DISPROPORTIONATE MORTALITY OF MALES IN A POPULATION OF SPRINGBOK (ARTIODACTYLA : BOVIDAE)

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ABSTRACT

The hypothesis that an imbalanced sex ratio, favouring females, in populations of springbok *(Antidorcas marsupialis)* is the result of disproportionate mortality of males is tested by comparing the sex ratio in a sample of 50 carcasses with that in a population of live springbok from the same geographical area. The results are consistent with this pypothesis. A suggested refinement of the hypothesis is that the disproportionate male mortality falls most heavily on young adult males which are in close association with springbok territories. Possible causes of this age- and sex-linked mortality are discussed.

INTRODUCTION

Bigalke (1970) hypothesized that an imbalanced sex ratio, favouring females, in populations of springbok (*Antidorcas marsupialis)* is the result of disporportionate mortality of males, possibly juvenile males less than 12 months old. This paper reports the results of a test of Bigalke's hypothesis.

METHODS

During October-December 1975, we collected 50 skulls from springbok carcasses found in a 200 ha section of Rooipoort estate (28° 45'S/24° 05'E), Kimberley district, South Africa. The collection area was equally divided between a calcrete pan, a preferred springbok habitat, and *Tarchonanthus* savanna, a suboptimal habitat (Bigalke 1972). This area was searched thoroughly by two or more observers at least once a week. Searches were conducted from a Land Rover, while driving transects 20 - 80 m apart. Transect width varied inversely with vegetation density. Records were kept of the number and sex of all springbok sighted in the collection area during October-December to derive an estimate of the sex ratio in the population. For all carcasses, the presence or absence of nearby (within a 20 m radius, the maximum conveniently searched area) trampled clearings heaped with

springbok dung was noted, since dung-heaped clearings are presumed to be signs of a springbok territory (Bigalke 1972). Skulls were classified according to the habitat in which they were found, and to their age and sex, based on horn shape and development (Rautenbach 1971; Liversidge unpubl. MS). Judging from carcasses of known age, all skulls were from animals which had died during March-December 1975.

RESULTS

Data for sex, age, habitat and proximity to dung-heaped clearings for the springbok skulls are summarized in Table 1. The sex ratio for 2492 sightings of springbok was 1,6 : 1, favouring females, and was significantly different from parity ($\chi^2 = 136,86$; $P < 0,001$). The sex ratio for the 50 skulls was 6,3 : 1, favouring males (Table 1), and was siginificantly different from the observed sex ratio ($\chi^2 = 34,21$; $P < 0,001$). The mean age of skulls from male springbok was 22,7 months, and for skulls from female springbok 26,6 months. These mean values are significantly different ($t = 2,16$; $P < 0,05$; Mann-Whitney U test). More than 83 per cent of the male skulls were from young adults 19 - 30 months old, and nearly 83 per cent of the latter skulls were found near a dung-heaped clearing (Table 1).

TABLE 1

Fifty springbok skulls collected at Rooipoort during October–December 1975 classified by habitat, sex, age and proximity to dung-heaped clearings.

Age (months)	*Habitat*									
	Calcrete Pan				*Tarchonanthus savanna*				*Both habitat & sexes*	
	Males		Females		Males		Females			
3–6	1	(0)*	0		0		0		1	(0)
7–10	0		0		0		0		0	
11–14	1	(1)	0		0		0		1	(1)
15–18	5	(1)	0		0		0		5	(1)
19–22	8	(6)	0		2	(2)	0		10	(8)
23–26	12	(10)	2	(2)	4	(4)	2	(0)	20	(16)
27–30	6	(5)	2	(1)	3	(2)	2	(0)	13	(8)
3–30	33	(23)	4	(3)	9	(8)	4	(0)	50	(34)

* number of skulls found near dung-heaped clearings.

DISCUSSION

There are several factors that could potentially lead to a sampling bias favouring males, both in counts of live animals, and in discovery of carcasses. These are listed in Table 2. Factors one to three tend to increase the probability of sighting males and counting the same male many times. Factors four to seven tend to increase the density, and the probability of sighting male carcasses. It is impossible to assess the effects of factors one through five, since the springbok in the collection area could not be identified individually, and it was impossible to age carcasses with an accuracy necessary to infer a precise sequence of mortality. Factors six and seven probably contributed little to any sampling bias. The collection area was searched thoroughly and regularly; therefore, it is unlikely that any carcasses were missed. There was no evidence of sex-linked differential wear in a sample of five skulls (three female, two male) from springbok that had died in March 1975, and had been exposed for more than eight months. Nevertheless, the true sex ratio in the springbok population frequenting the collection area was possibly somewhat more biased in favour of females than our data reflect, and the ratio for carcasses less biased in favour of males.

