CHAPTER 10

POPULATION VIABILITY ANALYSIS

Introduction

The primary causes of species decline are often obvious and deterministic, and include over-harvesting, conversion of the natural habitat which renders it lost to the particular species, pollution, local and global climate changes, exotic competitors, and predators among others. Although the primary causes of species decline are often easy to understand they are also much more difficult to reverse (Miller & Lacy 1999). An example of this is the recent near-demise of the free-living Arabian oryx population in Oman. Because of severe poaching, that population, which once numbered in excess of 400 animals in 1996, is no longer considered viable unless it is boosted by additional releases (Spalton, Lawrence & Brend 1999).

According to Caughley (1994) there are two different paradigms operating within conservation biology. These are the small population paradigm, which deals with the risk of extinction inherent in small numbers, and the declining population paradigm which is concerned with the processes by which populations are driven to extinction by agents external to them. The small population paradigm deals mostly with the population genetic and population dynamics problems faced by a population which is at risk of extinction due to its small size (Caughley 1994). The declining population paradigm focuses mainly on ways of detecting, diagnosing and halting a predicted or an actual population decline. In the declining population paradigm the problem is seen as a population that is in trouble due to something external that has changed. Consequently the size of the population is of no great relevance (Caughley 1994). All the effort is then aimed at determining why the population is declining and how the trend can be reversed. Both these approaches have much in common (Hedrick, Lacy, Allendorf & Soulé 1996), as they both focus on the fate of a given species. Although these two paradigms have been reconciled recently (Hedrick *et al*. 1996) and a broader understanding of the factors influencing endangerment and extinction*, through an inclusive approach to population viability analysis has been advised, they still form the basis for approaches to assessing extinction risk (Mace & Hudson 1999).

Population viability is the anticipation through data modelling of the likelihood that a population will persist for some arbitrarily chosen time into the future (Shaffer 1981; 1987). A concept that is closely related to population viability is minimum viable population analysis.

This type of analysis gives an estimate of the minimum number of organisms of a particular species that constitutes a viable population (Boyce 1992). Population viability analysis embraces the minimum viable population concept, without attempting to estimate the absolute minimum population necessary to keep the species viable (Soulé 1987). The viable population concept was formalised by Shaffer (1981) who presented four stochastic factors that affect population viability. These factors are demographic stochasticity, genetic stochasticity, environmental stochasticity and catastrophe. It has been stressed that the factors causing species extinction are interrelated and dynamic (Shaffer 1981; Gilpin & Soulé 1986). Subsequently Gilpin and Soulé (1986) suggested an integrated viability analysis for assessing the persistence of a species, which deals with demographic and genetic factors, while also introducing the concept that persistence expectations are probabilities.

Population viability analysis has been a popular modelling tool in conservation ever since its development (Ludwig 1999). It offers the prospect that sophisticated mathematical tools can be used to provide quantitative estimates of important quantities relating to threatened populations, such as the expected time to extinction or the probability of a population surviving for the next 100 years. There is, however, substantial disagreement in the literature regarding the usefulness of population viability analysis in conservation (Boyce 1992; Ludwig 1999). A concern often raised is the impression that population viability analysis provides exact results (Beissinger & Westphal 1998; Reed, Murphy & Brussard 1998). This has led to the suggestion that the results from the population viability models should be used in a relative fashion by comparing outcomes among model alternatives (Ralls & Taylor 1997; Beissinger & Westphal 1998). This has, for example, been done for the African elephant *Loxodonta africana* (Blumenbach, 1797) in Kenya (Armbruster & Lande 1993), African wild dogs *Lycaon pictus* (Temminck, 1820) in the Selous Game Reserve (Vucetich & Creel 1999), the lower keys marsh rabbit *Sylvilagus palustris hefneri* (Bachman, 1837) of Florida (Forys & Humphrey 1999) and a warthog population in the Andries Vosloo Kudu Reserve, South Africa (Somers 1997).

In the present study the computer prgram VORTEX (Miller & Lacy 1999) was used to model the future of the Arabian oryx population in the 'Uruq Bani Ma'arid Protected Area. The Conservation Breeding Specialist Group of the IUCN (Miller 1995; In: Brook, Cannon, Lacy Mirande & Frankham 1999) has used this particular program extensively in population viability analysis on a number of species, including the Cape mountain zebra *Equus zebra zebra* (Novellie, Miller & Lloyd 1996). VORTEX has also been used in modelling the Arabian oryx population in Oman (Spalton 1995) and a roan antelope population in Kenya (Magin &

Kock 1997). In addition the populations of blue crane *Anthropoides paradiseus*, wattled crane *Bugeranus carunculatus* and the grey crowned crane *Balearica regulorum* in the Mpumalanga province of South Africa have also been modelled with this program (Morrison 1998). VORTEX is considered to be the simulation program most widely used in population viability analysis (Caughley 1994).

The aim of this part of the study was therefore to assess the performance of the reintroduced Arabian oryx population over the short (10-year) and the medium (100- year) term and to answer the following principal questions:

- Could the population growth rate of the reintroduced Arabian oryx population in the 'Uruq Bani Ma'arid Protected Area have been increased through a stable age distribution?
- Which sex ratio would give the optimal growth rate for the reintroduced Arabian oryx population?
- What effect would catastrophes have on the medium term (100-year) survival of the reintroduced Arabian oryx population?
- What likely effect would the additional release of oryxes have on the population growth rate and the persistence of the reintroduced population?
- What would the likely effect on the reintroduced population be if oryxes were removed from the population in an uncontrolled manner such as through poaching?
- On which population parameters should management actions concentrate to ensure the survival of the reintroduced Arabian oryx population over the medium term?

Methods

VORTEX is based on a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental and genetic stochastic events on wildlife populations. In addition to environmental stochasticity, VORTEX can also model the effect of catastrophic events. Population dynamics are modelled by VORTEX, as discrete, sequential events that occur according to probabilities that are random variables, following user-defined distributions (Lacy 1993). A population is simulated over a specified time interval by stepping through a series of events that describe an annual cycle of a typical sexually reproducing, diploid organism. These events include mate selection, mortality, increment of age by one year, migration among populations, removals, supplementation, and the truncation to the ecological capacity, if necessary. The simulation is then iterated a number of times, as specified by the user, and produces a distribution of outcomes that the actual population might experience under similar conditions in the wild.

Basic model

The basic model was run over a 10-year period with 1000 iterations. The data used were those that were collected from March 1995 to February 1997. The assumptions made and the vital rates used in the basic model were as follows:

- Inbreeding depression was incorporated into the calculations by using the default values in VORTEX for the number of lethal alleles (3.14) and the percentage (50.0%) of the genetic load that is due to lethal alleles.
- Catastrophes were not included in the basic model.
- The mating system is polygynous and all the adult male oryxes (older than 4 years) were considered to be in the breeding pool.
- The age at first breeding for a female oryx, i.e. the age when the first calf is born, was taken as 3 years and the maximum age of reproduction was estimated to be 15 years.
- The ratio of males to females at the time of birth was taken to be 50.0%. Equal numbers of males and females were therefore born.
- Reproduction was density-independent.
- It was assumed that 80.0% of the breeding age females, with an estimated standard deviation of 15.0%, could breed during any year of the basic model. The maximum number of young that a female could produce within a time cycle of a year was two, and 21.0% of female oryxes produced twice within such a time. The remaining 79.0% of female oryxes that produced calves did so only once within a given year.
- The Arabian oryx population at the time of modelling was the 66 oryxes released into the ‘Uruq Bani Ma’arid Protected Area from March 1995 to February 1997 (Table 27).
- The ecological capacity of the ‘Uruq Bani Ma’arid Protected Area was estimated to be 400 Arabian oryxes, with a standard deviation of 80 animals (20.0%). This is an estimated figure, based on knowledge of the core protected area and the critical summer range as identified by Wacher (1997) as well as the low primary productivity in the area. A population of 400 oryxes in the 2500 km² core area of the ‘Uruq Bani Ma’arid Protected Area translates to a density of 0.16 oryx per kilometre squared. This density estimate is approximately midway between the observed minimum and maximum oryx densities of 0.1 and 0.4 oryx per kilometre squared as observed in Oman (Tear 1992). No trend in the ecological capacity was modelled.

