorables avec les autres membres de la population. En saison sèche, beaucoup de mâles territoriaux doivent subsister dans des endroits où la végétation n'a qu'une faible valeur nutritive et un contenu en eau réduit. Solitaires, les mâles territoriaux courent, plus que le reste de la population, le risque de servir de proie. De plus, pendant les pluies, il est possible qu'ils doivent se limiter à des endtoits couverts d'une végétation haute et être des proies encore plus exposées aux risques. En réponse à ces inconvénients, seuls 46% des territoires subsistent lorsque les conditions dans le veld sont les moins bonnes, malgré les avantages potentiels que représente le maintien d'un territoire pour la reproduction potentielle.

Introduction

Previous work on territoriality amongst ungulates has highlighted many of the potential costs to such individuals. A major cost is the loss of the benefits of group living in those polygynous ungulates in which territorial males spend much of their time alone e.g. wildebeest, *Connochaetes taurinus* Burchell, (Estes, 1969) and gerenuk, *Litocranius walleri* (Brooke) (Leuthold, 1978). The major benefits cited for group living include a reduction in predation pressure and increased feeding efficiency (Dehn, 1990; Fitzgibbon, 1990a). Fitzgibbon (1990b) found that in the Thomson's gazelle, *Gazella thomsoni* Günter, solitary individuals experienced a far higher rate of predation by cheetahs, *Acinonyx jubatus* (Schreber) than group members. Siegfried (1980) showed that as the size of springbok herds increases, so vigilance levels by individual group members decrease, facilitating an increase in their potential feeding time.

Another major cost is associated with territoriality itself. In establishing and maintaining a territory there is an increase in the risk of injury. This has been reported in the harem-holding red deer, *Cervus elaphus* L., (Clutton-Brock, Guiness & Albon, 1982). It is not unusual to find springbok rams with serious injuries such as broken legs, as a result of territorial disputes (Mills & Haagner, 1989). Also, through maintenance and sexual activities, males lose time in which to concentrate on essential activities such as grazing and ruminating: impala, *Aepyceros melampus* (Lichtenstein), show a marked decrease in feeding activity during the rut (Jarman & Jarman, 1973a).

Springbok rams are territorial (Bigalke, 1972; David, 1978; Williamson, 1987), with territories being maintained throughout the year (David, 1978; Williamson, 1987). This is in contrast to many other territorial ungulates which maintain territories only at specific times of the year, e.g. pronghorn, *Antilocapra americana* Kingsley, (Gilbert 1973), impala (Jarman & Jarman, 1973b) and red deer (Carranza, Alvarez & Redondo, 1990). Perennial territory defence by springbok is probably a response to their breeding capability, as they may breed throughout the year and may produce two broods per year (Skinner, Von la Chevalliere & Van Zyl, 1971). Both these features may be adaptive for the springbok in its arid environment, characterized by unpredictable rainfall (Skinner, Van Aarde & Van Jaarsveld, 1984). By maintaining perennial territories males are in a position to mate at any time of the year.

Springbok are highly mobile, capable of moving large distances in search of food or water, responding rapidly to rainfall and the subsequent growth of herbaceous plants (Mills & Retief, 1984; Williamson, 1987; Knight, Knight-Eloff & Bournman, 1988). The springbok population of the southern Kalahari is able to distribute itself freely in the area, except along the western border which is fenced. The ability of the population to respond rapidly to changing environmental conditions is therefore contrasted by the constraints males impose upon themselves by being territorial. The aim of the present study was to determine some of the costs to rams of being territorial and sedentary relative to the mobility of the rest of the population.

Study area

The study was conducted in the Kalahari Gemsbok National Park (KGNP), South Africa and the adjoining Gemsbok National Park, Botswana (Fig. 1). This is a total area of 36,200 km^2 (Mills & Haagner, 1989) in which springbok may roam undisturbed. The southern Kalahari is made up predominantly of red sand overlying a calcareous sandstone layer (Knight *et al.*, 1988). It can be classified into three habitat types: dunes, fossil riverbeds and calcareous pans (Leistner, 1967). The pans are characterized by alkaline soils with poor drainage and relatively high

