
Lineage Loss in Serengeti Cheetahs: Consequences of High Reproductive Variance and Heritability of Fitness on Effective Population Size

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Abstract: *In natural populations, many breeders do not leave surviving offspring, and as a result many potential genetic lineages are lost. I examined lineage extinction in Serengeti cheetahs (*Acinonyx jubatus*) and found that 76% of matrilineages were lost over a 25-year period. Production of future breeders was nonrandom and generally confined to a few families. Five out of 63 matrilineages accounted for 45% of the total cheetah population over the course of the study. Lineage persistence is perhaps best illustrated by the variance in lifetime reproductive success (LRS) and heritability in this parameter. In female cheetahs, variance in LRS was high, and new data show that this LRS was heritable. Variance in LRS and heritability in LRS have dramatic consequences for effective population size, N_e . I calculated N_e for cheetahs, taking into account fluctuating population size, unequal sex ratio, non-Poisson distribution of reproductive success, and heritability of fitness. The N_e was most strongly affected by variance in reproductive success and especially heritability in reproductive success. The variance N_e was 44% of the actual population size, and the inclusion of heritability further reduced N_e to only 15% of the actual population, a ratio similar to that of a social carnivore with reproductive suppression. The current cheetah population in the Serengeti is below numbers suggested by N_e estimates as sufficient to maintain sufficient genetic diversity.*

Pérdida de Linaje en Cheetas del Serengeti: Consecuencias de una Varianza Reproductiva Alta y de la Herencia de la Adaptabilidad en el Tamaño Poblacional

Resumen: *En poblaciones naturales, muchos reproductores no dejan descendencia sobreviviente y como resultado se pierden muchos linajes genéticos potenciales. Examiné la extinción del linaje en Cheetas del Serengeti (*Acinonyx jubatus*) y encontré que un 76% de las líneas maternas se pierden a lo largo de un período de 25 años. La producción de futuros reproductores no fue azarosa y generalmente estuvo confinada a unas pocas familias. Cinco de 63 líneas maternas fueron responsables de un 45% del total de la población de Cheetas a lo largo del estudio. La persistencia de linajes se ilustra quizá mejor por la varianza de la duración de la reproducción exitosa (LRS) y de la heredabilidad de este parámetro. En las hembras, la varianza de LRS fue alta y los datos muestran que esta LRS es heredable. La varianza en LRS y la heredabilidad en LRS tiene consecuencias dramáticas para el tamaño poblacional efectivo, N_e . Calculé N_e para los Cheetas tomando en consideración la fluctuación del tamaño poblacional, la proporción desigual de sexos, la distribución del éxito reproductivo diferente a la distribución de Poisson y la heredabilidad de la adaptabilidad en el éxito reproductivo. La varianza de N_e fue de un 44% de la población actual y la inclusión de la herencia redujo aún más N_e hasta solo un 15% de la población actual, una proporción similar a la de un carnívoro social con reproducción suprimida. La población actual de Cheetas en el Serengeti está por debajo de los números sugeridos por las estimaciones de N_e para mantener una diversidad genética suficiente.*

Introduction

The maintenance of genetic diversity in isolated populations depends primarily on the joint action of natural selection and random genetic drift (Nunney & Campbell 1993). Unless selection is strong, changes in allele frequencies in small populations are more strongly determined by random genetic drift than by natural selection (Kimura 1983; Lacy 1987). The importance of genetic drift is determined by the effective population size, N_e , the size of the ideal population that loses genetic variance at the same rate as a real population of size N (Wright 1931). The N_e is useful for predicting the magnitude of random genetic drift or the prevalence of inbreeding (Hill 1972). The N_e has no fixed relationship to N . Rather, it is calculated according to the most important discrepancies between the structures of the real and ideal populations (Nunney & Elam 1994; Caughley & Gunn 1996). In the absence of a direct measure of genetic variation, estimating N_e requires linking N_e theory to demographic and ecological data from the study population (Nunney & Elam 1994). For long-lived species this can be extremely difficult because of the need for detailed demographic data over many generations. Despite this difficulty, there are surprisingly fewer estimates of N_e than expected based on the number of long-term data sets (Creel 1998).

Although cheetahs (*Acinonyx jubatus*) are classified as an endangered species (Nowell & Jackson 1996), the Serengeti population does not appear to be systematically declining because, on average, it is nearly self-replacing ($\lambda = 0.997$) (Kelly & Durant 2000). The population, however, is still at risk of extinction due to demographic and environmental stochasticity (Kelly & Durant 2000), and, at 200–250 individuals (Caro & Durant 1995), the population is small enough to be influenced by genetic drift and inbreeding. Recent studies have shown that small natural populations do suffer from inbreeding depression and decreased fitness caused by low genetic variability, which makes accurate estimates of N_e important for wild populations (Saccheri et al. 1998).

The cheetah has been in the conservation spotlight because of its low genetic variability (O'Brien et al. 1983, 1985). This current lack of genetic variation, however, does not preclude cheetahs from potentially suffering further genetic depletion for at least three reasons. First, the amount of genetic variation in apparently healthy populations varies widely (Nevo 1978), with 30% of carnivore species exhibiting lower variability than cheetahs (Merola 1994). Second, recent studies have found more variation in cheetahs than suggested originally (Menotti-Raymond & O'Brien 1995). Third, in captivity cheetahs appear to suffer from inbreeding depression because offspring of related parents show higher levels of juvenile mortality than outbred offspring due to intrinsic factors such as stillbirths and congenital defects

(Wielebnowski 1996), implying that there is variation at loci affecting juvenile survival (Caughley 1994).

