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# New Insights on Cheetah Conservation through Demographic Modeling

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**Abstract:** *Researchers have recently argued that ecological factors, especially high levels of cub predation, are more important than genetic impoverishment in limiting wild populations of the endangered cheetah (*Acinonyx jubatus*). Despite considerable controversy, however, the forces actually driving cheetah population dynamics remain unclear. We used a combination of demographic techniques to investigate how variation in survival and reproduction might influence the population persistence of wild cheetahs. We parameterized our models using detailed demographic data from recently published, long-term ecological projects on cheetahs of the Serengeti. Results suggest that the influence of juvenile survivorship on population growth rate is relatively small compared to the large effects of adult survivorship. This result is consistent across a range of vital rates and is robust to deviations due to sampling error and environmental variability. These conclusions cast a new light on the current cheetah controversy and, more generally, counsel caution in the interpretation of ecological data for conservation and management.*

Nuevas Ideas para la Conservación del Leopardo Mediante Modelado Demográfico

**Resumen:** *Recientemente los investigadores han argumentado que los factores ecológicos, especialmente altos niveles de depredación de cachorros, son más importantes que el empobrecimiento genético en poblaciones silvestres limitadas del leopardo (*Acinonyx jubatus*), amenazado de extinción. Sin embargo, a pesar de considerables controversias, las fuerzas que actualmente conducen a las poblaciones del leopardo no son claras. Utilizamos una combinación de técnicas demográficas para investigar cómo la variación en la sobrevivencia y reproducción puede influir en la persistencia de poblaciones de leopardos. Nuestros modelos fueron parametrizados usando datos demográficos detallados de proyectos de largo plazo recientemente publicados de leopardos del Serengeti. Los resultados sugieren que la influencia de la supervivencia de juveniles en el crecimiento poblacional es relativamente pequeña en comparación con los grandes efectos de la sobrevivencia de los adultos. Estos resultados son consistentes a lo largo de un rango de tasas vitales y es robusto a desviaciones debidas a errores de muestreo y variabilidad ambiental. Estas conclusiones proyectan una nueva luz en la actual controversia sobre leopardos y en lo general aconsejan precaución en la interpretación de datos ecológicos para conservación y manejo.*

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## Introduction

The endangered cheetah (*Acinonyx jubatus*) has become the focal point in the debate over the role of genetics and ecology in the conservation of rare species.

O'Brien and colleagues (O'Brien et al. 1983, 1985, 1986; O'Brien 1994) have uncovered a surprising lack of genetic variation in cheetahs and have warned of the potential fitness consequences of this uniformity. This interpretation of the cheetah's predicament, however, has recently generated considerable controversy. Prompted by new evidence from both wild and captive populations (Laurenson et al. 1992; Caro 1993; Laurenson 1993; Lindburg et al. 1993; Caro 1994), recent papers

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have strongly argued that ecological factors, not genetic factors, are more important for cheetah conservation and management (Caro & Laurenson 1994; Caughley 1994; Merola 1994; Laurenson 1995; Laurenson et al. 1995a, 1995b). In particular, for many wild cheetah populations, exceptionally high rates of cub mortality, primarily due to predation by lions and hyenas, are argued to be of utmost importance in limiting cheetah populations; for example, only 5% of cheetah cubs survive to reach independence in the Serengeti (Laurenson et al. 1992; Caro 1994; Laurenson 1995).

Although considerable discussion has revolved around the "cheetah controversy" (May 1995), the relative strength of the forces actually driving cheetah population dynamics remain unclear. Demographic modeling of ecological data can provide insight into the influence of demographic parameters on population growth and persistence and can yield useful and sometimes counter-intuitive results that may alter management strategies (Crouse et al. 1987; Beier 1993; Crowder et al. 1994; Doak et al. 1994; Heppell et al. 1994). We adopt a quantitative approach to evaluate the relative importance of different life stages to the conservation of wild cheetah populations. We developed age-structured matrix models for cheetahs and, using both formal sensitivity analysis and a related technique recently pioneered by Wisdom and Mills (1997), analyzed how environmental variation in stage-specific vital rates influenced annual population growth rates. We parameterized our models using detailed demographic data from recently published, long-term ecological projects on cheetahs of the Serengeti (Laurenson et al. 1992; Caro 1994; Laurenson 1995); the models encompass a range of variation in vital rates. Our purpose is to generate robust predictions

on how variation in survival and reproduction can influence population persistence in wild cheetahs.

