CHAPTER 8

POPULATION DYNAMICS

Introduction

The survival ability of a species in a given area mainly depends on the ability of its members to maintain sufficient rates of nutrient intake. This, in turn, is reflected in the survival, growth and reproductive rates of the population (Knight 1991). Population dynamics therefore reflect the physiological and reproductive reaction of members of a population to various intrinsic or extrinsic factors. Extrinsic factors influencing the dynamics of a population are those factors that are not directly linked to the members of a population but which could influence the performance of such a population. Extrinsic factors include climate, primary productivity and the effects of disease or predators, amongst others. Intrinsic or density-dependent factors, also known as self-regulatory factors, are linked directly to a given population. These factors include the growth, age and sex composition, social organisation and the behaviour of a population (Bothma 1996). Both the extrinsic and intrinsic factors regulate the dynamics of a population but they operate effectively at different population densities (Caughley & Krebs 1983).

The aim of the reintroduction of the Arabian oryx into the 'Uruq Bani Ma'arid Protected Area was to establish a viable, self-sustainable population (Chapter 10). The reintroduction of ungulates involves understanding and the application of the significance of factors such as the ideal age for reintroducing individuals, ideal sex ratios, season for release, and more (IUCN 2000). In addition, it has been shown that population persistence is more likely when the number of founders is large, the rate of increase is high and the effect of competition is low (Griffith, Scott, Carpenter & Reed 1989; Stanley-Price 1989; Bothma 1996).

Mammals in general have two mortality phases. These are the high initial mortalities among young animals, which is followed by a phase in which further mortalities are low at first before increasing again (Bothma 1996). In many reintroductions large proportions of founder animals die shortly after release (Stanley-Price 1989). This suggests that the reintroduced animals are once again subject to the aboriginal, environmental factors which previously regulated their numbers. Analysis of the causes of mortality would reveal underlying patterns, which could be overcome through management action. In addition it gives a clearer understanding of the nature of the problems faced by the reintroduced population during establishment (Stanley-Price 1989).

The purposes of this part of the study were to report the basic facts on the reproductive performance of the reintroduced Arabian oryx population during the first 2 years after release, and to relate these facts to the age and sex class composition of the reintroduced population. This in turn will enable an evaluation of this particular reintroduction against the ideal circumstances as described by Stanley-Price (1989). The data and results presented here will also be used in a following chapter where a population viability assessment, through demographic modeling, will be done.

Methods

Data on the natality and mortality of the Arabian oryxes were collected in conjunction with data on the spatial distribution of the animals. Data collected included all the observations of mating behaviour, including activities such as circling* ("*paarungskreisen*") and goose-stepping* ("*laufschlag*") as described by Walther (1958) for captive oryx, and flehmen* as described by Schneider (1931). The identities of the animals involved and the dates of all such observations were noted.

Fecundity schedule

An age specific fecundity schedule was calculated for all the females and all the births to those females living in the 'Uruq Bani Ma'arid Protected Area during the study period. The fecundity rate of a particular age class was the product of all the females entering that age class and all the births to those females while in that age class. For example, during the study period 28 females entered the >2 to 3 year old age class, 16 of which produced calves. The age-specific fecundity rate for the >2 to 3 year old female Arabian oryxes therefore was 0.57 (16/28 = 0.57).

Seasonality of calving

The calving distribution is presented graphically by means of a frequency histogram. The calving distribution was tested for randomness on a seasonal basis only because sample sizes were too small for analysis on a monthly basis. The Chi-square analysis technique was used and the null-hypothesis tested for was that there is an equal chance of calving occurring during any season. The test was performed at the 95% confidence interval ($P<0.05$).

The date of conception was calculated by offsetting the date of calving by 9 months (Stanley-Price 1989). The time of conception was analysed for correlation with temperature by means of a linear regression and Pearson's correlation coefficient. The correlation between the length of daylight and the time of conception could not be analysed because no data on the daylength could be obtained from the Meteorological and Environmental Protection Agency (MEPA) in Riyadh, Saudi Arabia.

Mortality schedule

Data on the mortality of the Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area were collected whenever an animal was known to have died. Because of the intensive monitoring of the oryxes in the area, every reintroduced Arabian oryx that died was located. The cause of death was determined through the analysis of organ samples collected from dead animals. The rate of organ autolysis is, however, influenced by climatic conditions. Therefore in the 'Uruq Bani Ma'arid Protected Area the high ambient temperatures which accelerate the onset of autolysis*, make it imperative that all organ samples be collected from a dead animal within 4 hours after death (Ostrowski *pers. comm.*[5]).

Autopsies were performed on the animals if they were located within a reasonable time after death. All organ samples were stored in a 10% formalin concentration in a refrigerator until such time as the samples could be sent to a veterinary laboratory. The samples were either sent to the Veterinary Faculty at the University of Utrecht in the Netherlands or to *Laboratoire D'anatamo-Pathaologie* at the Veterinary Faculty of Maisons-Alfort in France.

An age-specific mortality schedule was calculated for the Arabian oryxes in the protected area during the study period. The mortality rate in the different yearly age classes was based on the number of animals entering that specific age class and the number that died while in that age class. For example, during the study period 53 Arabian oryxes entered the >2 to 3 year old age class, four of which died before entering the next age class. The age-specific mortality rate for the >2 to 3 year old age class therefore was 0.075 (4/53 = 0.075).

