

Chapter 5: Population viability of cheetahs in two contrasting habitats

5.1 INTRODUCTION

Cheetahs occur at low densities (Myers 1975; Hamilton 1986; Kelly & Durant 2000) across an increasingly restricted range in sub-Saharan Africa, inhabiting both woodland and open plains habitat (Caro & Collins 1987a). The main threats to cheetah populations are loss of habitat and persecution by humans (Myers 1975; Anderson 1983; Marker-Kraus et al. 1996); competition from other large predators (Caro & Laurenson 1994; Laurenson 1995; Laurenson, Wielebnowski & Caro 1995); and lack of genetic diversity (O'Brien et al. 1983; O'Brien et al. 1985; O'Brien, Wildt & Bush 1986; O'Brien et al. 1987). Competition with other large predators was identified as a major threat to cheetah populations when Laurenson (1994) found that the exceptionally high cub mortality (95%) on the Serengeti Plains was chiefly due to predation by lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*). Lions were the main predator accounting for 73% of cheetah cub deaths (Laurenson 1994). The extremely high rates of cheetah cub predation in the Serengeti, an open grassland system, may be associated with a shortage of available refuge sites for cubs and their extreme vulnerability on the short grass plains (Caro & Durant 1995; Laurenson 1995). Therefore, conditions in woodland habitats may be more favourable to cheetahs for avoidance of predation, because of increased availability of cover for refuges and concealment. In fact, cheetah populations in woodland savannas seem to have lower juvenile mortality rates (Hunter 1998; Purchase 1998), and therefore indeed may be exposed to less threat from predation than grassland savanna populations are.

Because animal species occurring in distinct habitat types may experience different development rates, life spans, and birth and death rates (Pulliam & Danielson 1991), different populations of the same species may show different rates of population growth and persistence across a spectrum of habitat conditions. In this chapter, a population viability analysis (PVA) was conducted, using the computer simulation model

VORTEX (Miller & Lacy 1999), to explore the population dynamics of cheetahs occupying contrasting habitats – a woodland and grassland savanna. The question asked here is: for a given population size, is cheetah population viability higher in a woodland savanna than a grassland savanna? A long-term data set from the Serengeti Plains in East Africa (Kelly & Durant 2000) provided the demographic data required to simulate the dynamics of a grassland savanna cheetah population. The Kruger National Park (KNP), having a population size (Pienaar 1969; Bowland 1994) similar to the Serengeti Plains population (Kelly & Durant 2000), was a hypothetical woodland savanna population. A cheetah study in the KNP (1987 – 1990; see Chapters 3 and 4) provided some demographic data for woodland savanna cheetahs; the remaining data were gathered from other cheetah studies in southern African woodland savannas (Berry et al. 1997; Hunter 1998; Purchase 1998).

The main objectives of this chapter are to: (1) assemble life history and demographic data on cheetahs inhabiting grassland and woodland savannas respectively; and (2) conduct a PVA to compare the viability of cheetah populations in those two contrasting habitats. Sensitivity analyses were used when demographic data were uncertain and for comparing viability under different scenarios. In this way, the PVA helps to identify parameters that the populations may be particularly vulnerable to (Lacy 1993). It is important to note that the model outcomes in this PVA are not meant to make any precise predictions or give absolute answers about the long-term persistence of the two cheetah populations. The value, however, lies in being able to compare the model outcomes of the two cheetah populations to understand how varying demographic parameters affects population viability and what implications this has for managing and conserving cheetahs. Demographic models are commonly used to make decisions for managing wild populations of threatened or endangered species (Beissinger & Westphal 1998), which has an important application for cheetah re-introductions into small parks and nature reserves. Finally, the relationship between cheetah cub mortality and cover availability is discussed.

5.2 METHODS

Population viability analysis is a process in which the probability that a population will become extinct is assessed within a specific period and under specific circumstances (Shaffer 1981). The computer simulation model VORTEX, version 8 (Miller & Lacy 1999) was used to perform the PVA. VORTEX models the deterministic and stochastic processes that determine population performance (Miller & Lacy 1999). In these analyses, general species and population specific parameters were assembled for cheetah populations in a grassland and woodland savanna (Table 5.1). Demographic data for the woodland cheetah population were collated from cheetah studies in the south eastern region of the Kruger National Park, South Africa (field data collected by M.G.L. Mills, 1987 – 1990); Matusadona National Park (MNP), Zimbabwe (Purchase 1998); Phinda Resource Reserve (PRR), South Africa (Hunter 1998); and on commercial livestock farmlands, Namibia (Berry et al. 1997) for the woodland savanna population. Data from the Serengeti Plains in East Africa were used for the grassland savanna population (Laurenson 1995; Kelly & Durant 2000).

5.2.1 General species parameters used in VORTEX for both populations

The VORTEX program was set for 500 reiterations projected at 100 years into the future. A population with a 95% probability of surviving over 100 years was assumed to be viable with an acceptable risk of extinction (Shaffer 1981). The following assumptions were made for the models: (1) no inbreeding depression was incorporated into the simulations; (2) no catastrophes were assumed for both populations; (3) environmental variation in survival was correlated with environmental variation in reproduction as cheetah mothers are known to abandon cubs if they cannot obtain enough food (Laurenson 1995; Purchase 1998); (4) populations were considered isolated and immigration was not included in the simulations as data for this were unavailable for both areas. Emigration, however, is incorporated into sub-adult and adult mortality rates (see below); (5) reproduction was assumed to be density independent as there is no evidence from previous cheetah studies to that show that the number of females which breed and

Table 5.1. Values for life history and demographic parameters used for input into VORTEX for simulating the population dynamics of two cheetah populations in contrasting habitats. Figures in brackets under mortality rates represent variations from baseline scenarios for sensitivity analyses. Data for the baseline scenario for the woodland savanna population were obtained from cheetah studies conducted in the south eastern region of Kruger National Park (this study); Matusadona National Park (Purchase 1998); Phinda Resource Reserve (Hunter 1998) and commercial livestock farmlands in Namibia (Berry et al. 1997). Data from the Serengeti Plains (Kelly & Durant 2000) were used for the baseline scenario for the grassland savanna population.