## Methods and Results

To investigate the demography of female cheetahs, we used age-structured population models (Leslie 1945, 1948) with post-birth censusing (Caswell 1989), partitioning the life cycle into seven 6-month intervals plus an adult stage. Our models incorporate data on six underlying biological stage classes of variable length (taken from Laurenson et al. 1992; Caro 1994; Laurenson 1995): newborn cubs, young cubs, weaned cubs, adolescents, young adults, and adults (Table 1). For each demographic rate we estimated an average, high, and low value; where no direct demographic data were available to estimate high and low values, we calculated  $\pm 50\%$  the mean value to approximate the extreme upper and lower bounds.

Whereas incorporation of the survival estimates into these matrix models is straightforward (Table 2), estimating fertility requires the consideration of an important biological complication. If a cheetah female loses her current litter to predation, she quickly enters estrous, conceives, and produces another litter (Laurenson et al. 1992; Caro 1994; Laurenson 1995). Therefore, cheetahs are able to partially compensate for high cub mortality by rapid reproduction after litter loss. To account for this factor, we constructed an equation for the mean interbirth interval (IB) as a function of the probabilities of litter loss at different cub ages and the subsequent times to rebirth:

**Table 1.** Stage classes, ages, durations, and vital rates used to construct population models for wild cheetahs.

Class	Age (months)	Duration (months)	Vital rates	Survival <sup>a</sup>		
				mean	low	high
Newborn cubs (birth to emergence from lair)	0	2	$S_{nc}$	0.288	0.144	0.432
Young cubs (emergence to weaning)	2	2	$S_{yc}$	0.306	0.153	0.459
Weaned cubs (weaning to independence)	4	14	$S_{wc}$	0.545	0.273	0.818
Adolescent adults (independence to age when fertile) <sup>b</sup>	18	6	$S_{aa}$	0.847	0.424	1.000
Young adult (age when fertile to average age at first reproduction)	24	18	$S_{ya}$	0.847	0.424	1.000
Adult (average age at first reproduction to death) <sup>c</sup>	42	—	$S_{ad}$	0.773	0.387	1.000
Days to rebirth						
young adults after death of litter <sup>d</sup>	—	—	$R_{ya}$	165	116	223
adults after death of litter <sup>d</sup>	—	—	$R_{ad}$	120	95	245
after cub independence <sup>d</sup>	—	—	$R_i$	65	26	146

<sup>a</sup>Newborn, young, and weaned cub survivorship are for the entire stage (Laurenson et al. 1992), whereas adolescent, young adult, and adult survival values are annual estimates (Laurenson 1995). Low and high survival probabilities are calculated as  $\pm 50\%$  mean value. Assuming absolutely no predation, high values for newborn, young, and weaned cubs are 0.809, 0.814, and 0.878, respectively.

<sup>b</sup>Adolescent adult stage ends at 2 years, the approximate age when cheetahs are first physiologically capable of reproducing (Adamson 1969; Schaller 1972; Caro 1994).

<sup>c</sup>Duration of adult class is allowed to iterate to zero.

<sup>d</sup>Lower and upper bounds for fertility value ( $F_x$ ) in matrix models were estimated by including the low and high values for  $R_{ya}$ ,  $R_{ad}$ , and  $R_i$ , derived from radio-telemetry data on individual cheetahs (Laurenson et al. 1992).