Survival rate

The survival rate of the Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area was calculated over the 2-year study period. The finite rate of survival of a population can be estimated with a sample of radio-tracked animals for a given period (White & Garrot 1990). The number of animals still alive at the end of the selected period (n_1) divided by the number of animals alive at the start of that period (n_0) gives an estimate of survival within the population.

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Therefore,

$$\hat{S} = n_1 / n_0$$

with the variance of √ being estimated by:

$$Var(\hat{S}) = \hat{S}(1 - \hat{S}) / n_0$$

because n_1 is a binomially distributed value (White & Garrot 1990). The 95% confidence interval for the variance ($\hat{S}$) is calculated as $\hat{S} \pm z_\alpha \sqrt{Var(\hat{S})}$, where z_α is the z-statistic for an appropriate probability level. For the calculated intervals to be correct the observations must be independent, since these procedures were developed from the binomial distribution (White & Garrot 1990). This means that the survival of one animal cannot be dependent upon the survival of another. Because of this assumption in the calculation of the survival rate the calves were not included in these calculations.

Population growth rate

The growth rate of a population changes continually in proportion to its varying size and structure and due to variation in the environmental resources (Bothma 1996). The growth rate in a population at any given time is known as the exponential growth rate (r).

Exponential growth implies that the growth rate of the population either increases or decreases with time as opposed to a constant growth rate (Bothma 1996). It is therefore practical to assign a value to the exponential growth rate of a population. The values assigned to the exponential growth rate can either be negative or positive. A benefit of these growth rate values is that the value zero (0) means that there is no growth in the population. Consequently a positive value of *r* means that the population is growing, while a negative value indicates that the population is declining. Another advantage of the exponential formulation of the growth rate is the ability to convert easily between time units (Caughley 1977; Bothma 1996).

The simplest way to calculate the exponential growth rate (r) from consecutive population counts is with the equation:

$\log_e(N_t) = \log_e(N_0) + r(t)$, where:

$\log_e(N_t)$ = the population size after time interval t

$\log_e(N_0)$ = the population size at the beginning of the time interval t

r = the exponential growth rate

The exponential growth rate (r) of the reintroduced Arabian oryx population was calculated separately for the period from March to December 1995 and from January 1996 to February 1997. As these two time periods differ in length the exponential growth rate is expressed as the exponential growth per month to facilitate comparison. Animals released over a 3-month period were considered to be from one release in this analysis. For example, in calculating the exponential growth rate for the period from March to December 1995, N_0 was taken as 31, or the 31 animals that were released during that year. In doing so, the calculated growth rate of the population only reflects the births and deaths recorded in the population during that time and not during any further releases.

Results and discussion

Natality

The Arabian oryx females fell into two groups, notably those that arrived in the protected area without having calved previously (n=35) and those that arrived after producing their first calf elsewhere (n=2). All of the females reintroduced into the 'Uruq Bani Ma'arid Protected Area reached sexual maturity during the study period. Both of the females that arrived after giving birth elsewhere produced calves within the protected area, while 26 (74.3%) of the females that had never calved before reintroduction calved at least once during the study period. During the study period 39 calvings, including five abortions were recorded.

The age at first calving ranged from 581 to 1121 days (Table 20), with a mean of 894.1 days ± 1 SD of 156 days. This agrees with what is known for oryx in captivity (Vié 1996) and for wild born oryx in Oman (Spalton 1992). The minimum age at first breeding in the captive population at the National Wildlife Research Centre in Taif, Saudi Arabia was 645 days (Vié 1996) indicating that females can become sexually mature and conceive at approximately 13 months of age. It should be noted that the minimum age at first breeding of 581 days, as observed in the present study is thought to have been an abortion as no calf was found even though it was obvious that the female had calved. The youngest female to produce and successfully raise a calf in the present study was 723 days (23.8 months) old.

During the study period 11 females produced their second calves in the protected area. The ages of these females ranged from 1021 to 1278 days with a mean of 1163.0 ± 79.5 days. The calving interval between the first and the second calf ranged from 265 to 359 days, with a mean calving interval of 306.1 ± 36.0 days. In addition, two females produced their third calves at a mean age of 1773.0 ± 56.6 days. The mean calving interval between the second and third calves was 283.5 ± 19.1 days. The calving interval for all females combined ranged from 265 to 359 days, with a mean calving interval of 297.3 ± 33.5 days.

Post-partum ovulation* is common in ungulates and has been recorded in various members of the Hippotraginae, including the addax (Densmore & Kraemer 1986), roan antelope (Joubert 1976), gemsbok (Dieckmann 1980), and the scimitar-horned oryx (Gill & Cave-Brown 1988). Post-partum ovulation was also observed in the captive Arabian oryx females at the National Wildlife Research Centre at Taif, Saudi Arabia. Based on an endocrinological study it was found to occur 18 days after parturition in captive female Arabian oryxes (Sempéré, Ancrenaz, Delhomme, Greth & Blanvillain 1996). At the same facility the mean length of the ovulation cycle in the Arabian oryx female was calculated as 22 ± 3.6 days (Vié 1996). By using a mean gestation period of 264 days (Stanley-Price 1989) it was calculated that 54.4%, 27.3% and 18.2% respectively of the conceptions of the second and third Arabian oryx calves in the present study occurred within 30, 60 and more than 90 days post-partum. This indicates that in the present study the majority of the conceptions in the multiparous females occurred during the post-partum oestrus* period.

