Annual reproductive pattern in the dassie *Procavia capensis*

M. van der Merwe and J.D. Skinner
Mammal Research Institute, University of Pretoria

Proximate factors influencing the reproductive pattern and rate in dassies are examined in an area subject to marked seasonal climatic variation. The influence of photoperiod is confirmed with no modifying influence by either temperature or rainfall during the period of the study. Testicular and ovarian activity was related, showing a peak in ovulation and fertilization between the period mid-March and mid-April. Of 49 pregnant females collected between June and December, 83% had either two or three embryos/fetuses. Growth curves for differing litter sizes have been calculated. Failure to increase litter size appears to be related more to a conservative ovulation rate than to ova not fertilized or fetal wastage, although ova loss increased with increasing ovulation rate.
S. Afr. J. Zool. 1982, 17: 130 – 135

Die faktore wat die voortplantingspatroon en -tempo in dassies onmiddellik beïnvloed is ondersoek in 'n gebied wat onderhewig is aan groot seisoenale klimaatskommelinge. Die invloed van dagliglengte is bevestig terwyl beide temperatuur en reënval geen wysigende invloed gedurende die studieperiode gehad het nie. Testis- en ovarium-aktiwiteite is gekorreleer met mekaar en 'n piek in ovulasie en bevrugting het vanaf middel Maart tot middel April plaasgevind. Van 49 dragtige wyfies wat versamel is tussen Junie en Desember, het 83% òf twee òf drie embrios/fetusse gehad. Groeikurwes vir verskillende werpselgroottes is uitgewerk. Beperkings in die toename van werpselgrootte blyk verband te hou met 'n konserwatiewe ovulasietempo eerder as met onbevrugte ova of fetale sterftes, alhoewel ova-verlies toeneem met toenemende ovulasietempo.
S.-Afr. Tydskr. Dierk. 1982, 17: 130 – 135

M. van der Merwe* and J.D. Skinner
Mammal Research Institute, University of Pretoria, Pretoria 0002, Republic of South Africa
*To whom correspondence should be addressed

Received 15 December 1981; accepted 11 February 1982

The rock hyrax or dassie (*Procavia capensis*), widely distributed throughout southern Africa, is a true testicond with the abdominal testes closely bound to the dorsal body wall (Glover & Sale 1968). In South Africa they reproduce once a year and have varying litter sizes. Due to their rapid increase in certain areas it has become necessary to control their numbers. However, before any culling programme can be carried out, knowledge about their population dynamics and ecology, with special emphasis on reproductive behaviour and physiology, is important (Millar 1971). Their seasonal breeding is characterized by a short period of sexual activity in both sexes during the second half of summer although the timing of this event varies with latitude (Millar 1971). The object of the present study was to examine seasonal patterns in reproduction in an area subject to marked seasonal climatic variation.

Study area and Methods

For features of the Willem Pretorius Game Reserve, including climatological data from 1962 – 1971 *vide* Bourquin (1973). The Reserve is situated in the summer rainfall area with an annual mean precipitation of 520,8 mm, 75% of which occurs between October and April. The mean minimum daily temperature for the coldest month (June) is –0,9 °C while the mean maximum daily temperature for the warmest month (January) is 34,2 °C. Temperatures and rainfall illustrated in Figure 4 are for Virginia (28°06′S/26°53′E), the nearest weather station (41 km) to the Game Reserve, for 1975 and 1976.

The 246 dassies (124 males, 122 females) were shot during the daytime, in the Willem Pretorius Game Reserve (28°18′S/27°15′E) in the central Orange Free State from March 1975 to March 1976, as part of an operation to reduce their numbers. It was decided to cull them on a monthly basis in order to obtain more information about the reproductive pattern over a 12-month period.

After the day's quota had been shot, the dassies were weighed and measured. The reproductive tracts were examined and preserved in A.F.A. i.e. a mixture of 95% ethyl alcohol, 40% formalin, glacial acetic acid and distilled water (3:1:1:5 by vol.). Fetuses were weighed and gonads were removed and weighed. Ovaries without corpora lutea (corpora lutea protrude from the ovaries and are easily recognizable) were embedded in paraffin wax and sectioned at 7 μm and stained with Delafield's haematoxylin and eosin. In those containing corpora lutea these were removed and their volume calculated. Morphology of the ovaries was related to reproductive state and site of fetal implantations.

