

Kelly MJ, Durant SM. 2000. Viability of the Serengeti cheetah population. *Conservation Biology* 14(3):786-97.

Keywords: 1TZ/*Acinonyx jubatus*/cheetah/conservation/extinction risk/lion/National Park/ population size/population viability analysis/Serengeti/stochasticity

Abstract: Most recent population viability analyses, especially those of long-lived species, rely on only a few years of data or data from a closely related species, combined with educated guesswork, to estimate model parameters and the variability surrounding those measures. This makes their conclusions or predictions difficult to evaluate. In our study, we used 20 years of demographic data on Serengeti cheetahs (*Acinonyx jubatus*) to conduct a population viability analysis. First we constructed a model of the deterministic growth rate and found that the cheetah population is nearly self-replacing ($A = 0.997$). Our model showed that population growth was most strongly influenced by adult survival followed by juvenile survival, which is typical of long-lived, iteroparous species. We then examined extinction risk and long-term projections of cheetah population size with our stochastic model, Popgen. We compared the projections with over 20 years of field data and found that demographic stochasticity trials produced a stable population size, whereas environmental stochasticity trials were slightly more pessimistic. Extinction risk was highly sensitive to both adult survival and juvenile survival (from 0-1 years). Decreasing the variance in survival rates also decreased extinction risk. Because lions are the major predator on cheetah cubs, we used our demographic records to simulate the effect of different lion numbers on juvenile survival. High lion abundance and average lion abundance resulted in extinction of nearly all cheetah populations by 50 years, whereas with low lion abundance most cheetah populations remained extant. Conservation of cheetahs may not rely solely on their protection inside national parks, but may also rely on their protection in natural areas outside national parks where other large predators are absent.

Viability of the Serengeti Cheetah Population

MARCELLA J. KELLY* AND SARAH M. DURANT†

*Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616, U.S.A..

email mjkelly@ucdavis.edu

†The Zoological Society of London, Institute of Zoology, Regent's Park, London, NW1 4RY, United Kingdom

Abstract: *Most recent population viability analyses, especially those of long-lived species, rely on only a few years of data or data from a closely related species, combined with educated guesswork, to estimate model parameters and the variability surrounding those measures. This makes their conclusions or predictions difficult to evaluate. In our study, we used 20 years of demographic data on Serengeti cheetahs (*Acinonyx jubatus*) to conduct a population viability analysis. First we constructed a model of the deterministic growth rate and found that the cheetah population is nearly self-replacing ($\lambda = 0.997$). Our model showed that population growth was most strongly influenced by adult survival, followed by juvenile survival, which is typical of long-lived, iteroparous species. We then examined extinction risk and long-term projections of cheetah population size with our stochastic model, Popgen. We compared the projections with over 20 years of field data and found that demographic stochasticity trials produced a stable population size, whereas environmental stochasticity trials were slightly more pessimistic. Extinction risk was highly sensitive to both adult survival and juvenile survival (from 0-1 years). Decreasing the variance in survival rates also decreased extinction risk. Because lions are the major predator on cheetah cubs, we used our demographic records to simulate the effect of different lion numbers on juvenile survival. High lion abundance and average lion abundance resulted in extinction of nearly all cheetah populations by 50 years, whereas with low lion abundance most cheetah populations remained extant. Conservation of cheetahs may not rely solely on their protection inside national parks, but may also rely on their protection in natural areas outside national parks where other large predators are absent.*

Viabilidad de la Población de Leopardos en el Serengeti

Resumen: *La mayoría de los análisis de viabilidad poblacional recientes, especialmente aquellos de especies de gran longevidad, se basan únicamente en datos de pocos años o de datos provenientes de una especie estrechamente relacionada, junto con reflexiones educadas, para estimar los parámetros de modelos y la variabilidad alrededor de estas mediciones. Esto dificulta la evaluación de las conclusiones o predicciones. En nuestro estudio usamos 20 años de datos demográficos de los leopardos del Serengeti (*Acinonyx jubatus*) para realizar un análisis de viabilidad poblacional (PVA). Primero construimos un modelo de la tasa determinística de crecimiento y encontramos que la población de leopardos se encuentra cercana al auto-reemplazo ($\lambda = 0.997$). Nuestro modelo indicó que el crecimiento poblacional fue influenciada más por la supervivencia de adultos, seguido de la sobrevivencia de juveniles, lo cual es típico de especies iteróparas, de gran longevidad. Posteriormente examinamos el riesgo de extinción y las proyecciones a largo plazo del tamaño poblacional de los leopardos usando nuestro modelo estocástico, Popgen. Comparamos las proyecciones de más de 20 años de datos de campo y encontramos que los ensayos de estocasticidad demográfica produjeron un tamaño poblacional estable, mientras que los ensayos de estocasticidad ambiental fueron ligeramente más pesimistas. El riesgo de extinción fue altamente sensitivo tanto a la sobrevivencia de adultos, como a la de juveniles (de 0 a 1 año de edad). Una disminución de la varianza de las tasas de supervivencia también disminuyó el riesgo de extinción. Debido a que los leones son los principales depredadores de los cachorros de leopardos, utilizamos nuestros datos demográficos para simular el efecto de diferentes números de leones en la sobrevivencia de juveniles. Una abundancia alta y una abundancia promedio de leones resultó en la extinción de casi todas las poblaciones de leopardos en 50 años, mientras que*

Paper submitted July 2, 1998; revised manuscript accepted September 29, 1999.

con una abundancia baja de leones la mayoría de las poblaciones de leopardos permanecieron. La conservación de los leopardos no puede depender únicamente de su protección dentro de los parques nacionales, sino que también puede depender de su protección en áreas fuera de los parques nacionales donde otros depredadores grandes estén ausentes.

Introduction

In the early 1980s the cheetah (*Acinonyx jubatus*) was diagnosed as having low genetic variability (O'Brien et al. 1983, 1985), and, given its low density in the wild and poor breeding performance in captivity, it became the prime example of how low heterozygosity might cause a species to become endangered. Later, however, detailed ecological studies showed that predation on cheetah cubs by lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) were chiefly responsible for low densities in the wild (Laurenson 1994), and better husbandry now appears to be the key to successful breeding in captivity (Wielebnowski 1996). Given the opaque link between genetic variation and population viability, we are as yet unable to determine the relative importance of genetic versus environmental factors in cheetah conservation, but we can assess the ecological viability of a protected population living with other large predators with a systematic population viability analysis (PVA).

The first attempt to model the population dynamics of wild cheetahs was made by Laurenson (1995), who used a simple model of birth, recruitment, and death to suggest that high juvenile mortality in Serengeti cheetahs was the factor responsible for limiting population growth rate in that ecosystem. Using a simulation model, Vortex, to examine population viability, Berry et al. (1996) focused on cheetahs in Namibia. Their results suggest that population growth rate is sensitive to "human induced adult mortality" (i.e., hunting pressure) and to cub mortality. More recently, Crooks et al. (1998) used published data on Serengeti cheetahs (Laurenson et al. 1992; Caro 1994; Laurenson 1995) to examine the sensitivity of the population growth rate to changes in demographic parameters. Their analysis suggests that variation in adult rather than juvenile mortality is the prime factor affecting cheetah populations in the wild, calling into question Laurenson's (1995) conclusion that predation on juvenile cheetahs has an important influence on the viability of the Serengeti cheetah population.