Fecundity

From March 1995 to February 1997 there were 39 births to 28 females. The fecundity schedule was therefore calculated for 39 births and all the oryx females in the wild. In five instances a female calved twice in the same age class (3 to 4 years old). Calving twice in the same age class is not surprising, given the aseasonal nature of breeding and early post-partum* conception in the Arabian oryxes (Spalton 1995). In Oman the data on the Arabian oryxes there suggested that calving twice in the same age class led to a subsequent delay in the following conception because the probability of calving in the next age class decreased. This observed delay in the following conception is a consequence of the greater nutritional demands of two consecutive births, and perhaps the inability to regain sufficient physical condition for early conception (Spalton 1995).

The fecundity schedule is illustrated in Figure 32 and the data for the schedule appear in Table 21. The fecundity of the female oryxes differed for the different age classes. The fecundity among females between 1 and 2 years old was only 9.0%, with one of 11 females in that age class giving birth. Even though the Arabian oryx females can breed at the age of 20 months (Spalton 1995), the mean age at first breeding in the present study was 29.4 ± 5.1 months, indicating a low fecundity rate at the age of first breeding. An increase in fecundity was observed with an increase in age. Maximum fecundity was observed in females between 4 and 5 years old. It should be noted that the sample size in the >4 to 5 year old age class was small with a calf produced by each of the two females aged between 4 and 5 years old. Due to the limited age distribution of the reintroduced population there were no females older than 5 years during the study period.

During the 2-year study period 69.6% of the oryx females that gave birth successfully did so before the age of 30 months. This is similar to the 70.0% observed for captive females at the National Wildlife Research Centre (Vié 1996). The fecundity schedule in large mammals follows a characteristic pattern (Eberhardt 1985) which starts with low fecundity rates in the age class in which it is first possible to breed (Spalton 1995). This low phase is followed by an increase in fecundity, which in turn is followed by a period where the fecundity rates remain relatively constant (Williamson 1991; Spalton 1995) before decreasing again (Clutton-Brock 1984; Green 1990). The fecundity schedule observed during the present study is similar to that described for the Arabian oryx in Oman (Spalton 1995) and also conforms well to the general pattern which is characteristic for large mammals.

Variation in the food supply is correlated with climatic variables such as rainfall and the population size increases and decreases in response to increasing and decreasing food availability in the habitat (Pellew 1983). Apart from food quantity, a definite link exists between the nutritional quality of the food plants and reproduction in mammals (Bronson 1985). Knight (1991), for example, related the number of gemsbok calves born in the Kalahari system to the rainfall that occurred in the previous summer, while Novellie (1986) found a correlation between the percentage of bontebok *Damaliscus dorcas dorcas* (Pallas, 1767) calves born in South Africa and the rainfall during the preceding 12-month period. Similarly, the breeding success of scimitar-horned oryx in the African Sahel was also linked to rainfall (Morrow, Wildt & Monfort 1999). It is interesting to note that although the number of breeding age Arabian oryx females in the 'Uruq Bani Ma'arid Protected Area increased linearly from 1995 to 2000, the proportion of such females with calves did not. The proportion of breeding age females with calves at heel increased from 62.5% during 1995 to 73.5% during 1996, before reaching a peak of 97.2% during 1997 (Wacher unpublished). This increase in the proportion of breeding age females with calves is linked directly with the widespread rain that occurred in the protected area during both 1995 and 1996. The effect that drought has on the productivity of the oryx females in the study area were also witnessed between September 1999 and June 2000 when only 13.7% of 51 identifiable (reintroduced) females had calves at heel (Strauss unpublished).

It is expected that the fecundity of the female oryxes in the 'Uruq Bani Ma'arid Protected Area will increase as the females become older, if the extrinsic factors such as environmental conditions allow it to happen. In Oman it was found that the primary factor that influences fecundity was the condition of the grazing resource, and that the probability of an oryx being fecund in any year decreased following low levels of crude protein in the diet in the preceding year (Spalton 1995). In the same study it was found that female Arabian oryxes reach constant high reproductive rates from the age of 6 years, and that maximum reproductive potential was recorded in the 11 to 12 year (n=6) and 12 to 13 year (n=4) age dasses.

Seasonality of calving

The Arabian oryx females produce calves throughout the year, with calves being born during all the months except April and July in the present study (Figure 33). There is, however a clear peak during December, when 31.6% of all the births during the study was recorded. There were too few births during the present study to test for randomness of distribution during the different months. On a seasonal basis, however, it was found that 63.2% of all the births occurred during the winter (December to February), and that the uneven distribution on a seasonal basis was significant ($\chi^2 = 30.814$, d.f. = 3, $P < 0.05$). Neither the distribution of the calvings nor of the conceptions was therefore randomly distributed on a seasonal basis. The Arabian oryxes reintroduced into Oman also produced calves throughout the year (Stanley-Price 1989; Spalton 1995) and a peak was observed from December to February for desert-born females, while no peak in calving could be distinguished for the reintroduced females (Spalton 1995). As could be expected due to the year-round favourable conditions and the occurrence of a post-partum oestrus, the Arabian oryxes in captivity produced calves throughout the year with no clear peak (Vié 1996).

As indicated previously, it was impossible to test the effect of daylength on Arabian oryx conception rates. It is, however, suspected that the effect of daylength will not be particularly important in influencing conception in the Arabian oryx in the Arabian Peninsula. In the temperate regions, photoperiod is a common environmental cue to time breeding events in seasonally reproductive species. In arid habitats, however, it is generally accepted that variations in temperature, rainfall and consequently food availability serve as the cues for regulating reproduction (Morrow *et al.* 1999). In Oman it was suggested that conceiving during the long-day months might have adaptive values for the Arabian oryx, as the females will then calve during the cooler months. Such a conception and consequently calving pattern would reduce the exposure of the calves to heat stress, while benefiting the water economies of the females through a reduced demand on lactation (Stanley-Price 1989). Spalton (1995), however, concluded that photoperiod was not involved in stimulating conception amongst the desert-born

Table 20: The age in days at first calving and the calving interval in days for individual Arabian oryx females reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia for the period March 1995 to February 1997.