The fetal mass at any stage of pregnancy varied according to the number of fetuses in the litter, with the fetuses of smaller litters tending to be heavier. This phenomenon is illustrated in Figure 1 where the cube root of the average fetal mass per litter was plotted against age. Because of this phenomenon it was decided rather to use total fetal mass in the construction of growth curves. Because the sizes of litters and therefore their ages varied considerably for each collection, and further because their real ages were not known, it was decided to work out their theoretical ages using the Hugget & Widdas (1951) equation. Hugget & Widdas (1951) have demonstrated that there is a direct relation between the cube root of fetal mass ($W^{1/3}$) and gestational age (t) as given by the equation $W^{1/3} = a(t - to)$.

The cube root of body mass ($W^{1/3}$) at birth was taken as the average of the two biggest litters (685,85 g and 505,0 g) collected on 6 November 1975 and 4 December 1975 respectively. The mean of these two litters (595,43 g) was taken to represent birth mass.

The gestational age (t) at birth was taken as 230 days from Millar (1971). The intersect on the t-axis (to) was given by Hugget & Widdas (1951) to approximate 0,2 × t for mammals with a gestation length between 100–400 days and will therefore be 46 days for the dassie. The specific fetal growth velocity (a) was calculated to be 0,0457. The theoretical growth curve for dassies according to the Hugget & Widdas (1951) equation is shown in Figure 2. With this equation $W^{1/3} = 0{,}0457\ (t - 46)$ the age ($t = \frac{W^{1/3}}{0{,}0457} + 46$) of all the litters was calculated.

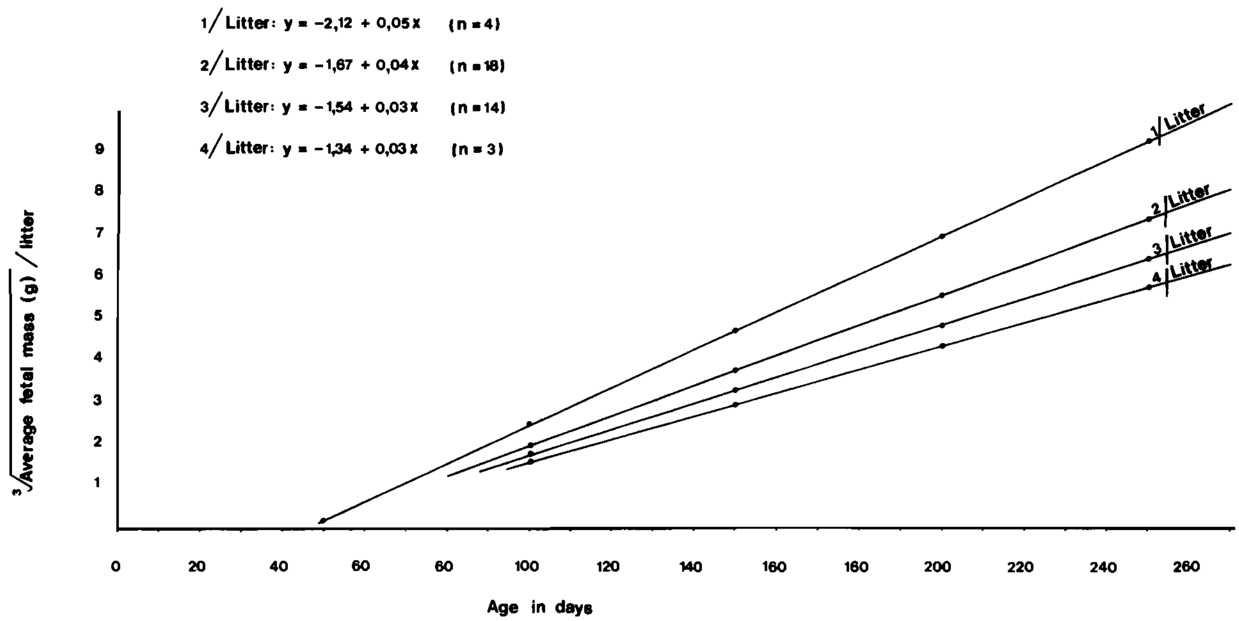

Figure 1 Theoretical growth curves of average fetal mass per litter plotted against age to show the differences in mass for varying litter sizes at the same age. Constructed from the Hugget & Widdas (1951) equation: $3\sqrt{W} = 0{,}0457\ (t - 46)$.