I used 25 years of data on Serengeti cheetahs to determine the rate of lineage extinction that resulted from some matriline (defined as lineages traced through the female line) having much greater reproductive success than others. I also present new data on the heritability of fitness in cheetah matriline and explore the potential causes. I then relate these factors to N_e for cheetahs. Effective population size is known to be affected by fluctuating population size, by imbalanced sex ratio (which affects inbreeding N_e), and especially by unequal reproductive success (which affects variance N_e) (Wright 1940; Lande & Barrowclough 1987; Harris & Allendorf 1989). Yet, in a survey of carnivores, Creel (1998) was able to incorporate these three factors for only two species, lions (*Panthera leo*) and dwarf mongooses (*Helogale parvula*). I extended Creel's (1998) work to include Serengeti cheetahs. In addition, I incorporated a new factor, heritability of fitness, in estimating N_e .

Methods

Cheetahs of the central plains of the Serengeti National Park, Tanzania, have been studied continuously since 1969 (Bertram 1978; Caro 1994; Kelly et al. 1998), but data are from 1970 to 1994. During most days, I searched for cheetahs over a predetermined area of the plains and woodland border (Sinclair 1979). Animals were recognized by unique patterns of banding on the tail (Caro & Durant 1991) and by spots on the body. Because cheetah spot patterns remain constant through life, those animals not immediately recognized in the field were photographed for identification at a later date. I used a computer-aided matching program to assist in matching the backlog of unidentified cheetahs (Caro & Kelly 2000). Relatedness of individuals could be traced only through the female line because extremely few matings have been observed in the wild (Caro 1994). Maternity was established by seeing a mother with her cubs in photographs. Later, those cubs were matched to photographs of adult animals.

Matriline Loss and Heritability of Fitness

I reconstructed life histories of female cheetahs and assigned related individuals to cheetah matriline. I mapped cheetah matriline in detail for as many as seven generations ($\bar{x} = 2.0$; SD = 1.4; range: 1–7). Individuals were counted as a member of a matriline if they survived to independence. Male cheetahs were included in a matriline if their mother or sister was a matriline member. I counted the total number of matriline that occurred from 1970 to 1994 and the number extant at the end of 1994. Gompper et al. (1997) show, however,

that lineage persistence is positively related to length of study period and inversely related to generation time, defined as age at first reproduction. Following Gompper et al. (1997), I incorporated study length and generation time by dividing number of years of the study by age at first reproduction (minimum generation time) and then used this figure to divide into the number of matrilineal lineages lost by the end of the study. This gave the rate of lineage loss per generation (Table 1).

Gompper et al. (1997) found that in animals that breed more than once, using age at first reproduction underestimates true generation time but allows one to examine lineage loss assuming the greatest possible number of generations or the maximum potential turnover. Therefore, I also examined lineage loss based on average generation time, calculated as the mean age of mothers at the time each offspring was born.

I regressed daughters' lifetime reproductive success (LRS) on that of their mothers to determine heritability, b^2 , which is the slope of the line in a parent-offspring re-

gression (Ridley 1993). I measured LRS of females in three ways. I used the common method of recording the total number of cubs raised to independence during the adult female's lifetime (Clutton-Brock 1988). I also calculated the number of cubs and the number of litters (defined as any number of cubs surviving) raised to independence per year, respectively. This was done by dividing the total number of surviving cubs or litters by the length of time the cheetah was known to be independent in the study area. Cubs per year is a more sensitive measure of reproductive success because partial litter mortality occurs in many litters after 4 months of age (Caro 1987; Laurenson 1994).

I was not able to include the reproductive success of male cheetahs in this analysis because of a complete lack of data on male LRS. To my knowledge, only two matings were witnessed between 1970 and 1999 in the Serengeti (T. M. Caro, personal communication; S. M. Durant, personal communication).

I compared mothers' and daughters' LRS using linear

Table 1. Percentage of lineages lost for large and small mammals through the course of a study and per generation.*

Species	Study period (years)	Lineages lost (%)	Lineages lost per generation (%)
Large mammals			
cheetah	25	76	6.1
<i>Acinonyx jubatus</i>			
black bear	23	8	1.7
<i>Ursus americanus</i>			
African lion	13	4	1.4
<i>Panthera leo</i>			
African wild dog	12	40	10.3
<i>Lyacon pictus</i>			
European badger	5	12.5	3.6
<i>Meles meles</i>			
white-nosed coati	7	40	11.4
<i>Nasua narica</i>			
elephant seal	21	7	1.2
<i>Marounga angustirostris</i>			
feral horse	6	8	2.8
<i>Equus caballus</i>			
red deer	17	3	0.4
<i>Cervus elaphus</i>			
yellow baboon	18	36.4	11.1
<i>Papio cynocephalus</i>			
Toque macaque	16	25	6.3
<i>Macaca sinica</i>			
Small mammals			
yellow-bellied marmot	23	87	8
<i>Marmota flaviventris</i>			
bush hyrax	6	54	24
<i>Heterohyrax brucei</i>			
plains viscacha	5	87.5	12.3
<i>Lagostomus maximus</i>			
thirteen-lined squirrel	4	80	20
<i>Spermophilus tridecemlineatus</i>			
Richardson's ground squirrel	4	80	20
<i>Spermophilus richardsoni</i>			