FEMALE NUMBER	AGE AT BIRTH OF FIRST CALF	CALVING INTERVAL	
		First to Second calf	Second to Third calf
1	914	286	-
7	980	274	-
9	921	357	-
12	-	-	270
14	-	-	297
15	900	308	-
17	854	265	-
18	817	281	-
20	899	306	-
21	1211	-	-
22	723	-	-
23	796	359	-
24	830	-	-
25	790	-	-
26	862	267	-
32	805	-	-
33	744	-	-
46	581	-	-
47	1209	-	-
49	934	-	-
54	1211	-	-
56	1023	-	-
64	929	-	-
65	873	-	-
66	871	-	-
73	1186	-	-
78	771	-	-
81	702	-	-
Mean	894.1	306.1	283.5

oryx in Oman. Instead it was shown that dietary crude protein in the grazing resource served as a link between rainfall and conception. The nutritional condition of the food plants at the time of conception, and not at parturition, therefore seems to be the driving force behind the timing of reproduction in the desert-born Arabian oryx females in Oman (Spalton 1995). No pattern in conception could, however, be distinguished for the reintroduced female oryxes in Oman (Spalton 1995) and conception in these females was not obviously influenced by nutritional factors.

There is a weak negative correlation ($r = -0.066$, d.f. = 10, $P > 0.05$) between conception in Arabian oryx females and the monthly ambient temperature, as illustrated in Figure 34. This suggests that ambient temperature may have little effect on the breeding patterns of a female Arabian oryx. A similar observation has been made in Oman, where no link between ambient temperature and the observed breeding pattern could be distinguished. The fact that calving during the summer months has been mostly avoided in Oman, has been attributed to the chance timing of the rainfall and the resultant nutritional conditions of the grazing resource in the area (Spalton 1995). The same is true for the present study, where the majority of conceptions took place during the spring.

Although no analysis of nutritional quality of the food plants of the Arabian oryxes has been done in the present study, the results correspond well with that obtained by Spalton (1995) for desert-born oryx females. Recent observations in the 'Uruq Bani Ma'arid Protected Area, where widespread rain has not fallen since 1997, indicates that the majority of oryx females are not conceiving and that few calves are being born (Strauss *pers. obs.*). A female in a good physical condition is more likely to conceive than one in a poor physical condition. This has also been found in the bontebok in South Africa (Novellie 1986). In domestic sheep it has been shown that the ovulation rate is affected by nutrition, with higher ovulation rates being associated with higher nutritional condition (Gordon 1983). These findings are in contrast to most of the seasonal breeding African ungulates where rainfall does not act on conception but where food quality at the time of parturition influences the timing of the births (Owen-Smith 1990). It can therefore be concluded that the Arabian oryx is an opportunistic breeder and that the females will conceive as soon as conditions allow it to do so. In general the opportunistic or aseasonal breeders occur in arid areas where the rainfall is unpredictable (Skinner & van Jaarsveld 1987). The populations of such animals can therefore crash in unfavourable conditions, but opportunistic breeding will allow an early recovery (Spalton 1995).

Mortality

Table 21: The age-specific fecundity schedule for 39 births that were recorded for the Arabian oryxes reintroduced into the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.

AGE CLASS IN YEARS	NUMBER OF FEMALES (A)	NUMBER OF OFFSPRING (B)	FECUNDITY (B/A)
0-1	12	0	-
>1-2	11	1	0.09
>2-3	28	16	0.57
>3-4	21	20	0.95
>4-5	2	2	1.00
Mean	-	-	0.65

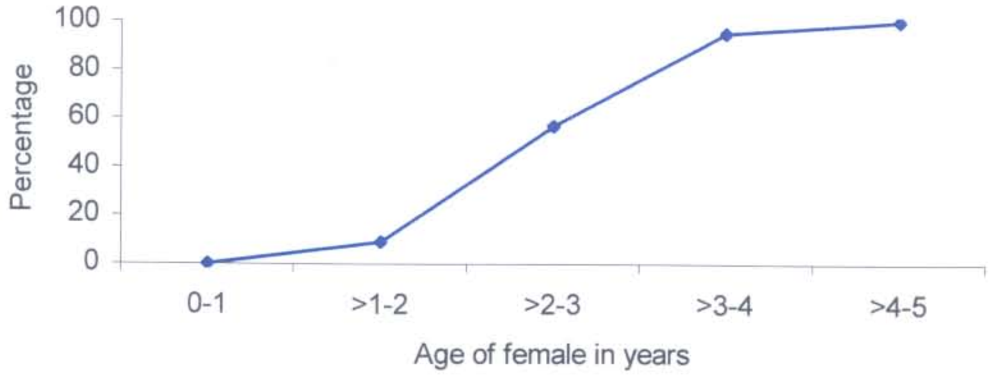

Figure 32: The percentage age-specific fecundity rate for 28 Arabian oryx females in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.