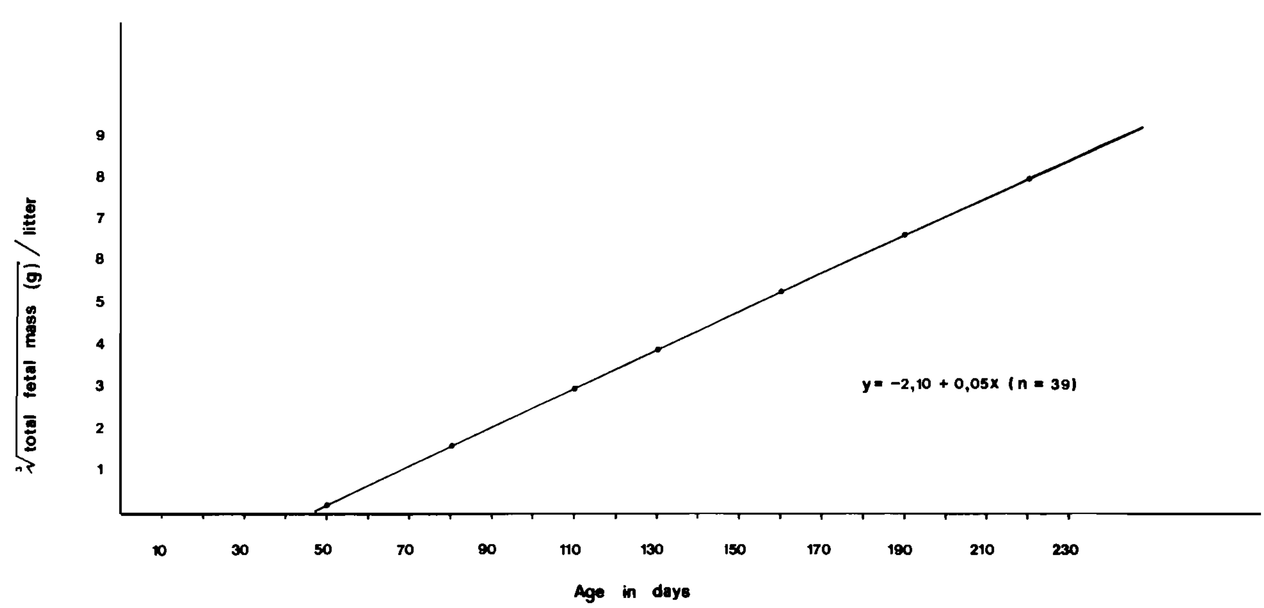

Figure 2 Theoretical growth curve of total fetal mass per litter plotted against age as constructed from the Hugget & Widdas (1951) equation: $3\sqrt{W} = 0{,}0457\ (t - 46)$.

Results

Of the 124 males shot 36% were less than 2,2 kg in weight and were not considered in any of the calculations as they represented sub-adult males with small and immature testes. In males weighing more than 2,3 kg great variation was found in the sizes of testes, even during the sexually quiescent months. In order to minimize statistical variation it was decided that all testes less than 30% of the maximum testes weight collected on a specific date were to be discarded. Using this criterion it was found that only one of the 67 males weighing more than 3 kg (i.e. 1,5%) had testes less than 30% (Figure 3), while 21 males weighing between 2,3 – 2,9 kg, 15 (i.e. 71,4%) had testes weighing less than 30% of the maximum testes mass (Figure 3). The mean mass ± 1 SD of the testes and epididymides of all the males within 30% of the maximum testes mass collected on a specific date was calculated and is illustrated in Figure 4. From this figure it is apparent that testes and epididymides mass peaked from March to May. In Figure 4 testicular and epididymal activity is also compared with proximate environmental factors such as temperature, rainfall and photoperiod. No significant correlation could be found with either temperature or rainfall. However, a good relationship was found between testicular activity and photoperiod. During the period between the shortest day (21 June) and the longest day of the year (21 December) testicular activity was