VORTEX parameter	Woodland savanna	Grassland savanna
Age at first reproduction	2 years*	2 years*
Maximum annual litter size	6 (1 litter)	18* (3 litters)
Litters size distribution*	1 – 6 cubs: 3.75, 3.75, 40, 32, 20 and 0.5 respectively.	1 – 18 cubs: 1.6, 2, 20, 16, 10, 8, 11.5, 11.5, 7, 4.5, 3.5, 2.4, 1.4, 0.5, 0.1, 0, 0, 0 respectively.
Proportion of females breeding per year (%)	68 ± 6.8	87.4* ± 8.74
Mortality rates (%)		
0 – 1 years	50 (and 25)	90* (85 – 95)
1 – 2 years	15 (– 65)	35* (30 – 40)
Adult > 3 years	15 (– 25)	15* (10 – 20)
Age of senescence	12*	12*

* Kelly & Durant (2000)

produce cubs decreases with increasing population size (Purchase 1998; Kelly & Durant 2000); and (6) all males were assumed to be in the breeding pool for both populations.

Caro (1994) found in the Serengeti that male cheetahs display two behavioural tactics for acquiring mates: either holding a mating territory or roaming in search of females. Therefore, it was assumed that most males would find and mate with at least one female (Purchase 1998).

Age at first reproduction for a single female cheetah in KNP was approximately 2.6 years. In Namibia, the average age of first reproduction for females was estimated at about three years in the wild farmland cheetah population or Etosha National Park (Berry et al. 1997). The average age of first reproduction in the Serengeti is 2.4 years (Kelly et al. 1998). Females are, however, capable of producing their first litters at two years of age (Schaller 1972; Berry et al. 1997; Kelly & Durant 2000). Therefore, Kelly & Durant's (2000) 'optimistic estimate' of two years for age of first reproduction for females was used for both populations as VORTEX does not allow fractional ages (Miller & Lacy 1999). Age of first breeding for males was also set at two years as male cheetahs are physiologically capable of breeding at this age (Caro 1994), but social constraints may limit breeding to older animals (Berry et al. 1997). Being a polygynous species, however, reproductive age is not considered to have a significant demographic effect on the model unless populations are extremely small (Berry et al. 1997). Differences in fecundity, such as the age at first reproduction, appeared to have little effect on the potential number of cubs produced compared with increasing cub survival by avoiding predators (Laurenson 1995). Age of first reproduction also appear similar for both cheetah populations, and therefore any effect on outcome would be applied to both populations.

A stable starting age distribution was used for both populations, wherein VORTEX assigns individuals to each age-sex class proportionate to the stable age distribution (Miller & Lacy 1999). In the initial analyses, a starting population size of 250 was used for both populations, as these are approximate to estimates established by Pienaar (1969) and Bowland (1994) for the KNP population and Kelly & Durant (2000) for the Serengeti Plains population. Starting population sizes of 15, 25, 50, 150 and 200 were also used to analyse for effects on extinction risk.

Carrying capacity was set at 500 individuals. This is an arbitrary selection that allows room for population growth before truncation (Kelly & Durant 2000). The cheetah population in the Serengeti also appears to show no signs of density dependence (Kelly & Durant 2000), and this was assumed for the woodland savanna cheetah population.

5.2.2 Population specific parameters

Female cheetahs are considered to produce between one and six cubs per litter (Berry et al. 1997; Purchase 1998; Kelly & Durant 2000; and KNP study). In the KNP, a female cheetah with four successive litters of cubs only produced a maximum of one litter per year (or six cubs per year). Berry et al. (1997) and Hunter (1998) used maximum litter sizes of five and six cubs respectively per year. Adult females, however, in the Serengeti with exceptionally high rates of cub mortality (estimated at 95%) conceive again rapidly (Laurenson, Caro & Borner 1992). Females mated, on average, within three weeks of losing the previous litter (Laurenson et al. 1992). Kelly & Durant (2000) assumed in their viability model that a cheetah mother in the Serengeti could give birth to a maximum of three litters per year, therefore producing a maximum of 18 cubs a year (VORTEX defines this as maximum annual litter size). They calculated probabilities for annual litter sizes ranging from 0 – 18, which were adapted slightly for use in the VORTEX model. Probabilities of giving birth to litter sizes of one to six cubs for woodland savanna cheetahs were obtained from Laurenson (1992, in Kelly & Durant 2000). Litter size distributions for both populations considered average litter size at birth to be approximately 3.5 cubs. This mean, however, is probably an underestimate as litters were only examined on average 15 days after parturition (Laurenson et al. 1992). Reports vary depending on when litter size was calculated. The average litter size in MNP was estimated at three cubs (Purchase 1998). Field data in Namibia yielded a mean litter size of 3.4 cubs (Berry et al. 1997). Both, however, appear to be underestimates, as litter sizes were estimated after emergence from the lair. Hunter (1998) recorded a mean litter size of 4.4 ± 0.94 cubs in PRR. The sex ratio at birth was set at 0.5 (Pettifer 1981; Laurenson et al. 1992; Berry et al. 1997).

In PRR, one female with three litters had an inter-litter interval of 16.5 months. In the KNP a female with three successive litters had a mean inter-litter interval of 18.6 ± 1.25 (SD) months. Combining the two areas, the average inter-litter interval was estimated at 17.6 months; i.e. 68% of female cheetahs will produce a litter in a given year. Berry et al. (1997) used estimates of 75% and 60% of the proportion of females producing litters in a given year. The standard deviation (SD) used by VORTEX for the percent females producing litters of offspring reflects environmental variation in reproduction (Miller & Lacy 1999). Insufficient data, however, prevented an estimation of this. Kelly & Durant (2000) were also unable to obtain a direct measure of this variation in the Serengeti, but entered a range of values in SD from 5% to 40% of the mean proportion breeding, and found no effect on extinction risk. Consequently, they set the SD equal to 10% of the mean, and the same was applied for the woodland savanna cheetah population.

