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Morphometrics and reproduction in a population of springbok *Antidorcas marsupialis* in the semi-arid southern Kalahari

J. D. SKINNER*, R. J. VAN AARDE, M. H. KNIGHT AND H. M. DOTT
Mammal Research Institute, University of Pretoria, Pretoria 0002, South Africa

Summary

The timing and duration of the male rut were monitored in a population of springbok in the Kalahari from 1984. Timing was random and could not be related to any proximate factor; the duration varied from 5 to 23 days. Springbok rams were shot or captured in the hot–wet, cold–dry and hot–dry seasons from 1988 to 1992. Body condition and testicular exocrine and endocrine functions were measured. Territorial and non-territorial rams were treated in the same way. All body measurements were lower for non-territorial than for territorial rams, but only neck girth differed significantly. Captured animals were stimulated with GnRH and plasma testosterone concentrations were measured over 90 min. Overall, non-territorials showed a greater response than territorial rams. The response of territorial rams to GnRH at the beginning of a rut was significantly less than the response 1 week later. Ewes came into oestrus shortly after the beginning of the male rut; in four of the past five years lambing peaked in the hot–wet season. Rams appeared to be physiologically capable of reproductive activity throughout the year, and responded to various stimuli by exhibiting rutting and/or mating behaviour. The possible stimuli are discussed.

Key words: Kalahari, rams, reproduction, rut, springbok

Résumé

On a surveillé l'occurence et la durée du rut des mâles dans une population de springboks du Kalahari depuis 1984. L'occurence semblait se faire au hasard et ne répondre à aucun facteur évident; la durée allait de 5 à 23 jours. On a tué des springboks mâles en saison chaude et humide, froide et sèche, et chaude et sèche, de 1988 à 1992. On a mesuré la condition physique ainsi que les fonctions testiculaires exocrines et endocrines. Les mâles ont tous été traités de la même façon, qu'ils soient territoriaux ou non. Toutes les mensurations corporelles étaient plus petites pour les mâles non territoriaux que pour les mâles territoriaux, mais seul le tour de cou différait significativement. On a stimulé des animaux capturés avec du GnRH et mesuré les concentrations de testostérone dans le plasma au bout de 90 minutes. En général, les mâles non territoriaux montraient une réponse plus forte que les mâles territoriaux. La réponse des mâles territoriaux au GnRH administré au début du rut était significativement

*Correspondence.

moindre qu'une semaine plus tard. Les femelles entraient en chaleur peu après le début du rut des mâles, et pour quatre des cinq dernières années, la mise-bas a culminé pendant la saison chaude et humide. Les mâles semblaient physiologiquement capables d'avoir une activité reproductrice tout au long de l'année et répondaient à différente stimuli en exhibant un comportement de rut ou d'accouplement. On discute des stimuli possibles.

Introduction

The springbok (*Antidorcas marsupialis*) is a gazelle which occurs in the arid southwestern parts of southern Africa (Skinner & Smithers, 1990). They are gregarious, usually moving in small herds during the dry seasons, although there have been sporadic appearances of large aggregations, numbering hundreds of thousands, trekking across the country (Skinner, 1993). Springbok can breed prolifically, the venison is of good quality (Skinner, 1972, 1989) and they can be restrained by normal small stock fencing. These characteristics make them suitable for game ranching (Skinner, 1985).

Data on their reproductive behaviour have been summarized by Skinner & Smithers (1990). Some males are territorial but may not remain on a territory throughout the year. Territorial rams experience a rut from time to time which is characterized by loud vocalizing, grunting and an increase in boundary marking by urination, defecation and horning of vegetation. They may also become less tolerant of non-territorial males and show a greater interest in females. Lambs may be born throughout the year, but in areas of summer rainfall the peak of lambing is in summer, and in winter rainfall areas the peak is in winter. In good conditions the females will produce and raise three lambs in 2 years (Skinner *et al.*, 1987), but if conditions are poor very few or no lambs may be born in a year. In other words, they are opportunistic breeders, but the cues responsible for triggering reproduction remain unknown. This is an important limitation if production is to be manipulated through management.

The aim of the present study was to identify some of these cues in an aseasonal breeding ungulate by measuring morphometric and reproductive characteristics in a population of springbok living in the semi-arid Kalahari, where climatic changes are extreme and rainfall is unpredictable. Observations were made in different seasons over a period of years in an attempt to distinguish between annual changes regardless of climatic conditions and changes that only occur prior to breeding. Climatic conditions and breeding success were also monitored.

Study area

The study was conducted in the vicinity of Nossob Camp (25° 25′S and 20° 36′E) in the Kalahari Gemsbok National Park, South Africa. The area is dominated by dunes underlined with calcareous sandstone which is exposed in the open wide riverbeds, pans and incipient pans (Leistner, 1967). The vegetation is characteristically Kalahari thornveld (Acocks, 1975). The mean annual rainfall measured during the summer rainfall season over the long term was 225.1 ± 12.9 mm [coefficient of variation (cv)=56.9%]. From 1985 to 1987 and in 1991/92, less than 20% of the mean rainfall fell. Single showers of less than 8.0 mm rain are ineffective in inducing vegetation to sprout (Knight, 1991), unless followed within 2 weeks by a similar rain shower (Leistner, 1967).

Irregular summer rainfall is accompanied by fluctuating high temperatures on a daily and seasonal basis. In summer, mean monthly temperatures exceed 20°C. The hottest month (January) has mean daily maximum and minimum temperatures of 36.6 ± 1.5°C and 19.8 ± 1.5°C respectively, cf. the coldest month (July) with temperatures of 22.8 ± 0.6°C and -0.1 ± 1.2°C respectively. In winter nocturnal temperatures frequently drop below freezing. The year can be divided into three seasons: cold–dry (May–September), hot–dry (October–December) and hot–wet (January–April) (Mills & Retief, 1984).