*Adapted from Gompper et al. (1997). Generation time is defined as age at first reproduction, which represents the minimum generation interval or maximum potential turnover. Using average generation for cheetahs yielded much higher lineage loss per generation at 16.1%.

regression. I also examined LRS of mother-granddaughter pairs by means of Spearman correlations because of small sample sizes. Cheetah pairs included in this analysis had to meet three criteria. First, only cheetahs known or assumed to be dead were included in this analysis and hence their reproductive efforts were over. Cheetahs were assumed dead if they had not been seen within two standard deviations of their average intersighting interval (Kelly et al. 1998). Second, because it is easy to lose track of females between sightings and subsequently miss independence of a litter, the fate of all litters and cubs born during the mother's lifespan on the plains had to be known with certainty. Third, cheetahs had to be seen as independent on the plains for a minimum of 20 months, the average time required to raise one litter—3 months gestation plus 17 months to independence (Kelly et al. 1998). Only those cheetahs independent from 1980 onward were included in the analysis because after 1980 the average reproductive success of cheetahs before this period was significantly different from LRS (Kelly et al. 1998). In addition few complete data sets exist on LRS for mother-daughter pairs before 1980.

To examine heritability of fitness in greater detail, I partitioned reproductive success into three components: age at first reproduction, litter size at independence, and reproductive lifespan. I compared these measures to the reproductive success of all cheetahs used in the parent-offspring comparisons and then compared the components of reproductive success between the mother-daughter pairs.

Estimates of N_e

The Serengeti cheetah population violates many of the assumptions of Wright's (1969) ideal population. The general assumptions are that the population size is stable, the sex ratio is 50:50, mating is random, and reproductive success follows a Poisson distribution. I used published methods for estimating effective population

size when these assumptions were not met. These methods are well developed in theory (Nei & Murata 1966; Wright 1969; Crow & Kimura 1970; Lande & Barrowclough 1987) and have been well reviewed by others (Lande & Barrowclough 1987; Nunney & Campbell 1993), but they rarely have been applied to data from wild populations because of lack of demographic information on known individuals over long periods of time (but see Nunney & Campbell 1993; Creel 1998). Using the long-term cheetah data set, I included four factors in N_e calculations: fluctuating population size, skew in the sex ratio (inbreeding N_e), variance in reproductive success or the family size effect (variance N_e), and heritability in fitness (equations relating N_e to these factors are given in Table 2).

For population-size estimates, only known resident adults (≥ 2 years old) were counted. Resident animals were those seen three or more times over the course of 1 year. The cheetah population size here is smaller than a previously published estimate that included transient cheetahs (Creel 1998). Because the fluctuating population-size equation for N_e (the harmonic mean, Table 2) applies directly to a population with discrete generations, I followed Lande and Barrowclough's (1987) correction for N_e per unit time for populations with overlapping generations.

The inbreeding N_e requires knowledge of numbers of breeding adults. I counted female cheetahs as breeding adults when they were 2 years old or older because 2 years is the youngest age at which female cheetahs begin reproducing (Kelly et al. 1998). There are no data on earliest age of reproduction for free-living male cheetahs. Captive studies have shown male cheetahs capable of reproduction by 15 months, but testosterone concentrations, which likely drive sexual aggressiveness and libido, do not reach adult levels until approximately 2 years of age (Wildt et al. 1993). Hence, I counted males as breeding adults only if they were ≥ 2 years old. The numbers I used for male and female adult population size are only slightly different from previous estimates of

Table 2. Effective population size of cheetah population calculated with different estimators.*

Estimator	n (years)	N or N_m, N_f	F	s^2	h^2	N_e	N_e/N	N needed to maintain	
								$N_e = 500$	
Fluctuating population size	$N_e = n/\sum(1/N_i)$	18	52.6	—	—	—	49.7	0.95	526
Inbreeding N_e (sex ratio bias)	$N_e = 4N_m N_f / (N_m + N_f)$	18	14.6, 37.9	—	—	—	42.2	0.80	625
Variance N_e (females only) (variance in reproductive success or family size)	$N_e = NF - 1/[F + (s^2/F) - 1]$	18	108	1.72	5.52	—	47.0	0.44	1136
Heritability of reproductive success (females only)	$N_e = N'_e / [(1 + 3h^2)(s^2/F^2) + (1/F)]$	13	40.4	1.60	4.91	0.88	6.1	0.15	3064

*N, average population size, except for variance N_e , for which N is the actual number of females; N_m, N_f , average number of males, females respectively; F, lifetime reproductive success; s^2 , variance in lifetime reproductive success; h^2 , heritability in lifetime reproductive success. $N'_e = N'L$, where N' is number born surviving to reproductive age and L is average generation length (calculated conservatively as average longevity, which was 6 years for cheetahs in this study).

population size that included any independent cheetah as an adult (average age at independence is 17.1 months) (Kelly et al. 1998).

Wright (1938) linked N_e to variance in reproductive success or family size, and numerous studies have shown that inclusion of this variance can have a dramatic effect on N_e (Crow & Morton 1955; Harris & Allendorf 1989; Rockwell & Barrowclough 1995; Creel 1998). Because of the difficulty in estimating variance in lifetime reproductive success, most studies assume a Poisson distribution of this parameter, but the available data suggest this is a poor assumption (Barrowclough & Rockwell 1993). Many birds have variances in reproductive success that exceed the mean (Newton 1989), and recent studies have shown this to be true for several mammal species (Clutton-Brock 1988), including cheetahs (Creel 1998; Kelly et al. 1998). I used previously published data on average lifetime reproductive success for cheetahs (Kelly et al. 1998) in estimating the variance N_e following Lande and Barrowclough (1987).