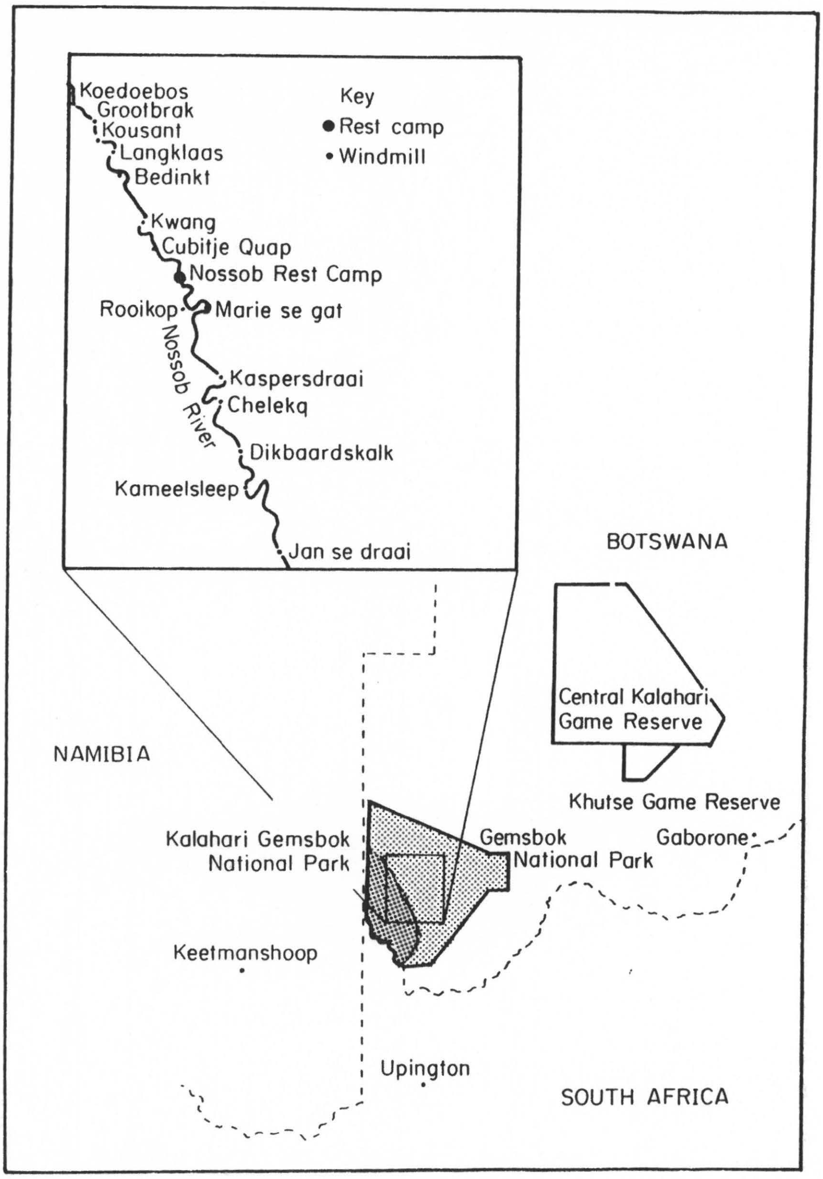

Fig. 1. Map of the southern Kalahari subregion with an inset of the study area along the Nossob riverbed.

nutrient levels. Riverbed soils are less alkaline and better drained than those of the pans, although they still exhibit a high nutrient content (Leistner, 1967) and support less ephemeral vegetation than the pans. The dunes support a lower quality of vegetation than the other two habitats but display a less marked decline in vegetative condition as the dry season progresses due to their relative ability to retain water (Leistner, 1967). Springbok are found in all three habitats, but show a strong preference for the pans and riverbeds (Knight *et al.*, 1988) on which male springbok maintain territories. The whole area is classified as semi-desert, falling between the 200 mm and 250 mm rainfall isohyets (Mills & Retief, 1984) with a patchy and unreliable rainfall.

The study area was centred at Nossob camp (Fig. 1) and can be divided into three regions in terms of the intensity of study. Monthly springbok counts were conducted along the course of the Nossob riverbed from Langklaas in the north to Dikbaardskalk in the South. Daily observations were made on individual springbok in the vicinities of Rooikop and Kwang waterholes. Vegetation biomass was measured in transects across springbok territories in the Nossob riverbed near Rooikop waterhole.

In the vegetation transects annual and perennial grasses and herbs were common. Dominant grasses included *Chloris virgata* Swartz, *Eragrostis porosa* Nees. *Setaria verticillata* (L.) Beauv. and *Tragus racemosus* (L.) All. *Schmidtia kalihariensis* Stent, predominant in the surrounding dunes, also fringed the borders of the riverbed in the sample area. Other common plants included the herbs *Amaranthus thunbergii* Moq., *Cucumis africanus* L.F., *Enneapogon branchystachyum* (Jaub & Spach.) Stapf = *E. Desvauxii, Heliotropium lineare* (A. DC.) C.H. WR. and *Tribulus terrestris* L. and the dwarf shrub *Lebekia linearifolia* E. Mey. Larger shrubs (e.g *Acacia mellifera* (Vahl) Benth, *Galenia africana* L., *Grewia flava* DC., *Rhigozum trichotomum* Burch. found in other areas of the riverbed were absent from the vegetation sample area.

Methods

Temperature and rainfall

Temperature records were taken at Nossob Camp. Rainfall was measured here and at four localities in the Nossob riverbed within 10 km of the camp. The readings from all five rain gauges were averaged.

Vegetation biomass

As grasses and herbs predominated in the sampling area, a disc pasture meter was used to provide an estimate of vegetation biomass (Bransby & Tainton, 1977). This involves measuring the height to which vegetation is crushed under a sliding disc allowed to drop down a rod from a fixed height. Four transects were made perpendicularly across the riverbed and a reading taken every twenty paces. The vegetation under the disc was collected at every third sample. This was weighed immediately to obtain a value of wet mass and again when it had been air-dried to constant mass, to yield a value for dry mass. The mean crush height was regressed against plant dry mass to obtain an estimate of vegetation biomass.

All records in which the only trees on the riverbed, *Acacia erioloba* (Mey), were noted were omitted from the final regression analysis. The procedure was repeated on a monthly basis and always on the same stretch of the riverbed in order to assess seasonal changes in biomass. The disc pasture meter was recalibrated every month because the degree to which vegetation is crushed under the disc varies according to its moisture content.

Vegetation height

The modal height of the predominant vegetation present in the riverbed was recorded every kilometre during the population census (see later) in March 1991. The modal height of the vegetation in which springbok were encountered was also recorded. Modal height was used rather than mean height as it more realistically reflects a springbok's field of vision and cover available to predators. Vegetation height was measured with a steel tape held perpendicular to the ground. These data were divided into three sub-sets; <35 cm (short), 35–69 cm (medium), $\geqslant 70$ cm (tall).

Springbok density on the riverbed

Springbok were counted along the course of the riverbed from Nossob camp. Counts were made, on a monthly basis, over a twelve month period from

September 1990 to August 1991. Two counts, separated by only a few days, were made over the course of a month, once up and once down the riverbed. All observations were made from a vehicle with the aid of 10 × 50 binoculars. During the cool-dry season (May–August) counts began an hour after sunrise to allow springbok to return to the riverbeds, as they tended to move off the river into the surrounding dunes at such times, possibly in response to the lower night-time temperatures on the riverbeds. At all other times of the year counts began at sunrise.

Data are presented over a standardized distance of 129 km, stretching from Langklaas to Dikbaardskalk waterholes. The odometer reading was taken every time a group of springbok was passed. If animals were found within 100 m of each other they were considered to be members of the same herd.

