OBSERVATIONS ON SPRINGBOK POPULATIONS

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The biology of the springbok, *Antidorcas marsupialis* (Zimm., 1780), like that of so many African antelopes, has not been studied in any detail. The main sources of published information are Cronwright-Schreiner (1925) and Shortridge (1934). Cronwright-Schreiner relates many personal observations of springbok and their behaviour, describes a mass eruption or "trek" which he observed in 1896 and reprints extracts from several older writings dealing with springbok and with their "trekking" habits. He discusses this phenomenon thoughtfully and in some detail. Shortridge (1934) brings together a good deal of general information from various sources (including Cronwright-Schreiner), many of them the books and diaries of early travellers and hunters. Walther (1966) in his recent general and comparative account of bovid behaviour, makes some mention of springbok, particularly of their stiff-legged jumping ("pronking") gait. There are other less important references of various kinds scattered through the literature but these will not be detailed here.

The present paper reports some of the findings resulting from a general study pursued sporadically and incidentally to other work during the period 1956 to 1964. Further papers are planned or in preparation.

STUDY AREA

The work was done mainly in three areas: the Etosha Game Park, South West Africa (approximately 15°-17°E, 18°-19°S); the Kalahari Gemsbok National Park, Cape Province, South Africa (20°-21°15′E, 24°31′-26°31′S); and privately owned land in the vicinity of Kimberley, Cape Province. Two large farms near Kimberley were visited frequently, the estate consisting of a number of adjoining properties and known as Rooipoort (approximately 24°50′E, 28°40′S—47,180 morgen) and Benaauwdheidsfontein (approximately 24°10′E, 28°40′S—12,978 morgen). A number of smaller farms in the same general area were visited occasionally. In addition, some observations were made on the Cape Provincial Wildlife Farm, De Hoop, situated to the south-east of Bredasdorp (approximately 20°02′E, 34°42′S—6,500 morgen). Some information was obtained from the S.A. Lombard Nature Reserve (25°31′E, 29°33′S) west of Bloemhof, Transvaal, and on the farm Grass Ridge (approximately 25°40′E, 32°S), north of Cradock, C.P.

The animals in the Etosha and Kalahari Gemsbok Parks are referable to the large race *A.m.angolensis* (nomenclature after Meester, 1964). In all other areas visited the smaller, nominate, race *A.m.marsupialis* occurs.

The writer was stationed in the Etosha Game Park from April, 1956 to March, 1958 and paid a subsequent visit there in April, 1962. The study was continued from mid-1958 to July, 1964, while working at the Alexander McGregor Memorial Museum, Kimberley. It was terminated as a result of taking up another appointment.

METHODS

Springbok were observed in the field whenever opportunities to do so arose, but particularly when activities of particular interest, such as rutting or lambing, were in progress. In the Etosha Game Park, movement was however severely restricted during the wet summer months, when most of the roads were impassable for long periods.

Because so many of the areas in which the work was carried out are extensive, it was necessary to traverse them by motor vehicle. Much of the springbok watching was thus carried out from a car or lorry. On occasion, where the country offered cover for concealment and when time permitted, this was supplemented by stalking on foot. Some observations were made while sitting in hiding at waterholes and drinking troughs.

The tools employed were simple ones: binoculars (8 × 30 and 10 × 50), a spotting telescope with interchangeable ocular lenses giving magnifications of 20×, 30× and 60× (a magnification of 20× was found to be satisfactory for most purposes), tally counters to facilitate counting and a notebook.

Springbok carcasses were only readily available for examination in any number during the winter months of June and July, the time of the shooting season. Shoots held on Benaauwdheidsfontein provided most of the material. Some animals were also examined at Rooipoort and other Kimberley farms and at Grass Ridge. At Benaauwdheidsfontein the number of carcasses brought into the farmyard during the latter half of a day's shooting was generally too large for anything but a rapid examination of each animal to be possible. As many carcasses as could be—and usually most or all of the bag was in fact handled—were weighed to the nearest ½ lb. on a 100 lb. spring balance (Salter) suspended from a wooden tripod.