Each of these studies has weaknesses. Laurenson's (1995) analysis relied primarily on a limited 3-year data set (1987-1990). Berry et al. (1996) used a combination of data from two different populations in Namibia and Serengeti to estimate demographic parameters in their simulation model. The large Namibian cheetah population (approximately 2500 individuals) suffers from high hunting pressure on farmlands outside protected areas

where other large predators are generally absent (Berry et al. 1996), whereas the Serengeti cheetah population is smaller and persists in the presence of other large predators. Berry et al. also relied on educated guesswork to estimate the variance in the demographic parameters. Finally, Crooks et al. (1998) analyzed only population growth rate (λ). Their finding that adult survival exhibits the strongest influence on deterministic population growth is not unusual in large mammals and is common in long-lived, iteroparous species (Goodman 1981; Crouse et al. 1987; Trites & Larkin 1989; Brault & Caswell 1993; Durant 1998a). Such a finding says little about a population's risk of extinction. Sensitivity analyses of lambda have been criticized (McCarthy et al. 1995) in part because populations that have positive population growth on average are still subject to extinction (Lacy 1993). The result of interest in a PVA is not solely the deterministic population growth rate but also the risk of stochastic decline or extinction (Shaffer 1990; Burgman et al. 1993).

In short, there is still a need for a PVA of Serengeti cheetahs based on robust, long-term demographic data that includes an overall estimate of population growth, analysis of extinction risks, and the effects of other large predators. We used 20 years of data on Serengeti cheetahs to construct such a PVA. We examined the deterministic growth rate, lambda, to determine if strong population trends exist and then used our stochastic model, Popgen, to project population size and analyze the sensitivity of extinction risk to changes in demographic parameters. Because different PVA simulation models can produce widely different projections even when input parameters are standardized across programs (Mills et al. 1996), we compared our model projections with the actual data. Finally, we incorporated the effects of different numbers of lions on juvenile cheetah survival.

Methods

Study Area and Population

Sightings of cheetahs were recorded across a 2200-km² study area in the southeastern plains and woodland borders of the Serengeti National Park in Tanzania since 1969 (Caro 1994). Cheetahs can be individually identified by distinctive spot patterns on their face, belly, and

haunches. Records taken before 1991 were matched with the aid of a computer recognition program, which ranked the most likely matches by using autocorrelation coefficients between photographs (M.J.K., unpublished data). Computer matches were confirmed by M.J.K. Records after 1991 were matched at the time of sighting, or soon after, with a photographic index. Some individuals were seen only once during the 25-year study. These cheetahs were designated as transients and were not used in our analyses.

Estimation of Demographic Parameters

We used data collected from 1975–1994 on Serengeti cheetahs to estimate vital rates. We did not use data from 1969–1974 and 1978–1979 because search effort was low during these years.

AGE OF FIRST REPRODUCTION, SURVIVAL, AND LONGEVITY

Average age at first reproduction is 2.4 years, and the youngest female observed to produce cubs was 2 years old (Kelly et al. 1998; S.M.D. et al., unpublished data). We used 2 years as an optimistic estimate of the age at which females begin breeding. Survival is lower for adult males than for females (Caro & Collins 1987; S.M.D. et al., unpublished data). In addition, males are more likely to disperse out of the study area, which further decreases measured survival rates (Caro 1994). We therefore calculated survival for adult females (≥ 2 years old) and adolescent females (1–2 years old) (Fig. 1), and the resulting figures were used for both males and females. Although we present the dynamics of adult females only, we accept that assuming equal survival for males may produce optimistic extinction risks, particularly at low population sizes.

Many cheetahs in the study population were seen infrequently, so the time of last sighting did not necessarily correspond to the time of death. We therefore calculated survival using a formula to estimate time of death from the intersighting interval for each individual. The formula calculates the probability that an individual is dead in a certain time interval given that it has not been seen, assuming that time of death and time between sightings follows an exponential distribution (S.M.D. et al., unpublished data). By calculating the interval that sets this probability equal to 0.5, the formula should therefore underestimate and overestimate time of death for equal numbers of individuals; hence, the estimated survival rate should be close to the actual survival rate. Once time of death was calculated, we estimated annual survival rates as the proportion of individuals surviving in each year.

Total variance in survival was composed of two components, demographic and environmental variance. We

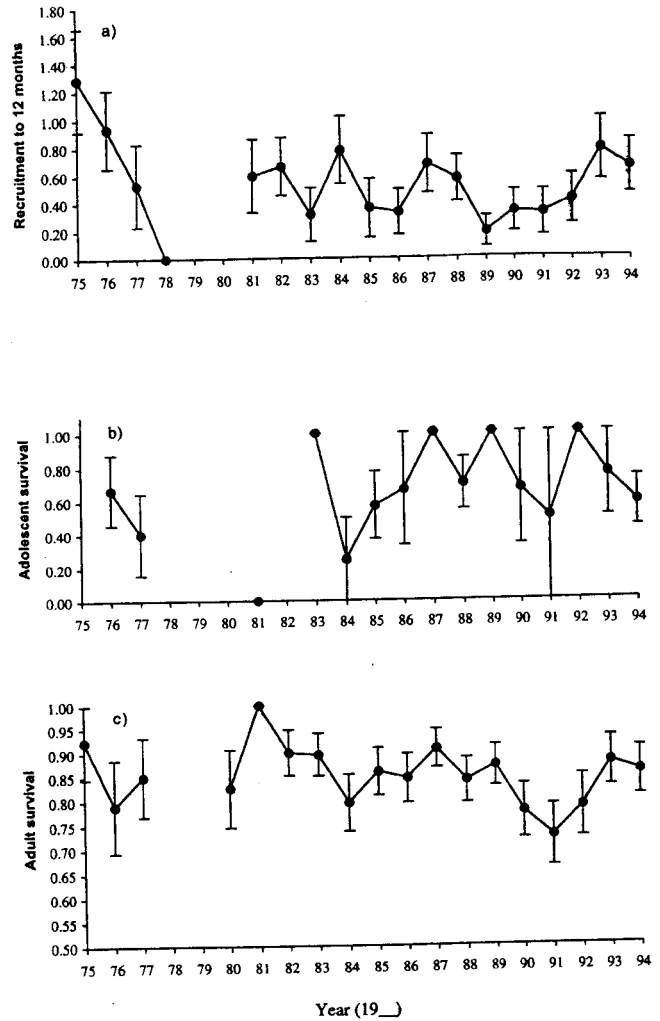


Figure 1. Estimates of survival for (a) recruitment to 12 months for each year of the study, (b) adolescent cheetahs (1–2 years), and (c) adult cheetahs (> 2 years). Error bars represent standard errors.

estimated environmental variance in the survival rate as that portion of the variance that was not accounted for by demographic stochasticity. This method does not exclude variance caused by sampling error. Although we expect this error to be low in the cheetah population because individuals were seen relatively frequently, sampling error inclusion increases environmental variability estimates. This is a conservative approach because it results in higher extinction risks.

It is often assumed that demographic stochasticity in the vital rates follows a binomial distribution (Durant & Harwood 1992). In Popgen, environmental variance is modeled as a series of discrete disasters exponentially distributed through time. For Popgen simulations, we adjusted the strength and frequency of disasters until the expected variance (E_{var}) was identical to that measured by means of the following equation:

$$E_{\text{var}} = \{e^{-\mu}(1-p)s[1 - (1-p)s] + (1 - e^{-\mu})ps(1 - ps)\} /$$

(demographic component)

$$N + \{e^{-\mu}(1 - e^{-\mu})[(1-p)s - ps]^2\},$$

(environmental component)

where p is the proportionate survival in a disaster year, μ is the frequency of disaster, s is the long-term survival, and N is the population size (Durant & Harwood 1992).

The oldest individual observed in the cheetah population was one female who reached 14 years of age. No female older than 12 years was seen to produce cubs, so we used this figure for longevity.

BIRTH RATE AND SURVIVAL TO ONE YEAR

During their first 2 months of life, cheetah cubs are confined to a den (Laurenson 1993). During this period and in the 2 months after they leave the den, they suffer high mortality, with approximately 11% of all cubs surviving to 4 months (Laurenson 1994). It was impossible to estimate how many cubs were born in each year of this study because females often were not seen for long periods and many births were unrecorded. Nevertheless we were able to measure recruitment to 12 months from our long-term data set (Fig. 1). Recruitment can be used to fix juvenile survival and birth rates at a value that ensures the same recruitment as observed in the long-term study. From the females known to produce a litter, we calculated recruitment for each year as the number of cubs that survived to 12 months per adult female. We did not include females if the fate of their cubs was unknown.