$$\left[ \sum_{t=1}^{120} (1 - \rho_1)^{t-1} (\rho_1)(t + R) \right] + \left[ (1 - \rho_1)^{120} \sum_{t=1}^{420} (1 - \rho_2)^{t-1} (\rho_2)(120 + t + R) \right] + [(1 - \rho_1)^{120} (1 - \rho_2)^{420} (540 + R_i)], \tag{1}$$

where  $\rho_1$ ,  $\rho_2$  are daily death rates for litters in the pre-weaning (0–120 days) and post-weaning (120–540 days) periods, respectively;  $R$  is the time to rebirth after death of a litter (which differs for young adults and adults); and  $R_i$  is the time to rebirth after cub independence (Table 1). Thus, we included the different susceptibility of litters to predation or other mortality factors in the pre- and post-weaning periods, and within each period we assume a constant daily probability of litter loss. To incorporate IB into our model, we then needed to express litter mortality rates ( $\rho_1$  and  $\rho_2$ ) in equation 1 as functions of individual cub mortality. Although the probability of litter loss is simply the joint probability of each cub’s death, this relationship is complicated by the correlation between cub deaths; there is a high probability that if one cub dies, then all the litter will be lost, especially if mortality is due to predators (Laurenson et al. 1992; Caro 1994; Laurenson 1995). Lacking detailed data to fully estimate this relationship, we assumed that if one cub in a litter dies with observed probability  $m_c$  ( $m_c = 1 - (S_{nc})(S_{yc}) = 0.911$  for pre-weaning cubs and  $m_c = 1 - S_{wc} = 0.455$  for weaned cubs), then there is an added risk of mortality ( $m_{ar}$ ) for each additional cub in the litter. We then related litter mortality ( $m_L$ ) to cub mortality ( $m_c$ ) over the entire pre- and post-weaning stages with the following:

$$m_L = m_c(m_c + m_{ar})^{n-1}, \tag{2}$$

where  $n$  is the starting litter size (3.5 and 2.25 for pre- and post-weaning litters, respectively). Using litter mortality rates (0.847 and 0.364 for pre- and post-weaning litters, respectively) observed by Laurenson et al. (1992), we could then calculate the estimates for  $m_{ar}$  (0.0598 and 0.3822 for pre- and post-weaning cubs, respectively) and substitute the resulting form of equation 2 into the IB equation, with  $\rho_1 = (m_L)^{1/120}$  and  $\rho_2 = (m_L)^{1/420}$ . Finally, we used IB to calculate  $L$ , the number of litters expected per 6-month interval:

$$L = (365/IB)(1/2). \tag{3}$$

To calculate the top-row elements ( $F_x$ ) of the matrix (Table 2), we multiplied  $L$  by young adult or adult survival ( $P_x$ ) and litter size (LS). Sex ratios of cheetah litters do not differ significantly from 1:1, so LS was estimated to be 1.75, 50% the average litter size of 3.5 cubs (Caro 1994).

Our estimates for interbirth interval from the IB equation (equation 1) were 256 and 213 days for young adults and adults, respectively. In comparison, data on the total number of days 20 wild female cheetahs were radio-monitored and the number of litters born during this period (Laurenson et al. 1992) yield rough estimates of interbirth intervals that average approximately 185 days. Thus, our model’s estimates for interbirth are similar to values actually found for individuals in the wild and in fact represent conservative estimates as to the rapidity with which female cheetahs reproduce after litter loss.

To analyze our demographic model, we first used analytical sensitivity analysis (Caswell 1989) to calculate the

**Table 2.** Mean population projection matrix for wild cheetahs.<sup>a</sup>

Time interval (age in months)							
0–6	6–12	12–18	18–24	24–30	30–36	36–42	42 (adult)
0.000	0.000	0.000	0.000	1.143 <sup>b</sup>	1.143 <sup>b</sup>	1.143 <sup>b</sup>	1.312 <sup>c</sup>
0.081 <sup>d</sup>	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.771 <sup>e</sup>	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.771 <sup>e</sup>	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.920 <sup>f</sup>	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.920 <sup>g</sup>	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.920 <sup>g</sup>	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.920 <sup>g</sup>	0.879 <sup>b</sup>

<sup>a</sup> Matrix is divided into seven 6-month intervals plus an adult stage. Fertility estimates ( $F_x$ ) and survival estimates ( $P_x$ ) for each 6-month interval are represented by the top row and subdiagonal, respectively. Footnotes b–h describe construction of these elements from underlying vital rates. Annual population growth rate,  $\lambda$ , is 0.956 for mean matrix.