Materials and methods

Meteorology

Climatic observations were made at Nossob camp. Precipitation was measured daily from a storage rain gauge, and temperatures in a Stevenson's screen. 'Effective' rainfall was grouped by half months. Relative humidity and maximum and minimum temperatures were monitored with a hygrothermograph.

Census methods

In February, July and October of each year from 1988 to 1992, total strip counts were made from the road along the river from Twee Rivieren to Nossob restcamps (160 km). Rams, ewes and lambs (<2 and <2 months of age) were counted in a 500 m strip centred on a fossil riverbed. Percentage lambing was calculated for each season using these counts. Rams were categorized by their behaviour as territorial or non-territorial.

Animals sampled—Shot animals

1 *Males.* Each year, five territorial and (since 1989) five non-territorial springbok rams were shot for rations in each representative season from February 1988 to February 1992. The animals were weighed and measured and the kidney fat index (KFI; Riney, 1955) was used as a measure of condition.

$$\mathrm{KFI} = \frac{\text{weight of capsula adiposa}}{\text{weight of both kidneys}}.$$

Reproductive organs were collected, weighed and examined histologically, and epididymal spermatozoa were counted. Plasma was stored at -20°C for subsequent measurement of testosterone concentration by radioimmunoassay.

2 *Females.* From 1989 to 1992, in February and July of each year, 10 ewes were shot, weighed and the KFI determined. Reproductive organs were collected for histological examination and foetuses, if present, were weighed and measured.

Animals sampled—Captured animals

Each season from 1989, five territorial and five non-territorial rams were immobilized with a mixture of 1 mg etorphine hydrochloride (M99, Reckitt & Coleman) and 10 mg xylazine hydrochloride (Rompun, Bayer) contained in darts fired from a dartgun (TelinjectSA, RSA). An additional 0.5 mg M99 was administered intravenously if the animal began to recover before the blood collection procedure had been completed. A 10 ml heparinized blood sample was collected as soon as the animal was immobilized and thereafter at 15 min intervals for 90 min. An intravenous injection of 0.05 mg gonadorelin (Relefact, Hoechst) was given immediately after the collection of the second sample. This procedure is necessary because immobilization inhibits LH secretion by the pituitary and consequently reduces secretion of testosterone by the Leydig cells. The animal was revived with diprenorphine hydrochloride (M5050, Reckitt & Coleman) injected intravenously at twice the M99 dose, and released. The length and breadth of the right incisor of all animals were measured with sliding callipers. No attempt was made to use the same animals on each occasion, although some were used more than once.

Behavioural observations

Since 1984, the timing and duration of the male rut have been noted. The distance between territories was measured each season to assess the relationship between climatic conditions and space use. In addition, mating behaviour, although only rarely observed even during intense male rutting, was recorded. Females in oestrus at other times were also noted.

Reproductive morphology and histology

The length and breadth of testes were measured with sliding callipers. The volume v was calculated from the length l and breadth b, on the assumption that the testis is an oblate spheroid, from

$$V = \tfrac{4}{3}\pi l b^2.$$

Testes of shot animals were fixed in Bouin's fluid and routinely prepared for light microscopy. They were serially sectioned at 7 μm and stained with haematoxylin and eosin.

The diameter of the seminiferous tubules and the thickness of the epithelium were measured with an image analysing computer (Quantimet 520, Cambridge Instruments, England). The diameter of the tubules (TD) was calculated from the area of the tubuli and the epithelial width was calculated from TD − LD, where LD is the lumen diameter. Tubules were considered circular when the ratio PD/TD was less than 1.3, where PD is the diameter calculated from the perimeter (10 circular tubules were selected at random).

Ovaries were examined morphologically, noting follicular development before slicing, then fixed in 70% alcohol, sectioned at 5 μm and stained with haematoxylin and eosin.

Conception dates were determined through back calculation using the growth constant and coefficient for springbok fetuses and a gestation length of 24 weeks (Van Zyl & Skinner, 1970).

Radioimmunoassay of testosterone

Plasma concentrations of testosterone were determined by radioimmunoassay using 0.1 ml duplicate, diethyl ether-extracted samples as described by Van Aarde & Skinner (1986). Antiserum was raised in rabbits against testosterone 3-carboxymethyl-oxime as described by Millar & Kewley (1976). Cross-reaction with most steroids was less than 0.1%, except for dihydrotestosterone for which it was 5.1%. Assay sensitivity was 10.0 pg ml^{-1} and the intra- and interassay coefficients of variation 7.8% and 9.8%, respectively. Plasma spiked with 0.5–2.5 ng ml^{-1} testosterone yielded expected values, and percentage binding in serially diluted plasma was parallel to that of the standard curve. Extraction efficiency was 95.5%.

Statistical analysis

The morphometric results and testosterone concentrations were analysed by three- or two-way analyses of variance to distinguish the variance due to status of the animal, season and year of collection.

Results

Census

The results of strip counts in the three seasons from 1988 to February 1992 are summarized in Table 1. No herds of non-territorial males were counted during October 1990 because they were integrated with the females. There was no discernible trend in population size, but numbers were highest during February for each year except 1988.

Morphometric analysis

Three-way analyses of variance of body mass, shoulder height, neck girth and testicular volume of animals shot between 1989 and 1992 showed that the interaction between year and season or year and status (non-territorial, territorial) were significant (Table 2).

Similar analyses of body mass, shoulder height and testicular volume of animals captured in 1990, 1991 and 1992 also revealed significant interactions (Table 2). The results for each year were analysed separately. Shot and captured animals were included in each analysis. The variance ratios, degrees of freedom and probability (P) of statistically significant differences are presented in Table 3. The means appear in the text.