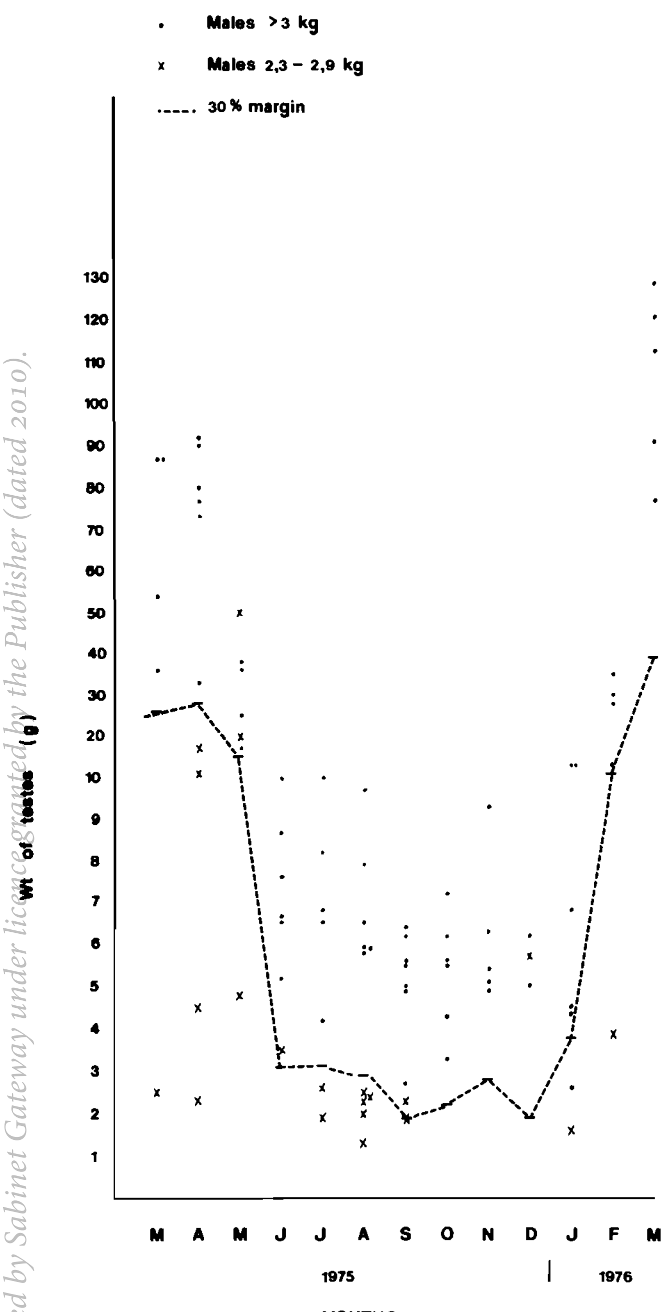

Figure 3 Distribution of the combined testes mass collected each month, with the 30% margin of the maximum testes mass for each collection indicated.