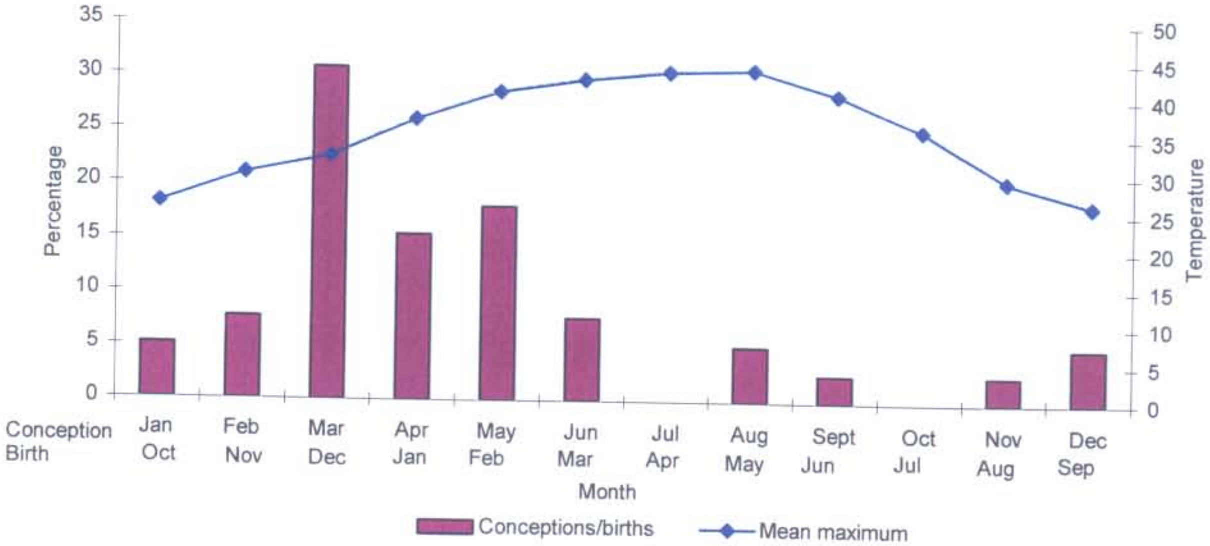

Figure 33: The monthly distribution of 39 Arabian oryx conceptions and births, and the mean maximum monthly temperature (°C) recorded in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia for the period March 1995 to February 1997.

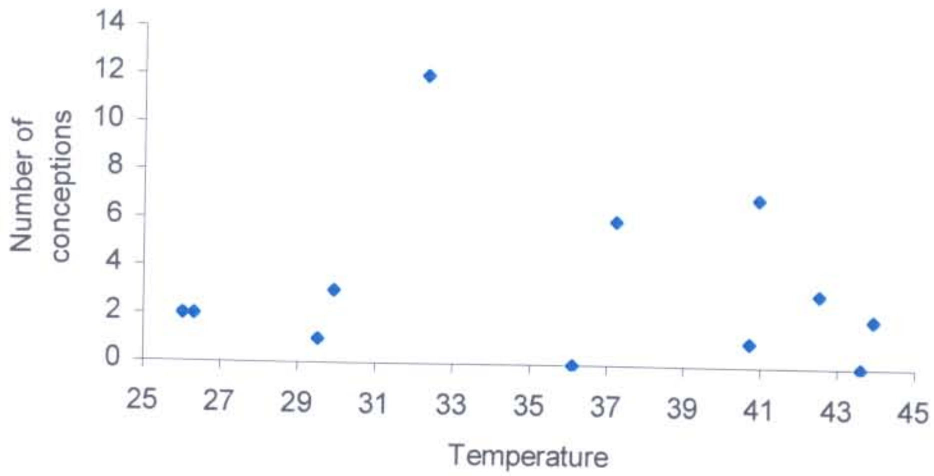

Figure 34: A scatter diagram indicating the relationship between 39 Arabian oryx conceptions and the mean maximum ambient temperature (°C) as observed in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997 (Pearson's correlation coefficient r = -0.006, d.f. = 10, P › 0.05).

From March 1995 to May 1996, a total of 66 Arabian oryxes were reintroduced into the study area. At the end of the study period, 60 of these reintroduced Arabian oryxes were still alive. The survival rate ($\hat{S}$) of the population from the official release in March 1995 to the end of February 1997 was 0.91 (91%), with a variance (Var $\hat{S}$) of 0.001 (1%). The 95% confidence interval, where $\alpha = 0.05$ and $z_{\alpha} = 1.96$ was 0.84 to 0.98 (84 to 98%). The deaths recorded for calves less than 1 year old represented 45.5% of all recorded mortalities. The mortality schedule, indicating age-specific mortality rates, is illustrated graphically in Figure 35, and the data that were used to calculate the mortality rates are presented in Table 22.

The mortality rate expressed as a percentage represents the proportion of all animals that entered a given age class and died before entering the next age class. The highest mortality rate (11.0%) was recorded for the juveniles (0 to 1 years old), while a 2.0% mortality rate was recorded for the yearlings (>1 to 2 years old). During the study period the mortality among the >2 to 3 year olds reached 8.0%, and included the only adult female to die during the study period. No deaths were recorded in animals more than 4 years old. In Oman the highest mortality rate was recorded for animals more than 13 years, while 17.0% of juveniles born in the area (n=178) died in that age class (Spalton 1995).