No data were available regarding age of senescence for KNP and PRR cheetahs, therefore, 12 years of age was used as the maximum age (Kelly & Durant 2000) in the model for both cheetah populations, and assumes that the animals can breed (at normal rates) throughout adult life.

Data for age-specific mortality rates for woodland savanna cheetahs are exceptionally sparse. The KNP data were able to provide some estimate of juvenile mortality rate from a single adult female cheetah with three successive litters of cubs. Here, juvenile mortality for 0 – 12 months was estimated at 45% ($n = 3$ litters). Litter size was estimated when cubs were approximately six weeks of age. Hunter's (1998) mortality rate for 0 – 12 months was 25%. Purchase's (1998) observations in MNP estimated mortality 0 – 2 years at 60% ($n = 2$ litters). Cub mortality from emergence to maturity was estimated by Pienaar (1969) as 50% in the KNP, and by Eaton (1970) and McLaughlin (1970, in Caro 1994) as 50% and 43% respectively in Nairobi National Park. Cub mortality of Namibian ranchland cheetahs between three months to one year of age was estimated at 46%, however, due to the absence of other predators in these areas, this statistic was disregarded. Considering the above, juvenile mortality (0 – 12 months) in the woodland savanna was set at 50% (for the baseline scenario) and 25%. These values may be considered optimistic, however, as mortality rates were not measured

immediately from birth. Laurenson (1994) estimated that 94.4 – 96% of cubs die before reaching independence at 14 months of age. The conservative figure, however, of 90% adopted by Kelly & Durant (2000) for the age-specific mortality rate 0 – 12 months was used in the VORTEX model for the grassland savanna cheetah population.

A three year study in the Serengeti by Laurenson (1995) estimated age-specific mortality for female cheetahs as 15.3% (adolescent, < 3 years), 22.7% (prime, 3 – 9 years) and 55% (old, > 9 years). Kelly & Durant's (2000) long-term data set on Serengeti cheetahs over 20 years, which estimates adolescent (1 – 2 years) and adult (> 2 years) female mortality as 35% and 15% respectively, however was used for the baseline scenario for simulating the grassland savanna cheetah population. While Laurenson's (1995) mortality estimates includes only those female cheetahs that died, Kelly & Durant (2000) estimates were based upon time of last sighting, which therefore includes those cheetahs that emigrated or dispersed out of the study area. This may explain the higher mortality estimates documented by the latter. The grassland savanna population was also modelled with Laurenson's (1995) sub-adult mortality estimate of 15%.

Data for sub-adult survival in woodland savannas proved the most problematic as no real studies have been conducted to estimate mortality rates for this cohort. Hunter (1998) used sub-adult mortality rates of 12.5% and 10% for males and females respectively, based on natural mortality estimates of Namibian cheetahs (Berry et al 1997). Berry et al. (1997), however, considers total annual mortality to range up to 30% with removal on farmlands by humans. A radio-telemetry study on 18 male and 8 female Namibian cheetahs reported by Berry et al. (1997) estimated crude annual death rates for cheetahs over one year of age to be 38.6% for males and 19.2% for females, of which four of the males were shot. Purchase (1998) estimated annual adult and sub-adult mortality at 20.5% using projected and actual population sizes observed over three years of study. These estimates also include those cheetahs that dispersed out of the study area. Considering the above statistics, baseline sub-adult mortality for the woodland savanna cheetah population was modelled at 15%, which was considered to exclude rates of emigration and dispersal. Mortality rates were then increased to include a percentage of cheetahs that may have dispersed or emigrated out of the population (Table 5.1).

The only recorded adult mortalities available for the woodland savanna population were from Hunter's study (1998) in PRR, which estimated male and female mortality at 17.85% and 12.5% respectively. The baseline scenario in this study used an average of 15% for the adult mortality rate. Sub-adult and adult mortality rates (including dispersion and emigration) were then predicted by varying the mortality rates until the population reached a stable or self-replacing state, i.e. growth rate (r) is close to zero and probability of extinction is less than 5%. Positive values of ' r ' are necessary for a population to survive or grow, and, in principle, a zero value characterises a stable population (Berry et al. 1997). No statistics were available for male cheetahs in either of the two habitats, although survival is considered to be lower for adult males than for females (Caro & Collins 1987b; Kelly & Durant 2000). This is mostly a result of intra-specific combat between males (Caro & Collins 1986), but also because non-territorial males are usually behaviourally and physiologically stressed and in poor health due to their nomadic lifestyle (Caro, Fitzgibbon & Holt 1989; Caro & Collins 1987a; Caro 1994). Males are also more likely to disperse out of the area than females, which further decreases measured survival rates (Frame & Frame 1980; Caro 1994; Kelly & Durant 2000). Evidence of this was observed in some woodland savanna cheetah populations. In PRR, sub-adult males were excluded from existing territories of other males and were killed on two occasions by cheetah coalitions (Hunter 1998). In the KNP, two nomadic, sub-adult male cheetahs moving through the study area were found to be in poor condition with mange - one died and the other disappeared. Therefore, males were considered to have higher mortality rates than females, but were initially modelled with equal age-specific mortality rates as females. Thereafter, sensitivity testing was used to assess the effects differential mortality rates may have on persistence by independently varying mortality rates of males and females. Sensitivity analyses were also used to assess the influence varying age-specific mortality rates may have on persistence by independently increasing and decreasing each mortality rate by 5% while holding all others constant (male and females with equal age-specific mortality rates were used for this set of simulations).