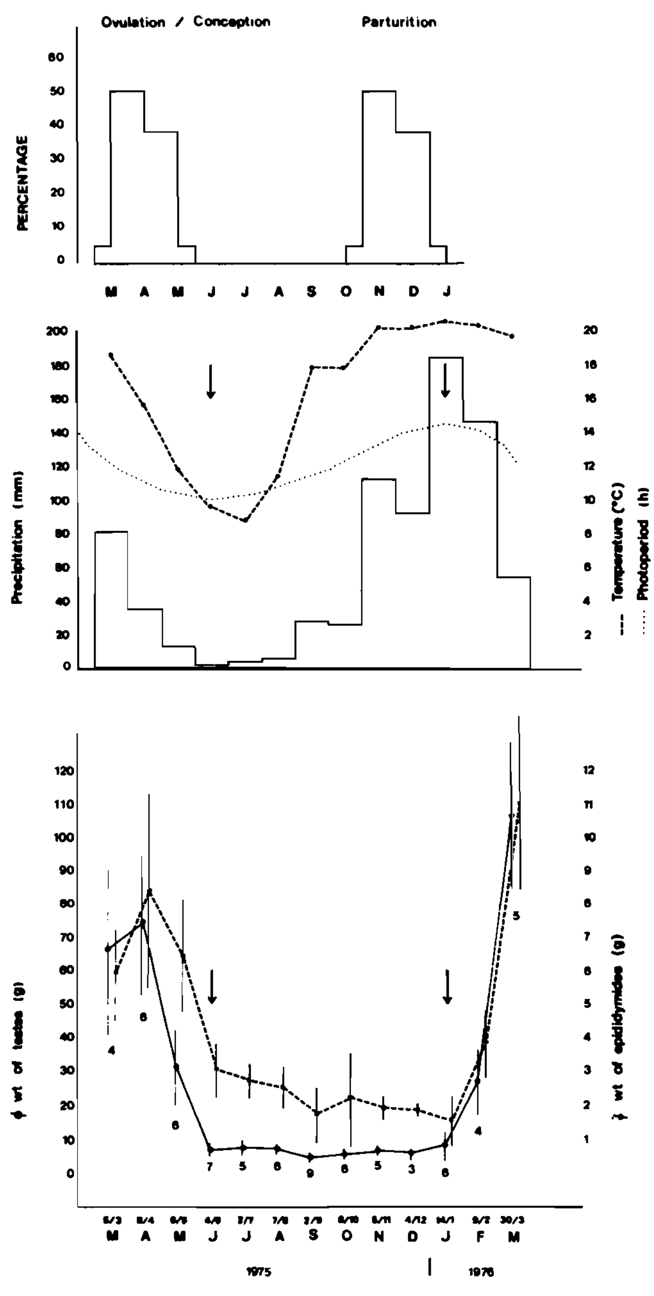

Figure 4 Climatic variables and the combined weights (mean ± 1 SD) of testes and epididymides. The number taken into consideration for the calculations as well as the specific date of collection per month are indicated. Arrows indicate the period between the shortest day (in June) and the longest day of the year (in January). Included are the estimated dates and percentages of ovulations/conceptions and parturition for fetuses, showing the distribution for the periods mid-March to mid-April and mid-April to mid-May as well as between November and December.

minimal, approximating a straight line. During both 1975 and 1976, however, maximum testes mass was attained during the decline in photoperiod.

Females

During the study period 122 females were shot. Of these 26 were not considered as they were nulliparous young and juvenile females of which the majority weighed less than 2,0 kg, the heaviest two being 2,2 kg. The reproductive status of the 96 parous females collected during the same period is illustrated in Table 1. The 49 females collected from June 1975 to December 1975 had embryos/fetuses large enough to count with ease. Amongst them these females had a total of 119 embryos/fetuses indicating an average litter size of 2,4 per female. The total number of embryos/fetuses and their distribution between the left and right uterine horns is given in Table 2, from which it can be seen that there was no significant difference in the distribution of the fetuses between the two horns. The percentages of females having litters of one or more are indicated in Table 3, from which it is apparent that twins are most common (51%) followed by triplets (33%). The occurrence of single young (8%) and four young (6%) were of the same order, five fetuses occurring in only one female. All the fetuses in the litters of four and five were in a healthy condition with no signs of resorption. The even distribution of the fetuses between the uterine horns was brought about by transuterine migration of the zygotes. This was deduced by noting the percentage of females in which the number of fetuses in a uterine horn differed from the number of corpora lutea in the ipsilateral ovary. In 38,8% of the females transuterine migration had occurred. In the majority of cases (73,7%) migration was from the left uterine horn to the right, indicating a dominant function of the left ovary. These transuterine migrations clearly illustrated the tendency to distribute fetuses evenly between the two uterine horns. This tendency was particularly apparent when examining females with two or four fetuses. In ten females having one fetus per uterine horn both ovulations were from one ovary alone. In one of the females having four fetuses, two per uterine horn, four corpora lutea were found in the left ovary. In some of the females, however, transuterine migrations did not occur. In two of the females (4%) both having litters of two, the two fetuses were in the horn corresponding with the ovary where the two corpora lutea were located.