Once an animal has attained adult status, the shoulder height remains constant and this measurement can be used as a criterion for the maturity of the animals. The mean shoulder height of males was 83.4 ± 2.51 cm ($n=178$). On only three occasions were there significant differences between groups of animals. In February 1989 the animals were significantly smaller than in the other two months (80.2 cf. 82.7 and 84.5 cm); in February 1990 the animals had greater shoulder heights than in July 1990 (84.5 cf. 81.8 cm), and in 1991 territorial animals had greater shoulder heights than non-territorials (84.3 cf. 83 cm, see Table 3).

Table 1. Total counts of springbok within a 500 m wide strip along the Nossob riverbed from Twee Rivieren to Nossob (160 km) in the last week of February (F), July (J) and October (O) from 1988 to 1992

	1988			1989			1990			1991			1992	
	F	J	O	F	J	O	F	J	O	F	J	O	F	J
Total	680	623	1610	1863	936	452	3068	1199	1728	1503	832	1308	1811	1402
Female herd size (mean)	108	20	150	113	72	18	111	62	—	43	23	24	30	11
Per cent lambs*	77	35	95	94	78	39	30	30	12	42	32	22	55	18
Per cent lambs<2 months old	96	12	47	43	79	0	50	15	0	89	25	17	73	0
Bachelor herd size (mean)	20	10	14	23	26	12	36	5	—	33	7	24	20	6

*Number of lambs as a percentage of mature females.

Table 2. The variance ratio (F), degrees of freedom and probability that differences were due to chance, from the three-way analyses of variance (year, season, status) of morphometric measurements of shot (1989–92) and captured (1990–92) springbok

Variable	Treatment interaction	Variance ratio (F)	Degrees of Freedom	Probability
Shot animals				
Body mass	year × season	4.19	6,94	$0.001>P$
	year × status	7.58	3,94	$0.001>P$
Shoulder height	year × season	5.56	6,94	$0.001>P$
Neck girth	year × season × status	2.42	6,94	$0.05>P>0.01$
Testicular volume	year × status	3.66	3,94	$0.05>P>0.01$
Captured animals				
Body mass	year × season × status	4.11	4,70	$0.01>P>0.001$
Shoulder height	year × season	6.79	4,72	$0.001>P$
Testicular volume	year × status	3.11	2,72	$P=0.05$

In 1989 and 1990 there were no significant differences in body mass between any of the groups, but the masses in 1989 were greater than in 1990 (44.0 cf. 41.9 kg, $t=2.586$, df=86, $0.02>P>0.01$). In July 1991 territorials were heavier than non-territorials (46.8 cf. 42.1). In February and July 1991, territorials were heavier than in October (45.5 and 46.8 cf. 39.5), and in July 1992 both territorials and non-territorials were heavier than in October (45.0 cf. 40.0, see Table 3).

KFIs varied widely (Table 4) with an overall mean of 57.2 ± 65.2 ($n=120$). The KFI in October was invariably lower than in other months (not always significantly) which is in accord with results obtained for body mass.

Toothwear was greater in territorials than in non-territorials in 1990 and 1992 (tooth height in 1990 was 10.7 cf. 13.6 mm; and in 1992 10.9 cf. 12.8 mm, see Table 3).

The neck girth of territorial rams was significantly greater than that of non-territorials in 1990 and 1991 (40 cf. 37.7; 40.5 cf. 38.2 cm) and in July 1989 (45 cf. 40.4 cm, see Table 3). The neck girth was smallest in October in at least one group of rams every year; in 1989 territorial rams in July had thicker necks than in October (45 cf. 38.3 cm); in 1990 and 1991 rams measured in February and July had thicker necks than those measured in October (1990, 39.1 and 40.6 cf. 37 cm; 1991, 41.2 and 40.2 cf. 36.7 cm); in July 1992 rams had thicker necks than those measured in February and October (41.8 cf. 37.9 and 36.8, see Table 3).

Reproductive variables

The variance ratios, degrees of freedom and probability of statistically significant differences between measurements of the testes and epididymides are presented in Table 5; the means appear in the text.

Testicular volume of territorial rams was greater than non-territorials in all four years, significantly so in two of the years. The volume was least in October

Table 3. The variance ratio (F), degrees of freedom and probability that differences were due to chance, from two-way analyses of variance (status, season) of morphometric measurements of springbok in 1989, 1990, 1991 and 1992 (see text for means)

Variable	Treatment interaction	Variance ratio (F)	Degrees of freedom	Probability
1989 (shot only)				
Shoulder height	J & O>F	6.18	2,20	$0.01>P>0.001$
Neck girth	TJ>BJ	5.33	2,20	$0.05>P>0.01$
	TJ>TO			
1990				
Shoulder height	F>J	4.94	2,43	$0.01>P>0.001$
Neck girth	T>B	6.28	1,43	$0.05>P>0.01$
	F & J>O	5.55	2,43	$0.01>P>0.001$
Tooth wear	T>B	3.21	2,66	$0.05>P>0.01$
1991				
Shoulder height	T>B	4.69	1,45	$0.05>P>0.01$
Body mass	TJ>BJ	3.41	2,45	$0.05>P>0.01$
	TF & TJ>TO			
Neck girth	T>B	9.08	1,45	$0.01>P>0.001$
	F & J>O	14.4	2,45	$0.001>P$
1992				
Body mass	J>O	8.25	2,43	$P=0.001$
Neck girth	J>F & O	14.15	2,45	$0.001>P$
Tooth wear	T>B	3.21	2,66	$0.05>P>0.01$

T, territorial; B, bachelor; F, February; J, July; O, October; TJ, territorial in July etc.