<sup>b</sup>  $(P_x)(LS)(L) = (P_x)(LS)[(365/IB)(1/2)] = (0.920)(1.75)[(365/256)(1/2)] = 1.144$ .

<sup>c</sup>  $(P_x)(LS)(L) = (0.879)(1.75)[(365/213)(1/2)] = 1.312$ .

<sup>d</sup>  $(S_{nc})(S_{yc})(S_{wc})^{2/14} = (0.288)(0.306)(0.545)^{2/14} = 0.081$ .

<sup>e</sup>  $(S_{wc})^{6/14} = (0.545)^{6/14} = 0.771$ .

<sup>f</sup>  $(S_{aa})^{1/2} = (0.847)^{1/2} = 0.920$ .

<sup>g</sup>  $(S_{ya})^{1/2} = (0.847)^{1/2} = 0.920$ .

<sup>h</sup>  $(S_{ad})^{1/2} = (0.773)^{1/2} = 0.879$ .

sensitivity of annual population growth rate,  $\lambda$ , to changes in each stage-specific mean vital rate. As our primary sensitivity measure we used elasticity, defined as the proportional change in  $\lambda$  given the proportional change in a single demographic element. Although many demographic studies calculate elasticities of just matrix elements, stage-specific survival rates are embedded throughout a Leslie matrix. For example, the cub, young adult, and adult survival values (Table 1) occur in both survival ( $P_x$ ) and fertility ( $F_x$ ) elements in our matrix (Table 2), and the IB function incorporates cub survival in complicated ways. Consequently, rather than calculating the elasticities of matrix elements, we calculated the elasticities of the stage-specific survival values (Caswell 1989), thereby providing a more direct measure of their effect on  $\lambda$ . For our elasticity calculations we used the mean vital rates presented in Table 1; mean cub survivorship rates were field-estimated values that included the risk of predation.

Results of our sensitivity analyses emphasize the importance of adult survival in determining population growth. Elasticities associated with mean survivorship for each cub stage, as well as for litter size, were nearly an order of magnitude smaller than the elasticity for the adult class (0.300). The majority of cub deaths, primarily due to predation, occur among newborn and young cubs; weaned cubs are fleet and usually evade predators (Laurenson et al. 1992; Caro 1994; Laurenson 1995). Nevertheless, even when survival through both the newborn and young cub stages was considered, their joint elasticity (0.041) was still over seven times lower than that for adult survivorship (Fig. 1).

Although elasticities indicate a primary importance for adult survival, the effects of low juvenile survivorship is most evident when sensitivity rather than elasticity values are used. Whereas elasticities measure proportional changes in vital rates, sensitivities calculate the change in population growth rate given an absolute change in a single demographic element (Caswell 1989). Elasticities are the standard approach (Crouse et al. 1987; Crowder et al. 1994; Doak et al. 1994; Heppell et al. 1994) because elasticities of individual vital rates, especially those with different absolute values, can be interpreted clearly (de Kroon et al. 1986).

In our model, sensitivities were high for pre-weaned cub and adult survivorship and relatively low for survivorship of weaned cubs, adolescent adults, and young adults as well as for litter size (Fig. 1). But because adult survival values were much higher than those for cub survival in our model (Table 1), a given absolute change in adult survivorship represents a much smaller proportional change than does the same absolute change in cub survivorship. Even when these relatively smaller absolute changes are considered, though, adult survival still had a large effect on population growth.

Interpretation of elasticities and sensitivities is compli-

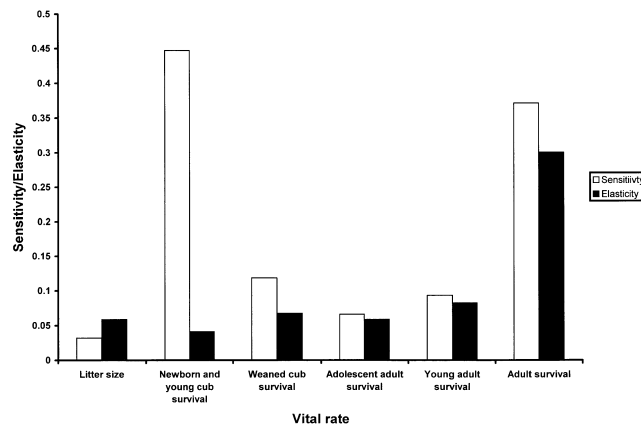


Figure 1. Elasticity and sensitivity of annual population growth rate,  $\lambda$ , associated with stage-specific vital rates for wild cheetahs. Elasticity is defined as the proportional change in  $\lambda$  given the proportional change in a single demographic element. Sensitivity is defined as the absolute change in  $\lambda$  given an absolute change in a single demographic element.