Status of individuals

Three subsets of adult springbok were recognized; territorial males, non-territorial males and females. Males were considered to be territorial if they were alone on the riverbed; territorial males spent 32·5% of their time alone in the KGNP (T. P. Jackson, pers. obs.). Herds of springbok on the riverbed were also considered to contain at least one territorial ram (if a ram was present). If more than one ram in a herd was seen to be behaving in a manner associated with being territorial they were also classified as having that status. These behavioural patterns include obvious sexual and aggressive activities, as well as the linked urination–defaecation sequence and horn rubbing, which are all performed predominantly by territorial rams in springbok and in many other antelope species (Walther, 1978, T. P. Jackson, pers. obs.).

Territory occupancy

To make a valid estimate of territorial male density on the riverbed, it was necessary to correct the data collected during the monthly censuses by the amount of time that males spent on their territories. Radio-collars were fitted and maintained throughout the study period on approximately ten territorial males, which were followed during the hours of daylight. The presence or absence of these males on their territories was recorded on an hourly basis.

Distance from permanent water sources

Permanent water is found in the KGNP in the form of water troughs supplied by windpumps. These are spread along the length of the riverbeds as well as in the surrounding dune system. Note was made of the distance between each windpump using the vehicle's odometer. The distances of herds from water was also recorded. If a herd extended over several hundred metres, the midpoint was taken as the average group distance from water. In this way the distance of animals from the nearest waterhole could be calculated. Animals were classed as either being <1 km, or $\geqslant 1$ km from water.

Results

Temperature and rainfall

Temperature and rainfall for the study period are given in Fig. 2. Between September and November precipitation was only 2% of the annual mean, whilst

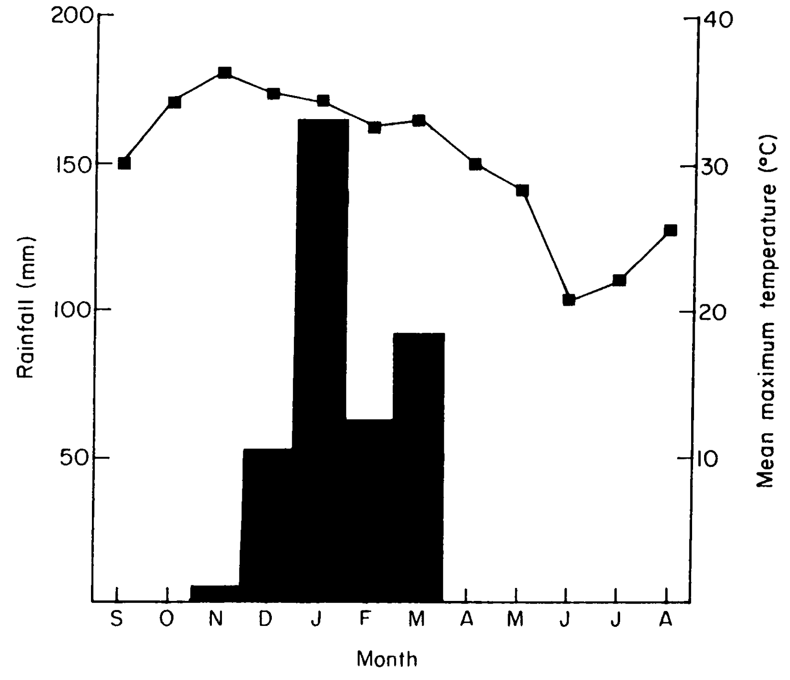

Fig. 2. Monthly variation in temperature and rainfall between September 1990 and August 1991 in the vicinity of Nossob Camp. Temperature –■–, Rainfall, bar chart.

mean monthly maximum temperatures did not decline below 30°C. These months represented the hot-dry season. The months from December to March were both hot and wet, contributing 98% of the year's rainfall, whilst the mean monthly maximum remained above 30°C. Total rainfall for the year was 380 mm, the highest level for 15 years. From April through to the end of the study period in August no rainfall was recorded. With the exception of April (mean max = 30·1°C) mean monthly maximum temperatures declined below 30°C (Fig. 2) and these months represented the cool-dry season.

Vegetation biomass

Vegetation biomass levels on the riverbed showed marked seasonal changes (Fig. 3). From a low of 10·0 gm^{-2} wet mass in November, at the end of the hot-dry season, levels increased and peaked in March (250 gm^{-2}), the last rainy month, three months after the onset of the rains. The dry biomass of vegetation peaked a month later in April (74·8 gm^{-2}) from a low of 8·1 gm^{-2}, at the end of the hot-dry season.

Springbok density on the riverbed

Overall springbok numbers on the riverbed are represented in Fig. 4. From a low of 5·4 km^{-1} on the riverbed in November, at the end of the hot-dry season, numbers peaked at 58·3 km^{-1} in April following the end of the hot-wet season; a 10·8 fold increase in population density. There was a significant monthly variation in the observed density of springbok on the riverbed compared with expected values had springbok density remained constant ($\chi^2 = 11521$, df = 11, $P < 0{\cdot}001$). The density of males occupying territories also fluctuated over the course of the year compared to that expected if their density was to remain constant ($\chi^2 = 140{\cdot}8$, df = 11,

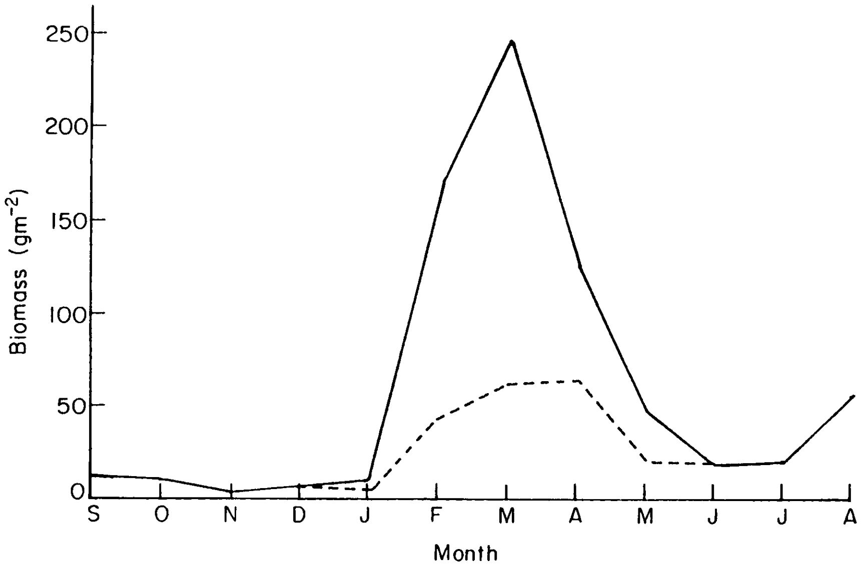

Fig. 3. Monthly variation in the wet and dry biomass of vegetation on the Nossob riverbed. Wet biomass ——, Dry biomass – – –.