Table 4. The three-way analysis of variance of the kidney fat index (KFI) of springbok rams

	Bachelor			Territorial		
	F	J	O	F	J	O
1989	107	31	23	94	32	7
1990	36	86	2	42	42	4
1991	89	113	4	133	9	5
1992	77	226	13	42	139	18

$F=2.53$; df=6,94; $0.05>P>0.01$; minimum significant difference (0.01)=62.9.

in all four years, significantly higher in July in three years and February in two years. In view of the consistency between years, the results of all years were analysed together; territorial rams had a significantly greater volume than non-territorials (319.2 cf. 278.3 ml). The volume was significantly lower in October than in the other two months (231.4 cf. 330.9 and 334.0 ml, see Table 5).

There were no significant differences in testes mass of territorials and non-territorials in any year or any month, but rams in February had heavier testes than those in October. This was significant except in 1992 (1989, 82.4 cf. 60 g; 1990, 70.6 cf. 49.7 g; 1991, 76.1 cf. 54.1 g). In 1989 and 1991 the July rams also had heavier testes than animals measured in October (1989, 78.2 cf. 60 g; 1991, 73.2 cf. 54.1 g, see Table 5).

Table 5. The variance ratio (*F*), degrees of freedom and probability that differences were due to chance, from three-way analyses of variance (year, status and season) of testicular measurements of springbok from 1989 to 1992 (testicular volume includes captured animals, see text for means)

Variable	Treatment interaction	Variance ratio (*F*)	Degrees of freedom	Probability
Testicular volume	T>B	11.55	1,166	$0.001>P$
	F & J>O	31.51	2,166	$0.001>P$
Testicular mass	year × season	2.41	6,92	$0.05>P>0.01$
1989	F & J>O			
1990	F>O			
1991	F & J>O			
Tubule diameter	year × season	3.22	6,91	$0.01>P>0.001$
1989	J>O			
1990	F>O			
Seminileous epithelium	year × season	9.12	6,91	$0.001>P$
1989	J>O>F			
1990	O>F & J			
Epididymal mass	year × season	7.75	4,72	$0.001>P$
1989	J>O			
1991	J>O			
1992	O>J			
Sperm numbers	T>B	4.7	1,65	$0.05>P>0.01$
	year × season	3.56	4,65	$0.05>P>0.01$
1989	O>J			
1991	O>F & J			

T, territorial; B, bachelor; F, February; J, July; O, October.

Each year the seminiferous tubule diameter was least in October; in 1989 it was significantly less than in July (200.3 cf. 232.5 μm) and in 1990 it was significantly less than in February (190.4 cf. 222.5 μm, see Table 5), but there were no significant differences between non-territorials and territorials. The seminiferous epithelium was thicker in October 1989 and 1990 than in February (56.1 cf. 38.3 μm and 77.1 cf. 62.7 μm); in 1990 it was also thicker than in July (77.1 cf. 59.9 μm), but in 1989 it was less than in July (56.1 cf. 70.6 μm, see Table 5). Both these characteristics had significantly different values between years, e.g. in July 1989 the animals had larger tubules than in July of the other three years. The tubules in July 1990 had a narrower epithelium than in July of 1991 or 1992.

Epididymal mass also varied from year to year; in October 1989 and 1991 it was less than in July (9.9 cf. 12.8 g, 8.8 cf. 11.3 g) whereas in October 1992 it was greater than in July (9.2 cf. 7.0 g); the mass in July 1992 (7.0 g) was significantly less than in 1989 (12.8 g), 1991 (11.3 g) and February 1992 (9.9 g, see Table 5).

Territorial rams had significantly more spermatozoa in the epididymis than non-territorials (1.48×10^{10} cf. 0.78×10^{10}), but there were differences between years. In October 1989 and 1991 the reserves were higher than in July (1989, 2.28×10^{10} cf. 0.19×10^{10}; 1991, 2.37×10^{10} cf. 0.36×10^{10}) and in October 1991 they were higher than in February (0.36×10^{10}, see Table 5).

Table 6. The variance ratio (F), degrees of freedom and probability that differences were due to chance, from three-way analyses of variance (year, status, season) of estimates of the concentration of testosterone in plasma of springbok, 1990–92 (initial concentration includes shot animals, see text for means)

Variable	Treatment interaction	Variance ratio (F)	Degrees of freedom	Probability
Initial test	year × status	5.54	2,157	$0.01>P>0.001$
1992	B>T			
	B & T>1990 & 1991			
	year × season	10.46	4,157	$0.001>P$
1992	J & O>F			
	1992 J & O> 1990 & 1991			
Response to GnRH	year × season	10.58	4,71	$0.001>P$
1992	O>F & J			
	O>1990 & 1992			
	J>1990			
Relative response	BO>TO	3.75	2,71	$0.05>P>0.01$

T, territorial; B, bachelor; F, February; J, July; O, October; TJ, territorial in July etc.

The concentration of testosterone in plasma of animals shot in February 1991 was higher (Table 6) than in July or October (3.82 cf. 1.52 and 1.25 ng ml^{-1}). The initial concentration of testosterone in plasma of rams captured in 1990 and 1991 did not differ significantly from season to season or between years; however, in October 1992 the concentration was significantly higher than in February or July (11.5 cf. 2.07 and 5.16 ng ml^{-1}), and it was also higher than in October of the previous two years (1990, 0.94 ng ml^{-1}; see Table 6). The response to GnRH stimulation (difference between the maximum and initial concentration) followed the same pattern with the addition that July 1992 was significantly higher than July 1990 (October 1992, 20.23 ng ml^{-1}; October 1990, 1.19 ng ml^{-1}; October 1991, 1.13 ng ml^{-1}; February 1992, 4.15 ng ml^{-1}; July 1992, 9.25 ng ml^{-1}; July 1991, 1.23 ng ml^{-1}; see Table 6). However, when the response was expressed as a fraction of the initial concentration (response/(response − initial), ie a value of 1 means the maximum was double the initial), there was no statistical interaction between year and season; instead the response of non-territorials in October was greater than that of territorials (5.27 cf. 1.18, see Table 6).