The apparent close association of springbok carcasses with springbok territories may be an artifact due to high density of dung-heaped clearings. This point is valid for carcasses from the calcrete pan habitat, since the mean distance between dung-heaped clearings in this habitat seemed to be less than 50 m. However, territories, and consequently dung-heaped clearings, are much more widely dispersed in *Tarchonanthus* savanna habitat (Bigalke 1972), and the close association between male carcasses and dung-heaped clearings in this habitat (Table 1) seems unlikely to be due to chance.

TABLE 2

Factors favouring male springbok in counts of live animals and discovery of carcasses.

	Counts
1.	Larger overall size (Bigalke 1970).
2.	Territorial springbok advertising display (Bigalke 1972).
3.	Strong fidelity of territorial males to their characteristically open domains (Bigalke 1972; David pers. comm.).
	Carcasses
4.	See Factor 3.
5.	Possible accumulation of carcasses due to deaths and successive occupation of a territory.
6.	Larger horns (Rautenbach 1971).
7.	Female skulls tend to weather more rapidly due to thinner bone structure (Skinner pers. comm.).

Assuming then that there was no great sampling bias, the skull data indicate disproportionate mortality of males in the springbok population frequenting the collection area. Thus, the results of this study are consistent with Bigalke's hypothesis. However, the results do not support his speculation that mortality is heaviest among males less than 12 months old. The greatest mortality appears to fall on young adult males between 19 and 30 months old, particularly those males in close association with springbok territories (Table 1). Therefore, a useful modification of Bigalke's hypothesis is: mortality of young adult males, particularly those living in or near springbok territories, contributes substantially to imbalanced sex ratios favouring females in springbok populations.

The causes of such heavy mortality of what should be animals in the prime of life remain obscure. Predation of healthy adult springbok is an unlikely major source of mortality, since the largest carnivore resident at Rooipoort is the black-backed jackal *(Canis mesomelas)*. Tracks of the brown hyena *(Hyaena brunnea)* have occasionally been seen at Rooipoort.

Intraspecific fighting, mainly restricted to disputes between holders of adjacent territories (David pers. comm.), may lead to some mortality; but battles rarely consist of more than vigorous horn wrestling (Bigalke 1972). However, the effect of intraspecific aggression cannot be dismissed as minimal without further investigation. The limited springbok hunting in the collection area is restricted to large, solitary, presumably territorial males. A result of such selective culling could be increased fighting over vacated territories.

Exhaustion, starvation and disease, three intimately related factors, seem to be the major sources of mortality of Rooipoort springbok. Since springbok have high energy and protein requirements, and low energy storage capacity in the form of fat (Vorster 1976), it would seem that they would be likely victims of these factors. Territorial males, particularly the young, inexperienced subordinate males would be especially vulnerable, since they would be forced to occupy suboptimal territories. A territory contains a limited amount of suitable food, which is utilized by its owner, conspecifics and other herbivores. Successful territorial occupation requires the output of considerable energy for patrolling and defending the domain and courting females (David pers. comm.; Schijf pers. comm.). Energy spent in these pursuits is at the expense of feeding time.

Thus, a territorial springbok can be thought of as walking an energetic tightrope. Should he not expend enough energy to maintain his territory, he will be displaced. Should he expend energy beyond that which his territory can support, he runs the risk of death through exhaustion, starvation and disease. If the modified version of Bigalke's hypothesis is correct, then it seems that young adult male springbok often gamble and lose.

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ADDENDUM

An astute colleague noted that if the Rooipoort springbok population is at an equilibrium, we should have found carcasses at a 1 : 1 sex ratio. A biased sex ratio favouring females would then be a consequence of a shorter life-span for males. We did find that male carcasses tended to be of younger individuals than were those of females.

However, the sex ratio of carcasses was more than 6 : 1 favouring males. This suggests that our sampling methods were somehow biased in favour of males (Table 2), and/or the population was not at equilibrium. We can test for non-equilibrial population, since there are accurate pre- and post-sampling estimates of the total springbok population at Rooipoort. There were approximately 2 500 springbok in 1974 and only 2 000 in 1977 These results show that the population was in a period of decline. Thus, until new data for springbok populations at equilibrium are gathered, our results have application only for declining populations.