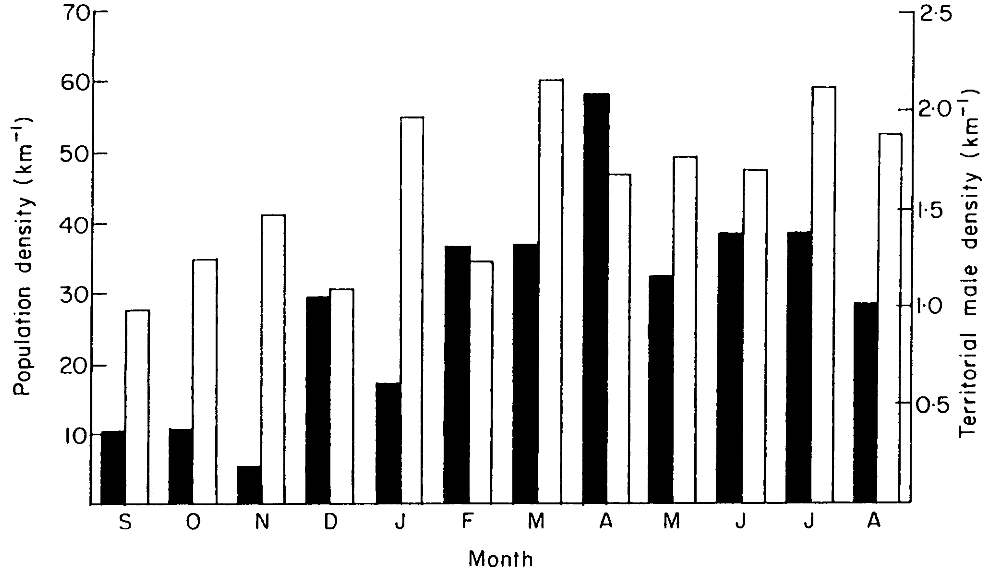

Fig. 4. Monthly variation in the density of the springbok population and of territorial males on the Nossob riverbed. Population ■, Territorial males □.

$P < 0{\cdot}001$). However, the fluctuation was less than that expected if it were to vary to the same extent as that of the whole population ($\chi^2 = 1025{\cdot}6$, df = 11, $P < 0{\cdot}001$), showing only a 2·2 fold increase. From a low of 0·99 territorial males km^{-1} in November, numbers peaked at 2·15 km^{-1} in July.

The springbok rutted both in late March and July; the peak in territorial rams in these months therefore corresponds to the two ruts. These data on the density of territorial males have been corrected to account for the time males spent off their territories (Table 1). For most months territory occupancy during the day was over 80%, but declined to 42·3% in November at the end of the hot dry season. It was also relatively low in March (68·3%) because some of the study animals had

Table 1. Time spent during the hours of daylight by radio-collared males on their territories in the Nossob riverbed between September 1990 and August 1991

	1990				1991							
Month	S	O	N	D	J	F	M	A	M	J	J	A
Total No. observations	220	136	151	128	188	145	88	60	83	38	89	74
No. observations on territory	168	94	64	117	163	142	60	56	79	36	88	62
% Time present on territory	76·3	69·1	42·4	91·4	87·7	97·9	68·2	93·3	95·2	94·7	98·9	83·2

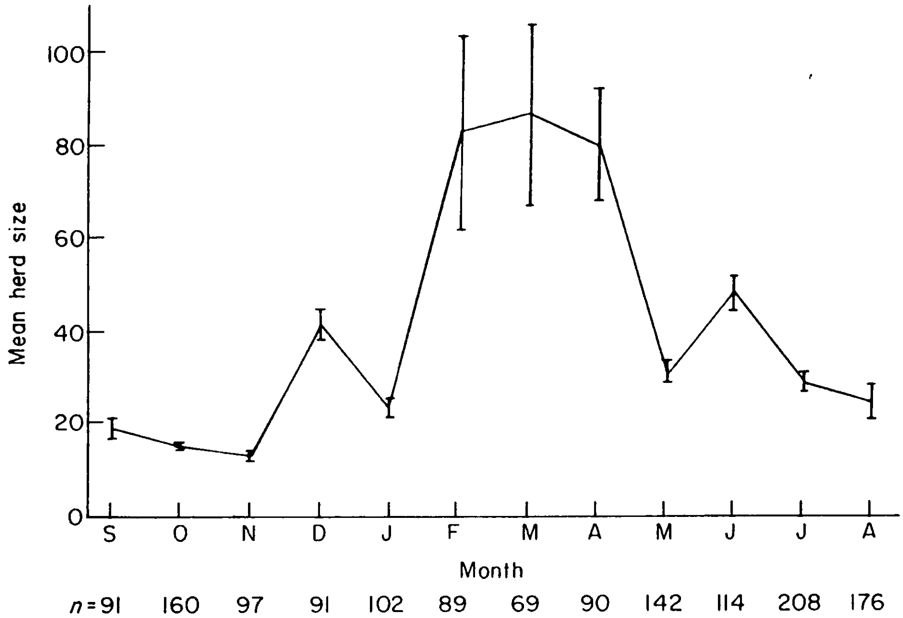

Fig. 5. Monthly variation in the mean springbok herd size (±SE) encountered on the Nossob riverbed.

territories in which the grass was very tall as a result of the good rains, and temporarily abandoned their territories or spent very little time on them. As the exceptionally long grass was a patchy phenomenon, our data on territory occupancy may be low, thus boosting the corrected figure for density of territorial males.