Loudon (1985) reported a 20.0% neonatal mortality rate for an expanding captive population of Arabian oryxes. Reduced juvenile survival has been associated with an increase in animal density and consequently an increase in competition for food (Skogland 1985). For example, in the state of Montana in the United States of America, the neonatal and summer fawn mortality rates of the white-tailed deer *Odocoileus virgianus dacotensis* (Zimmermann, 1780) ranged between 10.0 and 48.0% over a 5-year study period. In that study a positive linear relationship was found between the summer fawn mortality and the density of adult females (Dusek, Mackie, Herriges & Compton 1989). There are no data to suggest that the juvenile mortality in the 'Uruq Bani Ma'arid Protected Area was density-dependent. This agrees with the study of Spalton (1995) in Oman and, as in that study, it is because of the simultaneous increase in the number of animals in the area and the range used by them. Spalton (1995) did, however, relate juvenile survival to the condition of the grazing resource and found that survival in juveniles decreased at times of absolute food shortage. Conditions of food shortage have not yet been experienced in the 'Uruq Bani Ma'arid Protected Area.

The U-shaped mortality pattern as described by Caughley (1966) is characterised by high neonatal mortality, lower mortality during the middle age classes and an increase in mortality as senescence is approached (Eberhardt 1985). This mortality pattern, which is characteristic of most mammals, was not observed in the present study (Figure 35). This may be due to the

Table 22: The age-specific mortality rates for reintroduced and wild born Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.

AGE CLASS IN YEARS	NUMBER OF ANIMALS	NUMBER OF DEATHS	MORTALITY RATE
0-1	45	5	0.11
>1-2	49	1	0.02
>2-3	53	4	0.08
>3-4	26	1	0.04
>4-5	4	0	0.00
>5-6	2	0	0.00
>6-7	1	0	0.00
>7-8	1	0	0.00

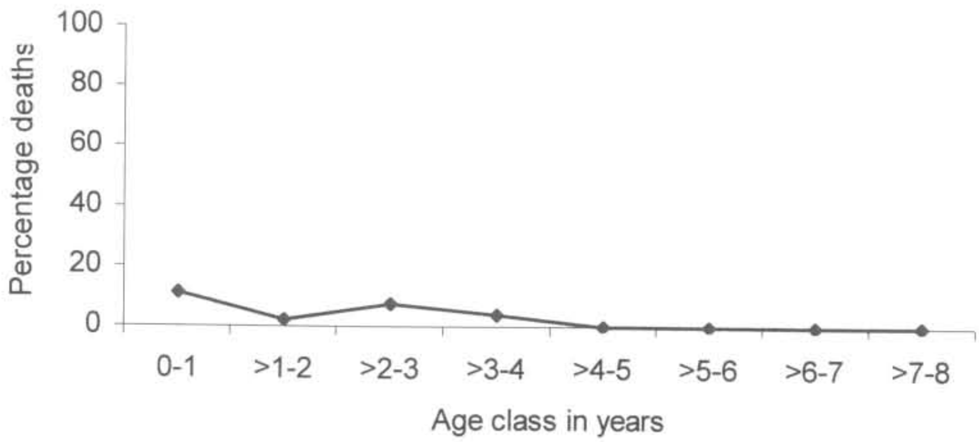

Figure 35: The mortality schedule for 11 deaths in the Arabian oryx in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.

limited age distribution of the reintroduced animals.

Perinatal mortality

The perinatal mortality, which is the sum of the neonatal mortality up to 10 days after birth, reached 12.8% (n = 5) during the present study. It is suspected that the dead calves were either stillborn or aborted as none of them was ever seen alive (Table 23). Perinatal mortality reached its highest levels in females calving for the first time and 80.0% of all instances of such mortality were recorded in primiparous females with 15.4% of all primiparous females losing their calves during the study period. The mean age of the primiparous females that lost their calves was 28.7 ± 9.4 months. This mean age was not significantly different ($t = 0.812$, $df = 24$, $P > 0.05$) from that of primiparous females whose calves survived the first 10 days after birth. The perinatal mortality figures recorded in the present study are relatively low when compared to those recorded in other wild ungulate populations. In Oman, perinatal mortality reached 21.0% in the reintroduced Arabian oryx population (Stanley-Price 1989). During 1998, 19.0% (n = 42) of the Arabian oryx calves born in the Mahazat As Sayd Protected Area in the Kingdom of Saudi Arabia were found dead before reaching 10 days of age. It is suspected, however, that as much as 55.0% of the calves born in the above mentioned protected area may have died before reaching the age of 10 days during 1998 (Ostrowski, *pers. comm.*).

The perinatal mortality figures for the captive Arabian oryx herds at the National Zoological Gardens in Pretoria, South Africa and at its breeding facility in Lichtenburg in the North West Province are approximately 9.0% and 13.0% respectively (Schoeman unpublished[6]). In captivity, perinatal mortality in scimitar-horned oryx under free-ranging conditions reached 13.3% (n = 15), and 29.0% for all artiodactyls at the Whipsnade Park in the United Kingdom (Kirkwood, Gaskin & Markham 1987). Gogan and Barrett (1987) reported perinatal mortality rates of 85.7% (n=21) in an expanding population of tule elk *Cervus elaphus namodes* that was reintroduced to California. The perinatal mortality rate for the Arabian oryx observed in the present study therefore compares favourably with that observed in oryxes in other areas and for other animals.

Causes of mortality

The mortality rate of the reintroduced oryxes reached 9.0% during the study period, as six animals of varying age, including one adult female died during this time (Table 23). Injuries incurred during dominance disputes between adult male oryxes caused the deaths of three

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(60.0%) of the adult males that died. The mean age of the adult male oryxes that died due to fighting was 35.8 ±3.5 months. Deaths due to fighting are not common in ungulates. It has, however, been reported for the Arabian oryxes in Jordan's fenced Shaumari Reserve (Abu Jafer & Hays Shahin 1989), the fenced Mahazat As Sayd Protected Area in Saudi Arabia (Greth & Schwede 1993) and in the unfenced Jiddat al Harrasis area of Oman (Spalton 1995). According to Spalton (1995) competition between Arabian oryx males is most intense between the ages of 5 and 8 years old, a time when 71.4% of the mortalities in male oryxes in that age category (n=7) result from fighting.