The environmental variation (EV) in mortality rates is reflected by the input of a standard deviation into the model for all mean age-specific mortality rates. These

variances, although shown in Kelly & Durant's (2000) viability study on the Serengeti cheetahs, were not available for woodland savanna cheetahs. Therefore, it was assumed that the differences in environmental variation between the two habitats, e.g. in predator and prey densities, were reflected by differences in the age-specific mortality rates. Therefore, EV was kept constant throughout by assigning zero standard deviations values to all age-specific mortality rates. The simulations varying each age-specific mortality rate by 5% will provide some measure of the effect further EV in mortality rates may have on population viability.

5.3 RESULTS

The results of the following set of simulations are presented in Table 5.2. When simulating the baseline scenarios for both cheetah populations, the *grassland savanna* population, although viable, showed a negative growth rate (r) and a 3% chance of extinction. In comparison, the *woodland savanna* population showed a high positive mean growth rate with no chance of extinction. When juvenile mortality of the woodland savanna population was lowered to 25%, mean growth rate climbed even higher. The grassland savanna population showed a positive mean growth rate when sub-adult mortality was lowered to 15%, according to Laurenson's (1995) estimate, and no chance of extinction. When increasing sub-adult mortality rates to 35%, according to Kelly & Durant's (2000) estimate, using the baseline scenario for the woodland savanna population, mean growth rate was still considerably higher than the grassland population with no chance of extinction. Comparing across all scenarios, lower cub mortalities produced higher mean growth rates. A hypothetical self-replacing woodland savanna cheetah population was generated when sub-adult and adult mortality was set at 60% and 23% respectively (with a 50% juvenile mortality), and 68% and 28% respectively (with a 25% juvenile mortality). Exchanging maximum litter size and litter size distribution between the two cheetah populations, while holding all other parameters constant, had a large impact on model outcomes. The probability of persistence for the grassland savanna population (using the baseline scenario) dropped to 0% (Fig. 5.1), while mean growth

Table 5.2. The results of population viability analyses using VORTEX simulating two cheetah populations in contrasting habitats. Demographic parameters used for input into the model are summarised in Table 5.1. Mortality rates are the same for both sexes. r = mean stochastic growth rate over 100 years; SD = standard deviation of r ; PE = mean probability of extinction over 100 years for extant and extinct populations; N = mean population size (across all extant and extinct populations) after 100 years.

Mortality rates			VORTEX results				Comments*
Juvenile	Sub-adult	Adult	r	SD	PE	N	
Grassland savanna							
90	35	15	-0.012	0.07	0.03	99	Baseline
90	15	15	0.04	0.036	0	498	Decrease sub-adult
90	35	15	-0.100	0.152	1.00	0	Adjust litter size = 6
Woodland savanna							
50	15	15	0.230	0.049	0	500	Baseline
25	15	15	0.339	0.058	0	500	25% juvenile
50	35	15	0.164	0.053	0	500	Increase sub-adult
25	35	15	0.266	0.064	0	500	Increase sub-adult
50	60	23	0.000	0.082	0	277	Hypothetical self-replacing population
25	68	28	0.004	0.098	0.01	334	Hypothetical self-replacing population
50	60	23	0.119	0.085	0	498	Adjust litter size = 18

* Comments indicate two baseline scenarios simulated for each population. Thereafter, alternative scenarios simulated with adjusted sub-adult mortalities; maximum litter size; and to generate hypothetical self-replacing populations.

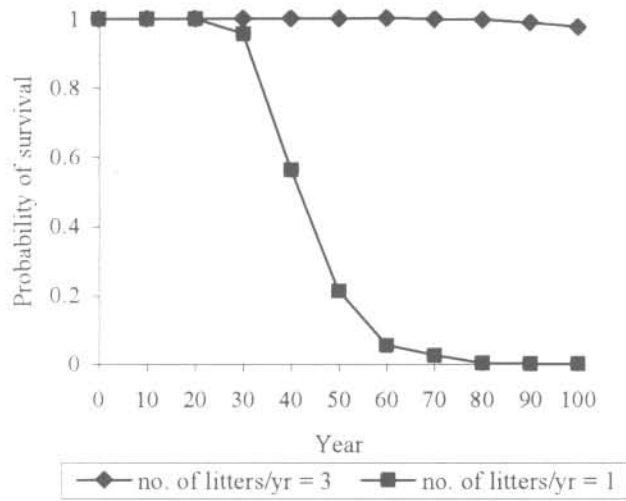


Figure 5.1. The effect of varying maximum litter size on the probability of a grassland savanna cheetah population surviving over 100 years. Three litters per year = maximum litter size of 18 while one litter per year = maximum litter size of six.

rate of the hypothetical self-replacing woodland savanna population increased from 0 to 11.9%. When independently increasing and decreasing age-specific mortality rates by 5% for both populations, mean growth rate and persistence of the *grassland savanna* cheetah population was most affected by changes in juvenile followed by adult mortality (Fig. 5.2a), while the *woodland savanna* population, with 50% juvenile mortality, was most affected by changes in adult followed by sub-adult mortality (Fig. 5.2b). The woodlandsavanna population, with 25% juvenile mortality, showed adult and sub-adult mortality to have an equal and larger effect on growth and persistence than juvenile mortality (Fig. 5.2c).

Using the baseline scenario (Table 5.1) and decreasing starting population size of the *grassland savanna* cheetah population, the probability of survival dropped below the threshold of 95% at a starting population size of 200 (Fig. 5.3). At a starting population size of 50 animals or less, there was a sharper decline in the probability of survival compared to other projections with larger population sizes (Fig. 5.3). The same scenario was then simulated but with sub-adult mortality of the grassland population adjusted to 15%, according to Laurenson's (1995) estimate. The results now showed that the grassland savanna population was still viable at a starting population size of 25 (probability of extinction (PE) = 3%), but not at a starting population size of 15 (PE = 14%). Comparatively, the *woodland savanna* cheetah population, using the baseline scenario (Table 5.1), still had a 100% chance of persistence at a starting population size of 15.