Females were examined while being degutted and the presence or absence of grossly visible embryos recorded. The greater part of the bag of females, and usually the whole bag, was studied in this way on most occasions. Body measurements could only rarely be taken.

A small number of animals was shot specifically for scientific examination. Unfortunately circumstances did not permit the regular collection of such specimens.

REPRODUCTIVE CYCLE

Springbok exhibit a marked seasonal cycle of reproduction. This is illustrated, for example, by the existence of discrete age classes within a population. They can be quite clearly recognised by morphological features, body size and weight, in spite of the fact that springbok cannot yet be accurately aged by the pattern of tooth eruption or any other method.

BODY WEIGHT

The distribution of body weights within population samples will be used to illustrate the existence of size and age classes. Discussion will be confined to springbok collected in 1962 and 1963 on the farm Benaauwdheidsfontein, where the population numbered approximately 2000 animals at the time of this study. In each year, data were gathered at three separate shoots, spaced so closely that they have been taken together to represent a single sampling

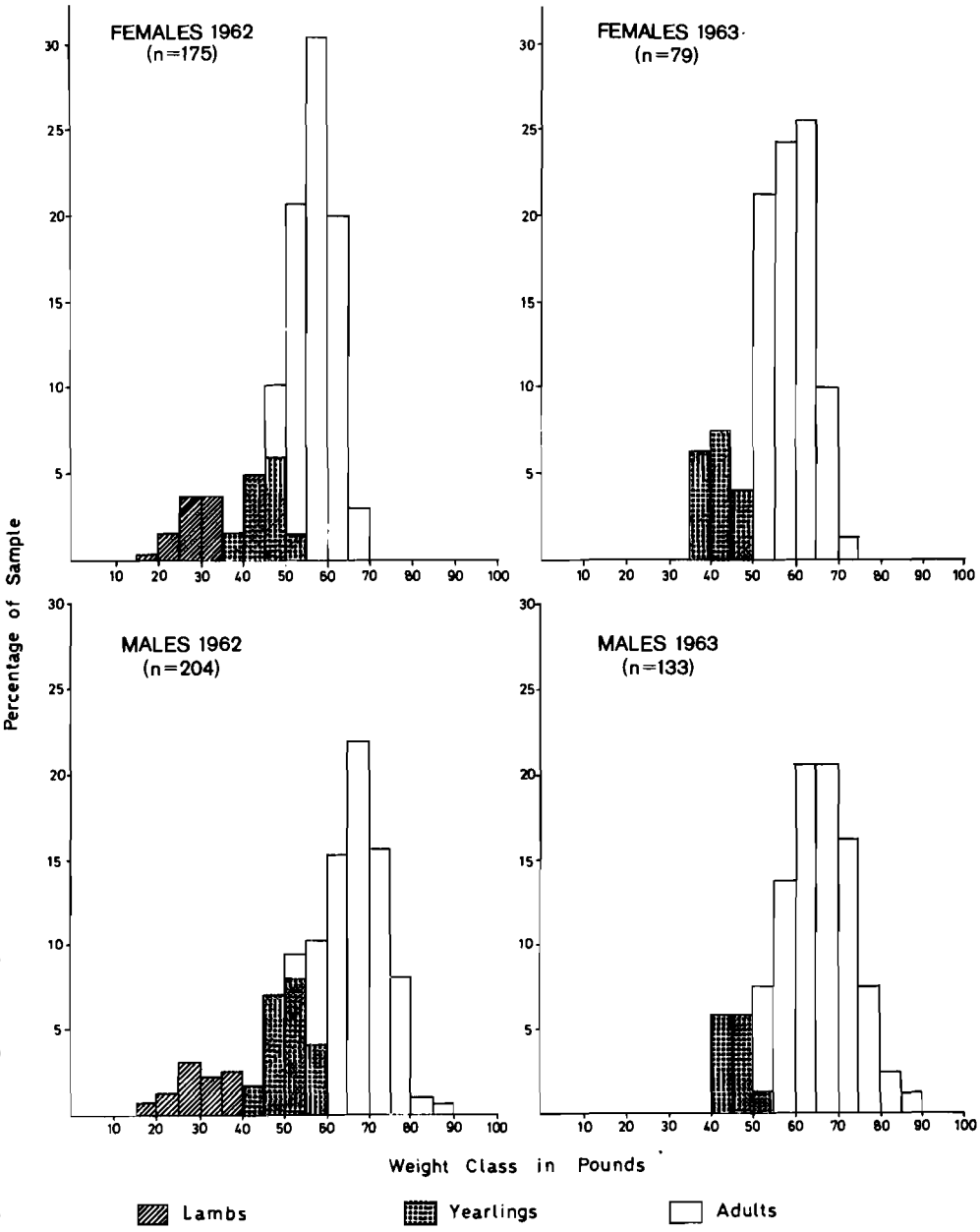

FIGURE 1
Percentage frequency of body weights amongst male and female springbok shot on Benaauwdheidsfontein in 1962 and 1963.

of the population during that year. In 1962 the shoots were held on 16 June, 11 July and 17 July while in 1963 they took place on 15 June, 21 June and 24 July.

The distribution of body weights, grouped into 5 lb classes and expressed as percentages, is illustrated separately for males and females in 1962 and 1963 (Figure 1).

Three age classes, lambs, yearlings and adults, are distinguished in the 1962 data and two in 1963. In 1963 the lamb class was absent from the sample, a point which will be taken up again below.

Animals were classified as lambs or yearlings on features of their external morphology—size; length and shape of horns; and proportions of the head. Those not considered to belong to either of these roughly defined but quite distinct categories were treated as adults. From observations on the times of year at which rutting and lambing took place (to be discussed below), and the knowledge that a gestation period of 171 days has been recorded (Shortridge 1934), the lambs were estimated to be approximately 4-5 months old, the 1962 yearlings 9-10 months old and those of 1963, 7-8 months old, when shot.