- The oryx population in the basic model was not supplemented and no harvesting took place.

Corrected basic model

The variables and assumptions used in this more realistic model is the same as those used in the basic model, unless otherwise specified. Due to the more realistic mortality figures the corrected basic model was used as the basis for all the subsequent models investigated through VORTEX. More realistic mortality figures, mimicking the characteristic u-shaped mortality curve in ungulates (Chapter 8) have been estimated. The new mortality figures (Table 27) are based on those observed in the present study and reported elsewhere (Stanley-Price 1989; Spalton 1995).

The corrected basic model was then used to model the reintroduced population over a 10-year period, for comparison with the basic model. The corrected basic model was also used for all the models over the 100-year period. Catastrophes were included in the latter models but not in the former.

Catastrophes

The catastrophes that were included in the corrected basic model and run over a 100-year period were all related to environmental conditions. Due to the variability of the annual rainfall in the southern parts of the Kingdom of Saudi Arabia (Mandaville 1990) four different drought scenarios of differing intensities, were modelled. Each of these scenarios influenced the productivity of the female oryxes and the survival rates of each of the age and sex classes recognised. A year of normal rainfall as used in this part of the study represents a year during which rain fell somewhere within the protected area, and which would result in fresh grazing being available to the animals. The drought scenarios modelled were:

- A year of normal rainfall followed by a year of no rainfall: Here the severity factor for reproduction was set at 0.75, while that for survival for all the age classes was set at 0.85. If, for example, 80.0% of the breeding age females reproduce within a year of normal conditions in this scenario, only 60.0% (80 x 0.75 = 60) of the breeding age females would reproduce during a year without rainfall. The severity factor for survival influences the survival of the different age and sex classes in a similar way. The probability of such a catastrophe occurring was estimated at 20.0%.

Table 27: The age and sex distribution of the starting population of Arabian oryxes in the 'Uruq Bani Ma'arid Protected Area of the Kingdom of Saudi Arabia, and their respective mortality rates (± 1SD) as observed from March 1995 to February 1997, and the more realistic age and sex class-specific mortality rates (± 1SD) as used in the corrected basic model.

AGE CLASS	ORYX NUMBER		MORTALITY RATE							
			BASIC MODEL				CORRECTED BASIC MODEL			
	Males	Females	Males	SD	Females	SD	Males	SD	Females	SD
0-1	2	4	5.5	5.0	5.5	5.0	20.0	20.0	20.0	20.0
>1-2	19	25	4.8	5.0	0.0	5.0	5.0	5.0	5.5	5.0
>2-3	5	7	22.0	5.0	2.9	5.0	5.0	5.0	5.0	5.0
>3-4	2	1	11.0	5.0	0.0	5.0	10.0	5.0	5.0	5.0
>4-5	0	0	0.0	5.0	0.0	5.0	10.0	10.0	5.0	5.0
>5-6	1	0	0.0	5.0	0.0	5.0	10.0	10.0	5.0	5.0
Total	29	37	-	-	-	-	-	-	-	-

- A year of normal rainfall followed by two consecutive years of no rainfall: Here the severity factor for reproduction was set at 0.50, while that for survival of the different age and sex classes was set at 0.75. The probability of a catastrophe of this nature occurring was estimated at 10%.
- A year of normal rainfall followed by three consecutive years of no rainfall: In this case the severity factors for reproduction and survival of the different age and sex classes were set at 0.20 and 0.75 respectively. The probability of the occurrence of this catastrophe was set at 10.0%.
- A year of normal rainfall followed by five consecutive years of no rainfall: Here the severity factors for reproduction and survival were set at 0.00 and 0.50 respectively. There was an estimated 10.0% probability of a catastrophe of this nature occurring. This catastrophe was included in all the VORTEX models, which were then run over a period of 100 years, with the exception of the corrected basic model where no possibility of a catastrophe was included.

The effect of management decisions on population growth

The main reason for this part of the analysis was to determine which management options would ensure the highest population growth rate under conditions similar to that observed during the present study. In addition, the extent to which the population and its persistence would be affected by various actions, including management, was investigated. To do so the following manipulations were done.

- The age distribution of the oryxes was changed from the actual observed age distribution to a stable age distribution. For this purpose only the size of the initial starting population was specified, whereafter VORTEX distributed those 66 animals according to the stable age distribution calculated from the life table as created by VORTEX.
- The actual sex ratio of the reintroduced population was changed to determine what ratio of adult female to male oryxes would be best for maximum population growth when reintroducing Arabian oryx. The number of breeding age females per male oryx that were modelled was 1, 2, 3, 5 and 10.
- The likely effect that additional releases would have on the reintroduced population was modelled through the additional release of oryxes during years three, four and five after the initial reintroduction. The total number of oryx released during such time was 55 at a ratio of 1.1 females per male (animals 2 years old and more).

- The effect that increasing mortality rates in the various age and sex classes would have on the population growth rate and the medium-term survival of the Arabian oryx population was investigated through sensitivity analyses.

Results and discussion

Basic model

Using the vital rates as recorded from March 1995 to February 1997 as well as the previously specified assumptions, VORTEX yielded a mean projected Arabian oryx population of 363.81 ± 65.37 (±1SD) animals after 10 years (Figure 45). The mean projected population growth rate ($r = 0.218$; ± 0.115) before truncation due to reaching the specified ecological capacity in the simulation model was lower than that observed during the study period ($r = 0.354$; Chapter 8). The final observed heterozygosity of the simulated populations were 0.994 ± 0.004. The probability of persistence over the modelling period was 1.00. This means that the model predicts certain survival over the 10-year modelling period.

Despite the vital rates used, the projected mean population growth rate as modelled here, was lower than that observed during the study period (Chapter 8). This is attributed to the stochastic nature of the modelling process and the differences in calculating the growth rates. The mean population growth rate as calculated in the basic model is, however, too optimistic, even though it is lower than that observed during the study period. The study period was characterised by above normal rainfall resulting in exceptionally favourable environmental conditions. Consequently the data on the vital rates collected during this time clearly cannot be taken as representative of normal long-term conditions.

Corrected basic model

In the corrected basic model the Arabian oryx population still showed positive growth ($r = 0.175 \pm 0.151$), but it increased slower than in the basic model (Figure 45). This is due to the more realistic mortality rates that were used in the corrected basic model. Over the 10 years that this population was modelled, the projected population increased from 66 oryxes at the time of release to 313 ± 66.97. The probability of persistence was still 1.00 after the end of the 10-year modelling period. The projected size of the final population is slightly lower than that of the basic model. This is of no particular importance and it is attributed to the stochastic nature of the models. In the population models used by Tear (1994) both ecological capacity and environmental variation were incorporated. The starting population of 89 oryxes in that model increased to a projected mean size of approximately 200 animals after a 10-year modelling period (Spalton 1995). The main reason for the differences in the final population sizes after 10 years in this study and in the models used by Tear (1994) is that different methods of analyses were used. This is also clear from the models used on the Arabian oryx in Oman where the VORTEX and RAMAS/age programs (Ferson, Rholf, Ginzburg, Jacques & Akcakaya 1990 In: Spalton 1995) were used. Due to the differences among the various packages, Brook *et al.* (1999) who used several packages in analysing whooping crane *Grus americana* viability, cautioned against interpreting the projections of a model that is based on a single population viability package only.