We partitioned recruitment into the two components used by our model, the birth rate and the survival rate from 0 to 1 year of age. Between 1987 and 1990, Laurenson conducted an intensive study of survival rates of cubs in dens. She estimated that between 4% and 5.6% of cubs survive to independence at 14 months of age (Laurenson 1994). Because this estimate was most likely made when the population was declining (S.M.D. et al., unpublished data), for the purposes of this analysis we assumed a slightly higher, conservative figure of 10%. The birth rate was then set to equal our measure of recruitment observed from the long-term data set divided by our figure for juvenile survival. The variance in juvenile survival for 0-1 years was set equal to the same proportion of the mean as in adolescent survival.

LITTER SIZE

Popgen requires the average litter size per year and the maximum number of young per litter per year. These can be difficult figures to obtain in a nonseasonal breeder such as the cheetah, that can produce more than one litter per year. We used the following methodology for converting litter sizes to annual parameters.

Cheetahs have a gestation time of 3 months. If a mother loses her cubs, she can come into estrus and conceive again quickly, often within 2 weeks (Laurenson et al. 1992). We therefore assumed that a cheetah mother could give birth to a maximum of three litters a year. This effectively divided each year into three 4-month periods, or litter-producing intervals, during which a female could produce a new litter. We used Laurenson's (1995) data to estimate litter size at birth. Cheetahs give birth to an average of 3.5 cubs, with litter size ranging from 1-6 cubs. We took the probability of a female giving birth to a litter of a given size as the proportion observed by Laurenson (Table 1). Therefore a cheetah could produce a maximum of 18 cubs in a year. We calculated the chance of annual litter sizes from 0 to 18 cubs as follows.

If p_l is the probability of producing a litter in each litter-producing interval, then P_n , the probability of producing n cubs in a year, equals

$$(1 - p_l)^2 p_l \times \text{probability a female produces } n \text{ cubs in 1 litter} +$$

$$(1 - p_l) p_l^2 \times \text{probability a female produces } n \text{ cubs in 2 litters} +$$

$$p_l^3 \times \text{probability a female produces } n \text{ cubs in 3 litters.}$$

We used this formula to calculate the probability of each litter size up to the maximum possible. For example, we calculated the probability of producing 6 cubs as

$$P_6 = 3p_1(1 - p_l)^2 p_6 +$$

$$p_l^2(1 - p_l)[6p_1 p_5 + 6p_2 p_4 + 3p_3^2] +$$

$$p_l^3[6p_1 p_2 p_3 + 3p_1^2 p_4 + p_2^3],$$

where p_n is the probability of producing n cubs per litter.

By doing this for each possible litter size, we generated a series of equations for P_0, P_1, \dots, P_{18} (Table 1) that we used to calculate the mean number of cubs produced per year:

$$\text{expected number of cubs} = \sum_{i=0}^{18} iP_i.$$

We set this equation equal to the birth rate and solved the equations iteratively for p_l . The proportion of females that did not produce cubs in a given year was then $(1 - p_l)^3$.

Our model does not deal with the fact that individual mothers who lose cubs will reproduce more quickly than mothers who do not, but this has no effect on the mean reproductive rate. Nonetheless, because we have not included the covariance between predation and litter production rates, the variance in our reproductive rate is likely inflated, which potentially increases extinction probabilities.

Table 1. Method for converting cheetah litter sizes into annual parameters.^a

Number of cubs per year ^b	Formula for probability calculation ^c	Cubs/year probabilities	Σ(cubs)	Σ(cubs ²)
0	$(1 - p_l)^3$	0.1260	0.0000	0.0000
1	$3(1 - p_l)^2 p_l \{p_1\}$	0.0141	0.0141	0.0141
2	$3p_l(1 - p_l)^2 \{p_2\} + 3p_l^2(1 - p_l) \{p_1^2\}$	0.0146	0.0293	0.0585
3	$3p_l(1 - p_l)^2 \{p_3\} + 3p_l^2(1 - p_l) \{2p_1p_2\} + p_l^3 \{p_1^3\}$	0.1515	0.4544	1.3632
4	$3p_l(1 - p_l)^2 \{p_4\} + 3p_l^2(1 - p_l) \{2p_1p_3 + p_2^2\} + p_l^3 \{3p_1^2p_2\}$	0.1321	0.5284	2.1134
5	$3p_l(1 - p_l)^2 \{p_5\} + 3p_l^2(1 - p_l) \{2p_1p_4 + 2p_2p_3\} + p_l^3 \{3p_1^2p_3 + 3p_2^2p_1\}$	0.0956	0.4781	2.3907
6	$3p_l(1 - p_l)^2 \{p_6\} + 3p_l^2(1 - p_l) \{2p_1p_5 + 2p_2p_4 + p_3^2\} + p_l^3 \{6p_1p_2p_3 + 3p_1^2p_4 + p_2^3\}$	0.0769	0.4614	2.7682
7	$3p_l^2(1 - p_l) \{2p_1p_6 + 2p_2p_5 + 2p_3p_4\} + p_l^3 \{6p_1p_2p_4 + 3p_1^2p_5 + 3p_2^2p_3 + 3p_3^2p_1\}$	0.1044	0.7306	5.1141
8	$3p_l^2(1 - p_l) \{2p_2p_6 + 2p_3p_5 + p_4^2\} + p_l^3 \{6p_1p_3p_4 + 6p_1p_2p_5 + 3p_1^2p_6 + 3p_2^2p_4 + 3p_3^2p_2\}$	0.1045	0.8356	6.6851
9	$3p_l^2(1 - p_l) \{2p_3p_6 + 2p_4p_5\} + p_l^3 \{6p_1p_3p_5 + 6p_1p_2p_6 + 6p_2p_3p_4 + 3p_2^2p_5 + 3p_4^2p_1 + p_3^3\}$	0.0646	0.5818	5.2359
10	$3p_l^2(1 - p_l) \{2p_4p_6 + p_5^2\} + p_l^3 \{6p_1p_3p_6 + 6p_1p_4p_5 + 6p_2p_3p_5 + 3p_2^2p_6 + 3p_3^2p_4 + 3p_4^2p_2\}$	0.0407	0.4070	4.0704
11	$3p_l^2(1 - p_l) \{2p_5p_6\} + p_l^3 \{6p_1p_4p_6 + 6p_2p_3p_6 + 6p_2p_4p_5 + 3p_3^2p_5 + 3p_4^2p_3 + 3p_5^2p_1\}$	0.0303	0.3336	3.6699
12	$3p_l^2(1 - p_l) \{p_6^2\} + p_l^3 \{6p_1p_5p_6 + 6p_2p_4p_6 + 6p_3p_4p_5 + 3p_3^2p_6 + 3p_5^2p_2 + p_4^3\}$	0.0240	0.2885	3.4624
13	$p_l^3 \{6p_2p_5p_6 + 6p_3p_4p_6 + 3p_4^2p_5 + 3p_5^2p_3 + 3p_6^2p_1\}$	0.0141	0.1830	2.3784
14	$p_l^3 \{6p_3p_5p_6 + 3p_4^2p_6 + 3p_5^2p_4 + 3p_6^2p_2\}$	0.0052	0.0735	1.0289
15	$p_l^3 \{6p_4p_5p_6 + 3p_6^2p_3 + p_5^3\}$	0.0012	0.0185	0.2776
16	$p_l^3 \{3p_5^2p_6 + 3p_6^2p_4\}$	0.0001	0.0012	0.0198
17	$p_l^3 \{3p_6^2p_5\}$	0.0000	0.0000	0.0005
18	$p_l^3 \{p_6^3\}$	0.0000	0.0000	0.0000

^aThe variance expected from this distribution can be calculated from $\Sigma(\text{cubs}^2) - \Sigma(\text{cubs})^2 = 11.285$. The proportion of females breeding can be calculated from $1 - (1 - p_l)^3 = 0.8740$.