In spite of the imprecision of the criteria available for classifying the animals before weighing, it will be seen from Figure 1 that there is no overlap in the body weights of lambs and yearlings. Such overlap as does occur is between yearlings and adults. This is much more marked in 1962 than in 1963. In 1962 the weight overlap is greater in females than in males.

The overlapping weights can be explained in several ways. We have already noted that the 1962 yearlings were probably a month or so older, and therefore of course larger, than those of the 1963 sample. It may also be that the writer's skill in distinguishing large yearlings from small adults had improved in the second year. It is not surprising that the greatest overlap occurs in the females; they are far more difficult to age by the size and shape of their relatively smaller horns than the males. There is also less difference in the relative body size of yearlings and adults. Thus the mean weight of the 1962 yearling female group is almost 80% of that of adults (Table 1). Yearling males, on the other hand, are smaller and lighter relative to adult males ($\frac{\text{yearling wt.}}{\text{adult wt.} \times 100} = 72{\cdot}6\%$). The difficulty of separating yearling from adult females becomes even greater when classifying living animals in the field. Then it is usually necessary to lump yearling and adult females together, whereas these two classes of males are quite easily distinguishable.

In Table 1 the marked differences between the mean body weights of the various age and sex classes are illustrated. The statistical significance of these differences has been examined by applying the "t" test. The results are presented in Table 2.

The fact that the 1962 yearlings are approximately a month older than those of 1963 is further illustrated by the highly significant differences between the mean weights of each sex. There is no such obvious reason for the differences between adult males and adult females in the two years and the point will not be pursued.