The projected population estimates that were derived from both the basic and the corrected basic models in the present study were substantially lower after 10 years than those projected for the reintroduced oryx in Oman (Spalton 1995). In that study VORTEX yielded a projected mean population size of 960 ± 378 oryxes after a 10-year modelling period. The starting population in those models consisted of 124 oryxes, with a ratio of two breeding age females per male. The differences in the mean projected population sizes as modelled in Oman and in the present study can be attributed to three factors in addition to the stochastic nature of the models. The first is the fact that Spalton (1995) used the median age of 2 years as the age of first breeding for the female oryxes in the models of that study. This was done based on the suggestion by Lacy (1993) that the median age at first breeding and not the earliest observed age of first breeding should be used in the VORTEX models. In the present study the median age at first breeding was 2.4 years. This figure is, however, based on actual data that were collected during a period of exceptional environmental conditions. Therefore it is not considered to be representative of more realistic environmental conditions. Consequently a more conservative age at first breeding of 3 years old was used for female oryxes in the present VORTEX modelling. Secondly, lower mortality rates were used in the Spalton (1995) models than in the present study. The higher mortality rates used in the present study were based on the harsher environmental conditions that the oryxes in the present study are subjected to, when compared to the population in Oman. Therefore it was decided to err on the conservative side, by underestimating rather than overestimating the projected population size. Thirdly, there were differences in the size and sex ratio of the starting populations in the two studies. In Oman the starting population was more than double that in the present study, and the sex ratio of two females per male (Spalton 1995) was more conducive to population increase than the approximately parity in the sex ratio in the present study.

Even though some of the vital rates in the corrected basic model of the present study were adjusted downwards to incorporate probable years of lower rainfall, no trends in the ecological capacity were modelled, neither were any catastrophes included. The projected results of the corrected basic model over a 10-year period should therefore still be treated with caution, especially so because a single population viability analysis program was used in the analysis. Nevertheless, the models show that the population will most likely increase continuously if environmental conditions remain similar to that observed during the study period, until ecological capacity is reached, and in the absence of any catastrophes.

Catastrophes

The projected effect that different catastrophes may have on the projected oryx populations is presented in Table 28. The simulation of drought conditions in the present study indicated that even in the worst case scenario (5 years of drought, no breeding, and a 50.0% survival rate) did the modelled populations show positive growth (r = 0.069 ± 0.319) over the medium term. Under such conditions a starting population of 66 oryxes reached a mean projected population size of 220.35 ± 129.07 after a 100-year modelling period. Furthermore, the models indicate that the oryx population would more than likely survive periods of up to 5 years without rain, given that these periods of catastrophe follow years of normal rainfall. After a 5-year drought the probability of extinction was 10.0%. During such a drought it is likely that no calves would be born, because of the decreasing nutritional value of the food plants, and consequently the decreasing physical condition of the breeding age females (Spalton 1995).

It is, however, more likely that more than one of the possible catastrophes would be encountered by an oryx population during a 100-year period. Of the four catastrophe combinations modelled, all but one resulted in excessively high probabilities of extinction during the modelling period. The worst case scenario where all the catastrophes are encountered during the modelling period resulted in a negative, mean projected population growth rate and a mean projected final population size of 45.92 ± 59.62 oryxes. The probability of persistence during the 100-year modelling period was 8.6%.

Mace and Lande (1991) indicated that populations with probabilities of extinction of 10.0% or more should be considered as vulnerable. Saltz (1996), however, suggested an even more conservative value of 1.0% or more, if factors other than demographic stochasticity (such as environmental stochasticity) are considered. Although these theoretical values might seem conservative, especially if applied across the board to all species, it would probably be wise

Table 28: The projected effect of different catastrophes of different intensity when acting individually or in combination on Arabian oryx populations modelled with VORTEX for a projected period of 100 years.

CATASTROPHE	SEVERITY FACTOR EFFECT ON		FREQUENCY	MEAN FINAL POPULATION	SD	MEAN FINAL HETEROZYGOSITY	SD	MEAN POPULATION GROWTH RATE	SD	SURVIVAL PROBABILITY
	Breeding	Survival								
Individual effects										
No catastrophe	No effect	No effect	-	343.06	59.99	0.951	0.016	0.164	0.142	0.998
One dry year	0.75	0.85	20	324.12	65.34	0.946	0.018	0.123	0.166	0.999
Two dry years	0.50	0.75	10	324.82	71.22	0.946	0.018	0.126	0.186	0.997
Three dry years	0.20	0.75	10	319.70	73.25	0.946	0.017	0.120	0.202	1.000
Five dry years	0.00	0.50	10	220.35	129.07	0.895	0.082	0.069	0.319	0.941
Combined effects										
One, 2 and 3 dry years	-	-	-	212.73	108.78	0.895	0.083	0.037	0.248	0.916
Two and 5 dry years	-	-	-	170.22	118.98	0.865	0.117	0.031	0.340	0.745
Three and 5 dry years	-	-	-	122.64	128.95	0.871	0.108	0.027	0.343	0.724
All catastrophes	-	-	-	45.92	59.65	0.780	0.195	-0.049	0.372	0.087

Note: The individual severity factors stay the same when various catastrophes are combined within a 100-year modelling period.

to consider the Arabian oryx population that was reintroduced into the 'Uruq Bani Ma'arid Protected Area as vulnerable, because relatively little is still known about the species in this variable environment. It is also too early to consider the reintroduction of the Arabian oryxes into the 'Uruq Bani Ma'arid Protected Area an unqualified success.

Management options

There are many facets to consider in the management of animals that are to be reintroduced. These include the background and age of the individual founders and the composition of the groups to be released. In many cases the chances of survival of a reintroduced population can be enhanced by management methods such as reproductive manipulation (Stanley-Price 1989). The criteria used for the selection of the founder population for the reintroduction in the present study have been discussed elsewhere (Chapter 3). In this section the effect that different group compositions in terms of the ratio of adult females per male will have on the population growth rates are investigated, as well as the effect that additional releases will have on these rates.

At the age of first breeding of a male and female Arabian oryx, the mean projected population growth rates in all the modelled populations were higher than that of a population with a stable age and sex composition, irrespective of the ratio of females to males (Table 29). This is because VORTEX automatically assigns a proportion of the starting population to most of the recognised age and sex classes when a population with a stable age structure is modelled. Inevitably VORTEX considers some of the animals as being below breeding age. The disadvantage of releasing a population with a stable age and sex structure is that there is a reproductive delay because a proportion of the animals still has to reach breeding age (Stanley-Price 1989). The release of a population with a stable age and sex structure does have advantages in that there is a set social structure at the time of release, which could reduce both inter- and intraspecific conflict, thereby enhancing the survival of the reintroduced animals, such as with the reintroduction of elephants into the Pilanesberg National Park in the North West Province of South Africa. At the time of that reintroduction no technique existed to translocate adult male elephants, while the translocation of subadult animals and adult females posed no problem. Due to the resulting unnatural social system that the subadult males found themselves in, various problems occurred, including interspecific aggression with white rhinoceroses *Ceratotherium simum* (Burchell, 1817) which led to the death of at least one white rhinoceros (Slotow, van Dyk, Poole, Page & Klocke 2000). Subsequently a recommendation was made only to move entire family groups