^bAssumes a female can give birth to a maximum of three litters each year.

^cProbabilities of giving birth to litter sizes of one to six cubs are, respectively, 0.0375, 0.0375, 0.4000, 0.3200, 0.200, and 0.0050 (Laurenson 1992). The probability of producing a litter in each litter-producing interval, p_l , was set to 0.4986 to ensure that the mean number of cubs per year was equal to 5.419 (equivalent to observed recruitment to 12 months divided by a survival of 0.1).

We were able to determine the proportion of females breeding per year, but because many female cheetahs in this study could have bred and lost a litter without being observed, we were unable to obtain from our long-term records a direct measure of variation in the proportion breeding. We entered a range of values in standard deviation from 5% to 40% of the mean proportion breeding and found no effect on extinction risk. Therefore, we set the standard deviation caused by environmental stochasticity equal to 10% of the mean.

Deterministic Model

Analysis of the deterministic model can indicate if strong population trends exist, and sensitivity analysis can determine which vital rates have the greatest effects on lambda (Beissinger & Westphal 1998). If a population has a stable age structure, then the growth rate (λ) is given by

$$l^\alpha m \lambda^{d-\alpha+1} - 2\lambda^{d+1} + 2p\lambda^d - l^\alpha m p^{d-\alpha+1} = 0,$$

where l is the annual juvenile survival rate, m is the reproductive rate, d is longevity, α is the age at first reproduction, and p is the annual adult survival rate (Durant 1998a). We determined the population growth by solving the equation for different values of each of the parameters while holding all other parameters constant at their mean values. We varied each parameter, solving for lambda, to examine the sensitivity of the growth rate to the different parameters in the model.

Simulation Model

There is a critical need to test PVA models to determine whether their projections accurately reflect the behavior of actual populations. Soulé (1987) suggests testing models by comparing their projections to field data from long-term studies. Brooks et al. (1997) compared the behavior of PVA simulation models to data collected over 15 years from Lord Howe Island Woodhens (*Tricholimnas sylvestris*) and found that the programs diverge dra-

matically from actual census numbers and from one another, depending on the details of the model and the input parameters. Lacy et al. (1995) advises using only packages that have undergone such retrospective testing. In light of these studies and recommendations, we modeled the cheetah population using an individual-based model and compared the results to the actual population size estimates over the past 20 years. We used the model Popgen (Durant 1991), which is not commercially available but has been described in previously published papers (Beudels et al. 1992; Durant et al. 1992; Durant & Harwood 1992; Durant & Mace 1994; Durant 1998a).

We tested our model by using the demographic parameters averaged from the entire study (1975–1994) (Table 2) as input and compared the model output with actual data from those years. Years 1978 and 1979 were excluded because there were no field researchers engaged in full-time study of cheetahs during those years (see Kelly et al. 1998). We present the population size for adult female cheetahs only. All modeling results were based on 1000 simulations.

In our simulations, density dependence was modeled as a population ceiling set at 1000 individuals. This is appropriate given that the Serengeti population does not appear to show signs of density dependence. Positive correlations were found between annual adult cheetah

Table 2. Values of demographic parameters calculated from the entire data set (1975–1994) used in long-term simulations of the Serengeti cheetah population.^a

Parameters	Annual rates of demographic parameters			
	mean	variance	expected variance	n (years)
Age at first reproduction	2			
Adult survival	0.8516 ^b	0.004085	0.003502	18 ^c
Adolescent survival (1–2 years)	0.6503 ^d	0.08439	0.005253	15
Recruitment	0.5419 ^e	0.08993	—	18
Juvenile survival (0–1 years)	0.10 ^f	0.00200 ^g		
Proportion breeding	0.8740			
Longevity	12			

^aAverage number of adult females is 38, and final population size in 1994 was 42 adult females ($\lambda = 0.997$).

^bExcludes from calculation individuals estimated to die in 1978 and 1979.

^cExcludes from calculation years 1978 and 1979.

^dExcludes years 1975, 1978–1980, and 1982 from calculations because there were fewer than three adolescents in these years.

^eExcludes years 1979 and 1980 from calculation because the recruitment rates were known for fewer than five females in these years.

^fUsed an optimistic figure based on Laurenson (1994).

^gVariance was set equal to the same proportion of the mean as in adolescent survival.

numbers and the total or average numbers of cubs raised to independence per year (Kelly et al. 1998). Also, prey biomass per cheetah is higher in the Serengeti than in any other protected area in Africa (Laurenson 1995), implying that prey availability is not limiting. The choice of 1000 individuals is somewhat arbitrary. Total adult population size in the Serengeti is estimated at 250–300 individuals (Caro & Durant 1995). Our model therefore allows room for population growth before truncation.

Popgen is an individual-based model that incorporates demographic stochasticity by determining the fate of individuals annually through sampling from a uniform distribution on the interval (0,1) using a pseudo-random number generator (Durant 1991; Durant & Harwood 1992). Environmental stochasticity is modeled as a series of discrete disasters distributed exponentially through time. These disasters reduce the mean survival or birth rate to a low value during the year in which they occur. The number of survivors or offspring are then calculated from a binomial distribution, in which the mean rate of survival or birth in a disaster year is substituted for that in a disaster-free year. Therefore, numbers of survivors and births are still distributed binomially in a disaster year, but their means are lower than they would be in a disaster-free year. We adjusted the strength and frequency of disasters until the expected variance was identical to that measured. Disasters in this sense did not correspond to actual events that occurred in the cheetah population but rather were used as a method of incorporating environmental variance. We did not incorporate catastrophes per se, although this way of modeling variance is equivalent to including minicatastrophes.

A PVA model requires a total starting population size. Because our most accurate population size estimates are for adult female cheetahs, we worked backwards from the stable age distribution to obtain a total starting population size. For example, 42 adult females (≥ 2 years old) were identified on the Serengeti Plains in 1994, the last year of this study. This results in an estimated total population size of 330 cheetahs, including young cubs, assuming a stable age structure. For long-term simulations based on our best estimates, we took 330 as the starting population size. For our model validation trials, we started with 301 cheetahs or 38 adult females, the average population size over the whole study.

Extinction Risk Simulations and Long-term Projections

We analyzed the sensitivity of extinction risk to changes in model parameters through simulation modeling. Extinction risk was defined as the proportion of extinctions out of 1000 population simulations over 50 years. We concentrated on the two parameters with the greatest effect on the population growth rate, adult and juvenile survival, as determined from the sensitivity analysis. Juvenile survival was further partitioned into two age

classes: 0-1 years old and 1-2 years old. We varied these three model parameters—juvenile survival (0-1 years), adolescent survival (1-2 years), and adult survival—one at a time while holding the other parameters constant at their mean. We also examined the sensitivity of extinction risk to changes in environmental variation surrounding these parameters by allowing environmental variance in the parameter of concern to vary in simulations and holding the environmental variance of the remaining parameters constant at values measured from the study.

Lion Trials

To estimate the effects lions have on the viability of the cheetah population, we used estimates of recruitment from an analysis of long-term trends in cheetah survival and recruitment in relation to the numbers of lions as estimated from a similar long-term study on lions (S.M.D. et al., unpublished data; C. Packer, unpublished data). A generalized linear model fitting recruitment to cheetah and lion numbers and controlling for prey and rainfall effects showed that recruitment was significantly related to cheetah and lion numbers through the interactions between cheetah and gazelle numbers and cheetah and lion numbers (S.M.D., unpublished data). When rainfall, gazelle, and cheetah numbers were fixed at their average values over the course of the study, this model predicted recruitment to be 0.09 cubs per adult female when lion numbers were at a maximum recorded during the course of the study, whereas recruitment was predicted to be 0.74 when lion numbers were at the minimum. The lowest number of lions, 72 adult females, occurred in 1975, the highest, 120 adult females, occurred in 1986. The average number of lions was 98, which resulted in a recruitment level of 0.24. We incorporated these three values for recruitment in our simulations by adjusting juvenile survival from 0 to 1 years.