Fig. 1 illustrates the initial concentration of testosterone and the response to GnRH stimulation of territorial rams from 1989 to 1992. Non-territorials were not captured in 1989. The analysis, which showed that 1989 did not differ from 1990 and 1991, was the same as that described above.

Rut

Males. The occurrence of rutting in different seasons and the significant cumulative precipitation (showers>8.0 mm) for 2-week periods over a number of years is illustrated in Fig. 2. There were 11 ruts in the period 1984–92, five of them in late June or July, and six between February and April in years when the summer rainfall had been good. In 1985 there was very little rain and in 1986, when there

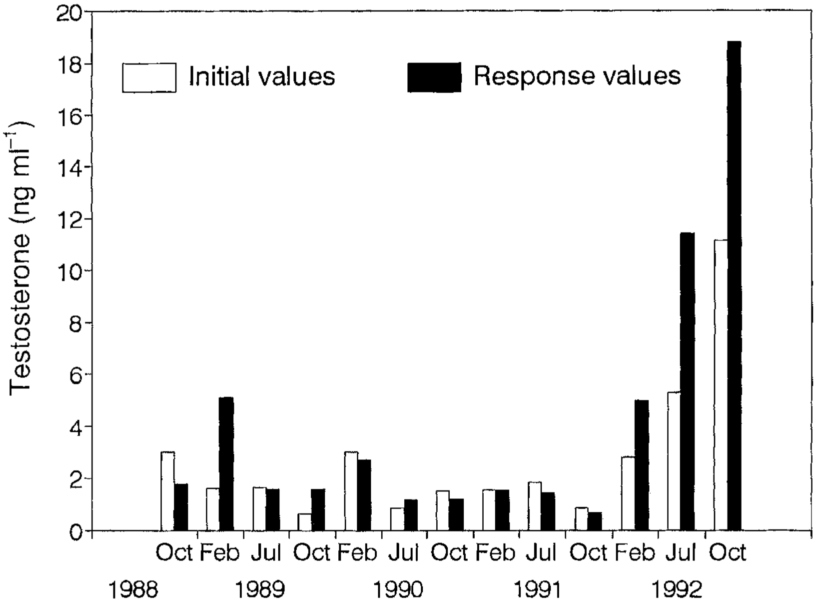

Fig. 1. Seasonal differences in testosterone production by immobilized springbok rams following GnRH stimulation from 1989 to 1991.

was virtually no rain, there was no apparent rut. The duration of the rut ranged from 5 to 23 days (mean=12.2 ± 6.3 days) and was not related to season. Subjective estimates of the intensity of the rut did not appear to be related to season.

In 1990 and 1991, ruts occurred from 10 April to 15 April and 4 July to 21 July and from 1 April to 9 April and 2 July to 25 July, respectively. These and other rutting dates did not correspond with a particular stage of the lunar cycle, nor were they related to cumulative rainfall beforehand.

In the two ruts in 1991, five rams were weighed and measured at the start of the rut and again 1 week later, this being the end of an intense rut in April but midway through the July rut. In July 1992, four rams were captured, but only two could be recaptured. The body measurements did not change (mass=46.0 ± 2.8 kg, shoulder height=82.3 ± 2.4 cm, neck girth=41.7 ± 1.8 cm) and the testis volume was unaffected (356.9 ± 67.7 ml). The initial concentration of testosterone in plasma did not differ significantly between rut and post-rut (2.19 ± 1.6 ng ml^{-1}), neither did the response to the GnRH challenge (2.14 ± 2.44 ng ml^{-1}), but the relative response was greater in the post-rut animals (0.73 cf. 2.43, F=6.33, df=1, 11, $0.05>P>0.01$).

Females. The results from the shot sample of springbok ewes are summarized in Table 7. Seasonal effects on body weight and condition of females are confounded by pregnancy and lactation. Ovaries tended to be quiescent in the hot–wet season (January–April), but as the sample was small and confined to one period, no generalizations could be made.

Ovulation following the onset of the rut in July 1990 and 1991 is illustrated in Fig. 3. The maximum and minimum temperature and day-length cycles in the area of Nossob camp are illustrated in Fig. 4.