I used the mother-daughter regressions of LRS to estimate heritability. I was not able to use the mid-parent value (average of mother's and father's LRS) because I did not know the reproductive success of the fathers. In such a case when only one parent is used, b^2 is equal to twice the slope of the parent-offspring regression ($b^2 = 2r_{po}$) (Maynard Smith 1989; Ridley 1993). I incorporated heritability into the N_e estimate following Nei and Murata (1966).

Results

Matriline Loss and Heritability of Reproductive Success

Over the course of the study, 76% of the cheetah lineages contained 4 or fewer individuals (Fig. 1). The most successful matriline contained 44 individuals. The 5 most successful matriline, each of which contained 20 or more individuals, accounted for 45% of the cheetah population (Fig. 2), excluding those males of unknown origin that could not be counted as a matriline member. The number of lineages lost over the course of the study was high (Table 1). Of the 63 matriline identified, only 15 (24%) persisted at the end of the 25-year study. Using minimum generation time, however, I found that cheetahs lost 6.1% of lineages per generation. Lineage loss per generation was much higher (16.1%) when I used the average generation time of 5.34 years ($n = 43$ females; $SD = 2.48$).

Lineage loss in cheetahs was nonrandom because persistent lineages contained highly successful mothers and daughters. Regressions of female cheetah reproductive rates against those of their mothers yielded positive and significant relationships for both cubs to independence per year ($n = 21$ pairs; $y = 0.466x + 0.155$, $r = 0.505$;

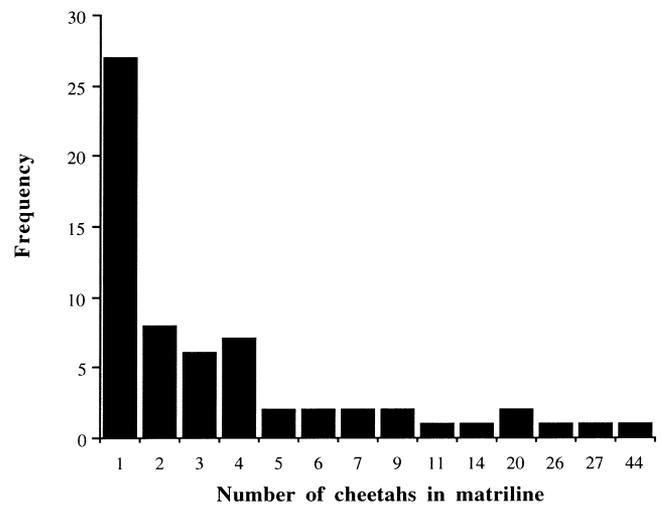


Figure 1. Size of cheetah matriline and their frequency of occurrence.

$p = 0.003$) and litters to independence per year ($n = 21$; $y = 0.444x + 0.138$; $r = 0.609$; $p = 0.020$) (Fig. 3). The reproductive lifespan (i.e., time seen independent) for cheetahs in my analysis ranged from 1.67 to 11.83 years, with an average of 6.35 years ($n = 31$ females; $SD = 3.15$), and the average number of reproductive attempts per reproductive lifespan was 3.65 ($SD = 2.01$). Although these data include cheetahs from only 1980 to 1994, reproductive success is still highly right-skewed, as it was for the entire study. I controlled for non-normality by repeating this analysis for mother-daughter pairs with log-transformed data and found similar results for cubs per year raised to independence ($n = 21$ pairs;

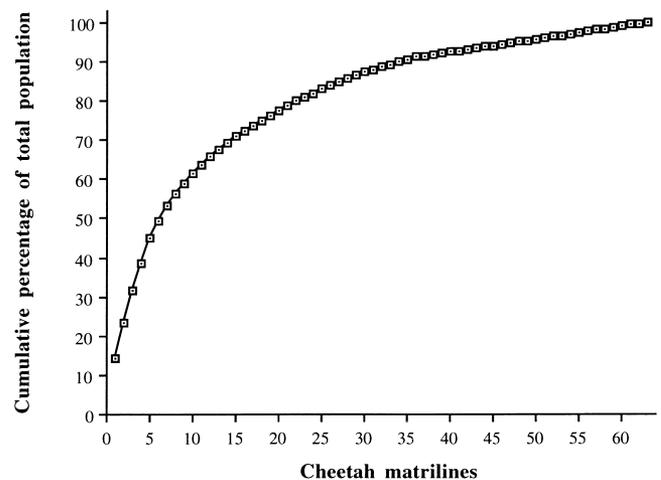


Figure 2. Cumulative percentage of total cheetah population represented by the 63 different matriline present over the course of the 25-year study. Matriline are plotted from the most to the least successful. The more cheetahs in a matriline, the more successful that matriline.