Results

Demographic Parameter Estimation and Deterministic Model

We calculated demographic parameters from the entire data set from 1975 to 1994 (Table 2). The mean and variance in annual recruitment to 12 months for this period were 0.5419 and 0.0899 cubs per adult female, respectively, for 410 individuals. This resulted in a mean birth rate of 5.419 cubs per year (assuming a survival rate of 0.1 to 1 year). We estimated a proportion of 0.8740 females breeding in any given year and calculated the annual litter-size distribution (Table 1).

The results of the deterministic model showed no strong population trend but rather, on average, that the cheetah population was nearly self-replacing ($\lambda = 0.997$). We examined the sensitivity of the population

growth rate using the survival parameters from Table 2. The growth rate was most sensitive to adult survival, followed by juvenile survival (Fig. 2). Adult survival was already high, however, and much greater increases in juvenile survival would be possible, perhaps representing greater potential for population increase. Growth rate was less sensitive to the birth rate and age of first reproduction and least sensitive to longevity.

Comparison of Model Outcomes to Data

To examine the performance of Popgen, we ran the model using demographic parameters estimated from the entire study (Table 2) and compared the output with actual population size during those years (Fig. 3a). All population size estimates for the simulations were averaged over only those trials that persisted, a process that inflates average population size estimates. There were, however, zero extinctions under demographic stochasticity and only eight under environmental stochasticity for the 20-year simulations. The average population trajectory under demographic stochasticity alone projected a stable population. With environmental stochasticity, Popgen produced lower average population sizes, but confidence limits were large (Fig. 3b). An inherent property of the models was that population fluctuations became much more dramatic when environmental stochasticity was added, and the range of pro-

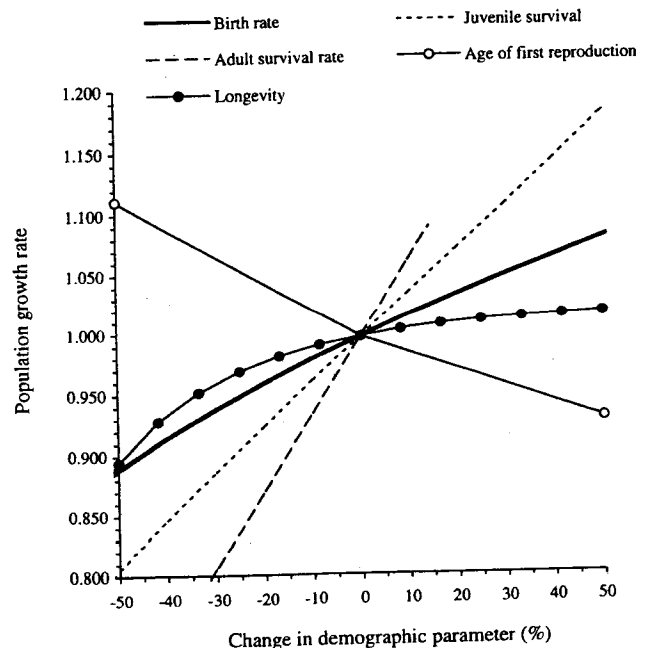


Figure 2. Sensitivity of the population growth rate (λ) to changes in the various demographic parameters. The bend in the line for age of first reproduction is an artifact of defining only integers for this parameter. The line for adult survival is truncated at the right because a 17% increase in this parameter results in 100% survival.

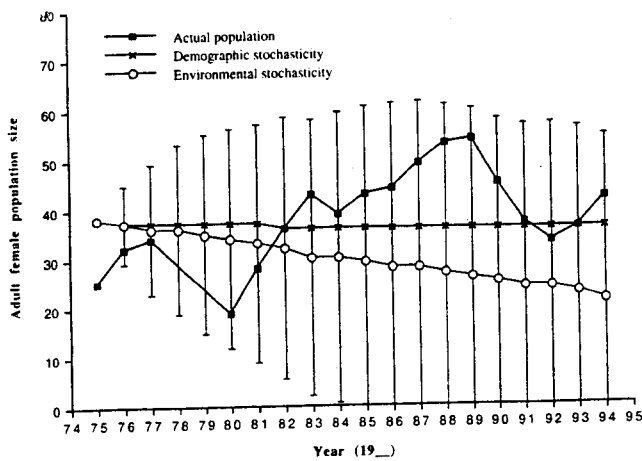


Figure 3. The average population size trajectory for Popgen simulations under demographic and environmental stochasticity plotted against the actual population size of adult female cheetahs. Vertical bars represent 95% confidence intervals for the environmental stochasticity simulations.

jections becomes enormous. Although actual population sizes fell within the projected range under environmental stochasticity, the large confidence intervals made it difficult to defend any single population projection.

Extinction Risk Sensitivity, Long-Term Model Predictions, and Lion Trials

Extinction risk was most sensitive to percentage changes in adult survival (Fig. 4a). When we examined actual survival values, however, juvenile survival (0-1 years) exerted a strong influence on extinction risk, comparable to that of adult survival (Fig 4b). Extinction risk was also sensitive to changes in environmental stochasticity in all survival rates (Fig 4c). Variance in adolescent survival, was already so high in the cheetah population, however, that it was only possible to increase it slightly. One-hundred-year population simulations showed, as expected, a much higher risk of extinction under environmental stochasticity (Table 3).

We adjusted juvenile survival to give the recruitment levels predicted for high, average, and low numbers of lions. This resulted in rates of juvenile survival to 1 year of 0.0172, 0.0446, and 0.1376 for high, average, and low numbers of lions, respectively. We used these values while holding all other parameters at their mean values. In 100-year simulations, high lion abundance and average lion abundance resulted in extinction of nearly all populations by 50 years with and without environmental stochasticity (Fig. 5). At low lion abundance, extinction risk remained close to zero, and the population size of cheetahs increased in number up to our arbitrary carrying capacity.

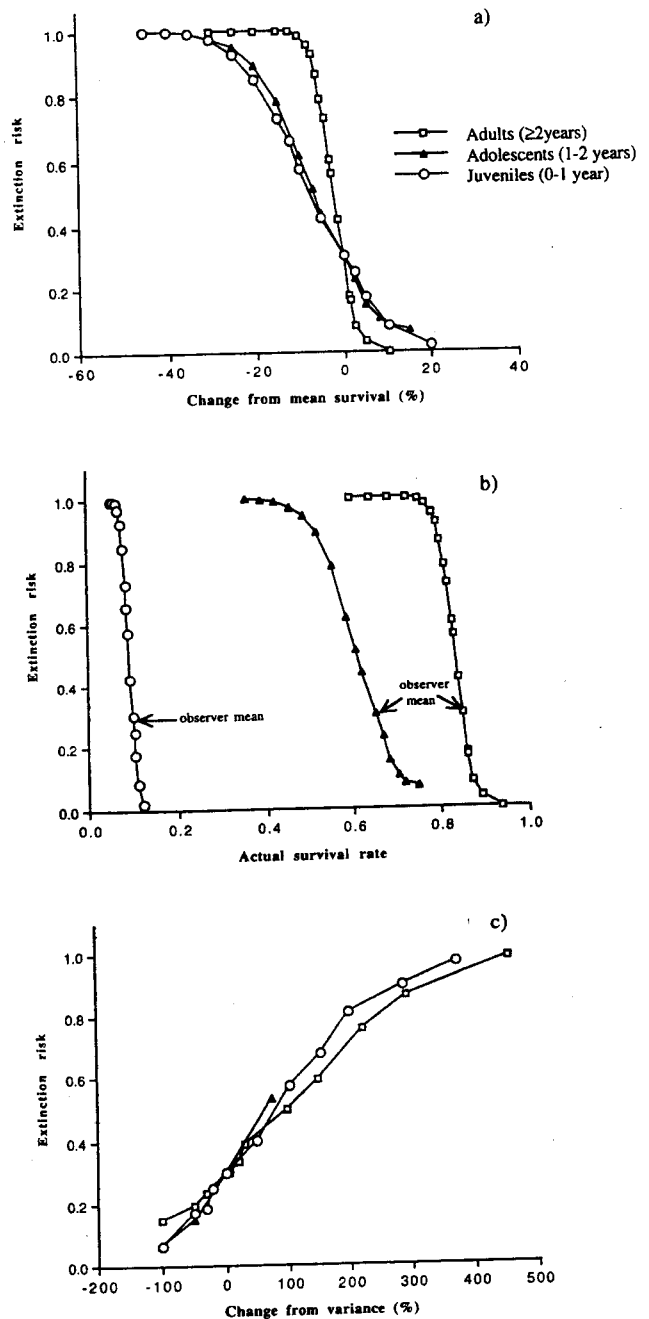


Figure 4. The relationship between changes in demographic parameters and extinction risk for 50-year cheetah population simulations for (a) percent changes in mean cheetah survival rates, (b) actual changes in mean survival rates, and (c) percent changes in the variance surrounding survival rates.