Autopsies were performed and organ samples were collected from one of the dead Arabian oryx males and from the female that died. The other four animals were not located soon enough after death to allow the collection of such samples. Analysis of the organ samples collected from the male oryx showed a congestion of the lungs and an acute oedema* in the lungs. Neither of the sets of organ samples collected showed any signs of infectious disease. A survey in the area, however, indicated that there are infectious diseases in the livestock in and around the area (Sandoka 1996). The female oryx that died had a 2.5-month old calf at the time of her death. Blood samples were collected from this calf to test for possible antigens that would have been passed to the calf from the mother if the mother had had an infectious disease. It was found that the calf presented a high positive serological titre to pasteurellosis *Pasteurella multocida* Type A (Ostrowski *pers. comm.*). It has, however, been suggested that the high *Pasteurella* titres encountered in the blood of this calf could be a reflection of its mother having been vaccinated rather than the calf being infected. Maternal antibodies only disappear from a juvenile's circulation at 3 months of age (Flamand, *pers. comm.*[7]).

Population growth rate

During 1995, the Arabian oryx population was established in the 'Uruq Bani Ma'arid Protected Area through three releases which took place during March, April and June of that year (Figure 36). In addition five calves were born, while two reintroduced animals died during the same period. The exponential growth rate for the period March to December 1995 was 0.092 (9.2%). During 1996 a further 35 oryxes were released while 29 calves were born. A further four oryxes died during this time. For the period January 1996 to February 1997 the exponential growth rate (r) was 0.309 (30.9%).

It is generally accepted that most wildlife populations display a similar growth curve form when

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Table 23: The causes of death of Arabian oryxes of different ages (months) in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997.

ANIMAL NUMBER	SEX	AGE	CAUSE OF DEATH
10	Male	25.0	Unknown, the animal was found approximately 1 week after death
24	Female	29.8	Unknown, an autopsy was inconclusive. *Pasteurella* titres were found in the female's 2.5-month old calf
19	Male	39.1	Physical injuries, an autopsy revealed congested lungs and acute oedema. No signs of disease
61	Male	16.8	Cause of death unknown. Died approximately 261 km from its release site
5	Male	32.2	Physical injuries
6	Male	36.0	Physical injuries
-	Unknown	0.0	The first calf of Female 46 who was 19.1 months old. The calf was never located
-	Unknown	0.0	The first calf of Female 21 who was 39.8 months old. The calf was partly scavenged when found
-	Unknown	0.0	The first calf of Female 81 who was 23.1 months old. The calf was never located
-	Unknown	0.0	The second calf of Female 26 who was 37.1 months old. The calf was never located

the number of animals in relation to time elapsed is presented graphically. The growth of an animal population follows a clearly defined pattern over time, and generally follows an S-shaped curve (Figure 37)(Caughley 1977; Odum 1983; Bothma 1996). In the initial establishment phase the births and deaths are about equal and the population increases slowly. After the initial slow establishment phase follows a period of exponential growth where the natural resources of the environment (extrinsic factors) are unlimited for a given species. As the exponential growth of the population continues, deficiencies of one form or another starts to influence the birth and survival rates of the population (Bothma 1996), while the effect of the intrinsic or density-dependent factors also becomes important in regulating the population. It is commonly accepted that population size is regulated by extrinsic factors such as food availability (Sinclair 1977; Fryxell 1987). This leads to a decrease in population growth and ultimately to a fluctuating equilibrium where the natural births and deaths balance each other (Bothma 1996).

During the first 9-month period (March to December 1995) after the official release, the births outnumbered the deaths by a factor of 2.5. The growth rate of 9.2% is higher than what one would expect from the establishment phase of a population where the number of births usually are only slightly higher than the observed deaths (Bothma 1996). The exponential growth rate (r) increased more than three-fold for the period January 1996 to February 1997 and the births outnumbered the deaths by a factor of 7.25. This increase in growth rate is due to a combination of factors. These factors are the increase in the founder population in the 'Uruq Bani Ma'arid Protected Area during 1996, when the number of breeding age females was increased by 425% from 8 to 34, as well as the good climatic conditions which resulted in an ample food supply of sufficient quality. This in turn resulted in the majority of the animals, and especially the females, being in excellent physical condition, which is ideal for conception.

During the period January 1996 to February 1997 the Arabian oryxes entered the exponential growth phase. This growth phase is characterised by unlimited resources (Bothma 1996) and the absence of density-dependent factors that could regulate the population growth. If the observed exponential growth rate (r = 30.9%) had remained constant, the oryx population would have increased to 200 animals within the next 3 years. Due to the good environmental conditions and the fact that the protected area is unfenced, intrinsic factors should still not have been prominent in regulating population growth in the 'Uruq Bani Ma'arid Protected Area. The primary factor in regulating the population growth in this area would be environmental, while density-dependent factors will always be secondary in that effect.