When modelling differential adult and sub-adult mortality rates for male and female cheetahs in the grassland and woodland savanna, female cheetahs had a considerably greater effect on mean growth rate and persistence than males. Increasing and decreasing female mortality rates by 5% resulted in the same outcomes to those observed in Fig. 5.2a for the grassland savanna and Fig. 5.2b and c for the woodland savanna cheetah population. In contrast, increasing adult or sub-adult male mortalities independently to 90%, for both populations, had little effect on PE and mean growth rate. When increasing them simultaneously in 10% increments, the probability of survival dropped below the 95% threshold for the grassland savanna population when adult and sub-adult mortality reached 55% and 75% respectively (PE = 9%), and when the

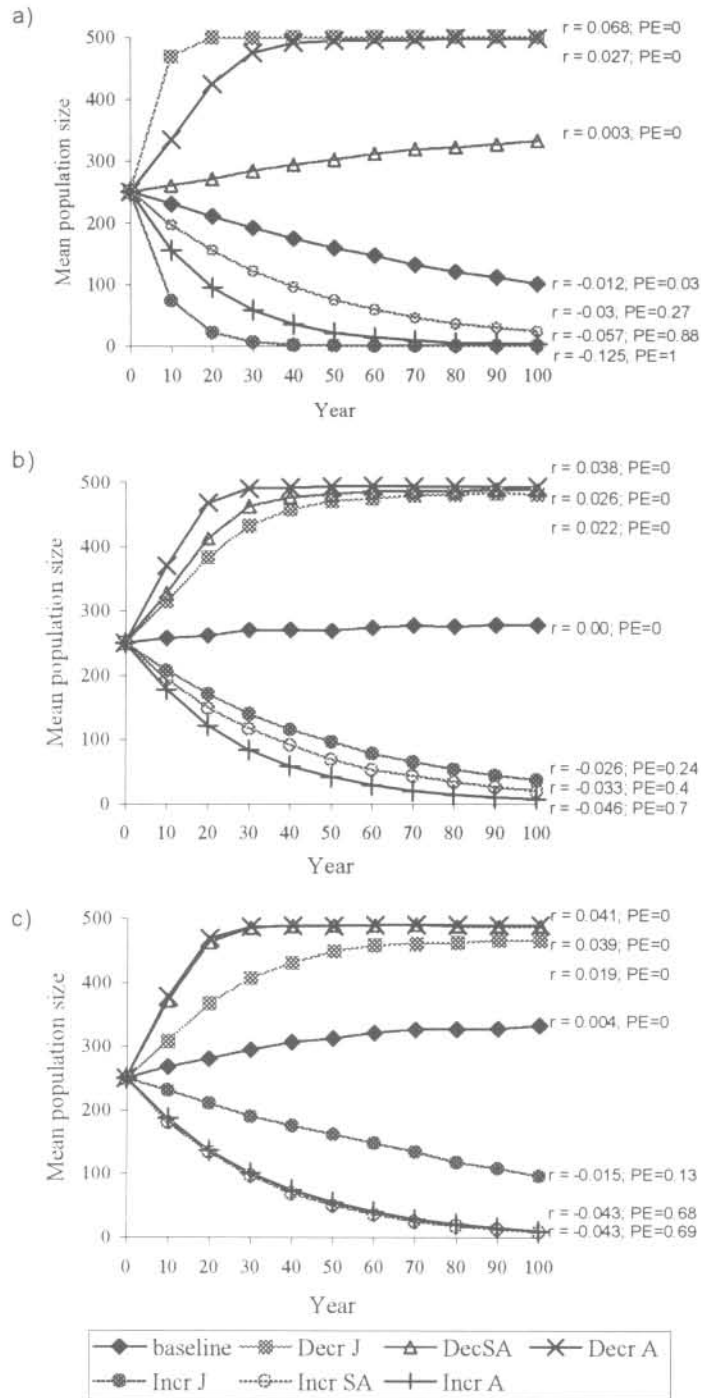


Figure 5.2. The effects of varying age-specific mortality rates by 5% on mean population size of cheetahs in a) grassland savanna with 90% juvenile mortality; b) woodland savanna with 50% juvenile mortality; and c) woodland savanna with 25% juvenile mortality. Baseline = 90%, 35%, 15% for grassland population; and 50%, 60%, 23% and 25%; 68%, 28% for woodland populations for J, SA and A mortality respectively. Decr = decrease 5%; Incr = increase 5%; J = juvenile; SA = sub-adult; A = adult; r = mean stochastic growth rate; PE = mean probability of extinction for extant and extinct populations.

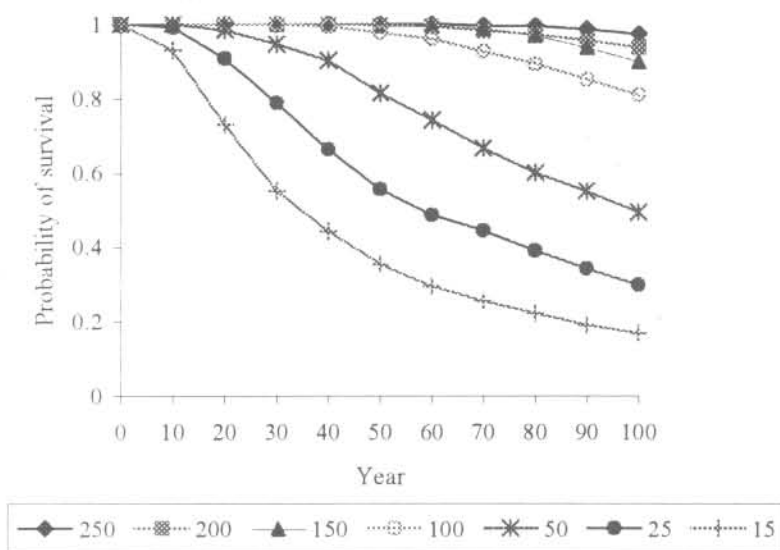


Figure 5.3. The effects of decreasing starting population size (from 250 individuals) on the probability of a grassland savanna cheetah population surviving over 100 years.

woodland savanna population reached 70% and 90% respectively (PE = 7%). There were no changes in mean growth rate for the woodland savanna population and only a slight reduction in mean growth rate ($r = -1.1\%$) for the grassland savanna population when increasing sub-adult and adult mortalities simultaneously.