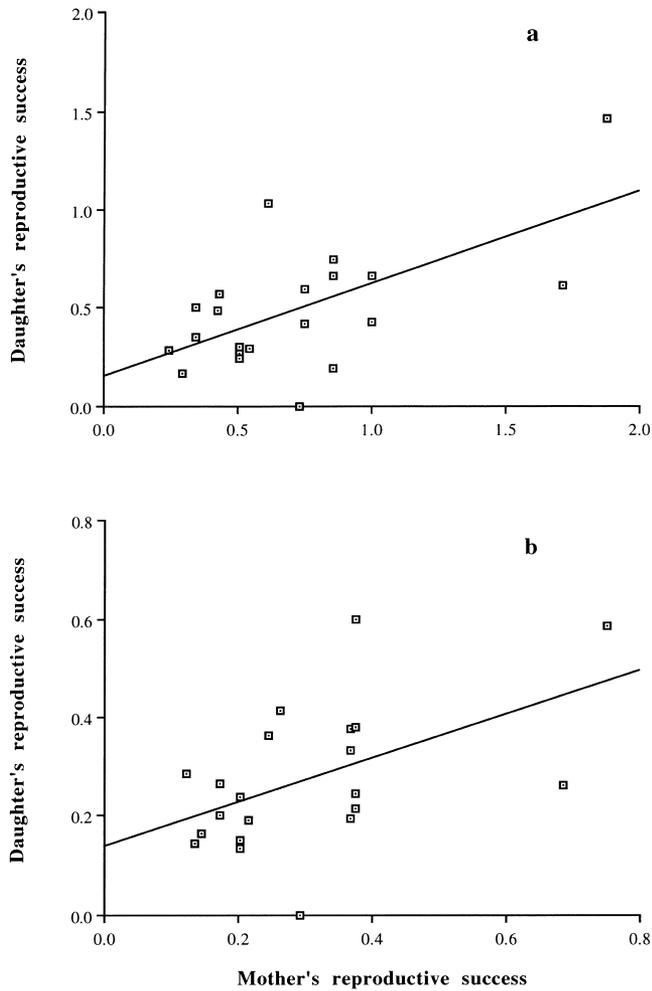


Figure 3. Parent-offspring regressions of lifetime reproductive success: (a) cubs to independence per year for mothers and their daughters and (b) litters to independence per year for mothers and their daughters.

$y = 0.500x + 0.052$; $r = 0.548$; $p = 0.010$) and litters raised to independence per year ($n = 21$ pairs; $y = 0.455x + 0.191$; $r = 0.498$; $p = 0.022$).

Correlations for mother-granddaughter reproductive rates (Fig. 4) were also positive and significant for cubs raised ($n = 8$ pairs; $r_s = 0.805$; $p = 0.033$) and litters raised ($n = 8$ pairs; $r_s = 0.638$; $p = 0.091$) to independence per year. The average reproductive lifespan of the 14 cheetahs in this restricted analysis was 6.2 years (SD = 2.8; range = 1.67 – 11.83 years), and the average number of reproductive attempts per reproductive lifespan was 3.86 (SD = 1.88).

Through linear regression, I compared the reproductive rates of all the cheetahs used in the parent-offspring comparisons to three components of reproductive success: age at first successful reproduction, average litter size at independence, and longevity or reproductive lifespan. Reproductive rate, measured as the number of litters raised to independence per year, was inversely related to both age at first reproduction and reproductive

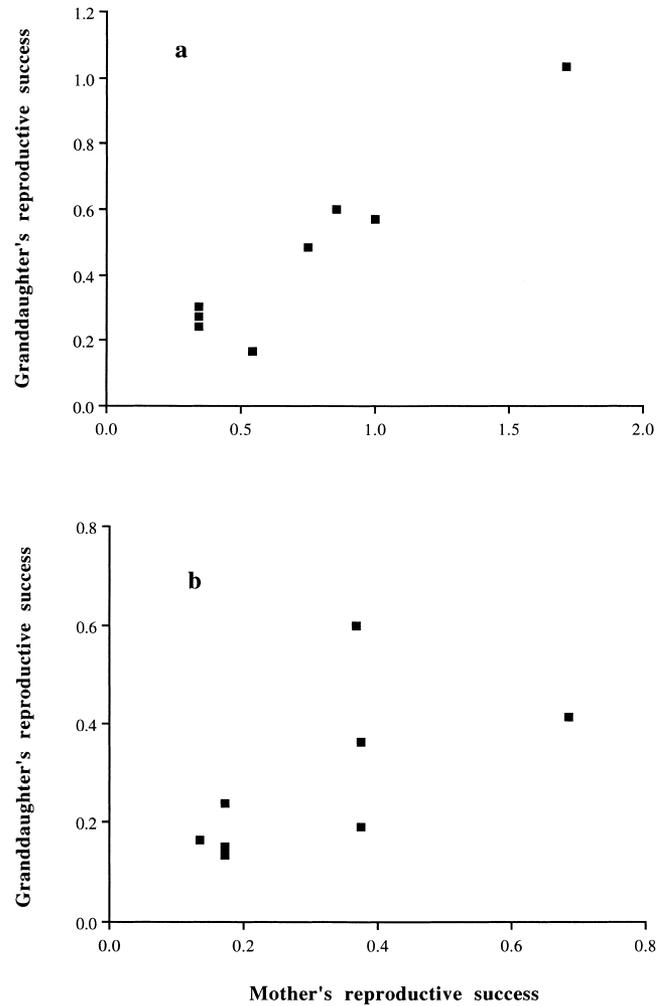


Figure 4. Parent-grand offspring Spearman correlations of lifetime reproductive success: (a) cubs to independence per year for grandmothers and their granddaughters and (b) litters to independence per year for grandmothers and their granddaughters.