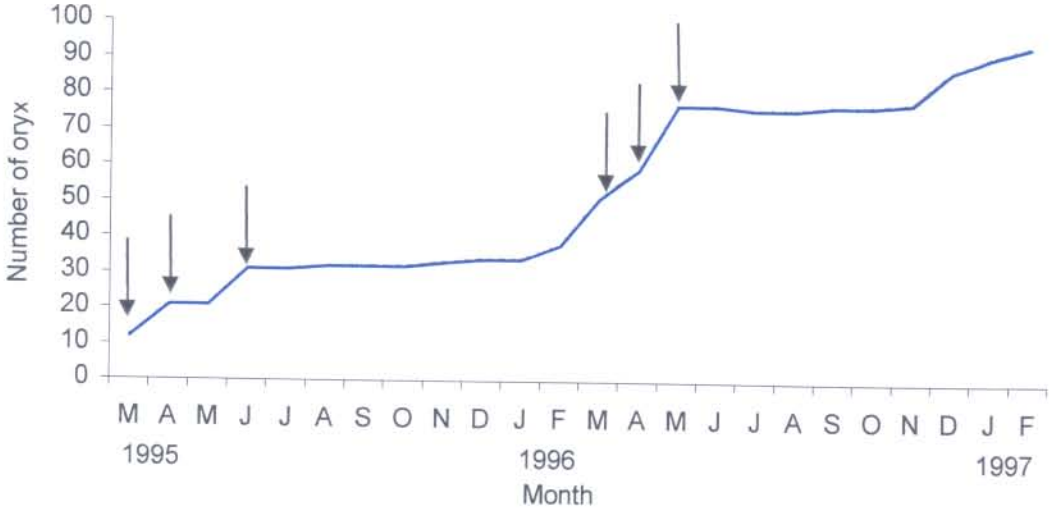

Figure 36: The actual growth of the Arabian oryx population in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia from March 1995 to February 1997. Arrows indicate the six months of release.

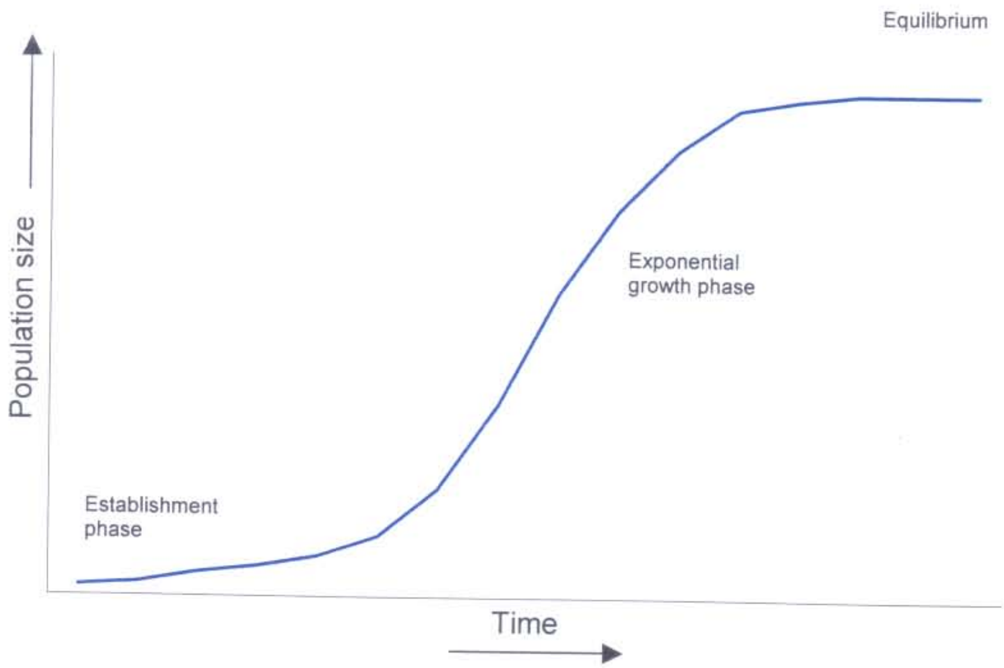

Figure 37: The characteristic growth phases of animal populations (Bothma 1996).

Conclusions

Shortly after the release of the first group of Arabian oryxes into the 'Uruq Bani Ma'arid Protected Area, widespread rain fell in the area. Because of the good environmental conditions, the condition of the vegetation, and the resulting physical condition of the female oryxes, calves were born during both years of the study. For the period 1996 to 1997, 75% of the females of breeding age had calves at heel. During surveys conducted in 2000, only 13.7% of identifiable breeding age females had calves, confirming the fact that food quality is the driving force behind the productivity of the Arabian oryxes in the Arabian Peninsula.

Releasing older females of higher fecundity instead of mainly primiparous females, might have increased the productivity of the reintroduced oryx population. Since no signs of infectious diseases were found in the organ samples collected from some of the dead animals, it is not quite clear why 12.8% of the new calves died during or shortly after birth, unless one attributes it to the inexperience of the females. The fact that the majority of the multiparous females conceived during the post-partum oestrus period not only confirms the good environmental conditions, but it also attests to the fact that the limited age structure of the reintroduced population did not noticeably impinge on the productivity of the population.

Ultimately the successful reintroduction of a species partly depends on a clear understanding of the possible effects that both the extrinsic and intrinsic factors can have on the dynamics of the reintroduced population, as well as the levels at which these factors operate. Based on the results from this study it is suggested that the reintroduced Arabian oryx population is regulated by extrinsic factors such as environmental conditions. Due to the unfenced nature of the 'Uruq Bani Ma'arid Protected Area and the ranging behaviour of the species it also suggested that intrinsic factors will always be secondary in regulating the dynamics of this population.