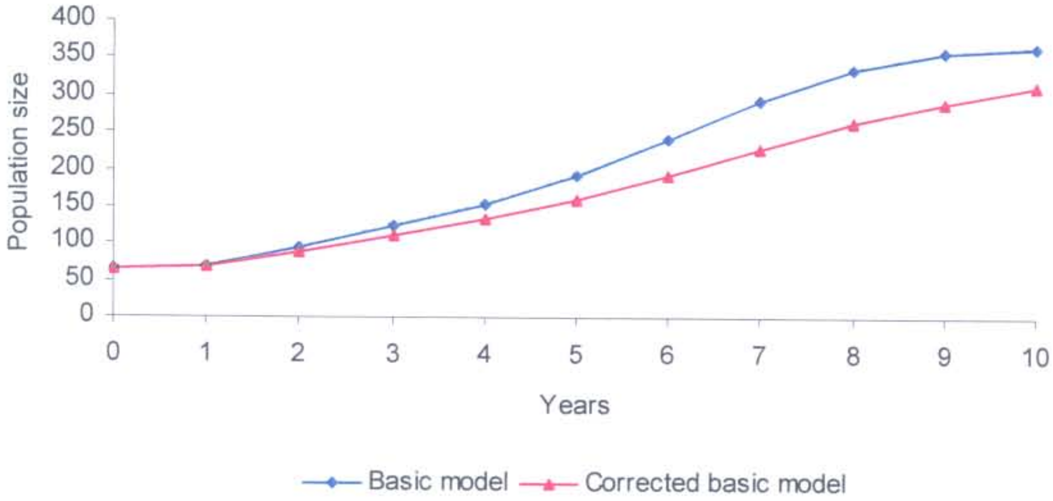

Figure 45: The comparative projected mean growth curves of modelled Arabian oryx populations. The vital rates in the basic (blue) and the corrected basic (red) models were the same, with the exception of more realistic mortality figures being used in the latter model.

Table 29: The mean projected population growth rates (r) for Arabian oryx populations with different ratios of breeding age females per male at the time of release, as modelled over a 10-year period.

FEMALES PER MALE	MEAN POPULATION SIZE AT YEAR					MEAN GROWTH RATE	SD
	2	4	6	8	10		
1	107.60	149.36	211.68	278.41	324.07	0.184	0.153
2	123.57	182.86	258.56	317.26	338.24	0.209	0.162
3	132.57	199.59	277.28	326.78	342.39	0.222	0.168
5	142.06	213.64	292.13	336.25	348.09	0.232	0.175
10	150.19	228.49	301.42	339.48	349.34	0.238	0.182
Stable age	93.69	132.71	186.69	249.18	300.57	0.167	0.145

of elephant, including adult males. No such problems have occurred since. These problems experienced are not surprising because release groups mimicking the natural social structures are considered as the single most critical factor in attempting to ensure successful reintroductions in animals that are not asocial (Stanley-Price 1989).

The highest mean projected population growth rate (r = 0.238 ± 0.182) was attained in a modelled population when the sex ratio was 10 breeding age females per male. A ratio of five breeding age females to a single breeding age male yielded a similar projected mean growth rate (r = 0.232 ± 0.175) after 10 years. The latter growth rate resulted in a projected mean population of 255.02 ± 61.71 after a 5-year period, which is comparable to the mean population size of 270.02 ± 64.58 after the same number of years when the sex ratio used was 10 breeding age females per male (Figure 46). Elsewhere it has been shown that the size of the reintroduced population is critical to successful reintroduction and that the more rapid the population grows the higher the probability of the reintroduction will be of being a success (Dixon, Mace, Newby & Olney 1991). The rate of increase of a population largely depends on the breeding biology of the species in question, notably the age at first breeding and the calving interval. Therefore animals such as the Arabian oryx are more likely to be reintroduced successfully than for example the orang-utan *Pan troglodytes* (Blumenbach, 1775). This is so because the Arabian oryx first breeds at a relatively young age, and at short intervals thereafter, while the orang-utan starts to breed late in life and has long breeding intervals (Stanley-Price 1989).

When the modelled Arabian oryx population was augmented with an additional release of 55 animals over a 3-year period, it increased from 66 to a projected mean population size of 343.84 ± 60.74 over a 10-year period (Figure 47). During the years of supplementation the projected mean population growth rate (r) was 0.439 ± 0.151. During the rest of the years the projected mean population growth rate was 0.158 ± 0.145. Across the entire 10-year modelling period, the mean projected growth rate was 0.215 ± 0.184, before growth ceases when the ecological capacity would be exceeded. The high standard deviation in the mean projected growth rate across the modelling period is indicative of the differences which will occur in the growth rates during years of supplementation as opposed to those years without additional releases.

In these models the additional releases had a positive effect on the reintroduced population in that the initial establishment phase of the population was short. Within 2 years after the initial release, the modelled Arabian oryx populations were already in the exponential growth

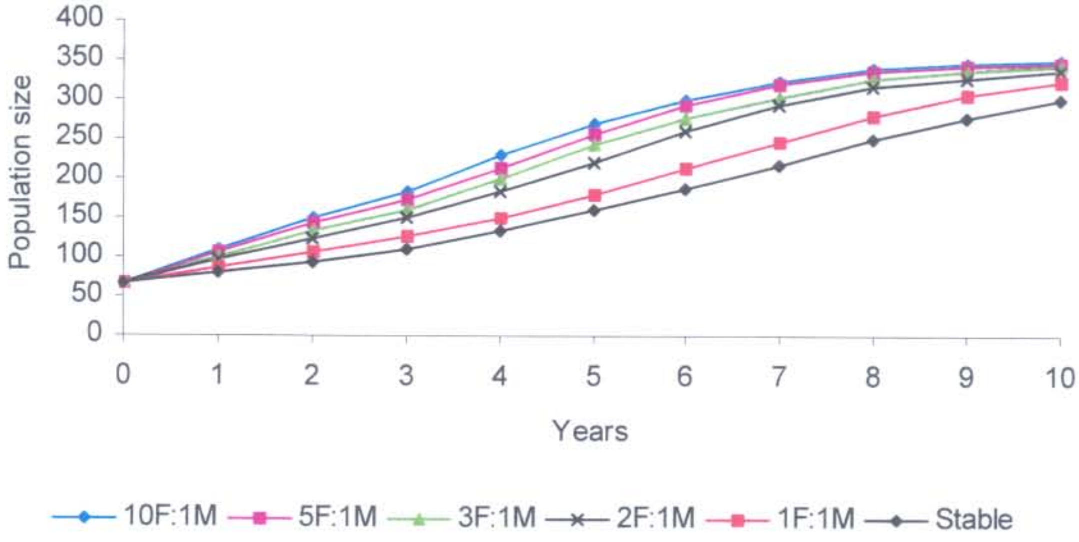

Figure 46: The comparative growth curves of Arabian oryx populations with different ratios of breeding age females per male, as modelled over a 10-year period, indicating the mean projected annual population size after 1000 iterations.