5.4 DISCUSSION

5.4.1 Population Viability Analysis

The woodland savanna cheetah population appeared to have a greater viability than the grassland savanna population over 100 years, using demographic data gathered from the literature and KNP study. The woodland savanna population had high positive mean growth rates and was viable at small population sizes, while the Serengeti Plains population had a negative mean growth rate and was not viable at population sizes smaller than 200. A population size of less than 100 cheetahs on the Serengeti Plains appears to be the population size whereby stochastic processes begin to have a greater impact on the ability of the population to persist (Miller & Lacy 1999). This appears evident because of the steeper decline in survival probabilities compared to other projections using larger starting population sizes (Fig. 5.3). A population size of 250 cheetahs in the grassland savanna with no change in mortality rates may not persist in the long-term, as a sustained negative growth rate inevitably leads to extinction (Berry et al. 1997). When lowering the sub-adult dispersal rates on the Serengeti Plains to those recorded by Laurenson (1995), which seemed to exclude those cheetahs that dispersed or emigrated (following Kelly & Durant 2000), the grassland population reflected a positive mean growth rate, and was viable at a starting population of 25 cheetahs over a 100 years. Therefore, in this PVA and possibly in Kelly & Durant's (2000) viability study, including emigration without immigration rates into the simulations will result in pessimistic predictions for population persistence. The difference between the two mortality rates may indicate some measure of emigration and dispersal of cheetahs on the Serengeti Plains (20%).

The high growth rates shown by the woodland savanna population (Table 5.2) are reflected by the low juvenile mortality rates coupled with low adult and sub-adult to those estimated by Kelly & Durant (2000) in the Serengeti still showed high positive mean growth rates. In order to generate hypothetical self-replacing cheetah populations, with mean growth rates close to zero and $PE < 0.05$, sub-adult mortality had to be increased substantially. Sub-adult mortalities were raised to 60% and 68% for populations with 50% and 25% juvenile mortality respectively (Table 5.2). Like the grassland savanna population, the difference between the natural mortality rates estimated by Berry et al. (1997) and those predicted for sub-adult mortality in this PVA may provide an indication of the dispersal rates of sub-adult cheetahs in woodland savannas (45% and 54% when juvenile mortalities are 50% and 25% respectively). Although probably an overestimate, because of certain parameters 'optimistically' used or excluded in the PVA (see Methods), this high sub-adult mortality rate is feasible as high emigration probabilities have been recorded in other large carnivores. Lindzey et al. (1988) recorded a 50% dispersal rate for mountain lions (*Felis concolor*), with more males dispersing than females. Waser (1998) tabulates emigration probabilities for lions (87% males, 38% females); gray wolves *Canis lupus* (29% males, 26% females), spotted hyaenas (43% males, 6% females) and coatis *Nasua narica* (46% males, 23% females). Waser (1998) also found that significantly more males than females emigrate, as is the case in cheetahs (Caro 1994; Kelly et al. 1998), which is significant because the model allowed for far higher mortality rates in males than females without increasing extinction risk. The cheetah, being a polygynous breeder probably allows for this.

The higher dispersal rates predicted for the woodland savanna cheetahs are probably due to a high recruitment of juveniles into the sub-adult cohort due to high cub survival. Greater cub survival in woodland savannas may be due to an increased availability of cover, which offers greater concealment from predators (this is discussed later). The greatest influence on population growth and persistence, detected in this PVA, is that females are able to produce up to three litters per year by rapid resumption of breeding following litter loss (Laurenson et al. 1992; Kelly & Durant 2000). This was evident when substituting the maximum litter size of 18 (three litters per year) to six (one litter per year) for the grassland savanna population, resulting in a 100% probability of

extinction (Fig. 5.1). This is considered to be an evolutionary strategy of cheetahs compensating for their high cub mortality (Hamilton 1986; Caro 1994)

Crooks et al. (1998) and Kelly & Durant (2000) modelled demographic data of cheetahs on the Serengeti Plains and found that adult survivorship was the most important factor contributing to population increase, but that extinction risk was highly sensitive to both adult and juvenile survival. Kelly & Durant (2000), however, contended that it is typical for adult survival to exhibit the strongest influence on population growth in large, long-lived mammals, but such a finding says little about a population's risk of extinction. In this PVA, the grassland savanna population was most sensitive to 5% variations in juvenile mortality, while the woodland savanna population was more sensitive to variations in adult mortality, more so when juvenile mortality was low (i.e. 25%). These analyses seemed to show that when juvenile mortality is exceptionally high, adult mortality has a less important influence on viability. Vucetich & Creel's (1999) results of a PVA, using VORTEX, also suggested that population persistence was relatively insensitive to juvenile mortality in wild dogs *Lycaon pictus* unless it is severe (71%) and persistent.

The results of Kelly & Durant's (2000) viability study found a self-replacing cheetah population in the Serengeti with a deterministic growth rate of 0.997. This value, however, is largely affected by demographic or environmental stochasticity and excludes rates of immigration (Kelly & Durant 2000). It appears that a source of immigrating cheetahs, which this PVA also did not include, is the greatest security from extinction for the Serengeti Plains cheetah population. Vucetich & Creel (1999) found that population persistence of wild dogs increased substantially even at low immigration rates. A demographic study by Kelly et al. (1998) found that 60% of male and 50% of female cheetahs on the Serengeti Plains were of unknown origin. Kelly & Durant's (2000) study of the Serengeti cheetahs also indicated that the population had not reached carrying capacity. This implies that the Serengeti Plains may be a sink for cheetahs (Kelly et al. 1998). For many populations, a large fraction of the individuals may regularly occur in 'sink' habitats, where reproduction is insufficient to balance local mortality; however, populations may persist in such habitats being locally maintained by continued immigration from more-productive 'source' areas nearby (Pulliam 1988). With the

predicted high rates of sub-adult dispersal, nearby woodland savannas may be this source. The relationships found between lion (Packer 1985; Hanby, Bygott & Packer 1995) and bank vole *Clethrionomys glareolus* (Mazurkiewicz 1994) populations in two contrasting habitats are striking examples of what may also be occurring between the grassland and woodland savanna cheetah populations in the Serengeti National Park.