lifespan ($n = 23$; $y = -0.004x + 0.460$; $r = 0.422$; $p = 0.045$; and $n = 27$; $y = -0.002x + 0.441$; $r = 0.385$; $p = 0.036$; respectively), whereas the reproductive rate measured as the number of cubs raised to independence per year was positively related to the average litter size at independence ($n = 28$; $y = 0.207x + 0.200$; $r = 0.379$; $p = 0.043$). In general, cheetahs with high reproductive success reproduced early, had a short lifespan, or raised large litters to independence. Comparing these components of reproductive success between mothers and their daughters, however, yielded no significant relationships (age at first successful reproduction: $n = 13$; $y = -0.157x + 36.940$; $r = 0.127$; $p = 0.679$; average litter size at independence: $n = 17$; $y = 0.430x + 0.813$; $r = 0.318$; $p = 0.172$; reproductive lifespan: $n = 21$; $y = 0.191x + 62.549$; $r = 0.175$; $p = 0.448$). Hence, no one particular component of reproductive success appeared to be passed on from mother to daughter.

Estimates of N_e

The N_e estimators I used when assumptions of the ideal population were not met are presented in Table 2. Effective population size is generally expressed as a proportion of the mean adult population size, N_e/N , to allow for comparisons between species (Nunney & Elam 1994). Fluctuating population size had little effect on the genetic effective size of the cheetah population as N_e was 95% of the original population (Fig. 5). This result is similar to the previous estimate of N_e for cheetahs (at 97% of original), which included transient cheetahs (Creel 1998).

An imbalanced sex ratio had a stronger effect on N_e than fluctuating population size. The effective population size was reduced to 80% of the actual population size. This result does differ substantially from that of Creel (1998), who estimated the inbreeding N_e to be 98% of the actual cheetah population. The inclusion of transient cheetahs in that estimate will equalize the sex ratio because male cheetahs are more likely to be unknown transients than females are (Kelly et al. 1998).

Cheetah lifetime reproductive success follows a skewed distribution (Fig. 6). Most female cheetahs raised no cubs to independence, whereas a few raised many. The average number of cubs raised to independence over the entire study was 1.72 ($n = 108$ females; $s^2 = 5.52$). A non-Poisson distribution in LRS proved to have a strong effect on N_e , reducing the effective population size to 44% of the actual size.

Mother-daughter regressions yielded slopes of 0.444 and 0.466 for cubs raised per year or litters raised per year, respectively (Fig. 3). These resulted in heritability estimates of 0.888 and 0.932. I chose the lower, more conservative value, 0.888, for my heritability measure. The most drastic reduction in N_e came with the addition of heritability in reproductive success: N_e was only 15% of the actual population size.

Discussion

The initial flurry of research papers on homozygosity and its consequences in cheetahs (O'Brien et al. 1983, 1985, 1986) highlighted the importance of genetic variation for population viability. Later, ecological studies implicated high cub predation in limiting cheetah population size (Laurenson 1994) and suggested that genetics may have been over-emphasized in the plight of cheetahs (Caro & Laurenson 1994). Although demographic and ecological factors brought on by habitat loss and fragmentation are undoubtedly an immediate threat to most endangered species, long-term maintenance of genetic variation is relevant to species conservation, especially for small populations. Responses of populations to demographic and environmental changes are affected by genetic variation (Frankham 1995), but it is difficult to demonstrate that an extinction was influenced by low genetic variability and a consequent lack of adaptive potential in the wild. Evidence is now accumulating, however, that wild and semiwild populations are suffering inbreeding depression and decreased fitness due to low variability (Frankham 1995; Lacy 1997; Caro 2000). Saccheri et al. (1998) provide the first direct evidence that inbreeding contributes to the extinction of wild populations. They found that populations of Glanville fritillary butterflies (*Melitaea cinxia*) with less genetic variation were more likely to become extinct even after all known demographic, ecological, and environmental causes of extinction were accounted for. In addition, Frankham and Ralls (1998) cite several indirect lines of evidence implying that the results from the Glanville butterfly can be extended to other wild species.

Matriline Loss and Possible Causes of Heritable Fitness

Only recently has the importance of lineage loss in natural populations become a conservation concern. Studies

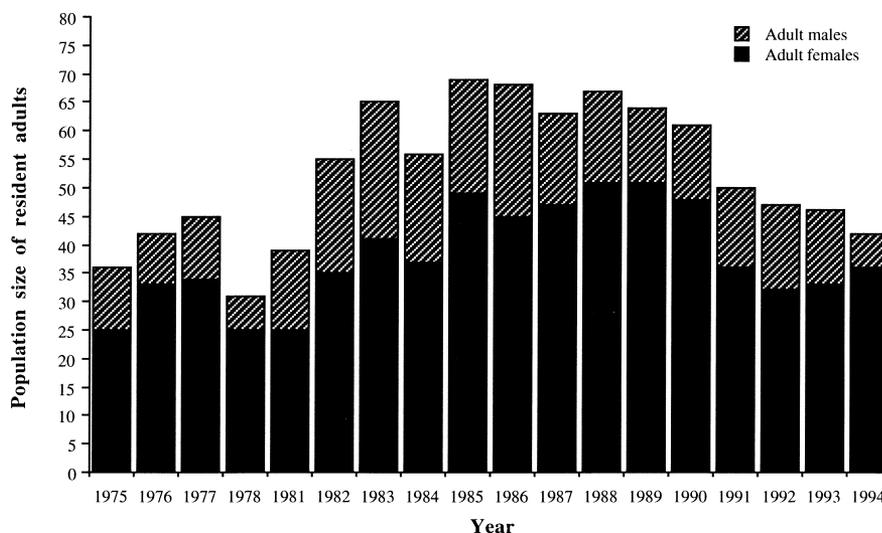


Figure 5. Population size of resident adult (≥ 2 years) cheetahs on the Serengeti Plains. Years 1979–1980 are absent because a shortage of researchers in the field lead to inaccurate cheetah counts.