cated by the fact that these values are themselves functions of the vital rates and will vary with differences in these rates because of sampling error and spatiotemporal environmental variability. Further, elasticities are only an approximate measure of a vital rate's effect on  $\lambda$ , and in particular may misguide prediction of how large changes in rates will affect population growth (Caswell 1989). Thus, the elasticity for a single mean set of vital rates may not provide a robust index of each rate's effect on population dynamics (Wisdom & Mills 1997). Therefore, following the approach of Wisdom and Mills (1997), we also used our high and low estimates of each vital rate (Table 1) to construct 500 population matrices, randomly choosing each vital rate from a uniform probability distribution bound by its high and low estimate. We used a uniform distribution to fully explore how a wide range of vital rates may affect population growth; this procedure thus provided multiple matrices that span a range of possible values for cheetah demography. Using the calculated  $\lambda$  for each of these 500 matrices as our sample, we performed regression analyses to determine the influence of variation in each vital rate on population growth. A reduction in the variation of a vital rate will also reduce  $r^2$  values in a regression between that rate and  $\lambda$ . Simulations by Wisdom and Mills (1997), however, indicated that even relatively large changes in the range encompassed by a given demographic parameter only slightly affected  $r^2$  and did not influence the relative rankings of either  $r^2$  or elasticity values across replicate matrices. In all, unlike the simple elasticities presented above, these regression analyses measured the effect of large, simultaneous, and disproportionate changes among demographic parameters on realized population growth rates.

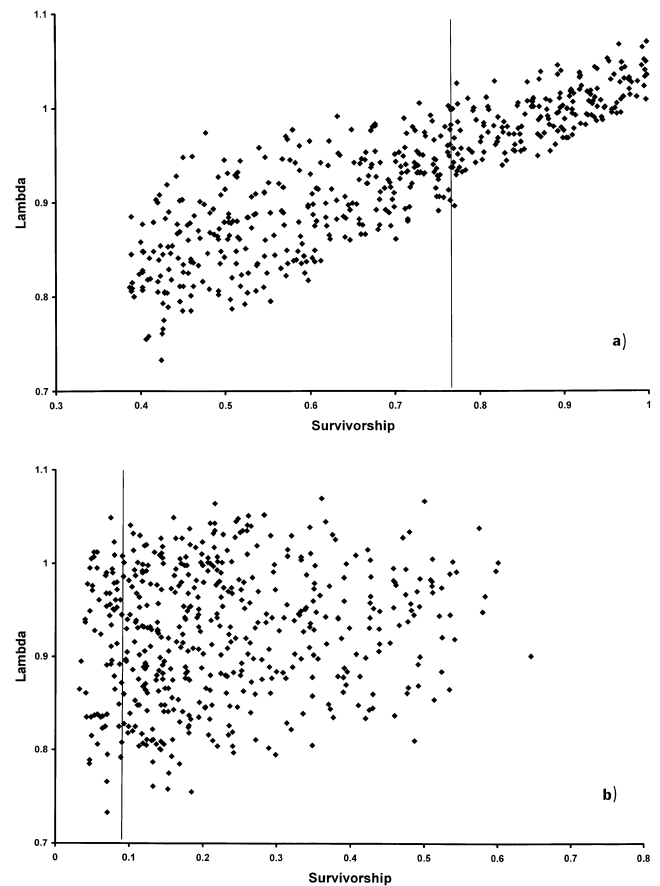
Adult survivorship accounted for nearly all of the variation in  $\lambda$  ( $r^2 = 0.877$ ), whereas little variation in  $\lambda$  was explained by survivorship of newborns ( $r^2 = 0.015$ ), young cubs ( $r^2 = 0.004$ ), weaned cubs ( $r^2 = 0.061$ ), or even combined variation in the newborn and young cub stages, during which predation is the main cause of mortality ( $r^2 = 0.018$ ). In other words, although adult survivorship explains 88% of the variation in  $\lambda$ , the inclusion of survival variation in all cub stages only improves this by an additional 8%.