SEASONAL RUTTING AND PARTURITION

It was not possible to observe springbok uninterruptedly throughout the year. Consequently no detailed information was obtained on the dates when rutting behaviour and parturition

TABLE 1

WEIGHT CLASSES IN SAMPLES OF SPRINGBOK COLLECTED ON THE FARM BENAAUWDHEIDSFONTEIN

Group No.	*Sex*	*Age Group*	*Year*	*n*	*Mean Weight (lb)*	*S.D.*
1	♂	Lambs	1962	18	30·7	5·2
2		Yearlings	1962	41	50·2	4·0
3		Adults	1962	144	69·1	6·3
4	♀	Lambs	1962	14	27·6	4·4
5		Yearlings	1962	24	45·7	4·3
6		Adults	1962	137	57·6	6·5
7	♂	Yearlings	1963	18	46·2	3·2
8		Adults	1963	115	65·8	9·6
9	♀	Yearlings	1963	14	42·1	3·5
10		Adults	1963	65	60·0	5·2

TABLE 2

SIGNIFICANCE OF DIFFERENCES BETWEEN THE MEAN BODY WEIGHTS OF AGE CLASSES OF SPRINGBOK COLLECTED ON THE FARM BENAAUWDHEIDSFONTEIN

Difference tested	*Level of significance*
Different classes, 1962	
♂ Lambs— ♂ Yearlings	$P<0·001$
♂ Yearlings— ♂ Adults	$P<0·001$
♀ Lambs— ♀ Yearlings	$P<0·001$
♀ Yearlings— ♀ Adults	$P<0·001$
♂ Lambs— ♀ Lambs	$P<0·001$
♂ Yearlings— ♀ Yearlings	$P<0·001$
♂ Adults— ♀ Adults	$0·005>P>0·001$
Different classes, 1963	
♂ Yearlings— ♂ Adults	$P<0·001$
♀ Yearlings— ♀ Adults	$P<0·001$
♂ Yearlings— ♀ Yearlings	$0·005>P>0·001$
♂ Adults— ♀ Adults	$P<0·001$
Equivalent classes, 1962/1963	
♂ Yearlings	$P<0·001$
♂ Adults	$0·005>P>0·001$
♀ Yearlings	$0·025>P>0·01$
♀ Adults	$0·01>P>0·005$

started, reached a peak and ended. It was also impossible to document fully the changes in herd size and composition which accompany these two significant events in the springbok calendar. However, the existence of the discrete size and age classes described in the preceding section, varying remarkably little in weight (as well as in other, less easily measurable, characteristics not dealt with here) is only explicable by assuming that mating, and hence parturition, is exceedingly accurately synchronised within the entire population.

Information collected about the time of year when springbok mate and lamb is presented in the sections which follow.

HERD COMPOSITION CHANGES AND RUTTING

The associations between springbok of different sexes and ages which were encountered in this study, are illustrated in Table 3.

TABLE 3

RELATIVE ABUNDANCE OF VARIOUS SOCIAL GROUPS IN SAMPLES FROM TWO SPRINGBOK POPULATIONS AT DIFFERENT SEASONS

Area	*KGNP*		*Etosha G.P.*	
Month	*March*		*July*	
Kind of group	*No.*	%	*No.*	%
Solitary ad. ♂	11	33·3	27	26·2
Herd ad., juv.; ♂, ♀	14	42·4	32	31·1
Herd ad. ♂	5	15·2	19	18·4
Herd ad. ♂, ♀	1	3·0	8	7·8
Herd ad. ♀; juv. ♂, ♀	1	3·0	6	5·8
Herd ad. ♂; juv. ♂, ♀	—	—	4	3·9
Others	1	3·0	7	6·7
	33	99·9	103	99·9

KGNP = Kalahari Gemsbok National Park
Etosha G.P. = Etosha Game Park

In both population samples, mixed herds occur most frequently, followed by solitary males and then adult male herds. Other associations are infrequent. The close similarity between the social structures of the two samples from different areas suggests that the three groups of real importance in the social life of springbok are mixed herds of adults and juveniles, solitary adult males and adult male herds.