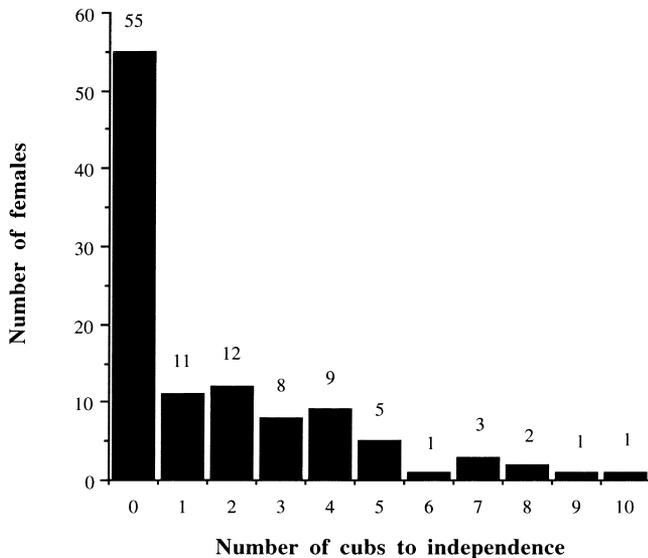


Figure 6. Number of cheetah cubs raised to independence over a female's lifetime for the entire study (1969-1994). Adapted from Kelly et al. (1998).

by Berger and Cunningham (1995) and Gompper et al. (1997) point to the fact that, once matriline losses are considered, genetic diversity may be lost at a much more rapid rate in natural populations than expected. For cheetahs, only a few lineages (8%) produced nearly half of the total population in the Serengeti over the course of the study (1970-1994). Over similar spans of time (approximately 20 years), cheetahs lost family groups much more rapidly than did other large mammals. Cheetahs lost 76% of matriline, whereas other large mammals lost from 3% to 40% ($n = 10$ species; $\bar{x} = 18\%$). Small mammals lost lineages at a rate of 54-87.5% ($n = 5$ species; $\bar{x} = 78\%$) over the course of the studies shown (Table 1). Once I converted to minimum generational rates, however, cheetahs lost 6.1% matriline per generation, similar to rates for both large and small mammals. For species that breed more than once, however, it is perhaps more appropriate to calculate lineage loss using the average generation interval rather than the minimum. In cheetahs, the average generation time of 5.3 years is much higher than the minimum generation interval of 2.0 years. Cheetahs lost matriline much more quickly, at 16.1% per generation, when average rather than minimum generation time was used. Calculating average generation time is difficult because it requires knowing the age at which an individual female gives birth to each of her young over her lifespan; unfortunately, there are few such data on other species for comparison.

The matriline effect is perhaps best demonstrated by unequal LRS and heritability in LRS. It is not clear why heritability in female reproductive success is so high in cheetahs. In general, heritability is expected to be small for traits directly contributing to fitness (Fisher 1930).

When some individuals in a population possess good genes, selection acts to fix those good genes; hence, variance in genetic quality should be eliminated (Maynard-Smith 1989; Ridley 1993). If the environment changes, however, selection may not have sufficient time to fix good genes. Some evidence for environmental change exists as lion density has increased on the Serengeti Plains during the 1980s (Hanby et al. 1995), and lions are a major source of juvenile mortality in cheetahs (Laurenson 1995). Furthermore, we know that cheetah reproductive success was significantly lower from 1980 to 1994 than it was from 1970 to 1980, which parallels the increase in lion numbers on the plains (Kelly et al. 1998).

Although age at first reproduction, litter size at independence, and reproductive lifespan are correlated with a cheetah's overall reproductive success, no single component appears to be heritable from mother to daughter. Yet the overall LRS was heritable not only from mother to daughter but also from mother to granddaughter. Which specific components of fitness are correlated across generations are unknown, and nothing is known about the extent to which variation in LRS is due to genetic variation. Durant (1998) has shown that cheetahs actively avoid areas with high numbers of lions and that cheetahs with higher reproductive success react more strongly to playbacks of lion calls than do cheetahs with poor reproductive success (Durant 2000). Successful mothers appear more vigilant and "nervous." In contrast, a behavioral study on captive cheetahs found that "calm" cheetahs were more likely to breed successfully than tense individuals (Wielebnowski 1999). Unfortunately, it is unknown whether there is a genetic component to nervous or calm behavior in cheetahs.

Predation is a major source of cheetah mortality (Laurenson 1995) and hence potentially results in high lineage loss in cheetahs. The extent to which matriline loss has occurred in cheetahs in the past is unknown. On the one hand, cheetahs exhibit life-history traits such as large litters and early age at maturity which point to their long evolution with extrinsic causes of high cub mortality (Caro 1994). In addition, more reproductively successful female cheetahs exhibit higher vigilance against potential predators than unsuccessful cheetahs do (Durant 2000). On the other hand, predation pressure may be ephemeral, at times relaxing the selection pressure for high vigilance. In 1993, for example, canine distemper virus killed two-thirds of the lion population in the Serengeti (Roelke-Parker et al. 1996), potentially resulting in lower cheetah cub predation. Also, cheetahs' high mobility may allow them to avoid areas of high predator concentration (Durant 1998). At the moment, questions about lineage loss in the past remain unresolved.