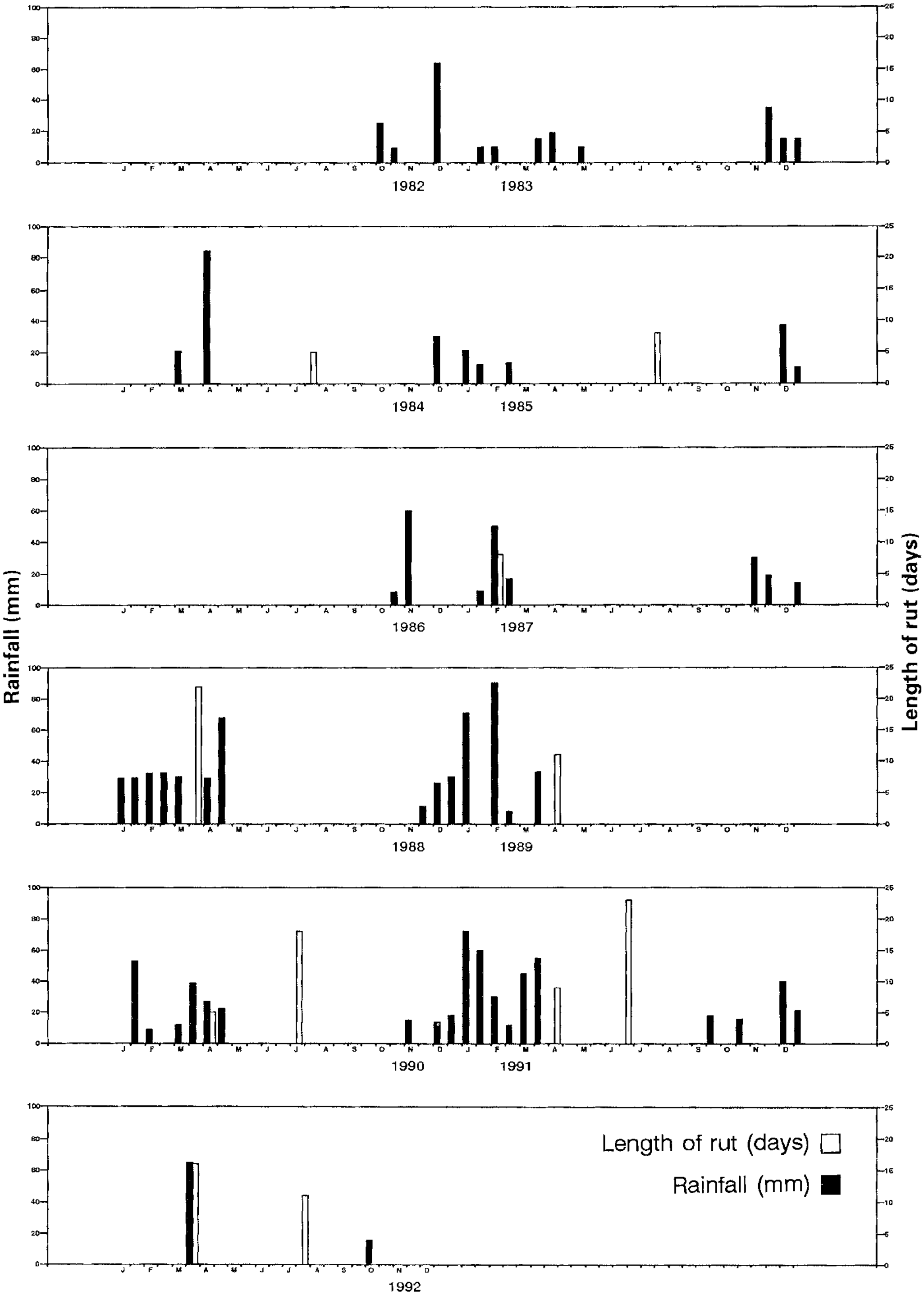

Fig. 2. The effective (precipitation > 8.0 mm) rainfall pattern over 10 years at Nossob Camp, with timing and duration (days in parentheses) of the springbok male rut over nine years in the Kalahari Gemsbok National Park.

Table 7. Conception rate in springbok ewes shot in the last week of February and July in the Kalahari

Year	Veld condition	*N*	Mean mass (kg)	KFI	Pregnant	Lactating	Conception date	Ovarian morphology
February								
1989	Good	10	37.4	43	1	7	End October	2/10 large follicles rest quiescent
1990	Very poor	10	29.7	39	0	1	—	Quiescent
1991	Verdant	10	33.6	51	1	2	End August	9/10 quiescent
1992	Very poor	10	34.2	15	0	7	—	Quiescent
Additional observations								
1989 noted 2 newborn lambs 24 February								
July								
1988	Good	10	38.7	120	8	0	6 end February 2 April	3/10 corpora lutea 2/10 quiescent
1989	Good	10	36.0	56	10	0	9–14 July 1–12 June	 10/10 corpora lutea
1990	Medium	10	34.0	205	5	0	5–21 July	5/10 corpora rubra 3/10 Graafian follicles
1991	Medium	10	36.6	213	8	1	8–24 July	8/10 corpora rubra 8/10 Large Graafian follicle 1/10 quiescent
1992	Poor	10	37.7	193	1	0	1–23 July	1/10 corpus rubrum
Additional observations								
1991 newborn lamb 21 July								
1991 pregnant female shot with 4-week-old foetus, ie conceived June								