Table 1 Reproductive status of parous dassie females sampled each month

Month	Total	No. not pregnant	No. pregnant	No. lactating
4 March 75	8	7	0	1
9 April 75	5	2	3	0
5 May 75	5	0	5	0
4 June 75	8	0	8	0
3 July 75	7	0	7	0
7 August 75	7	0	7	0
2 September 75	9	0	9	0
2 October 75	13	2	11	0
5 November 75	5	0	5	0
4 December 75	7	1	2	4
14 January 76	8	1	0	7
9 February 76	10	1	0	9
4 March 76	4	4	0	0

Table 2 Number of females with specific litter sizes and the distribution of the embryos/fetuses between the two uterine horns

Number of pregnant females	Number of embryos/fetuses per female	Distribution of the embryos/fetuses between the left and right uterine horns: Left	Right
4	1	3	1
25	2	25	25
16	3	24	24
3	4	6	6
1	5	3	2
49		61	58

Table 3 Percentage of females having different litter sizes

Number of embryos/fetuses	% of females
1	8,2
2	51,0
3	32,7
4	6,1
5	2,0

Ova loss became apparent when comparing the number of corpora lutea with the number of fetuses per litter. In this manner it was found that an 8,5% ova loss occurred amongst 20,4% of the females. Only in one of the females were indications of fetal loss evident. In a female collected on 7 October 1975 two corpora lutea were found, one in each ovary, but no indications of fetuses could be found in either of the uterine horns, although both of them were slightly enlarged. The mammary glands as well as the teats were small. It appeared that abortion rather than resorption had occurred.

In order to establish the potential litter sizes if ova loss had not occurred, the number of corpora lutea per female was counted and taken to represent the original litter sizes. In this manner it was found that the mean litter size without ova loss would have been 2,7. There was a significant increase in ova loss with increasing litter sizes from two to four. This ranged from 10% in females which had originally shed two ova and lost one to 29% in females which had originally shed three ova to 40% in those which originally had shed four ova. No ova loss was found amongst litters of one and five but there was only one female where five corpora lutea were found. The extreme rarity of litters of five would appear to result from a deficient ovulation rate rather than ova loss reducing such litters. Nevertheless, although there was an increase in ova lost with ovulation rate, in all but one of the females only one ova was lost, one female losing two of four ova.

It appeared that the corpus luteum established a baseline production of progesterone with the placenta playing an increasing role in the production of progesterone with increasing fetal age. This assumption has been based on the fact that no correlation could be found between corpus luteum volume and fetal age (y = 0,001 + 11,14; r = 0,0168 where y = corpus luteum volume and x = fetal age) indicating that maximum corpus luteum volume is reached during early pregnancy.

Fetal growth

With the age of the litters known on each date of collection, the estimated dates of conception and birth of the litters were calculated and are illustrated in Figure 4. This confirms the seasonal nature of breeding in this species with most of the births occurring during November and December (Figure 4).

From this figure it can be seen that the most active period for ovulations/conceptions was between mid-March and mid-May and that for births during November and December (Figure 4). Maximum testes and epididymides weights were found from mid-March to mid-April (Figure 4). During the same period 51% of the ovulations/conceptions occurred followed by the period from mid-April to mid-May when 39% of the ovulations/conceptions occurred. This corresponds with the data on the males in that epididymides mass was at its second highest on 6 May 1975, indicating second highest activity from mid-April to mid-May (Figure 4). The corresponding period when 51% of the births occurred was in the whole of November (Figure 4). One litter not considered in the calculations was apparently conceived very late after the peak of conceptions during March and April. On 4 December 1975 a female was collected with only one fetus weighing 135,83 g. The age of this fetus was calculated to be 163 days, indicating conception on 25 June 1975. Birth of this fetus should have taken place around 10 February 1976.