The size and composition of the mixed herds studied in March (KGNP) and July (Etosha) differ markedly (Table 4). In the March sample, the herds are larger and only very few of them contain only one adult male. In the July sample, herds are small and more than half of them

TABLE 4

COMPARISON OF THE KALAHARI GEMSBOK PARK AND ETOSHA PARK MIXED HERDS (AD., JUV.; ♂, ♀: TABLE 3)

Area	*KGNP*	*Etosha G.P.*
Month	*March*	*July*
Total animals	820	598
Herd size range	7—182	3—90
Mean size	58·6	18·7
SD	61·9	16·4
Total No. herds	14 (100%)	32 (100%)
No. herds with 1 ad. ♂	2 (14·3%)	17 (53·1%)
No. herds with 2 ad. ♂♂	3 (21·4%)	4 (12·5%)
No. herds with 3 + ad. ♂♂	9 (64·3%)	11 (34·4%)

KGNP = Kalahari Gemsbok National Park
Etosha G.P. = Etosha Game Park

have only one adult male. In March no rutting behaviour was observed in the Kalahari Gemsbok Park. In July the rut was in full swing amongst the springbok seen in the Etosha Game Park.

TIME OF RUTTING AND LAMBING

In the Etosha Game Park active mating behaviour was seen mainly in June, July and August. The impression was gained that a peak may have been reached at about the end of July. On this assumption, most lambs should have been born in about mid-January. There are few summer records from Etosha because the roads were, at the time of this study, often impassable during that season. Nevertheless newly born lambs were recorded in January. The statements "In Angola the breeding season is between the end of December and the beginning of January"—Penrice, and "In Angola they breed in January"—Blaine, quoted by Shortridge (1934), support this finding.

In the Kimberley area and at the S.A. Lombard Nature Reserve, rutting and parturition occur much earlier in the year. Observations on lambing made at Rooipoort and Benaauwdheidsfontein, and information obtained from the S.A. Lombard Reserve, provide the best evidence for this statement. These data are presented in Table 5.

The months listed in Table 5 are those in which most lambs appear to have been born in each year. The records are not very precise and it is not known over exactly what period parturition extended. However, the peak period seems to fall within a month at the most and is possibly shorter. In only a few cases were many lambs born as early as August or as late as November. October was the most important month. There was some variation in different years. It has been noted that Benaauwdheidsfontein yearlings were heavier when shot in the

TABLE 5

RECORDS OF SPRINGBOK LAMBING PEAKS

	Area	*SAL*	*Rpt.*	*Ben.*
1953	.. ..	Oct.	—	—
1954	.. ..	?	—	—
1955	.. ..	Oct.	—	—
1956	.. ..	Aug.	—	—
1957	.. ..	Nov.	—	—
1958	.. ..	Nov./Dec.	Sept./Oct.	Nov.
1959	.. ..	Oct./Nov.	Oct.	Oct.
1960	.. ..	—	Oct.	Sept./Oct.
1961	.. ..	—	Sept.	Aug./Sept.
1962	.. ..	—	Oct./Nov.	Oct./Nov.
1963	.. ..	—	Oct.	—

SAL = S.A. Lombard Nature Reserve
Rpt = Rooipoort
Ben = Benaauwdheidsfontein

winter of 1962 than in 1963. This reflects the fact that the lambing peak fell in August/September in 1961, but only in October/November in 1962.

These findings agree with the observations summarised by Shortridge (1934); there the months of September, October and November are mentioned by several early authors.

If, for the purpose of argument, 15 October is taken as a "mean peak lambing date", then the "mean peak rutting date" should be approximately 171 days earlier—at the end of April. Rutting behaviour was most commonly observed in the months of March, April and May in the Kimberley area. The writer gained the impression that mating was most actively pursued in late April and early May.