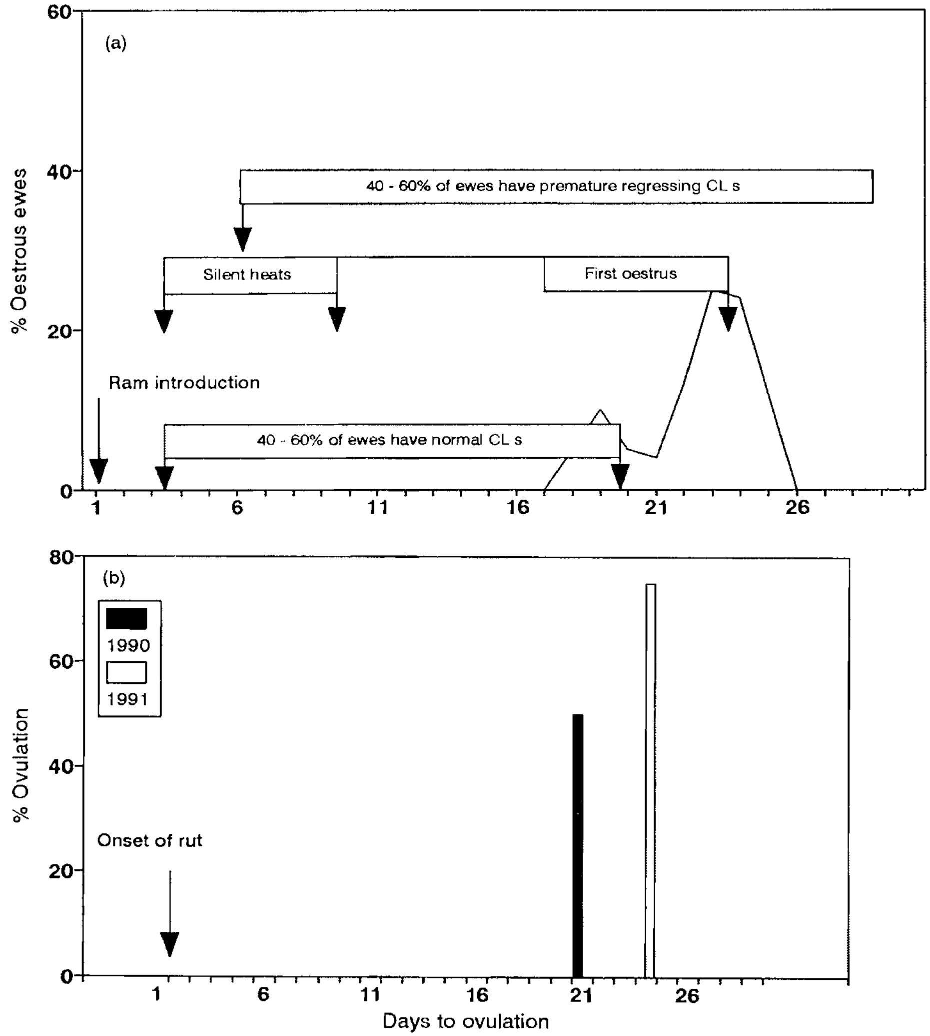

Fig. 3. A schematic diagramme of (a) the time after ram introduction (*Ovis aries*) on the onset of ovulatory and oestrous activity and the premature regression of the corpus luteum (from Knight, 1983) and (b) ovulation in springbok (*Antidorcas marsupialis*) following onset of the rut. Oestrous cycle length 16 days for both species.

Male behaviour

Territorial rams remained on their territories for most of the year, only vacating them when they were forced to move out of the riverbed and into the dunes in search of food in the late hot–dry season. The census along the Nossob riverbed showed that the distance between rams varied from 0.4 to 2.9 km depending on the season and whether the rams were rutting. The dry riverbed averages 0.25 km wide (Jackson T. P., pers. comm.), and if it is assumed the distance between rams represents one dimension of the territory, then territory size varies from 0.1 to 0.73 km^2 (mean 0.46 ± 0.25 km^2).

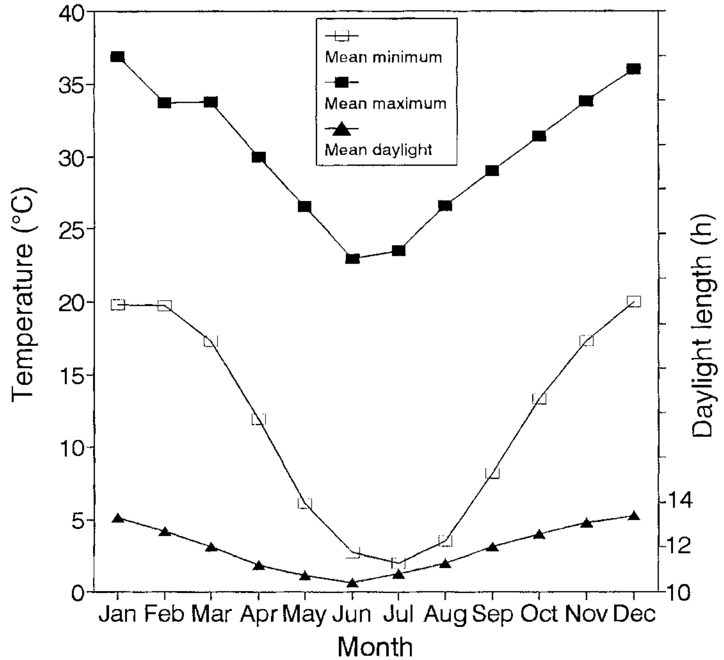

Fig. 4. The annual temperature and daylength cycles in the Kalahari Gemsbok National Park.

In July 1988 five males, occupying territories approximately 1.5 km north of Nossob Camp at Cubitje Quap, were shot. They were replaced within 1 month by new rams. In 1989 this was repeated in all three seasons with the same result, although replacement in February and October took 2–3 months in 1990 and 2 months in October 1991.

Discussion

The abrupt reduction in numbers coincident with the lack of rain in 1989 and the sharp increase in numbers by April 1990 (Table 1 and Fig. 2), which cannot have been produced by the resident population, illustrate the nomadic habits of the springbok. This feature of their behaviour makes it impossible to draw any firm conclusions on reproduction from the census data alone.

The unpredictable nature of the climate, and its influence on resident animals, is reflected in the variability of morphometric measurements of male springbok, in particular body mass and KFI, in the same season from year to year. However, it is apparent from the KFI that October, at the end of the cold–dry season, is the month with the lowest reserves. In both male Thompson's (*Gazella thomsoni*) and Grant's (*Gazella granti*) gazelles, seasonality in body condition was shown to be related to the rainfall pattern, suggesting a correlation with forage quality which declined substantially in the dry season (Stelfox & Hudson, 1985). Body mass also appears to be affected by the status of the animal, with territorial rams being the heavier, possibly because they occupy the 'best' part of the range.

The attrition of teeth suggests that territorial rams are older than non-territorials, but we know from the shoulder height that the latter were mature and their response to GnRH was equal to, and on some occasions greater than, that of territorials; a similar result has been reported for hippopotamus *Hippopotamus amphibius* (Skinner, Scorer & Millar, 1975). This would suggest that the observed failure of non-territorial springbok to mate is not due to immaturity or an inability of the testis to respond to stimulation, but instead to an absence, or suppression, of communication between the sensory organs and the hypothalamus. Whatever the mechanism, it can be quickly activated because there are always non-territorial rams in condition to occupy a territory, which is confirmed by the rapidity with which a territory is occupied after the removal of a territorial ram, even when a rut is not imminent. Further information is required to discover if all non-territorials are always in condition to occupy a territory.