Discussion

In South Africa mating in the dassie generally occurs during the second half of the summer but varies in timing at different localities, being later with a wider distribution at the lower latitudes (Millar 1971). Photoperiod has been shown to be the proximate cause of seasonal sexual activity in dassies and that annual variation in temperature and rainfall may only have a modifying influence (Millar 1971; Millar & Glover 1973). However, Millar & Glover (1973) maintain that a critical photoperiod length could not be the cue but rather a critical rate of decrease in photoperiod. This view is supported in the present study where testes mass peaked during the decline of the photoperiod in both 1975 and 1976. Prevailing environmental conditions, especially nutritional conditions, are proximate factors causing variation in litter size and will influence litter size via ovulation rate and prenatal mortality (Millar 1971). Even within a relatively small area, litter size can vary due to differences in rainfall and vegetation with drought having a particularly adverse effect resulting in a reduction in ovulation rate and an increase in fetal wastage (Skinner, Nel & Millar 1977). Therefore, the physical condition of the females, as a result of the prevailing environmental conditions, before and during the mating season, will be an important cue for the ovulation rates that can be expected. During spring and summer there is relatively more foliage than during autumn and winter, with the initial increase in the amount of food starting in September and reaching maximum quantities during summer (Steyn 1980). During spring and summer the available foliage is quantitatively more nutritious as the plants are then sprouting new green leaves and plant growth is maximal, with its moisture content closely following the increase and decrease in rainfall (Steyn 1980). Therefore, the condition of the veld during spring and especially summer will have a direct effect on the physical condition with which the females will enter the mating season from the beginning of autumn.

The importance of prenatal mortality in reducing litter size, especially during stressful periods, may not be overlooked. However, the methods applied in determining prenatal mortality may not always be valid and may lead to incorrect deductions. During the present study 130 corpora lutea were counted compared to 119 embryos and fetuses. This, however, does not imply that 11 (i.e. 8,5%) conceptuses were lost. Because no embryos or fetuses were found in any state of resorption (except the one possibility discussed earlier) it implies that most, if not all of the 'conceptuses' were lost before implantation. As there is no means to determine whether they were fertilized ova or not, it can merely be accepted that many of them, if not all, were unfertilized ova. Therefore, ova loss in the dassie may be a normal phenomenon with no significant implication.

In view of this background some comparisons can be made to see whether any significant changes have occurred in the reproductive rates of the dassies at the Willem Pretorius Game Reserve during the seven years since 1969. During that period (1969 – 1975) a significant increase in spring and summer rainfall occurred (Table 4) which implies better and more abundant plant growth. The low spring-summer rainfall of 1972/3 could easily have been buffered by the good rainfalls of the previous and subsequent years. In this respect the nutritional conditions have increasingly improved during the spring and summer months since 1969. No significant long term changes occurred in the average daily maximum and minimum temperatures for the months January to May from 1969 to 1975. Over a ten-year period Bourquin (1973) has given the mean of the maximum daily temperatures of the hottest month (January) as 34,2 °C and that for the coldest month (June) as –0,89 °C. Between 1969 and 1975 these two limits have not been exceeded

Table 4 Average precipitation (mm) for the spring and summer months (September – February) for the seasons 1968/69 – 1974/75

Months	Precipitation (mm)
Sept. 1968 – Feb. 1969	39,97
Sept. 1969 – Feb. 1970	44,30
Sept. 1970 – Feb. 1971	63,97
Sept. 1971 – Feb. 1972	85,72
Sept. 1972 – Feb. 1973	39,35
Sept. 1973 – Feb. 1974	82,98
Sept. 1974 – Feb. 1975	99,42

Table 5 Average daily maximum and minimum temperatures (°C) per month for the months January to May 1969 – 1975

Month	Average daily maximum temperatures per month for the years							Biggest difference for the same month between succesive years	Average daily minimum temperatures per month for the years							Biggest difference for the same month between successive years
	1969	1970	1971	1972	1973	1974	1975		1969	1970	1971	1972	1973	1974	1975	
January	32,9	31,1	28,7	27,8	33,0	27,7	28,8	5,3 (1973/74)	17,2	17,0	16,8	16,7	17,0	17,3	15,1	2,2 (1974/75)
February	30,7	30,3	27,5	28,2	27,5	27,0	26,6	2,8 (1970/71)	17,2	16,3	15,1	15,1	15,5	16,5	15,4	1,2 (1970/71)
March	26,5	29,9	29,1	24,6	29,4	26,0	24,2	4,8 (1972/73)	14,5	13,9	14,2	14,5	15,7	13,9	13,1	1,8 (1973/74)
April	23,6	25,7	24,3	24,1	22,9	21,6	22,9	2,1 (1969/70)	10,2	10,3	9,4	10,4	10,5	9,7	8,3	1,4 (1974/75)
May	19,2	20,7	19,0	20,3	20,6	19,9	20,6	1,7 (1970/71)	5,4	5,5	5,1	3,0	3,8	3,9	3,2	2,1 (1971/72)