To further test the possibility that dramatic reductions in cub mortality could significantly improve population growth rate, we also performed analyses with a different and higher upper bound for the newborn and young cub stages, basing these estimates on a reduction to zero of predation-caused mortality in these vulnerable stages (Table 1). Even with these very high upper bounds on cub survival—predation accounts for 75% of the mortality in these stages (Caro 1994)—adult survivorship still explained most of the variation seen in  $\lambda$  ( $r^2 = 0.750$ ), whereas survivorship of the combined newborn and young cub stages was still only of minor importance ( $r^2 = 0.025$ ) (Fig. 2). Thus, even when a range of scenarios is considered, including the complete prevention of predation, the survival of adults and not survival of early life stages has by far the largest influence on population growth.

## Discussion

Juvenile mortality among wild cheetahs, high compared to that of other felids, is now widely viewed as a primary threat, especially in protected areas such as the Serengeti where populations of lions and spotted hyenas may be artificially high and where habitat destruction and direct persecution by humans, serious concerns for cheetah conservation, are reduced (Laurenson et al. 1992; Caro 1994; Caro & Laurenson 1994; Laurenson 1995). Our quantitative models for cheetah demography suggest that cub survival was in fact less important than adult survival in influencing population growth. Moreover, this pattern was consistent across a wide range of vital rates, demonstrating robustness to environmental variability and sampling error (Wisdom & Mills 1997).

The importance of adult survival for population growth has been documented for many moderate- to long-lived species (Crouse et al. 1987; Caswell 1989; Crowder et al. 1994; Doak et al. 1994; Heppell et al. 1994). Because adult survival acts upon individuals of high reproductive value repeatedly, changes in this demographic rate are likely to strongly affect population growth. The influential role of adult survivorship on population growth in cheetahs, however, is also in part attributable to the compensatory effect of rapid reproduction for increased neonatal mortality, a life-history



*Figure 2. The annual population growth rate,  $\lambda$ , of simulated wild cheetah populations regressed on annual adult survivorship ( $r^2 = 0.750$ ) (a) and combined survivorship of the newborn and young cub stages ( $r^2 = 0.025$ ) (b). Survivorship values were selected randomly from a uniform probability distribution to build 500 Leslie matrices that were used to calculate  $\lambda$ . The vertical line in each figure represents the mean vital rate (Table 1). Upper bounds for survival of newborns and young cubs in (b) were estimated using absolutely no predation in these stages, thus testing the maximum possible effect of predation reduction on population growth. More points fall toward smaller survivorship values in (b) because we multiplied two uniform distributions with relatively small values (newborn and young cub survival) to calculate combined survivorship for the entire pre-weaning stage.*

characteristic that we explicitly included in our models. Indeed, cheetahs have experienced high cub mortality due to predation throughout their recent evolution; savannah habitats where cheetahs have occurred have supported a large migratory prey base and high predator densities. Thus, cheetahs have likely responded through larger litter sizes and rapid resumption of breeding following litter loss (Caro 1994). Our models, however,

were parameterized with data from cheetahs of the Serengeti, a potentially declining population (Laurenson 1995) with high levels of cub predation. Although no detailed demographic data on cheetahs has been published from other locales, such studies would provide useful information on the generalizability of our model to other cheetah populations.