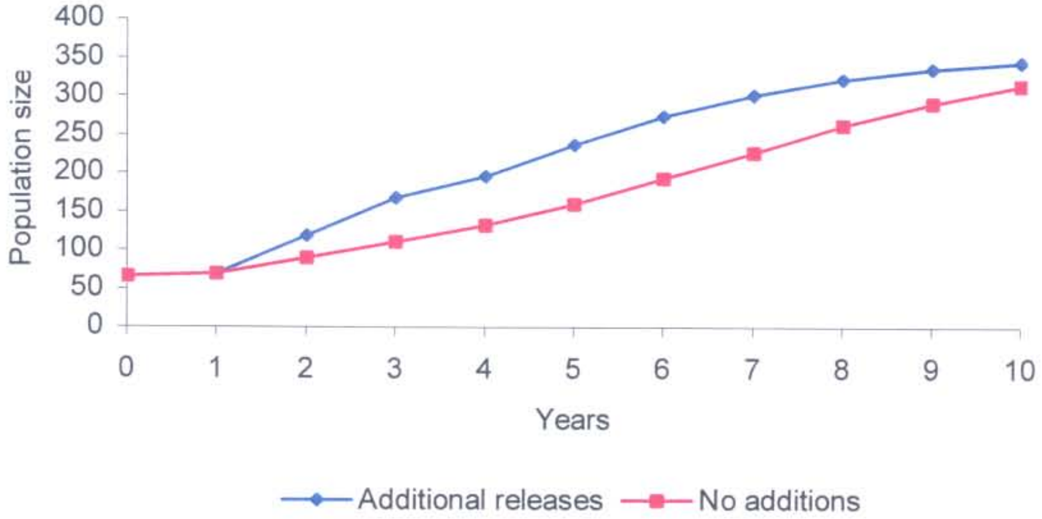

Figure 47: The comparative population growth curves of Arabian oryx populations with (blue) and without (red) the additional release of 55 animals during the third, fourth and fifth years of a simulation before ecological capacity is reached.

phase. In the exponential growth phase the resources available to the population are unlimited and population growth occurs unhindered (Bothma 1996). This exponential growth is not due to a sudden increase in productivity, however, because the ratio of calves to adult females was virtually the same in all the models whether using additional releases (65.0% calving rate) or not (64.3% calving rate). Rather, the modelled populations entered the exponential growth phase because of an increase in the number of breeding age females, which was a direct result of the additional releases. This increase in the number of females of breeding age, combined with the favourable environmental conditions in the models, led to more females conceiving and giving birth successfully. Not only did the modelled populations with additional releases grow more rapidly, but they also reached greater population sizes and mean projected population sizes. Based on the models used in this part of the study and the assumptions associated with these models the additional release of 55 oryxes over a 2-year period was beneficial to the reintroduced Arabian oryx population because it accelerated the population growth.

The additional release of oryxes into the population over the medium term (100 years) was not modelled because the corrected basic model indicated that the population growth rate levels off and becomes asymptotic after about 10 years into the model, when the ecological capacity is reached. The additional release of animals into a population close to its ecological capacity will, therefore have little positive effect on the population, because it cannot significantly increase its population size without a concomitant increase in the ecological capacity of the area. Whether it would have any negative effects is not clear. It is, for example, known that the additional release of adult male mountain gazelles into the wadi systems of the 'Uruq Bani Ma'arid Protected Area disrupted the established social hierarchy among the males (Wacher, *pers. comm.*[8]). This in turn could result in increasing competition between these males, increasing adult male mortality rates and finally lowering lamb production. Elsewhere such disruptions of the social structure have also been observed while it has also been noted that additional releases could introduce pathogens to populations (Cunningham 1996).

It is likely that future additional releases of Arabian oryxes into the protected area will have a significant effect on the population growth when these releases take place at the end of catastrophic droughts, provided that the resident population is not yet at or close to the ecological capacity of the area. This will allow the number of breeding age animals once

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again to be increased, which in turn could result in increased population growth provided that the environmental conditions allow it to happen.

The effect of increasing mortality on population persistence

The projected effect that an increase in the mortality rates of adult male and female Arabian oryxes would have on the size of a population over the medium term is illustrated graphically in Figure 48. An increase of 5.0% in the mortality rate of adults resulted in a mean projected population size of 186.02 ± 120.50 animals after 100 years of simulation. The mean maximum population size that would be reached after such time is 201.21 ± 119.02, or approximately half the estimated ecological capacity of the area. The mean projected population growth rate during this modelling period is $r = 0.038 \pm 0.320$. As could be expected, increases of 10.0% and 15.0% in the adult mortality rates resulted in even lower projected population growth rates and mean population sizes after a 100-year period. In the worst case scenario where adult mortality was increased by 15.0%, the modelled populations experienced a projected mean negative growth rate ($r = -0.22 \pm 0.323$). Subsequently the mean population size after 100 years of modelling would be 103.65 ± 103.19 animals. Such increases in the mortality rates of adult male and female Arabian oryxes will result in 71.1% of all the modelled populations becoming extinct within 100 years (Figure 49). The first extinction will occur after a mean of 51.55 ± 24.45 years since the original release.

The modelled populations were relatively insensitive to an increase in the mortality rate of the juvenile male oryxes only. In the worst case scenario where the juvenile mortality rate of the males was set at 60.0%, the modelled populations still reached a projected mean population size of 233.77 ± 121.20 animals after 100 years. During that time the projected mean population growth rate was $r = 0.067 \pm 0.318$ and the probability of persistence was 0.899 (Figure 50). This indicates that 89.9% of the modelled populations will survive the modelling period, despite the fact that 60.0% of the juvenile males did not survive. At the end of the modelling period the final projected heterozygosity was 0.879 ± 0.089. In contrast, the modelled populations were sensitive to an increase in the mortality rate of the juvenile females. In this instance the worst case scenario resulted in a projected negative population growth rate ($r = -0.019 \pm 0.302$) over a period of 100 years, with a final mean projected population size of 78.65 ± 88.86 oryxes. The majority (65.2%) of the modelled populations will become extinct during the modelling period (Figure 50) and the final projected heterozygosity of the modelled populations was 0.836 ± 0.165. However, such a skewed juvenile mortality rate, where the juvenile female oryxes disappear from the population at a much higher rate than the juvenile males, seems unlikely to occur under normal circumstances. It does, nevertheless, illustrate the sensitivity of the populations to increasing mortality rates in the juvenile females.

A simultaneous increase in the mortality rates of juvenile male and female oryxes through disease, drought or predation would also affect the reintroduced population adversely (Figure 51). An increase in the mortality rate of juvenile Arabian oryxes to 50.0%, for example, will decrease the probability of oryx populations persisting over a period of 100 years to 0.60, indicating that 40.0% of all the populations are likely to face extinction within that time frame. Such levels of mortality among the juveniles are not considered to be unrealistic. Mace (*pers. comm.* In: Magin & Kock 1997) suggested that the mortality rate of juvenile roan antelope could reach levels of up to 60.0% due to predation, because the young of these animals hide during the first few weeks after birth. Fryxell (1987) reported mortality rates of up to 50.0% in the white-eared kob *Kobus kob leucotis* (Erxleben, 1777) calves, while Somers (1997) used a 55.0% first year mortality rate in modelling a warthog population. According to Beudels, Durant & Harwood (1992) a decrease in the calf mortality of the roan antelope within the national parks of Burundi could result in substantial annual population growth, thereby reducing the probability of extinction of these small and isolated populations. In cheetah populations it was, however, found that increased cub survival plays a minor part in increasing population growth or population persistence (Crooks, Sanjayan & Doak 1998). That study revealed that the protection of adult cheetahs was more important in maintaining viable populations than a decrease in cub mortality due to predation, for example. That is partly attributed to the breeding biology of the cheetah where females have relatively large litters and where such litters can be produced rapidly after the loss of a previous litter.