There was also a marked variation in the size of herds with which animals were associated during different months (ANOVA, $F = 8{\cdot}89$, df = 1428, $P < 0{\cdot}001$; Fig. 5). Mean herd size reached its lowest in November ($\bar{x} = 12{\cdot}8$, $n = 97$) at the end of the hot-dry season before increasing to a peak in March ($\bar{x} = 86{\cdot}7$) during the hot-wet season. Both mean herd size and population density showed an anomalous decline in January. The density of territorial males was high during this month. It should be noted that the January count was made at a time when the riverbed was waterlogged. Thus although males remained on their territories, there was a tendency for

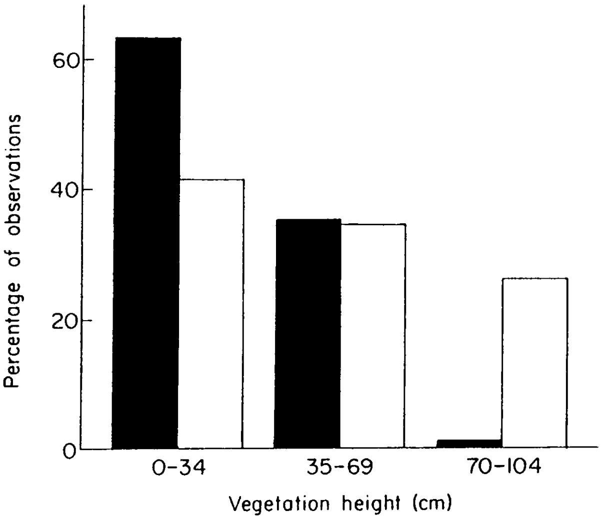

Fig. 6. Distribution of springbok on the riverbed relative to vegetation height at the end of the hot-wet season. Observed ■, Expected □.

other springbok to seek refuge on the neighbouring dunes until the conditions on the riverbed improved.

The time of peak population density on the riverbed coincides with that of peak vegetation biomass, being correlated to both wet ($r_s = 0{\cdot}66$, $P < 0{\cdot}05$, $n = 12$) and dry biomass ($r_s = 0{\cdot}71$, $P < 0{\cdot}05$, $n = 12$). However, neither the density of territorial males within the population, nor the time males spent on their territories were significantly related to vegetation biomass (wet or dry) on the riverbed ($r_s = < 0{\cdot}46$, $P > 0{\cdot}1$, $n = 12$). Thus the factors influencing the density of the majority of the population and that of territorial males appear to be different. It was also found that the springbok population density *per se* was not significant in determining the density of territorial males on the riverbed ($r_s = 0{\cdot}42$, $P < 0{\cdot}2$, $n = 12$).

Distribution of springbok on the riverbed

1 Proximity to permanent water. The distribution of all springbok, excluding territorial males, relative to permanent waterholes was found to be different over the three seasons ($\chi^2 = 1502{\cdot}6$, df = 5, $P < 0{\cdot}001$). More animals were found within 1 km of water during the two dry seasons than expected. The distribution of territorial males showed no seasonal variation, but remained the same throughout the year ($\chi^2 = 0{\cdot}23$, df = 5, $P > 0{\cdot}99$). During the hot-wet season there was no difference in the distributions of territorial males, non-territorial males and females relative to permanent water sources (Friedman two-way ANOVA, $\chi^2_r = 0{\cdot}3$, df = 4, NS). The average distance of territorial males from water was greater than that of females during the two dry seasons (Wilcoxon matched pairs, $T = 1$, $n = 7$, $P < 0{\cdot}05$), which was itself greater than that of non-territorial males during these months (Wilcoxon matched pairs, $T = 0$, $n = 7$, $P = 0{\cdot}01$).

2 Vegetation height. When the height of the vegetation was recorded during March, at the end of the hot-wet season, all springbok showed a marked preference for areas of low cover, < 35 cm high ($\chi^2 = 1430{\cdot}5$, df = 2, $P < 0{\cdot}001$.) in which herbaceous plants were dominant (Fig. 6). Given that springbok prefer areas of low cover, the distribution of different sub-sets of the population was examined to see if they differ from that of the overall population. In areas of the shortest cover the occurrence of territorial rams, non-territorial rams and ewes was similar

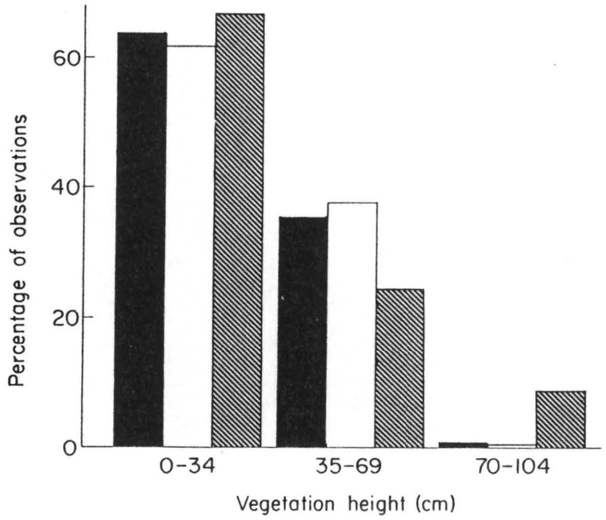

Fig. 7. Distribution of territorial male, non-territorial male and female springbok on the riverbed relative to vegetation height at the end of the hot-wet season. Females ■, Non-territorial males □, Territorial males ▧.