High sensitivity values demonstrate that extremely low juvenile survivorship can certainly affect cheetah populations. But elasticity values and regression analyses, especially the simulations excluding predation-related mortality, clearly indicate that cub survivorship does not influence population growth as strongly as adult survival does. Neither elasticity, sensitivity, nor regression techniques, however, explicitly address the costs or logistics of actually altering different vital rates in real-world situations (Wisdom & Mills 1997). To date, low cub survivorship naturally has focused attention on minimizing predator-induced mortality to benefit cheetah populations. Because cub survival is a small value, increasing survivorship by a few cubs would result in a relatively large percent increase in the vital rate. Unfortunately, opportunities to actually reduce cub mortality in the wild are limited. Potential options include culling or translocating lions and hyenas, constructing artificial lairs, and breeding or raising cheetah litters in protected enclosures. But such efforts are logistically, financially, and morally problematic (Caro 1994). Further, our results suggest that focusing on cub mortality to the exclusion of adult survivorship may be inefficient or even detrimental to population growth.

It has also been proposed that conservation efforts for cheetahs be focused outside of national parks where lions and hyenas are less abundant and juvenile mortality is lower (Laurenson et al. 1992; Caro 1994). Our models, however, predict that even a slight decrease in adult survivorship of cheetahs outside of protected areas—for instance due to poaching, persecution by ranchers, or reduced prey—may counteract the benefits of a reduction in predation-related mortality in juvenile stages in such locales. For conservation efforts focused outside of parks, management plans that target adult cheetahs may be especially effective. Such may be the case for cheetahs in Namibian farmlands, where strategies including education, incentives, and guard dogs are currently reducing the large number of adult cheetahs killed by ranchers (Marker-Kraus et al. 1996).

In a broader context, the cheetah has become a touchstone in the debate over the role of genetics and ecology in the conservation of rare species. Both ecological and genetic factors play an important role in the persistence of all populations, including cheetahs (Jimenez et al. 1994; Mills 1996; Hedrick et al. 1996). For wild cheetahs, high levels of cub predation are an extrinsic force that certainly decreases population persistence. Moreover, adult survivorship, of primary importance in our

demographic models, is undoubtedly influenced by ecological factors such as habitat loss and direct persecution by humans. Other processes at least partially under genetic control, such as metabolic efficiency (Mitton & Grant 1984; Koehn 1987; Teska et al. 1990; Pogson & Zouros 1994) or disease susceptibility (O'Brien & Evermann 1988; Thorne & Williams 1988; Vrijenhoek & Leberg 1991), may also influence adult and cub survivorship and, therefore, according to our model, cheetah population persistence. Without doubt, ecological studies are essential because they can provide valuable data such as those used in our models (Schemske et al. 1994). We advise caution, however, because ecological data need to be analyzed in an appropriate fashion before they become the basis for important management decisions. Often, the dramatic nature of the data themselves lead to conclusions that, although seemingly intuitive, may be misleading (Crouse et al. 1987). Quantitative and synthetic analysis of demographic data is needed before it can be reliably used to draw management inferences. Conservation of the cheetah will rest upon our ability to understand how a combination of ecological and genetic factors work in concert to affect cheetah populations.

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## Literature Cited

- Adamson, J. 1969. *The spotted sphinx*. Collins, London.
- Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. *Conservation Biology* 7:94-108.
- Caro, T. M. 1993. Behavioral solutions to breeding cheetahs in captivity: insights from the wild. *Zoo Biology* 12:19-30.
- Caro, T. M. 1994. *Cheetahs of the Serengeti plains: group living in an asocial species*. The University of Chicago Press, Chicago.
- Caro, T. M., and M. K. Laurenson. 1994. Ecological and genetic factors in conservation: a cautionary tale. *Science* 263:485-486.
- Caswell, H. 1989. *Matrix population models*. Sinauer Associates, Sunderland, Massachusetts.
- Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215-244.
- Crouse, D., L. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68:1412-1423.
- Crowder, L. B., D. T. Crouse, S. S. Heppell, and T. H. Martin. 1994. Pre-

- dicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecological Applications* **4**:437-445.
- de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* **67**:1427-1431.
- 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.
- Hedrick, P. W., R. C. Lacy, F. W. Allendorf, and M. E. Soulé. 1996. Directions in conservation biology: comments on Caughley. *Conservation Biology* **10**:1312-1320.
- Heppell, S. S., J. R. Walters, and L. B. Crowder. 1994. Evaluating management alternatives for Red-cockaded Woodpeckers: a modelling approach. *Journal of Wildlife Management* **58**:479-487.
- Jimenez, J. A., K. A. Hughes, G. Alaks, L. Graham, and R. Lacy. 1994. An experimental study of inbreeding depression in a natural habitat. *Science* **266**:271-273.
- Koehn, R. K. 1987. The importance of genetics to physiological ecology. Pages 170-188 in M. E. Feder, A. F. Bennett, W. W. Burggren, and R. B. Huey, editors. *New directions in ecological physiology*. Cambridge University Press, Cambridge, United Kingdom.
- Laurenson, M. K. 1993. Early maternal behavior of wild cheetahs: implications for captive husbandry. *Zoo Biology* **12**:31-44.
- 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: research, conservation and management 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.
- Laurenson, M. K., T. M. Caro, P. Gros, and N. Wielebnowski. 1995a. Controversial cheetahs? *Nature* **377**:392.
- Laurenson, M. K., N. Wielebnowski, and T. M. Caro. 1995b. Extrinsic factors and juvenile mortality in cheetahs. *Conservation Biology* **9**:1329-1331.
- Leslie, P. H. 1945. On the use of matrices in population mathematics. *Biometrika* **33**:183-212.
- Leslie, P. H. 1948. Some further notes on the use of matrices in population mathematics. *Biometrika* **35**:213-245.
- Lindburg, D. G., B. S. Durrant, S. E. Millard, and J. E. Oosterhuis. 1993. Fertility assessment of cheetah males with poor quality semen. *Zoo Biology* **12**:97-103.
- Marker-Kraus, L., D. Kraus, D. Barnett, and S. Hurlbut. 1996. Cheetah survival on Namibian farmlands. USAID Environmental Education Project, Rossing Publishers, Windhoek, Namibia.
- May, R. M. 1995. The cheetah controversy. *Nature* **374**:309-310.
- Merola, M. 1994. A reassessment of homozygosity and the case for inbreeding depression in the cheetah, *Acinonyx jubatus*: implications for conservation. *Conservation Biology* **8**:961-971.
- Mills, L. S. 1996. Cheetah extinction: genetics or extrinsic factors. *Conservation Biology* **10**:315.
- Mitton, J. B., and M. C. Grant. 1984. Associations among protein heterozygosity, growth rate and developmental stability. *Annual Review of Ecology and Systematics* **25**:45-69.
- O'Brien, S. J. 1994. The cheetah's conservation controversy. *Conservation Biology* **8**:1153-1155.
- O'Brien, S. J., and J. F. Evermann. 1988. Interactive influence of infectious disease and genetic diversity in natural populations. *Trends in Ecology and Evolution* **3**:254-259.
- 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* **227**:1428-1434.
- O'Brien, S. J., D. E. Wildt, and M. Bush. 1986. The cheetah in genetic peril. *Scientific American* **254**:84-92.
- Pogson, G. H., and E. Zouros. 1994. Allozyme and RFLP heterozygosity, as correlates of growth rate in the scallop *Placopecten magellanicus*: a test of the associative overdominance hypothesis. *Genetics* **137**:221-231.
- Schaller, G. B. 1972. *The Serengeti lion: a study of predator-prey relations*. University of Chicago Press, Chicago.
- Schemske, D. W., B. C. Husband, M. H. Ruckelshaus, G. Goodwillie, I. M. Parker, and J. G. Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. *Ecology* **75**:585-606.
- Teska, W. R., M. H. Smith, and J. M. Novak. 1990. Food quality, heterozygosity, and fitness correlates in *Peromyscus polionotus*. *Evolution* **44**:1318-1325.
- Thorne, E. T., and E. S. Williams. 1988. Disease and endangered species: the black-footed ferret as a recent example. *Conservation Biology* **2**:66-74.
- Vrijenhoek, R. C., and P. L. Leberg. 1991. Let's not throw the baby out with the bathwater: a comment on the management of MHC diversity in captive populations. *Conservation Biology* **5**:252-254.
- Wisdom, M. J., and L. S. Mills. 1997. Sensitivity analysis to guide population recovery: Prairie-Chickens as an example. *Journal of Wildlife Management* **61**:302-312.