(Table 5) and there is therefore no reason to believe that significant long term changes in temperature had occurred. Therefore it is doubtful that any stress conditions could have resulted because of annual fluctuations in temperature. During 1969, under much drier environmental conditions, Millar (1971) found an average litter size of 3,0 at the Willem Pretorius Game Reserve, but unfortunately, has shown no standard deviation of the mean. During the present study the average litter size was 2,4 ± 0,9. Therefore, although the mean litter size was lower during the present study than during 1969, this can not be shown to be statistically significant.

The number of young a mammal can produce at a time is genetically determined and environmentally influenced. It would therefore appear that dassies living in the same locality for many generations have become adapted to the short-term environmental fluctuations occurring there, and that an ideal litter size for that area has been established. Short-term fluctuations in environmental conditions will therefore cause fluctuations in the ovulation rate although these will not necessarily be statistically significant. Because of the increasingly better seasons since 1969, environmental conditions would have been beneficial for the survival of young dassies, especially as the young are born during the period October to December when plants are generally sprouting new leaves and plant growth is maximal. Therefore, if other factors such as predation, disease or insufficient shelter have not placed increasing pressure on the dassie population (for which there is no evidence) their numbers should have increased considerably during the seven years since 1969.

Because litters of four and even five have been found during the present study there is no reason to believe that they were living under stressful conditions, especially as such stress could have been negated by the increasingly good seasons. However, as overgrazing by dassies at the Willem Pretorius Game Reserve has already been reported (Bourquin 1973) an expected increase in their numbers, after a prolonged series of good seasons, may intensify this problem. Especially if a prolonged series of good seasons is followed by a prolonged series of dry seasons. In the latter case, if factors such as disease do not reduce their numbers considerably, the dassies will be forced to compete heavily for foliage which may cause considerable damage to the habitat. Moreover, not only will the dassies compete amongst themselves for available foliage, but also with other herbivores utilizing the same resources. Under drought conditions the dassies will be superb competitors and conditions will have to become very severe before it will have a significant effect on them. The reason is that they are very adaptable and can vary their diet so widely that it is possible for them to maintain an adequate nutritional state under various conditions (Fairall 1981).

Acknowledgements

We are grateful for the assistance of J. Langerman, J. Breytenbach and R.D. Carr during collection of specimens, and the Division of Nature Conservation of the Orange Free State for co-operation and hospitality.

References

BOURQUIN, O. 1973. Utilization and aspects of management of the Willem Pretorius Game Reserve. *J. Sth Afr. Wildl. Mgmt Ass.* 3: 65 – 73.

FAIRALL, N. 1981. A conceptual integrated scheme for the control of the hyrax (*Procavia capensis*) in South Africa based on preliminary research. *Wld Furbearer Conf. Proc. Univ. Maryland.* 1875 – 1884.

GLOVER, T.D. & SALE, J.B. 1968. The reproductive system of the male rock hyrax (*Procavia* and *Heterohyrax*). *J. Zool. Lond.* 156: 351 – 362.

HUGGETT, A. St.G. & WIDDAS, W.F. 1951. The relationship between mammalian foetal weight and conception age. *J. Physiol.* 114: 306 – 317.

MILLAR, R.P. 1971. Reproduction in the rock hyrax (*Procavia capensis*). *Zool. Afr.* 6: 243 – 261.

MILLAR, R.P. & GLOVER, T.D. 1973. Regulation of seasonal sexual activity in an ascrotal mammal, the rock hyrax, *Procavia capensis*. *J. Reprod. Fert.* Suppl. 19: 203 – 220.

SKINNER, J.D., NEL, J.A.J. & MILLAR, R.P. 1977. Evolution of time of parturition and differing litter sizes as an adaptation to changes in environmental conditions. In: Reproduction and evolution. Ed. Calaby, J.H. & Tyndale-Biscoe, C.H. *Proc. IVth Symp. Comp. Biol. Reprod.* pp.39 – 46.

STEYN, D. 1980. Reproduction in the hyrax, *Procavia capensis* in relation to environmental factors. M.Sc. thesis, University of Natal.