($\chi^2 = 1{\cdot}25$, df = 2, $P < 0{\cdot}3$; Fig. 7). In areas of intermediate vegetation height fewer territorial and more non-territorial males were found than one would predict $\chi^2 = 7{\cdot}84$, df = 2, $P < 0{\cdot}05$). However, the most significant deviation from the norm was seen in areas with the tallest vegetation cover where many more territorial males were present than would be expected ($\chi^2 = 103{\cdot}6$, df = 2, $P < 0{\cdot}001$). These areas were dominated by dense stands of the annual grass *Schmidtia kalahariensis* and the shrub *Galenia africana.*

Discussion

Food availability and quality in the Nossob riverbed fluctuates markedly over the course of the year. There is a strong tendency for the springbok population as a whole to move widely, concentrating on the riverbed when grazing is good and dispersing into the dunes as conditions deteriorate. The dune habitat is most extensively utilized at the end of the hot-dry season (Williamson, 1987; pers. obs.), a time of year during which springbok largely browse (van Zyl, 1965; Mills & Retief, 1984). Browsing is preferred to grazing on the lignified grasses available on the riverbed at this time (Davies & Skinner, 1986). The dunes can therefore be seen as a food reservoir during the dry periods as the herbaceous annuals associated with the river habitat show considerable variation in nutrient and moisture content, whilst the woody browse plants maintain relatively high levels of both throughout the year (Schijf, 1978).

Although springbok can survive long periods without water (Child, Parris & LeRiche 1972), animals remaining on the riverbeds tended to keep close to permanent waterholes during the dry seasons, but distributed themselves more evenly along the course of the riverbed during the wet period. Thus while the majority of the population gained nutritional and drinking advantages by their seasonal movements, territorial males gave up these opportunities by being more sedentary, showing no seasonal movement towards waterholes and using the dunes to a much lesser extent.

Unlike other members of the population, a territorial male's movements along the course of the riverbed are constrained by its attachment to a particular territory. If a ram is to remain territorial it is unable to respond to changing conditions inside or outside the territory, such as an absence of vegetation during the dry season or an excess after the rains. Thus, after the rains significantly more territorial males were seen in areas in which the vegetation cover was high, relative to the distribution of other springbok. Cheetahs are believed to be the major predator of adult springbok (Hofmeyr & Louw, 1987; R. Liversidge, pers. comm.), and Fitzgibbon (1990b), found that they hunted a greater proportion of gazelle groups available to them in high than in low vegetation. As a disproportionate number of territorial males were found in tall vegetation, this may be a factor leading to higher predation rates on them than on other sub-sets of the population. Thus, by being territorial and hence more sedentary and not able to respond to changing environmental conditions in the same way as the rest of the population, territorial males impose upon themselves additional nutritional costs and predation risks.

Springbok have been observed to copulate and lamb at all times of year and, with a six month gestation period, may even produce two offspring per year (Skinner *et al.*, 1971; T. P. Jackson, pers. obs.). This is in marked contrast to many species whose gonadal development and reproductive activity is seasonally restricted (Skinner, Van Zyl & Oates, 1974). Such species are generally found in areas where changes in environmental variables are relatively predictable. Due to the unpredictability of environmental variables in the arid south-west of Africa where springbok are endemic, they are not seasonal but opportunistic breeders, though they do still have rutting peaks. To date, only territorial males have been seen to copulate with females (T. P. Jackson, pers. obs.), suggesting that they achieve at least most of the copulations with receptive females.

The number of territorial rams peaks during the rut, when the probability of mating is at its highest. A similar increase in the number of solitary rams, which are most probably territorial, has been noted in the Etosha National Park, Namibia (Bigalke, 1972). We suggest that rams are perennially territorial primarily in order to be established on territories at the start of the rut, whenever it occurs, while they may also gain chance matings outside the rut. The fact that springbok may rut and may lamb twice in one year (Skinner *et al.*, 1971) should further increase the motivation to maintain perennial territories. Although the density of territorial males on the riverbed fluctuated much less than that of the whole population, there were clearly some males which established territories opportunistically during the rut, thus avoiding the costs of maintaining a perennial territory. At present it is not known to what age group these new territory holders belong, but it is possible that many are young, first time males temporarily taking advantage of the rut. Whilst maintaining a perennial territory may be energetically more costly, it may offer a greater guarantee of mating opportunities than to join the scramble for vacant territories at the start of the rut.

Acknowledgments

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The "Ram effect" in three species of African Ungulates

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UNGULATE
BLESBOK
DAMALISCUS DORCAS
IMPALA
AEPYCEROS MELAMPUS
SPRINGBOK
ANTIDORCAS MARSUPIALIS
RAM EFFECT
REPRODUCTION
SOUTH AFRICA

ABSTRACT – Heap (1901) suggested the presence of the male could influence the onset of oestrus. This has subsequently been found to occur in sheep *Ovis aries*, goats *Capra hircus* and cattle *Bos indicus*. In wild ungulates, restricted breeding has resulted from climatic changes, particularly at high latitudes. In such seasonally breeding wild ungulates synchronization of births is further enhanced to ensure that a large percentage of young are born within a short space of time. The influence of the ram in this finer tuning has long been suspected and has now been demonstrated in seasonally breeding blesbok *Damaliscus dorcas*, impala *Aepyceros melampus* and opportunistically breeding springbok *Antidorcas marsupialis*. Reasons for synchronization are discussed.

Results from experiments where blood was sampled regularly from blesbok ewes in a mixed herd, ewes separated from a ram by a fence and ewes with no ram nearby for a year and then a ram introduced are reported. Plasma levels of progesterone were measured. Blood was also taken from impala ewes in mixed herds. For springbok, observations on behaviour and ovulation are reported.

INTRODUCTION

Heap (1901) was the first to suggest that the presence of the male influenced the onset of oestrus. This has subsequently been found to occur in sheep *Ovis aries* (Underwood, Shier & Davenport, 1944), cattle *Bos indicus* (Skinner & Bonsma, 1964), goats *Capra hircus* (Skinner & Hofmeyr, 1969) and red deer *Cervus elaphus* (McComb, 1987). In seasonally breeding wild ungulates the synchronization of births is further enhanced to ensure that a large percentage of lambs are born within a short space of time – in blesbok *Damaliscus dorcas*, for instance, three out of four lambs are born within a 16-day period (Du Plessis, 1972). Sinclair (1977) suggested that this finer tuned synchronization was to swamp the predators. Experiments ware carried out on blesbok, impala and observations made on springbok examining the role of the ram in the finer tuning of oestrus and ovulation.

METHODS

Blesboks were divided into three groups. Group 1 consisted of a mixed herd, Group 2 consisted of five ewes and one ram separated by a mesh fence and Group 3 consisted of six ewes separated from a ram for a year.