Discussion

Population viability analysis models are no better than the data upon which they are based (Doak et al. 1994). Extinction probabilities, as well as minimum viable populations and time to extinction, are highly influenced by

Table 3. Extinction probabilities for cheetah population simulations under demographic and environmental stochasticity.

Features of model	Year of simulation									
	10	20	30	40	50	60	70	80	90	100
Demographic stochasticity	0.000	0.000	0.000	0.000	0.004	0.008	0.022	0.037	0.051	0.071
Environmental stochasticity	0.000	0.001	0.055	0.156	0.309	0.454	0.608	0.708	0.789	0.840

how accurately model parameters are estimated (Taylor 1995). Predictions are often unreliable because of poor-quality data and difficulties in estimating variance in demographic rates (Beissinger & Westphal 1998). Most studies of long-lived, iteroparous species rely on few years of data and often have poor estimates of variation in demographic parameters (Shaffer 1983; Lande 1988a; Boyce 1992). In using PVA as a predictive tool or to provide suggestions for management, it is essential to scrutinize the robustness of parameter estimation and model projections (Boyce 1992). We used a comprehensive 20-year data set to estimate means and variances in model parameters, and we compared our model projections with the actual field data. Although the actual cheetah population size fluctuated, the average population projection for our demographic stochasticity model reflected a relatively stable population size with no fluctuations. Such is the nature of taking an average over 1000 simulations. Demographic stochasticity trials suggested stability, but the environmental stochasticity trials were slightly more pessimistic.

The deterministic model produced a nearly stationary deterministic growth rate for the cheetah population ($\lambda =$

0.997). Although lambda estimates should increase in accuracy with the length of time over which parameters are estimated, we hesitate to suggest that the cheetah population is stable in the long term. We do not know the proportion of immigrants to the study site or if the population depends on supplementation from elsewhere. Furthermore, only when a population is at its stable age distribution is the overall growth rate measured by lambda. This assumes that no environmental or anthropogenic perturbations have altered relative ratios of demographic parameters and different age classes in recent times (Burgman et al. 1993). This is perhaps an unrealistic assumption for most endangered species. Nevertheless, it is still encouraging that our deterministic results did not show a strongly decreasing population trend.

Examining the sensitivity of the deterministic growth rate gives us an idea of how variability or uncertainty in estimations of particular demographic parameters will affect our results. Our finding that lambda is most sensitive to changes in adult survival followed by juvenile survival is not unusual for large mammals. Individual female reproductive success, however, is significantly lower in the latter half of this study, most likely because of a decline in survival of 0- to 1-year-old cheetahs (Kelly et al. 1998). Lions affect cheetah recruitment (Laurenson 1995; S.M.D. et al., unpublished data), and lion numbers on the Serengeti Plains have dramatically increased, peaking in 1986 and again in 1993 (Hanby et al. 1995). An epidemic of canine distemper virus reduced lion numbers by one-third at the end of 1993 and beginning of 1994 (Roelke-Parker et al. 1996), but the lion population is currently recovering.

Given the fluctuating nature of the cheetah population, it is particularly important to examine the results of our environmental stochasticity trials. Even when the population growth rate is one or greater, populations are still subject to extinction due to stochasticity. We therefore examined the sensitivity of extinction risk to changes in demographic parameters. We found that extinction risk was most sensitive to proportional changes in adult survival. Nevertheless, a proportional change in a number close to 1.0 (adult survival) versus a number close to zero (juvenile survival) results in very different actual numbers of cheetahs. By examining actual survival values (Fig. 4b), rather than proportional change from the mean, we see that increasing survival of 0- to 1-year-olds from the mean of 0.10 to 0.12 decreases extinction risk to zero. This 20% increase is equivalent to

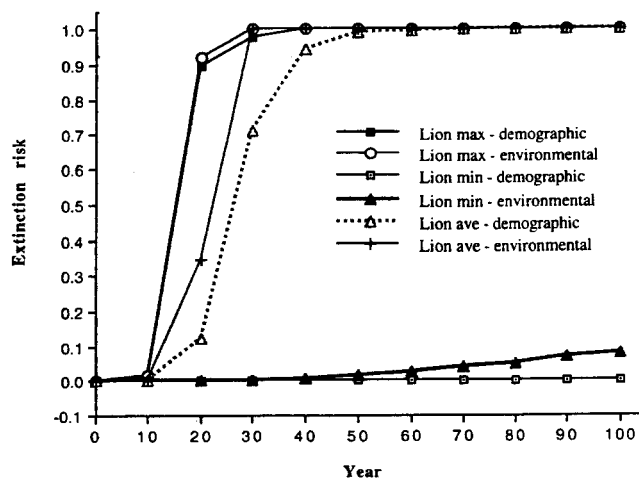


Figure 5. Projected extinction risk under both demographic and environmental stochasticity for cheetah populations subjected to different lion densities. Low lion density, 72 adult female lions, corresponds to the minimum recorded over 20 years of lion study; high density, 120 adult female lions, corresponds to the maximum recorded; average lion density is 98.

an increase in survival of only 2 cubs per every 100 cubs born. Changing adult survival from the mean of 0.85 to 0.91, to obtain a zero extinction risk, requires the survival of an additional 6 adult cheetahs per every 100 adults. This is a much smaller proportional change (7%) but requires more animals. Hence, when parameter means are very different from each other, it is advisable to examine the sensitivity of actual survival parameters rather than only proportional changes from mean values. The lack of feedback between cub survival and reproduction in our stochastic model, however, is a potential reason for our finding more emphasis on cub survival than have previous studies (Crooks et al. 1998).

Although extinction risk was sensitive to all three parameters, increasing environmental variance surrounding adult and juvenile survival (0–1 years) caused similar large changes in extinction risk. This was not the case for variation in adolescent survival, which was so high already that it was not possible to increase variance much further in the model.

Incorporating environmental variation into models causes projections to fluctuate dramatically in a manner that is magnified over time. Confidence limits for projections rapidly increase into the future (Fig. 3b), making any single estimate of minimum viable population or time to extinction difficult to defend (Boyce 1992). Yet models that do not incorporate environmental variability produce overly optimistic estimates of population persistence (Goodman 1987; Pimm et al. 1988). It is instructive to see that we have little ability to predict the fate of any single population, including the cheetah population. Real systems with moderate levels of annual fluctuations are unpredictable, as our model suggests.

We did not include our genetic modeling of the cheetah population here because many have argued against the use of genetic modeling in PVA (Dawson et al. 1987). Walters (1991) describes genetic models as imprecise because they are based on idealized (N_e) populations. Although the relationship between the size of an idealized population and loss of genetic variability is well understood, the link between genetic variability and population viability remains to be established (Shaffer 1981; Lande 1988b; Simberloff 1988; Nunney & Campbell 1993). Cheetahs exhibit low levels of heterozygosity and as a result have been hypothesized to suffer decreased fitness and hence increased vulnerability to extinction (O'Brien et al. 1985), yet the species has survived the hypothesized bottleneck and has spread.