From comparative observations of the size of the lambs seen in the Kimberley area and in the Kalahari Gemsbok Park at the same time of year, the Park springbok seem to mate and give birth at much the same time as those at Kimberley. It would be interesting to establish how the timing of these activities changes as one proceeds northwards from the latitude of the Kalahari Park to that of Etosha.

At Kimberley courtship and mating behaviour was also observed at the time when lambs were born in or about October. Ewes which conceived at this time would be expected to lamb in early April. Newly born young were in fact recorded in March and April, a few also as early as February and as late as June.

AUTUMN LAMBS

In most years of the study period, these autumn lambs were few in number and were not considered to contribute significantly to population growth. However, in 1962 a distinct

autumn crop was produced on Benaauwdheidsfontein. In a sample of 478 animals classified during the last week of March, newly born young constituted 5·4%.

This is a much smaller contribution to the population than that of the "spring" (October) young, which usually made up about 25% of the population (Table 6). However, the figure of 5·4% may be too low. It may have been higher had a count been made in April when the lambs would have been more active and easier to see. It should also be noted that there were about half as many lambs as yearlings amongst the springbok shot in June and July (Table 1—$\frac{32 \text{ lambs}}{65 \text{ yearlings}} = 49{\cdot}2\%$). Although small, the autumn crop of 1962 may in fact have been bigger than the March counts indicate.

A substantial crop of autumn lambs was also recorded (indirectly) in the Kalahari Gemsbok Park in 1962. On a visit in March of that year, juveniles born in the previous spring and estimated to be about 6 months old, constituted 25·8% of one sample of 416 animals and 29·2% of another sample of 858 animals. A few newly born young were seen on this occasion. In September, 1962 the Park population was again sampled. Once again a juvenile class of animals, estimated to be perhaps 5 months old, was present. These were clearly animals that had been born after the previous visit in early March. They made up 25·4% of one sample of 492 springbok.

In this case then, the autumn crop seems to have contributed about as many animals to the population as did the previous spring crop of lambs. Within a period of some six months, the Kalahari Gemsbok Park springbok population produced two crops of young, apparently of approximately equal size, one in the spring of 1961 (counted as juveniles in March, 1962), and one in the autumn of 1962 (counted as juveniles in September, 1962).

Some further information about the occurrence of autumn lamb crops comes from the S.A. Lombard Reserve records. A second lambing peak occurred in April, 1954 and a number of young lambs were noted in early May, 1955.

Unfortunately one can only speculate about how often the remarkable reproductive performance of producing two groups of young within six months occurs. At Kimberley it was noted only once in five years. In the S.A. Lombard Reserve it happened once and perhaps twice in seven years. Autumn lamb crops could be produced in one of two ways. Ewes experiencing post-partum oestrus after lambing in October could conceive then and lamb again in March or April. Alternatively yearling ewes, most of them sexually immature when six months old at the time of the autumn rut (but see below) could come into oestrus in October when one year old. They would then also lamb in autumn. It is likely that both classes of females are involved.

It is interesting and significant that springbok have a mechanism for rapid reproduction, but hardly surprising. The range of the species extends over the dry desert and semi-desert areas of western South Africa. The populations of species inhabiting such inclement regions tend to fluctuate quite violently. One can imagine periods of rapid population growth induced by a fortuitous succession of "good years", with (at least sometimes) two increments a year, preceding the well-known springbok "treks". However, not only absolute population size but also density within a given area and environmental factors (e.g. quality of food available)

must have been important in determining when "treks" occurred. It is a pity that "treks" such as the one which took place in south-western Botswana in 1959 (Eloff 1961) have not been studied in detail.

POPULATION STRUCTURE

In this concluding section, the structure of populations sampled in the Etosha Game Park and Kalahari Gemsbok Park will be discussed. The information is presented as absolute numbers and percentages in Table 6.