The rut is a pattern of behaviour exhibited by mature males in a number of species in which the male holds a territory. It is characterized by intense territorial behaviour by the males for a short period once a year; during the rut most mature females come into oestrus (e.g. impala *Aepyceros melampus*, Murray, 1982). The latter results in mating which seems to be part of rutting behaviour; thus, the rut has become synonymous with the mating season. The springbok is different: territorial males mate with any female in oestrus at any time of the year. However, the rut may occur once or twice a year, or not at all, and the proportion of females that come into oestrus during the rut varies.

The dissociation between the rut and mating is illustrated by the morphometric measurements and the measurements of reproductive activity. Neck girth is an indication of breeding condition, but the significant differences noted were not correlated with a recent, or impending, rut. Testicular volume and/or mass both tended to be lower in October when no rut was observed, but variations in the more direct measures of breeding potential, such as spermatozoa in the epididymis, histology of the testis and endocrine status, were not associated with a rut.

Gosch & Fischer (1989) found that testicular volume in live fallow deer (*Dama dama*) increased before the rut, also evident in seasonally breeding African plains antelope (Skinner, Van Zyl & Oates 1974), and was strongly correlated with other testicular parameters such as semen volume and quality. The start of a rut in springbok is unpredictable, but our records provide no evidence of an increase in testicular size.

The dissociation is also evident in the rutting dates shown in Fig. 2 and the conception dates in Table 7, bearing in mind that gestation is 25 weeks.

One result which might indicate a link between the rut and reproductive activity is the increase in relative response to stimulation by GnRH 1 week after the start of the rut. This may result from a build-up in Leydig cell activity during the rut. Alternatively, the response of the rams to some extrinsic factor that initiated the rut may not have been complete at the onset. In springbok we have to look for at least two stimuli, one acting on the male to initiate rutting behaviour, and the other on the female to initiate oestrus.

The effect of adequate rainfall on vegetative growth, particularly on the richer alluvial soils of the fossil riverbed, is quite dramatic. Within days, plants sprout and grow in profusion. The growth continues until cold–dry conditions prevail but there is no sudden transition at the end of the hot–wet season. When this study commenced it was thought the rut was due to 'flushing' (Hammond, 1957) but the springbok have not shown any apparent response to green growth since then, apart from rams remaining on territories and all other springbok concentrating on the verdant green patches in the riverbeds. In the southern Kalahari, July appears to be the most favourable time for mating; lambs would then be born in the middle of the hot–wet season (Table 1), and ruts were observed in five of the nine years for which data were available. There are records of lambing peaks in the second half of summer (Knight, unpubl.). This pattern would fit Baker's (1938) hypothesis of ultimate factors influencing reproductive patterns. Some ruts have occurred in the hot–wet season, but mating then would produce lambs in the cold–dry season.

The irregular interval between ruts (Fig. 2) seems to exclude the possibility of an annual rhythm, but in five of the nine years a rut was observed in July which is close to the inflexion in the day-length curve on 21 June (Fig.4), which might well be a trigger in springbok as it is in some other species (e.g. *Ovis aries*, Lincoln & Davidson, 1977; Dott, unpubl.). In two of the years (1986 and 1987) when a July rut did not occur the previous summer, rainfall was sparse and well below average for the area, and in 1988 there was a prolonged rut in March/April. One might postulate an underlying seasonal rhythm with an ability to suppress the annual rhythm when conditions (external or internal) are unsuitable, but it is apparent from the 1992 observations that some factor has been overlooked. The ruts that were observed during, or towards the end of, the hot–wet season when rainfall had been good, might have been a response by the males to post-partum behaviour by a few females. A spontaneous post-partum oestrus is dependant on the female being in exceptionally good condition, a possibility in the hot–wet season but not at the end of the cold–dry season. Therefore, it is unlikely that a July rut would be initiated by female behaviour.

From direct observations in 1990 and 1991 on ovarian morphology (Fig. 3) and subsequent census data it is apparent that the onset of the rut induced some females to come into oestrus through a classic ram-effect (Knight, 1983; Skinner, Jackson & Marais, 1992). The only effect observed on the ram is that of enhancing the relative response to GnRH challenge.

Synchronization of oestrus and subsequent parturition occurs widely in ungulates with a restricted breeding season, and Estes (1976) has suggested that this finer tuned synchronization is an adaptation to swamp predators. These results support that hypothesis, but this is the first time it has been shown in an opportunistically breeding ungulate.

In ewes, body weight and condition were confounded by pregnancy so that both weight and KFI as a measure of condition were greater in July, when 80% of the ewes shot were pregnant or had just ovulated, cf. less than 1% in February when 70% were also lactating, in 1989 and 1992, imposing a further drain on body reserves (Table 7).

Much has been published about African antelope, including their reproduction, and summarized in comprehensive publications (Perry & Rowlands, 1969; Kingdon, 1982; Skinner & Smithers, 1990). There seems little doubt that many seasonal breeders use the annual photoperiodic cycle to time their reproduction, possibly with some other cue to fine tune the process; e.g. Sinclair (1977) has referred to the possible importance of the lunar cycle in the reproduction of wildebeest (*Connochaetes taurinus*) in eastern Africa. The timing of the rut in springbok bears no relation to the lunar cycle; we do not have sufficient detailed information on lambing to establish a relationship with the phase of the moon. Barometric pressure may also influence parturition in springbok (Skinner & Van Jaarsveld, 1987); falling barometric pressure as a result of rainfall may help synchronize births. We have been unable to confirm this. It is possible that springbok can use photoperiod and the influence of available nutrients (Laing, 1957) in combination to produce most of their lambs when conditions are most conducive to their survival.

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