Across both woodland and grassland savanna habitats, it is apparent that the survival of adult cheetahs, particularly females, needs to be ensured. A number of factors threaten adult survival and ultimately cheetah density; the most important identified as habitat loss and direct persecution by humans (Crooks et al. 1998). In Namibia, adult survival is a major concern to population persistence as cheetahs are considered 'pests' in the farming areas and shot (Marker-Kraus et al. 1996). Habitat suitability, however, may also affect cheetah densities (Chapter 3), as parks, particularly small, isolated parks, may not be able to support adequate densities for viable populations (Purchase 1998). High lion densities in restricted areas may also outcompete cheetahs, as cheetahs seek out spatio-temporal 'competitive refuges' with low predator densities, which enables them to coexist with their superior competitors (Durant 1998; Durant 2000a). Durant (1998) suggested that cheetahs, with high mobility and low competitive ability, may only be able to persist in areas that are large enough to sustain sufficient spatial heterogeneity.

5.4.2 Implications to management and conservation

A grassland savanna population (like the Serengeti Plains) may be threatened with extinction if cub mortality continues to increase or is persistently severe; but probably the greatest threat is a lack of immigrating cheetahs. 'Sink' habitats may support very large populations despite the obvious fact that the 'sink' population would eventually disappear without continued immigration (Pulliam 1988). Therefore, maintaining 'source' or highly cheetah-reproductive habitats would be of prime conservation consideration. Cheetahs are known to flourish outside protected areas, where other large predators have been removed (Laurenson et al. 1992; Laurenson & Caro 1994; Burney 1980 in Laurenson 1995), and therefore the conservation of cheetahs may rely on their protection outside as well as within national parks (Kelly & Durant 2000). Further demographic studies are

required of woodland savanna cheetah populations, which may act as important ‘source’ habitats. Pulliam (1988) warns that species conservation based on ‘sink’ habitats alone can lead to very misleading conclusions and inappropriate management decisions. Autecological studies of populations in ‘sink’ habitats may yield little information on the factors regulating population size if population size in the sink is largely determined by the size and proximity of sources (Pulliam 1988).

According to this study and Hunter’s (1998) PVA, re-introduced cheetahs into woodland savannas can establish viable populations, even at small population sizes. This is mostly due to rapid recruitment rates from high cub survival. The success of cheetah re-introductions, however, is questionable as high sub-adult recruitment and dispersal rates may lead to conflict with bordering land use areas, or else increased adult mortality rates or stress-related factors from competing for space with conspecifics and other predators. In PRR, MNP and Suikerbosrand Nature Reserve, re-introduced cheetahs were frequently reported snared, shot or in conflict with bordering areas (Cohen et al. 1978; Zank 1995; Hunter 1998; Purchase 1998) because of the natural tendency for cheetahs to disperse (Cohen et al. 1978; Frame & Frame 1980; Caro 1994). Conflict with people on reserve borders is a major cause of mortality in wide-ranging carnivores, so that border areas represent population sinks and may contribute more to their extinction than stochastic processes (Woodroffe & Ginsberg 1998). Although predators lower the reproductive success and density of cheetahs (Laurenson 1995; Durant 2000b; Kelly & Durant 2000), an absence of predators may result in a very opposite outcome. In Suikerbosrand Nature Reserve, where cheetahs were the top predator, an 85% cub survival rate led to a rapid increase in cheetahs and a decimation of abundant prey populations, which resulted in the cheetahs’ eventual removal (Cohen et al. 1978, Pettifer et al. 1981). Similarly, the average litter size in Namibia of 10 month old cubs was four on ranchlands, where lion and hyenas have been eliminated (McVittie 1979). This gives an indication of the recruitment potential into the sub-adult cohort in the absence of predators. In order to counter balance high recruitment rates, sub-adults need to be “removed” from the population, either through dispersal, and if the system is a closed one then management intervention may be required. Dispersal opportunities may be provided by removing fences, enlarging reserves or creating corridors for movement. These are

some of the considerations needed for re-introductions into small, isolated woodland savanna habitats. Re-introductions into small, isolated grassland savanna habitats with high predator densities and few refuges for escape and concealment may not produce viable cheetah populations, unless supplementation occurs. Zank (1995) ran a PVA using life history data from the Serengeti Plains, with 95% cub mortality, to establish the viability of re-introduced cheetahs in MNP and found that a founder population of 20 cheetahs required a supplementation of at least three cheetahs every three years to prevent probable extinction.

5.4.3 Juvenile survival and benefits of cover

Although records and observations of cub survival in woodland savannas are limited and poorly researched, these reports, including the few observations in the KNP indicate that cub survival is higher than on the Serengeti Plains. This may be due to the benefits of increased cover availability for concealment from predators. An increase in cub mortality, however, seems predominantly associated with an increase in predator density (Table 5.3). Lion density has a negative impact on cheetah density (Laurenson 1995) and reproductive success (Kelly et al. 1998; Durant 2000b; Kelly & Durant 2000). There is, however, no estimate of cub mortality for the Serengeti Plains during the early period (1967 – 1979), when lion density was lower than the later period (Table 5.3). Using the same proportionate decline in average lifetime reproductive success from early to late periods (Kelly et al. 1998), cub mortality may be estimated at approximately 70% for the early period. The Serengeti Plains, however, during the early period (1967 – 1979) had a similar lion density to the KNP but KNP cub mortality is only 45%. Similarly, one would expect juvenile mortality rates in KNP and Serengeti Plains during the later period (1985 – 1991) to be more similar, considering that differences in lion densities between these two areas were not that large. The differences in cub mortality may be associated with the greater availability of cover and refuges for concealment in woodland savannas. Furthermore, in MNP, Purchase (1998) estimated a 60% juvenile mortality between 0 – 2 years old (i.e. including the age of maturity and dispersal), which seems comparatively low judging from the exceptionally high lion density found there.