Animals were immobilized with xylazine and fentanyl and blood was sampled from all three groups thrice weekly during the breeding season and throughout the year for Group 2. During winter and when pregnant Groups 1 and 3 were sampled monthly. Blood was collected into heparinised venojets for progesterone assay following van Aarde (1985). Forty-four impala ewes were immobilized on an opportunistic basis from January (mid-summer) to September (spring) and blood was sampled and assayed as for blesbok.

Ten springboks ewes were shot in each of two years three weeks after the rut and the reproductive tracts examined. The springboks were also observed during the rut and lambs were counted to indicate the relationship of rutting to subsequent lambing.

RESULTS

Blesbok ewes and rams could interact freely in Group 1. All ewes showed cyclic activity during March, April and May (autumn breeding season) and pregnancies were detected from mid-April. Ewes in Group 2 experienced ovarian cyclicity throughout the year with progesterone baseline levels ranging from ~0.05 ng/ml to ~1.0 ng/ml. The expected winter anoestrus did not materialise. This was attributed to the proximity of the territorial ram and the good body condition of the ewes as their diet was supplemented. The length of the oestrous cycle, as determined by the cyclic production of progesterone, was 28 - 32 days or probably half this, namely 16 days.

In Group 3 ewes, progesterone concentrations were high (> 0.5 ng/ml) during the first month of translocation away from the ram in February but for the remainder of the year declined to a baseline of ~ 0.05 ng/ml (fig. 1). However, immediately after introducing a ram to Group 3 in February twelve months later, he established a territory and herded the ewes. His presence had a dramatic impact on progesterone concentrations which increased within a week in all the ewes. Moreover, the ewes cycled in synchrony in March and all had conceived by 7 April. It is apparent from figure 1 that the ewes experienced unfertilized cycles.

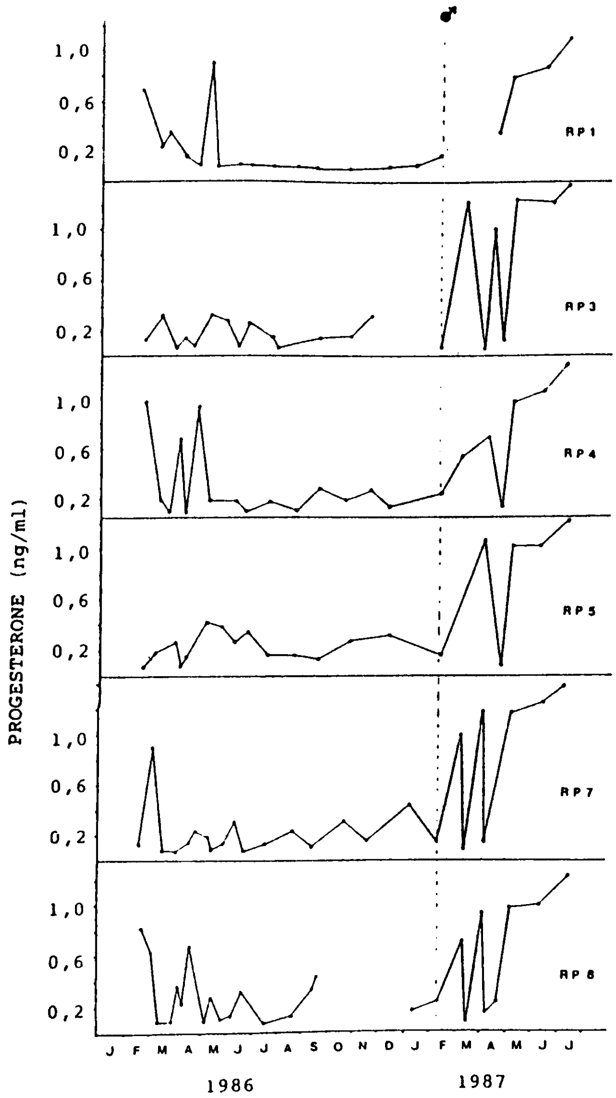

Figure 1 : Circulating concentrations of progesterone in blesbok ewes in Group 3 during 1986 and 1987. ♂ denotes the introduction of the ram.

In the impala ewes, ovarian activity was apparent during May and June (autumn) when progesterone concentrations were > 0.5 ng/ml. Pregnant impala had levels of 1.8 ng/ml progesterone by September when darting ceased (fig. 2). There was insufficient evidence for silent heats in impala, although no ovarian activity was noted before May, which is the peak conception month (Fairall, 1972). Ewes not pregnant by the end of June lapsed into anoestrus with baseline levels of progesterone. Oestrous cycles in impala ewes were limited to the latter half of May, coinciding with the lunar cycle as postulated by Warren (1974) and supported by Murray (1982).

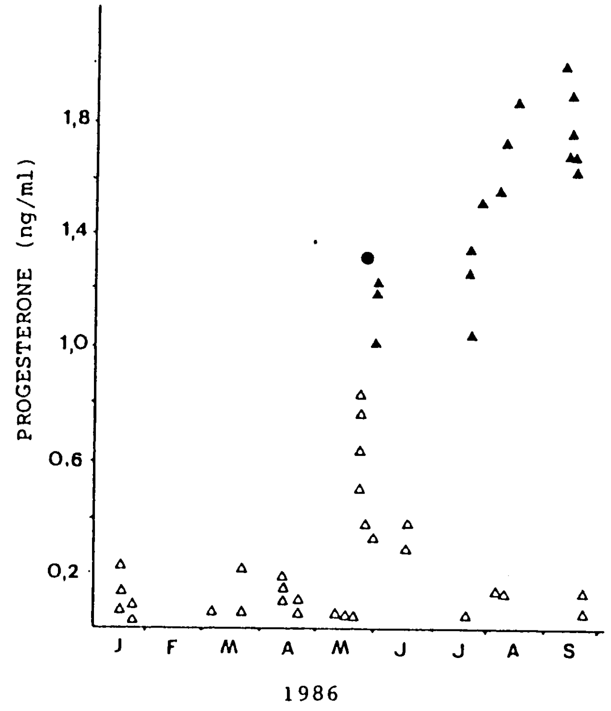

Figure 2 : Circulating concentrations of progesterone in impala at Derdepoort during 1986.▲ denotes pregnant animals, and ● denotes the full moon.