Currently predation is not likely to cause high mortality rates in the Arabian oryx within the 'Uruq Bani Ma'arid Protected Area. This is due to the absence of predators larger than the red fox *Vulpes vulpes* (Linnaeus, 1758) in the area as revealed by trapping (Seddon & van Heesnik, *pers. comm.*[9]) and a lack of any signs that suggests otherwise (Strauss, *pers. obs.*). Cognisance should, however, be taken of the potentially devastating effect that a lack

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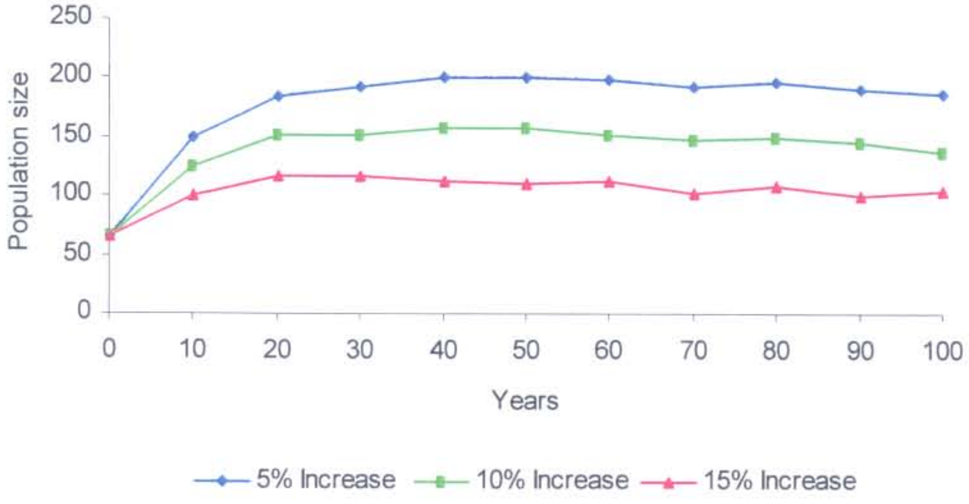


Figure 48: The comparative effect that an increasing mortality rate in adults will have on the growth of the modelled Arabian oryx populations over a period of 100 years.

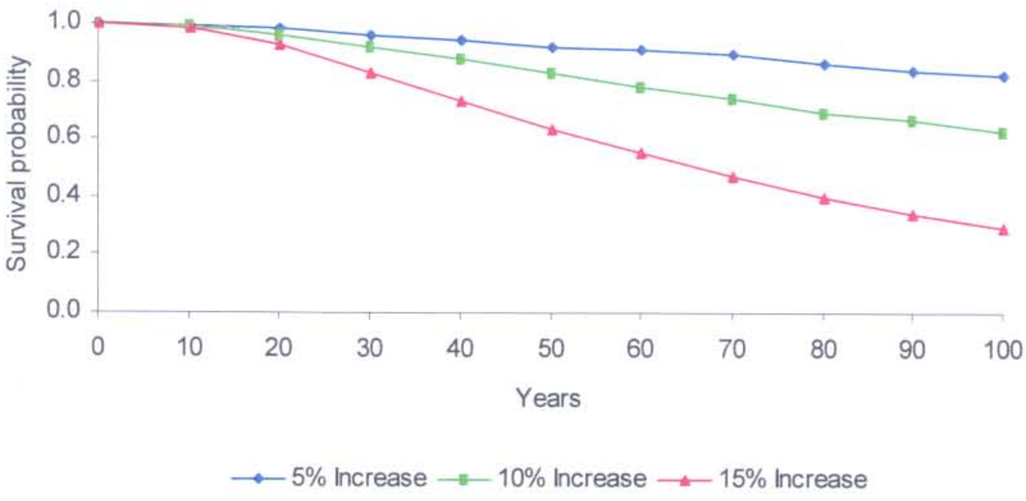
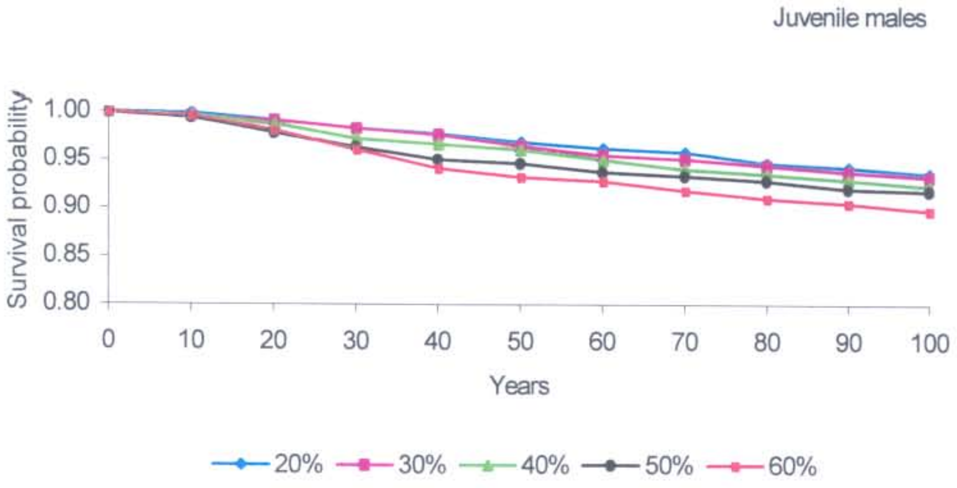


Figure 49: The effect of increasing mortality rates in adults on the survival probabilities of the modelled Arabian oryx populations over a period of 100 years.



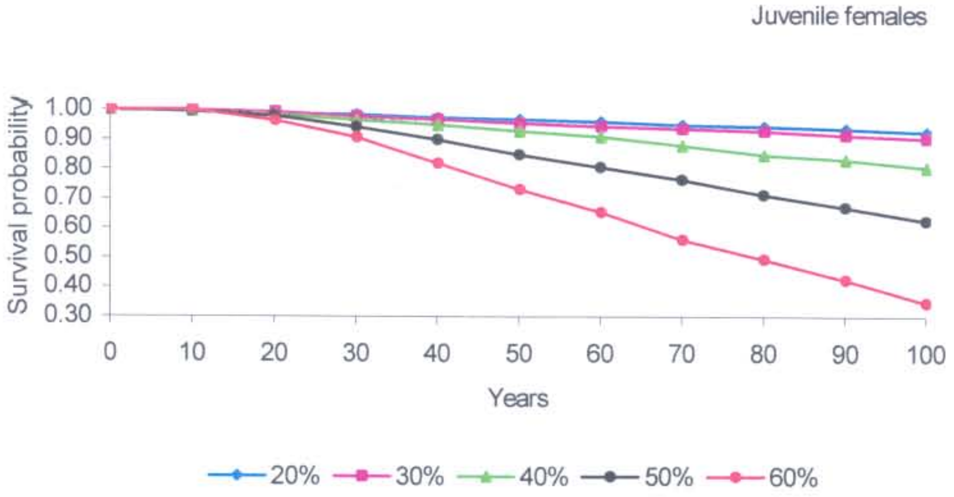


Figure 50: The effect of increasing mortality rates in juvenile males and juvenile females on the survival probability of modelled Arabian oryx populations during the medium term (100 years) when the mortality rates of the adult males and females are kept constant.