Table 5.3. Lion and spotted hyaena density and cheetah juvenile mortality across five protected areas of southern and East Africa.

Protected area	Lion density* (animals per km ²)	Hyaena density* (animals/km ²)	Juvenile mortality 0 – 12 months (%)
Suikerbosrand Nature Reserve (SNR)	none	none	15
Phinda Resource Reserve (PRR)	0.08	0.05	25
Kruger National Park (KNP)	0.07 – 0.1	0.135	45
Matusadona National Park (MNP)	0.317	0.13	60 (up to 2 years)
Serengeti Plains (1967 - 1979)	0.079 - 0.094	0.12-0.17	No estimate**
Serengeti Plains (1985 – 1991)	0.14	0.82	95

*Densities collated from Stander (1991) and Creel & Creel (1996).

** Average lifetime reproductive success was higher during this period than 1980 – 1994 (Kelly et al. 1998).

These figures, however, must be interpreted with caution, as cub mortality estimates in the woodland savannas may be underestimates due to mortality rates not being recorded immediately following birth.

Cheetahs may benefit from a greater availability of cover when cubs are immobile and in the lair (< 2 months). Cubs in the lair are typically hidden in long grass, rocky outcrops or dense vegetation (Labuschagne 1979, Laurenson et al. 1992). Lions located female cheetahs with cubs in the lair by seeing them sit up in the lair, or by noticing the mothers resting nearby (Laurenson et al. 1992; Laurenson 1994). Laurenson (1994) found that lying low in the lair was a good anti-predator strategy. Cubs are most vulnerable just after emergence until four months as they are not yet fast enough to escape from predators (Laurenson 1994). On the short-grass plains, where cheetahs can be spotted from as far away as 2.5 km (Caro 1994), cubs are particularly vulnerable. Hanby & Bygott (1979) considered the reduction in dry-season fires over a ten-year period may have benefited cheetahs by providing more cover for safe concealment of cubs. Therefore, in woodland savannas, a greater availability of cover may substantially reduce cheetah mortality (most obviously before four months of age) when compared to an open grassland system like the Serengeti Plains. Woodlands may provide far greater concealment of the lair and the mother and a greater opportunity for escape. In PRR and MNP, cheetah cubs were observed escaping from predators into dense bush (Hunter 1998; Purchase 1998). The effects that other environmental factors may contribute to differences in cub mortalities are indeterminate, although they may not play a large role. Laurenson (1994) found that about 21% of juvenile mortality on the Serengeti Plains is due to environmental causes, such as abandonment, fire and exposure, while Pettifer (1981) recorded a 15% juvenile mortality in Suikerbosrand Nature Reserve (in the absence of other large predators). Finally, it must be noted that although cub survival may seem higher in the KNP than on the Serengeti Plains, further evidence is required before any such conclusions can be drawn.

5.4.4 Reflections on the model

Beissinger & Westphal (1998) believe predictions from quantitative models of endangered species are unreliable because of poor quality data. As with any other study, this PVA is open to the criticism that population persistence predictions are no more reliable than the data on which the predictions are based (Reed, Murphy & Brussard 1998; Miller & Lacy 1999). The aim of this PVA, however, was not to make any absolute predictions about either of the two cheetah populations, but was more interested in comparing cheetah population dynamics in contrasting habitats using different demographic and life history parameters. Unfortunately, environmental variation in mortality rates could not be included in the models for reasons explained above (see Methods). Extinction risk tends to increase with increasing environmental variation in survival rates (Mills et al. 1995; Kelly & Durant 2000). Therefore, excluding this variation probably produced overly optimistic estimates of persistence for both cheetah populations. Although most extinctions are a function of steady population decline due to deterministic causes rather than chance events (Caughley 1994), the random fluctuations that increase as populations become smaller can cause the final extinction (Beissinger & Westphal 1998). A positive population growth rate, without modelling environmental variation or catastrophes, can lead to a false sense of security (Beissinger & Westphal 1998). In a predictive capacity, including environmental variation would have either raised the extinction risk or resulted in lowered adult and sub-adult mortality rates to attain hypothetical self-replacing populations. Lowering sub-adult mortality rates was possible for the grassland savanna population as these mortality rates included those cheetahs that disappeared out of the study area, and had not necessarily died (Kelly & Durant 2000).

5.5 CONCLUSIONS

Overall, this PVA indicates that the persistence of cheetah populations depend on the ability of female cheetahs to conceive again rapidly after litter loss; adult survival, except when cub mortality is very high and persistent; and immigration into populations experiencing low cub survival rates. Similar conclusions were found from a PVA conducted on wild dogs, which is also a low density, wide-ranging carnivore that is

highly sensitive to competition with lions (Vucetich & Creel 1999). The importance of the continued persistence of 'source' populations in the Serengeti National Park, either outside the park or from the woodland population within the park, may be paramount to the continued persistence of the Plains population. When compared to the Serengeti Plains cheetah population, very little is known about the population dynamics of cheetahs in woodland savannas. Demographic data on cub survival, sub-adult recruitment and dispersal, and adult survival in woodland savannas are required, as woodland savanna populations may be critical 'source' populations for other depleted areas. This information would also be more far more representative of cheetah populations inhabiting southern Africa, and may provide a better indication of the cheetah's ability to persist across a fragmented and diminishing range.

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