It is unlikely that inbreeding depression is causing a decrease in fecundity in wild cheetahs. Recent work has shown that the captive cheetah population does not exhibit symptoms of inbreeding depression, low fecundity, or higher juvenile mortality than other captive felids (Wielebnowski 1996). In addition, the same study showed that inbred zoo cubs had lower survival than noninbred cubs, indicating that variation exists at the loci affecting

juvenile survival (Wielebnowski 1996), as has been suggested (Pimm 1991; Hedrick 1992; Caughley 1994).

Implications for Conservation

Fortunately, Serengeti cheetahs are not showing a drastic deterministic decline to extinction, as their population growth rate on average is close to 1.0. Extinction risk may still be relatively high because of environmental stochasticity, however, particularly surrounding adult and juvenile survival, and high lion numbers can increase extinction risk through their effect on young juveniles (0–1 years old). Unfortunately, it may not be logistically feasible to increase either biological rate within the Serengeti National Park. Decreasing extinction risk or increasing growth rate by increasing adult survival is extremely unlikely because cheetahs are well protected within the borders of the national park. Increasing juvenile survival in the wild is also difficult because culling lions and hyenas within protected areas to reduce predation is politically unpopular. Constructing artificial lairs or raising cheetahs in protected enclosures is financially and logistically difficult and its effectiveness unpredictable. Within the national park, it is likely that adult survival will remain consistently high and that young juvenile survival will fluctuate depending on predation pressure.

Generally, for any large, long-lived species, population growth will likely be most sensitive to changes in adult survival. But if adults are already protected within a reserve, it may be more important to focus conservation efforts on other parameters that do not affect population growth as strongly. Hence, for cheetah conservation, it is important to continue to monitor lion numbers and their effect on cheetah cubs.

Cheetahs are highly mobile in the Serengeti. The average home-range size of females has been estimated at 833 km² (Caro 1994), and they are capable of moving from the center of the park out into surrounding game reserves in a matter of days. In Namibia it has been suggested that cheetahs emigrate out of protected reserves because these reserves have high densities of other predators that are themselves likely to be seeking refuge from hunting pressure in surrounding reserves (95% of cheetahs occur outside of protected areas in Namibia; Berry et al. 1996). Also, in Namibia, litter size when cubs are 10 months old is 4.0, twice that of the Serengeti (McVittie 1979), indicating that cheetahs exhibit signs of predator release and hence can potentially rear large litters in the absence of predation.

Cheetahs perhaps provide a good example of a fugitive vertebrate species (Levin & Paine 1974; Hanski 1990; Shorrocks 1991; Tilman 1994; Tilman et al. 1994). They are excellent dispersers but poor competitors in comparison to other large predators, always losing in di-

rect competition for food and suffering high mortality from predation (Durant 1998b). Cheetahs do actively avoid lions (Durant 2000), however, and they appear to seek out "competition refuges" with low densities of lions and hyenas. Their mobility is likely the key to their continued co-existence with other predators (Durant 1998b).

Conservation of cheetahs may rely on their protection outside protected areas as well as within core areas of national parks. The secretive and elusive nature of cheetahs may allow them to exploit edges of parks where other large, aggressive, and gregarious predators are exterminated by human hunters. Although edge effects have received negative attention in conservation biology (Wilcove 1985; Wilcove et al. 1986; Simberloff et al. 1991), edge effects can be positive for certain species. Lovejoy et al. (1986) point out that secondary successional forest, rather than primary core forest, provides better shelter and food for tamarins and marmosets, especially in the absence of competitors and predators. In game reserve areas surrounding the Serengeti National Park, hunters and pastoralists preferentially hunt other predators but rarely hunt cheetahs. Such buffer zones would require minimal management effort and may then support high numbers of cheetahs. Aside from this possibility, we are forced to conclude that cheetahs will remain at low density and at risk from extinction even in protected areas where adult survival is high, if these areas support high numbers of other large predators.

Acknowledgments

We thank the Government of Tanzania, Tanzania National Parks, and the Serengeti Wildlife Research Institute (SWRI) for permission to conduct this research. We thank G. and L. Frame for access to records of cheetahs seen prior to 1980, T. Caro for access to records between 1980 and 1990, S. Albon and T. Caro for making this collaboration possible, and S. Albon, P. Beier, S. Beissinger, T. Caro, M. Johnson, R. Lacy, G. Mace, and two anonymous reviewers for constructive comments on early drafts of this manuscript. We are grateful to T. Caro, S. Cleaveland, T. Collins, C. FitzGibbon, G. and L. Frame, L. Gilby, I. Graham, K. Laurenson, and L. Turnbull for data collection. We are also grateful to our fellow workers at SWRI for providing additional photographs and sighting information. The project benefited from logistical support provided by M. Borner, C. Trout, S. and S. Tham, P. Hetz, M. Kuitart, G. and M. Russel, and H. van Lawick and his "team." Over the years the project has been funded by The African Wildlife Foundation, The Fauna and Flora Preservation Society, the Frankfurt Zoological Society, The Institute of Zoology, Leverhulme, The Max Planck Institute fur Verhaltensphysiologie, The Messerli Foundation, the National Geographic

Society, The Royal Society, Sigma Xi, the University of California at Davis, Wendy Keller, World Wildlife Fund (U.S.A.), and The Zoological Society of Philadelphia.

Literature Cited

- Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62:821-841.
- Berry, H., O. Forge, L. Marker-Kraus, K. Nowell, and U. S. Seal. 1996. Life-history/vortex modeling: working group report—cheetahs in Namibia. Draft report. Species Survival Commission, Otjiwarongo, Namibia.
- Beudels, R., S. M. Durant, and J. Harwood. 1992. Assessing the risks of extinction for local populations of roan antelope (*Hippotragus equinus*). *Biological Conservation* 61:107-116.
- Boyce, M. S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23:481-506.
- Brault, S., and H. Caswell. 1993. Pod-specific demography of killer whales (*Orcinus orca*). *Ecology* 74:1444-1454.
- Brooks, B. W., L. Lim, R. Harden, and R. Frankham. 1997. Does population viability analysis software predict the behaviour of real populations? A retrospective study on the Lord Howe Island Woodhen *Tribolima sylvestris* (Slater). *Biological Conservation* 82:119-128.
- Burgman, M. A., S. Ferson, and H. R. Akçakaya. 1993. Risk assessment in conservation biology. Chapman and Hall, New York.
- Caro, T. M. 1994. Cheetahs of the Serengeti Plains: group living in an asocial species. University of Chicago Press, Chicago.
- Caro, T. M., and D. A. Collins. 1987. Ecological characteristics of territories of male cheetahs (*Acinonyx jubatus*). *Journal of Zoology* London 211:89-105.
- Caro, T. M., and S. M. Durant. 1995. The importance of behavioral ecology for conservation biology: examples from Serengeti carnivores. Pages 451-472 in A. R. E. Sinclair and P. Arcese, editors. *Serengeti II: dynamics, management, and conservation of an ecosystem*. University of Chicago Press, Chicago.
- Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215-244.
- Crooks, K., M. A. Sanjayan, and D. Doak. 1998. Cheetah demography and conservation: a modeling approach. *Conservation Biology* 12: 889-895.
- Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68:1412-1423.
- Dawson, W. R., J. D. Ligon, J. R. Murphy, J. P. Myers, D. Simberloff, and J. Verner. 1987. Report of the scientific advisory panel on the Spotted Owl. *Condor* 89:205-229.
- Doak, D., P. Kareiva, and B. Klepetka. 1994. Modeling population viability for the desert tortoise in the Western Mojave desert. *Ecological Applications* 4:446-460.
- Durant, S. M. 2000. Living with the enemy: predator avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology: in press*.
- Durant, S. M. 1998a. A minimum interventionist approach to conservation: the influence of social structure. Pages 105-129 in T. Caro, editor. *Behavioral ecology and conservation*. Oxford University Press, New York.
- Durant, S. M. 1998b. Competition refuges and coexistence: an example from Serengeti carnivores. *Journal of Animal Ecology* 67:81-92.
- Durant, S. M. 1991. Individual variation and dynamics of small populations: implications for conservation and management. Ph.D. dissertation. Cambridge University, Cambridge, United Kingdom.
- Durant, S. M., and J. Harwood. 1992. Assessment of monitoring and management strategies for local populations of the Mediterranean monk seal *Monachus monachus*. *Biological Conservation* 61:81-92.
- Durant, S. M., and G. M. Mace. 1994. Species differences and popula-