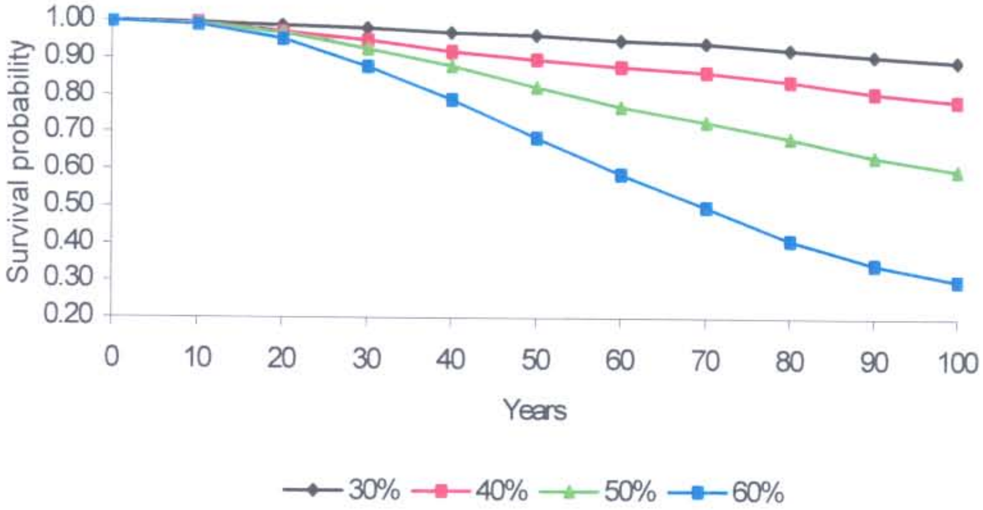


Figure 51: Sensitivity analyses indicating the survival probabilities of the modelled Arabian oryx populations over a period of 100 years, at increasing rates of mortality in juveniles and constant rates in the adults.

of female recruitment could have on the population, due to the potential decrease in the number of females reaching breeding age. It is known that mainly female oryxes have been targeted in the live-capture of oryx in Oman. The devastating effect that that has had on the resident population has been well-documented (Spalton, *et al.* 1999).

It is likely that the mortality rates of various age and sex classes would increase simultaneously in the event of large-scale poaching. With a simultaneous increase in the mortality rates of more than one age group, the effect on the population parameters over 100 years is amplified. Various scenarios regarding the mortality rates of juvenile, adult male and adult female oryxes were modelled in an attempt to simulate this. The results are illustrated graphically in Figures 52 and 53. A medium level of poaching was simulated by setting the mortality rate of the juveniles at 30.0% and that of the adult females and males at 10.0% and 15.0% respectively. This resulted in a mean projected population growth rate of $r = 0.020 \pm 0.315$ after a 100-year modelling period. This means that the projected population will increase from the initial 66 oryxes to a mean of 152.07 ± 118.04 during the modelling period. In 1000 simulation over 100 years, 772 (72.2%) of the modelled populations will survive. The final projected heterozygosity of the modelled populations was 0.860 ± 0.124.

A further increase in either the mortality rate of the juveniles, the adult males or the adult females will cause negative, mean projected population growth rates over the modelling period. For example, a juvenile mortality rate of 40.0% in addition to mortality rates of 10.0% and 15.0% respectively in adult females and males resulted in a mean projected population size of 118.93 ± 106.40, from a mean projected population growth rate of $r = -0.004 \pm 0.312$ over the 100-year modelling period. The survival probability of populations with such mortality rates is 0.51. Such an increase in the mortality rates furthermore will result in a decrease in the final projected heterozygosity to 0.839 ± 0.137 in the modelled populations.

These results show that relatively small simultaneous increases in the mortality rates of the different age and sex classes, due to poaching for example, could have a devastating effect on the future survival of the Arabian oryx population. Apart from environmental catastrophes, poaching is probably the biggest potential threat to the reintroduced Arabian oryx population. Poaching has also been found to be major threat in other antelope populations. In Kenya, for example, the poaching of roan antelope between 1985 and 1990 reduced the population from approximately 110 individuals to between 30 and 35 animals, representing an increase of 10.0% in the mortality rate of the adults over the estimated 5.0% natural mortality rate in

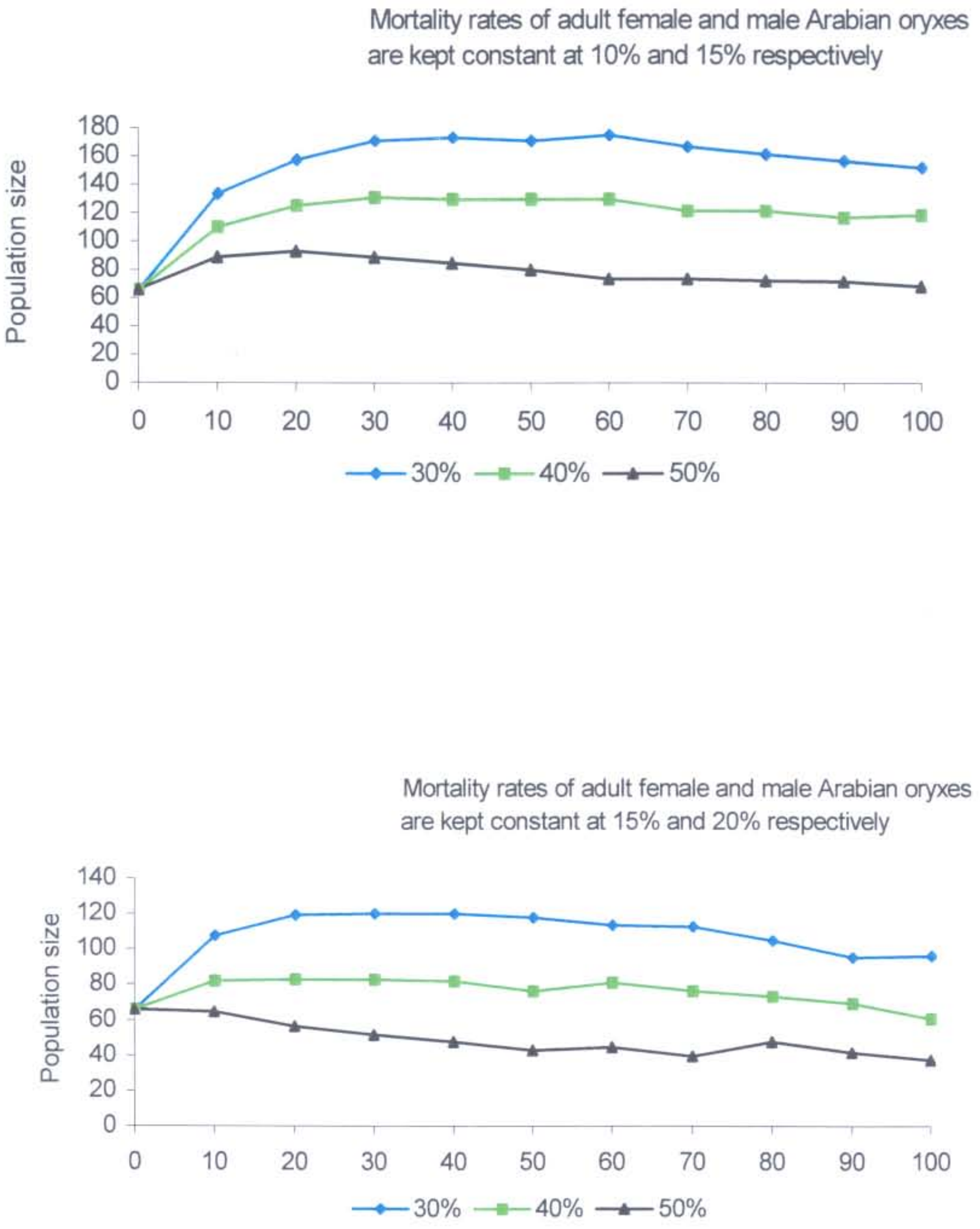
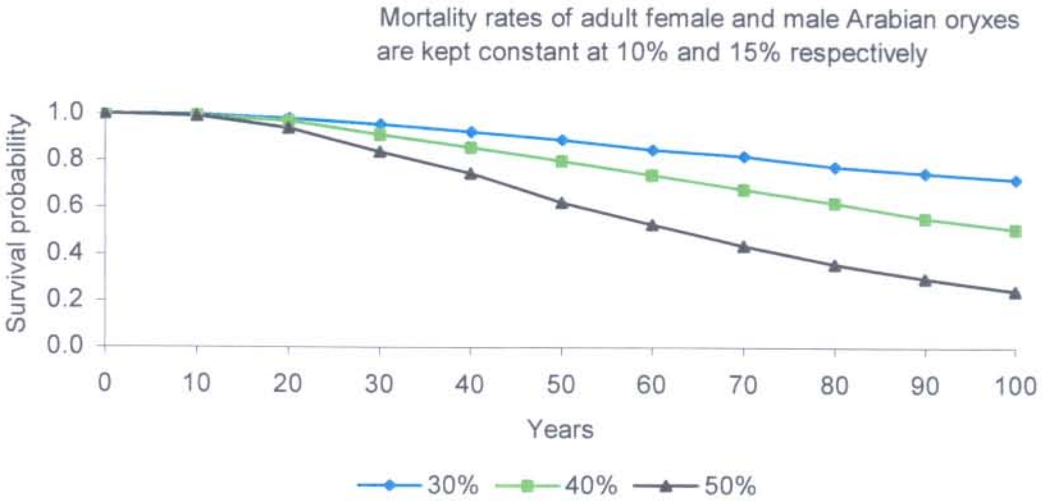