TABLE 6

STRUCTURE OF ETOSHA AND KALAHARI GEMSBOK PARK SPRINGBOK POPULATIONS

	Adult ♂♂		*Adult* ♀♀		*Juveniles*		
Area and Date	*No.*	*%*	*No.*	*%*	*No.*	*%*	*Total*
Etosha, July, 1957 ..	224	27·6	394	48·6	193	23·8	811
Etosha, April, 1962 ..	264	22·7	618	53·2	279	24·1	1161
KGNP Auob 2/3/62 ..	110	26·4	199	47·8	107	25·8	416
KGNP Auob 3/3/62 ..	203	23·7	404	47·1	251	29·2	858
KGNP Nossob 4/3/62 ..	94	22·0	203	47·5	130	30·4	427

KGNP = Kalahari Gemsbok National Park

In Table 7 the figures from Table 6 are expressed as ratios.

TABLE 7

SEX AND AGE RATIOS OF ETOSHA AND KALAHARI GEMSBOK PARK SPRINGBOK POPULATIONS

Area and Date	*Ratio* ad. ♂ : ad. ♀ : juv.	*Ratio* juv./100 ad. ♀♀
Etosha, July, 1957	1·2 : 2·0 : 1	48·9
Etosha, April, 1962	0·9 : 2·2 : 1	45·1
KGNP Auob 2/3/62	1 : 1·9 : 1	53·8
KGNP Auob 3/3/62	0·8 : 1·6 : 1	62·1
KGNP Nossob 4/3/62	0·7 : 1·5 : 1	64·4

From both Tables 6 and 7 it is evident that the relative proportion of adult males, adult females and young of the year are surprisingly constant in these population samples taken at different times in different areas. The difference between the numbers of adult males and females is large indeed, and likely to be real rather than an artefact of biassed sampling. The mortality rate in males must therefore be considerably higher than in females, as is the case in a number of animal species. Juvenile males which leave the maternal herds at the time of

the rut, when they are about six months old, are probably a particularly vulnerable class of animals. In the absence of more detailed information on the age structure of the adult male and female groups, the question of sex and age specific death rates cannot be further discussed.

The fact that there is about one juvenile to two adult females may be explained by assuming that most ewes bear their first young at age two and that a very high proportion of them continue to reproduce annually thereafter. Some information was collected on pregnancy rates and on the age of sexual maturity in females by examining the animals shot during the winter. The findings are presented in Table 8.

TABLE 8

SPRINGBOK EWES EXAMINED FOR PREGNANCY ON BENAAUWDHEIDSFONTEIN

Date	*Group*	*Examined*	*Pregnant*
15/7/61	Adult	36	34 (94·4%)
	Yearl.	15	3 (20%)
16/6/62	Adult	72	36 (50%)
11/7/62	Adult	48	38 (79·2%)
	Yearl.	9	0
17/7/62	Adult	14	11 (78·6%)
	Yearl.	4	0
15/6/63	Adult	34	23 (67·6%)
	Yearl.	7	0
24/7/63	Adult	26	22 (84·6%)

Yearl. = yearling

The adult female pregnancy rates vary from 50% to 84·6%. The figures collected in June, when the embryos are usually still quite small and therefore easy to overlook in a cursory examination, are probably inaccurate and too low. If they are excluded the rate of adult pregnancies is found to vary from 78·6% to 94·4%. Of the small number of yearlings (i.e. animals usually about 9-10 months old in June and July) examined, 20% of the 1961 sample was found to be pregnant.

We see that it is physiologically possible for these young animals to conceive at the age of about 6 or 7 months and thus to lamb at the age of one year. It does not seem as though this very early sexual maturity occurs in a large proportion of the first year females. However, only small samples were available for examination. As in other species, the rate would probably depend very greatly on a factor such as condition and nutritional status.

In any event this ability to conceive at an early age is another feature of the springbok reproductive mechanism which would enable populations to increase rapidly under favourable conditions and thus to recover from the catastrophic blows which the fluctuations of a harsh environment must be presumed to deal out to those animals with the plasticity and adaptability to survive them.

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