Springbok are arid adapted opportunistic breeders (Skinner & Van Jaarsveld, 1987). The rams also experience a rut, although not necessarily at the same time of the year in consecutive years. In the Kalahari, springbok rams rutted in April for two weeks and again for the month of July in both 1990 and 1991. Subsequently, the effect of conceptions during these ruts could be assessed by an increase in the number of new-born lambs (fig. 3).

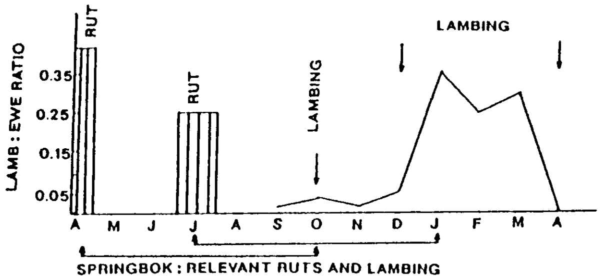

Figure 3 : Illustrating the rut and subsequent lambing peaks for springbok during 1990 in the Kalahari Gemsbok National Park.

Following the onset of the July rut, 10 ewes were shot 21 and 23 days later and 5% or more had just ovulated (fig. 4). As the oestrous cycle length is 16 days (Liversidge & De Jager, 1984), the same as in sheep, a silent heat is indicated as the ewes come out of anoestrus and mate at the second ovulation (fig. 4) (Knight, 1983).

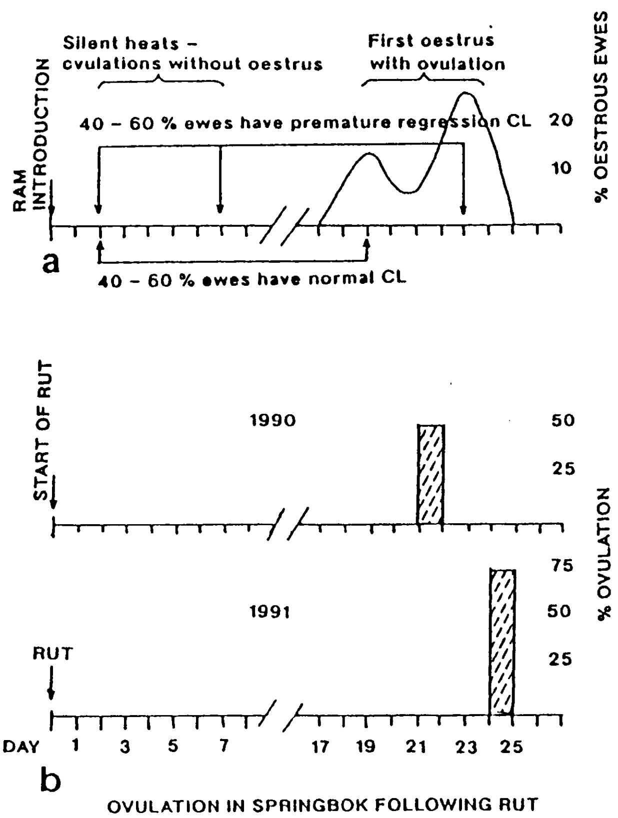

Figure 4 : A schematic diagram of (a) the time after ram introduction (*Ovis aries*) of the onset of ovulatory and oestrous activity and the premature regression of the corpus luteum (from Knight, 1983) and (b) ovulation in springbok (*Antidorcas marsupialis*) following the onset of the rut.Oestrous cycle length 16 days for both species.

DISCUSSION

The three species of ungulates discussed here are prominent in game ranching in southern Africa (Skinner, 1990). Manipulating reproduction is important for increasing productivity per hectare on the ranch. All three species responded to external stimuli. Blesbok showed a capacity to cycle throughout the year in the presence of the ram and adequate nutrition. Impala appear to be less flexible physiologically, indeed this confirms Fairall's (1983) observations that they experience only two oestrous cycles in autumn. Our results indicate that they may well experience a silent heat prior to the first overt oestrus as is indicated in the springbok and apparent in the blesbok.

At the onset of the rut in all three species, rams begin to grunt or "roar" and to chase ewes. This induces ovulation and, in the two seasonal breeders, concentrates births at the start of the lambing season. In the springbok, births are also synchronised but, in the arid regions, there is no apparent advantage in terms of growth and development (Clutton-Brock *et al.*, 1987).

In all three species, the advantage to the male in bringing the ewes out of anoestrus is an increased mating success and long-term fitness. The territory cannot be maintained for long as males lose body condition, particularly in impala (Skinner, 1971) where the ram only has two opportunities to fertilize the ewe. In springbok the rut apparently embraces only one oestrus but ewes may continue cycling as evidenced in figure 3 and will breed at any time of the year.In addition, McComb (1987) calculated for red deer that a failure of the stags to roar would retard conception by an average of six days and this would retard mating success by over 20%.

Bringing ewes out of anoestrus advances conception date to fall within the period the ram occupies a territory. Failure to conceive at the first oestrus (after silent ovulation) will result in a delay of 16 days. Clutton-Brock *et al.*, (1987) study on factors influencing survival of young in red deer showed that such a delay results in a loss in fitness. In their study, calf mortality increased by approximately 1% per day for every day of delay of birth after the median calving date of the group.Synchronization of the breeding season, even in seasonal breeders, by day length is coarser and would result in a spread of births over the period of two or three cycles. The finer cue of the "ram effect" skews this distribution, resulting in 75% of blesbok lambs being born within 16 days. In impala there is the same effect. This advancement of the median birthdate is advantageous for their growth and fewer parasites are present in early summer. In addition, the birth of more lambs in a defined short period, as also for springbok, affords lambs greater protection from predators through swamping. Also, this mechanism ensures that the fittest rams, which are more likely to occupy territories at the peak mating period, can fertilize all those ewes in his territory before his condition deteriorates.

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