Figure 52: Sensitivity analyses showing the comparative projected population growth curves of the modelled Arabian oryx populations with increasing mortality rates of juveniles at different rates of mortality in the adult males and females.



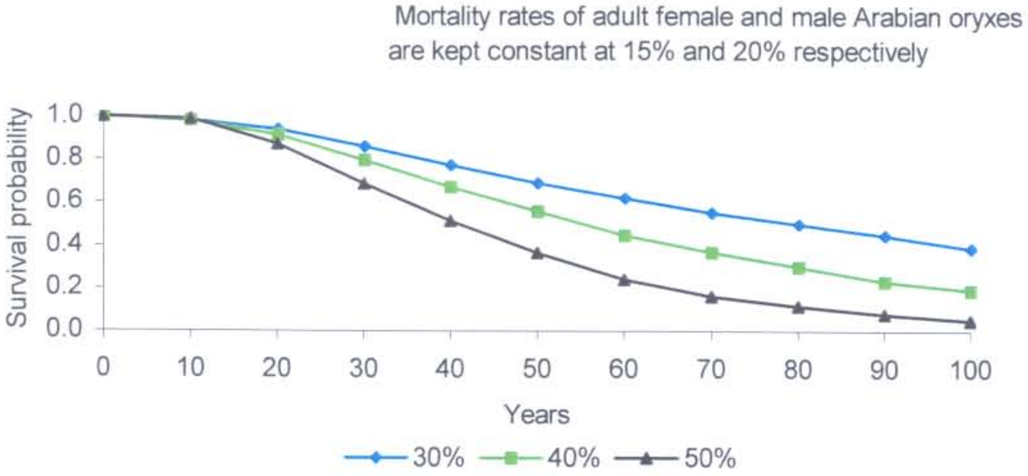


Figure 53: Sensitivity analyses showing the survival probabilities of the modelled Arabian oryx populations over a period of 100 years with increasing mortality rates in the juveniles at different rates of mortality in the adult female and male oryxes.

adult roan antelope (Magin & Kock 1997). Similarly the Arabian oryx population in Oman decreased from an excess of 400 individuals in October 1996 to 138 individuals in September 1998 because of poaching (Spalton *et al.* 1999). This represents a 65.5% decrease in the size of the Arabian oryx population over a 2-year period.

The results of the models in this part of the study also indicate that the survival of especially the female oryxes is of particular importance to the persistence of the Arabian oryx population in the 'Uruq Bani Ma'arid Protected Area. The importance of adult survival for population growth is well documented for many moderately to long-lived species (Casswell 1989; Emlen & Pikitch 1989; Lande 1991; Doak, Kareiva & Klepetka 1994; Heppell, Walters & Crowder 1994). Tear (1994) suggested that management action in Oman should be focused on maintaining survivorship of young oryx. Therefore, supplementary food and water should be supplied to herds where young animals can be found during periods of drought. Since droughts develop over time it would seem, however, that a monitoring program focussing on the well being of especially the breeding age females could be particularly useful in determining and predicting the effect of the drought on the population. As is the case with the brown bear *Ursus arctos* (Linnaeus, 1758) in Spain (Wiegand, Naves, Stephan & Fernandez 1998) the survival of females should be the principal management target in the 'Uruq Bani Ma'arid Protected Area because the females are critical to the recovery of the population. Similar conclusions were reached in studies of grizzly bears *Ursus arctos horribilis* in Yellowstone National Park (Knight & Eberhardt 1985).

Recent work done on the Arabian oryx in the Mahazat as Sayd Protected Area in the Kingdom of Saudi Arabia has suggested that the Allee effect influenced population growth in that area (Treydte, Williams, Bedin, Ostrowski, Seddon, Marshall, Waite & Ismail 2001). The Allee effect is characterised by the inability of the social structure of small populations to function once the size of the population decreases to below a certain level. This results in decreased productivity because the animals are unable to find mates once the population density decreases below a certain level. This, in turn, leads to an even smaller population, worsening the problem (Primack 1998). Although VORTEX caters for the analysis of the Allee effect in the population models, this option was not included in any of the models in the present study. Monitoring during the present study indicated that 62.0% of the breeding age females conceived and delivered calves during 1995. During the same year 25.0% of the breeding age females, or 40.0% of those females that calved, conceived in captivity at either the National Wildlife Research Centre or in the protected area enclosures before release. During 1996, however, 73.5% of the breeding age females in the protected area produced calves, while 97% of such females gave birth during 1997 (Chapter 8). These results strongly suggest that the Allee effect did not influence the birth rate in the 'Uruq Bani Ma'arid Protected Area.

Conclusions

The prediction models presented in this study indicate that under the observed environmental conditions and subject to the specified assumptions within the models, the Arabian oryx population in the 'Uruq Bani Ma'arid Protected Area is secure over the short term, but could become vulnerable over the medium term.

Release groups with stable age distributions showed lower projected population growth rates and consequently lower final population sizes than all the other release groups where varying ratios of female to male oryxes were modelled. A ratio of 10 adult females per male showed the highest projected population growth rates. A ratio of five adult females per male is, however, more ideal because of the high attrition rate among the adult males when compared to the females. The latter ratio will result in population growth rates that are similar to a ratio of 10 adult females per male.

The Arabian oryx populations that were modelled here showed that catastrophes such as a 5-year drought period will affect the reintroduced population, but it will not be enough to drive the population to extinction. Various combinations of catastrophe, however, will mostly prove to be fatal for the modelled populations. Because of the effect that such catastrophes could have on the population, the oryx females, especially the adult females, should be the focus of management activities during periods of drought. This has been confirmed through sensitivity analyses. While the projected populations seem to tolerate increasing mortality rates in the males, they are sensitive to increasing mortality rates in the females. The additional release of animals has the potential to impact positively on the population already established, provided that the population has not yet reached the ecological capacity for the habitat.

This chapter has focussed on some of the direct causes of population decline which could eventually lead to the extinction of the Arabian oryx population that was reintroduced into the 'Uruq Bani Ma'arid Protected Area. The causes of endangerment and possible extinction are manifold (Primack 1998), however, and include direct causes such as those modelled here, others such as habitat destruction, or even less direct pathways to extinction. Less direct pathways, which could also influence persistence time, include the mechanisms by which females choose their mates and the effect that those mechanisms have on the effective population size (Blumstein 1998). Bearing this in mind there are many factors that could potentially influence the future survival of the reintroduced Arabian oryx in the ‘Uruq Bani Ma’arid Protected Area. It is therefore imperative that the population be monitored continuously, that the data collected are analysed continuously and that those hypotheses that are formulated from the data are tested in the field.