Missing from my study is information on the male reproductive contribution to variance or heritability in reproductive success. If there is a lack of congruence be-

tween patriline and matriline (e.g., if males from different or "unsuccessful" lineages are fathering offspring in successful matriline), the problem of lineage loss may be offset, or lineage loss may be inflated in my study. Unfortunately, no data exist on male reproductive success in free-living cheetahs.

Current evidence suggests that lineage loss in mammals and birds is common and nonrandom because only a few individuals are responsible for production of a large percentage of the future breeders (Gompper et al. 1997). This phenomenon is perhaps best exemplified by the high variance in reproductive success occurring in many natural populations (Clutton-Brock 1988; Newton 1989), including cheetahs (Kelly et al. 1998). Such asymmetry in reproductive success becomes even more pronounced when the number of offspring that become breeders is taken into account (Gompper et al. 1997). This is best exemplified by incorporating unequal LRS and heritability of LRS into estimates for N_e (i.e., variance N_e and heritability N_e).

Estimates of N_e

An imbalanced sex ratio reduced the N_e to 80% of the actual population size, which differs substantially from Creel's (1998) estimate of 98%. This difference was due to the exclusion of transient males in my estimation of male population size, which equalizes the sex ratio. If transient males breed, then Creel's (1998) estimate of inbreeding N_e is more realistic. It is unknown whether transient males father offspring, but they remained in the study area for only short periods. If transients occasionally breed, the actual inbreeding N_e will fall between the two values given above.

Variance in lifetime reproductive success had a much stronger effect on N_e than did fluctuating population size or sex-ratio skew. The effect of a non-Poisson distribution in LRS reduced the effective population size to 44% of the actual size. In comparison with variance N_e estimates for other species, cheetahs have the lowest known N_e/N , ratio with the exception of dwarf mongooses (Nunney & Elam 1994; Creel 1998). Addition of heritability in reproductive success further reduced N_e . There is currently no other study incorporating measured heritability into N_e estimates that can be compared with those of cheetahs.

Few data are available on heritability of fitness in natural populations. Of the 24 studies of reproductive success in wild populations presented by Clutton-Brock (1988), only 2 examined heritability. Van Noordwijk and van Balen (1988) found heritabilities of about 40% ($b^2 = 0.40$) for clutch size in the Great Tit (*Parus major*), and Smith (1988) found no evidence of heritability in breeding success for Song Sparrows (*Melospiza melodia*). Gustafsson (1986) found heritabilities close to zero for components of LRS for Collared Flycatchers (*Ficedula*

albicollis), whereas research on red deer (*Cervus elaphus*) indicates that juvenile survival is related to genetic differences (Pemberton et al. 1988).

Mating systems are a major determinant of lifetime reproductive success (Nunney 1991) such that social species, especially those with reproductive suppression, have extremely high variance in LRS. For dwarf mongooses, variance in LRS is 18 times the mean (Creel 1998), whereas for female cheetahs variance in LRS is three times the mean. Creel (1998) found that N_e/N for dwarf mongooses varied from 0.17 to 0.34, depending on how many subordinates were estimated to reproduce. Cheetahs do not exhibit reproductive suppression in the wild. Rather, most females have the opportunity to reproduce, and it is likely that both resident territorial and floater males do also (Caro & Kelly 2001), although data are lacking for male LRS in cheetahs. Nonetheless, based on female heritability of fitness, N_e/N for cheetahs is reduced dramatically to 0.15 (Table 2), a value similar to that estimated for dwarf mongooses, a species with reproductive suppression (Creel 1998).

Franklin (1980) and Soulé (1980) initially suggested that the N_e needed to maintain adaptive potential should be at least 500 individuals. If free-living populations are subject to ecological or behavioral processes causing directional selection rather than just genetic drift, the N_e may need to be higher (Lande 1995). In any case, satisfying the Franklin-Soulé rule of thumb for cheetahs requires an actual population size for cheetahs of 1136 for variance N_e and 3064 for heritability N_e (Table 2). How realistic it is to achieve such numbers depends greatly on cheetah population size in the greater Serengeti-Mara ecosystem, an area of 25,000 km². Caro and Durant (1995) roughly estimated that 200–250 cheetahs occur in this ecosystem. At this level, the cheetah population is well below the level necessary to buffer against genetic drift and loss of variation due to inbreeding. This population-size estimate, however, was based on cheetah population size on the Serengeti Plains, an area that is only 2,200 km², or 9% of the total area. The Serengeti Plains are surrounded by woodland areas, and it is generally assumed that cheetahs occur at lower densities in woodland areas than on the plains (T. M. Caro, personal communication). It is unclear if this assumption is realistic. Actual data do not exist on cheetah numbers in the woodland areas that comprise most of the Serengeti ecosystem, and there is not much information on emigration from or immigration to the woodland areas surrounding the Serengeti Plains. Nevertheless, even under the optimistic assumption of the woodlands holding densities similar to those of the plains (53 adults on average), the total would come to approximately 530 individuals, which is still well below the variance and heritability N_e estimates.

If lineage loss in natural populations is as common as has been suggested (Gompper et al. 1997) and is related

to unequal reproductive success and heritability in LRS, as in cheetahs, it is then important to examine these factors in other species and determine their effect on effective population size. Otherwise, N_e estimates will be far more optimistic than they should be.

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