- tion structure in population viability analysis. Pages 67-91 in P. J. S. Olney, G. M. Mace, and A. T. C. Feistner, editors. *Creative conservation: interactive management of wild and captive animals*. Chapman & Hall, London.
- Durant, S. M., J. Harwood, and R. Beudels. 1992. Monitoring and management strategies for endangered populations of marine mammals and ungulates. Pages 252-261 in D. R. McCullough and R. H. Barrett, editors. *Wildlife 2001*. Elsevier Applied Science, New York.
- Goodman, D. 1981. Life history analysis of large mammals. Pages 415-436 in C. W. Fowler and T. D. Smith, editors. *Dynamics of large mammal populations*. Wiley, New York.
- Goodman, D. 1987. The demography of chance extinction. Pages 11-34 in M. E. Soulé, editor. *Viable populations for conservation*. Cambridge University Press, Cambridge, United Kingdom.
- Hanby, J. P., J. D. Bygott, and C. Packer. 1995. Ecology, demography, and behavior of lions in two contrasting habitats: Ngorogoro Crater and the Serengeti Plains. Pages 315-331 in A. R. E. Sinclair and P. Arcese, editors. *Serengeti II: dynamics, management, and conservation of an ecosystem*. University of Chicago Press, Chicago.
- Hanski, I. 1990. Dung and carrion insects. Pages 127-145 in B. Shorrocks and I. R. Swingland. *Living in a patchy environment*. Oxford University Press, Oxford, United Kingdom.
- Hedrick, P. W. 1992. Genetic conservation in captive populations and endangered species. Pages 45-68 in S. K. Jain and L. W. Botsford, editors. *Applied population biology*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Kelly, M. J., M. K. Laurenson, C. D. FitzGibbon, D. A. Collins, S. M. Durant, G. W. Frame, B. C. R. Bertram, and T. M. Caro. 1998. Demography of the Serengeti cheetah population: the first 25 years. *Journal of Zoology*, London **244**:473-488.
- Lacy, R. C. 1993. Vortex: a computer simulation model for population viability analysis. *Wildlife Research* **20**:45-65.
- Lacy, R. C., K. A. Hughes, and P. S. Miller. 1995. Vortex: a stochastic simulation of the extinction process. Version 7. Chicago Zoological Society, Chicago.
- Lande, R. 1988a. Demographic models of the Northern Spotted Owl. *Oecologia* **75**:601-607.
- Lande, R. 1988b. Genetics and demography in conservation biology. *Science* **241**:1455-1460.
- Laurenson, M. K. 1992. Reproductive strategies in wild female cheetahs. Ph.D. dissertation. University of Cambridge, Cambridge, United Kingdom.
- Laurenson, M. K. 1993. Early maternal behavior of wild cheetahs: implications for captive husbandry. *Zoo Biology* **12**:31-43.
- Laurenson, M. K. 1994. High juvenile mortality in cheetahs (*Acinonyx jubatus*) and its consequences for maternal care. *Journal of Zoology* London **234**:387-408.
- Laurenson, M. K. 1995. Implications of high offspring mortality for cheetah population dynamics. Pages 385-399 in A. R. E. Sinclair and P. Arcese, editors. *Serengeti II: dynamics, management, and conservation of an ecosystem*. University of Chicago Press, Chicago.
- Laurenson, M. K., T. M. Caro, and M. Borner. 1992. Female cheetah reproduction. *National Geographic Research and Exploration* **8**:64-75.
- Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences of the United States of America* **71**:2744-2747.
- Lovejoy, T. E., R. O. Bierregaard Jr., A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H. Harper, K. S. Brown Jr., A. H. Powell, G. V. N. Powell, H. O. R. Schubert, and M. B. Hays. 1986. Edge effects and other effects of isolation on Amazon forest fragments. Pages 257-285 in M. E. Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts.
- McCarthy, M. A., M. A. Burgman, and S. Ferson. 1995. Sensitivity analysis for models of population viability. *Biological Conservation* **73**:93-100.
- McVittie, R. 1979. Changes in social behaviour of South West African cheetah. *Modoqua* **11**(3):1171-1184.
- Mills, L. S., S. G. Hayes, C. Baldwin, M. J. Wisdom, J. Citta, D. J. Mattson, and K. Murphy. 1996. Factors leading to different viability predictions for a grizzly bear data set. *Conservation Biology* **10**:863-873.
- Nunney, L., and K. A. Campbell. 1993. Assessing minimum viable population size: demography meets population genetics. *Trends in Ecology and Evolution* **8**:234-239.
- O'Brien, S. J., D. E. Wildt, D. Goldman, C. R. Merrill, and M. Bush. 1983. The cheetah is depauperate in genetic variation. *Science* **221**:459-462.
- O'Brien, S. J., M. E. Roelke, L. Marker, A. Newman, C. A. Winkler, D. Meltzer, L. Colly, J. F. Evermann, M. Bush, and D. E. Wildt. 1985. Genetic basis for species vulnerability in the cheetah. *Science* **221**:1428-1434.
- Pimm, S. L. 1991. *The balance of nature*. University of Chicago Press, Chicago.
- Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. *American Naturalist* **132**:757-785.
- Roelke-Parker, M. E., et al. 1996. A canine distemper virus epidemic virus in Serengeti lions (*Panthera leo*). *Nature* **379**:441-445.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *BioScience* **31**:131-134.
- Shaffer, M. L. 1983. Determining minimum viable population sizes for the grizzly bear. *International Conference on Bear Research and Management* **5**:133-139.
- Shaffer, M. L. 1990. Population viability analysis. *Conservation Biology* **4**:39-40.
- Shorrocks, B. 1991. Competition on a divided and ephemeral resource: a cage experiment. *Biological Journal of the Linnean Society* **43**:211-220.
- Simberloff, D. 1988. The contribution of population biology to conservation science. *Annual Review of Ecology and Systematics* **19**:473-511.
- Simberloff, D., J. A. Farr, J. Cox, and D. Mehlman. 1991. Movement corridors: conservation bargains or poor investments? *Conservation Biology* **6**:493-504.
- Soulé, M. E. 1987. Where do we go from here? Pages 175-183 in M. E. Soulé, editor. *Viable populations for conservation*. Cambridge University Press, Cambridge, United Kingdom.
- Taylor, B. L. 1995. The reliability of using population viability analysis for risk classification of species. *Conservation Biology* **9**:551-558.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* **75**:2-16.
- Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. *Nature* **371**:65-66.
- Trites, A. W., and P. A. Larkin. 1989. The decline and fall of the Pribilof fur seal (*Callorhinus ursinus*): a simulation study. *Canadian Journal of Fisheries and Aquatic Sciences* **45**:1437-1445.
- Walters, J. R. 1991. Application of ecological principles to the management of endangered species: the case of the Red-cockaded Woodpecker. *Annual Review of Ecology and Systematics* **22**:505-523.
- Wielebnowski, N. 1996. Reassessing the relationship between juvenile mortality and genetic monomorphism in the captive cheetahs. *Zoo Biology* **15**:353-369.
- Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* **66**:1211-1214.
- Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237-256 in M. E. Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts.

