Abstract: Preservation of genetic diversity within declining populations of endangered species is a major concern in the discipline of conservation biology. The endangered cheetah, *Acinonyx jubatus*, exhibits relatively little genetic variability (polymorphism = 0.02-0.04, heterozygosity = 0.0004-0.014). Since the discovery of the cheetah's relative homozygosity, this species has been frequently cited as an example of one whose survival may be compromised by the loss of genetic diversity. The cheetah's genetic uniformity is generally believed to be the result of an historical population bottleneck followed by a high level of inbreeding. Evidence offered in support of this hypothesis includes the cheetah's present low level of genetic variability and symptoms of inbreeding depression in captive populations. Using available data on fluctuating asymmetry and genetic variation in other carnivores, I question the assumption that the present level of genetic diversity in the cheetah is indicative of a loss of former variability. Carnivores exhibit significantly lower levels of genetic variation than other mammals, and several carnivores for which data are available exhibit lower levels of heterozygosity and polymorphism than the cheetah does. Measures of fluctuating asymmetry do not support the hypothesis that the cheetah is suffering an increased level of homozygosity due to genetic stress. Many of the phenotypic effects attributed to inbreeding depression, such as infertility, reduced litter sizes, and increased susceptibility to disease, are limited to captive individuals and may be explained as physiological or behavioral artifacts of captivity. In sum, the genetic constitution of the cheetah does not appear to compromise the survival of the species. Conservation efforts may be more effectively aimed at a real, immediate threat to the cheetah's future: the loss of its natural habitat.

A Reassessment of Homozygosity and the Case for Inbreeding Depression in the Cheetah, *Acinonyx jubatus:* Implications for Conservation

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Abstract: *Preservation of genetic diversity within declining populations of endangered species is a major concern in the discipline of conservation biology. The endangered cheetah,* Acinonyx jubatus, *exhibits relatively little genetic variability (polymorphism = 0.02–0.04, heterozygosity = 0.0004–0.014). Since the discovery of the cheetah's relative homozygosity, this species has been frequently cited as an example of one whose survival may be compromised by the loss of genetic diversity. The cheetah's genetic uniformity is generally believed to be the result of an historical population bottleneck followed by a high level of inbreeding. Evidence offered in support of this hypothesis includes the cheetah's present low level of genetic variability and symptoms of inbreeding depression in captive populations. Using available data on fluctuating asymmetry and genetic variation in other carnivores, I question the assumption that the present level of genetic diversity in the cheetah is indicative of a loss of former variability. Carnivores exhibit significantly lower levels of genetic variation than other mammals, and several carnivores for which data are available exhibit lower levels of heterozygosity and polymorphism than the cheetah does. Measures of fluctuating asymmetry do not support the hypothesis that the cheetah is suffering an increased level of homozygosity due to genetic stress. Many of the phenotypic effects attributed to inbreeding depression, such as infertility, reduced litter sizes, and increased susceptibility to disease, are limited to captive individuals and may be explained as physiological or behavioral artifacts of captivity. In sum, the genetic constitution of the cheetah does not ap-*

Resumen: *Una de las principales preocupaciones en el área de la biología de la conservación es la preservación de la diversidad genética dentro de las problaciones de especies en peligro de extinción. Una de estas especies, el cheetah* Acinonyx jubatus *exhibe poca variabilidad genética (polimorfismo = 0.02–0.04, heterocigosidad = 0.0004–0.014). Desde el descubrimiento de la homocigosidad relativa, del cheetah el ha sido frecuentemente citado como un ejemplo de aquellas especies cuya supervivencia esta comprometida por la pérdida de la diversidad genética. Se piensa que la uniformidad genética del cheetah se debe a un histórico cuello de botella poblacional, seguido por un alto nivel de endogamia. Los bajos niveles de variabilidad genética en el cheetah y los síntomas de depresión de endogamia en las poblaciones en cautiverio son considerados como evidencias que apoyan esta hipótesis. Usando datos disponibles sobre la fluctuación asimétrica y la variación genética en otros carnivoros, considero cuestionable la suposición de que el presente nivel de diversidad genética en el cheetah se debe a la pérdida de la variabilidad genética que habría poseido en el pasado. En comparación con los demás mamiferos, los carnivoros presentan un nivel de variabilidad genética significativamente menor. Más aún, varios carnivoros, de los cuales se dispone de datos, tienen niveles de heterocigosidad y polimorfismo menores que el cheetah. Las medidas de fluctuación asimétrica no apoyan la teoría de que el cheetah esta sufriendo un aumento en el nivel de homocigosidad debido a tensiones genéticas. Muchos de los*

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efectos fenotípicos atribuidos a la depresión ae endogamia, tales como la infertilidad, reducción en el tamaño de las camadas y aumento en la susceptibilidad a las enfermedades, se han limitado a observaciones de individuos en cautiverio. Tales efectos, pueden ser explicados como el resultado de artificios fisiológicos o de comportamiento ocasionados por el cautiverio. En pocas palabras, la constitución genética del cheetah no parece poner en peligro la supervivencia de esta especie. Los esfuerzos de conservación podrían ser dirigidos en forma másefectiva para enfrentar un peligro real e inmediato que amenaza el futuro del cheetah: la pérdida de su hábitat natural.

Introduction

The preservation of genetic diversity is a top priority in conservation biology (Foose 1977: Chesser et al. 1980; Schonewald-Cox et al. 1983). Since the discovery that the endangered cheetah, *Acinonyx jubatus*, exhibits near genetic uniformity, this species has become a symbol for the conservation of genetic diversity (see O'Brien et al. 1983). The cheetah's lack of generic variability has traditionally been interpreted as the result of a drastic reduction in former genetic diversity due to one or more population bottlenecks, followed by extensive inbreeding. The relative homozygosity of the cheetah has been widely accepted as an explanation for the difficulty experienced in trying to breed this species in captivity; problems encountered have been diagnosed as symptoms of inbreeding depression in the captive populations (O'Brien et al. 1985: Yuhki & O'Brien 1990). Furthermore. the cheetah's genetic invariability is frequently cited as posing a critical threat to the future of the species in both the popular and scientific literature (see Allendorf & Leary 1986; Steinhart 1992).

The cheetah's low level of genetic variation does not appear to negatively affect the surviving wild population, estimated in 1974 to number approximately 20,000 individuals. but possibly as few as 10,000 (Myers 1976). The reduction in wild populations of cheetahs is largely attributable to habitat loss (Myers 1975). As wild cheetah populations continue to decline, increasing emphasis is placed upon captive breeding programs for the preservation of the species. This analysis considers the evidence for a loss of genetic variation in the cheetah using published measures of fluctuating asymmetry, and it compares the cheetah's level of genetic variability with that of other terrestrial carnivores. Alternative interpretations are posed for factors often cited as evidence of inbreeding depression. suggesting that problems in captive breeding may be rooted more in the husband? than in the genetic constitution of the cheetahs. The contribution of homozygosity to the decline of wild cheetah populations is increasingly questionable (Merola 1993; Caro & Laurenson 1994). In considering conservation strategies, the emphasis upon the cheetah's genetic composition may be misdirected as habitat critical to the survival of the species continues to disappear

The Importance of Genetic Diversity

Genetic diversity is commonly represented by two measures: polymorphism *(P)*, the proportion of loci known to vary in the population, and heterozygosity (H), the proportion of loci which vary in the average individual. A number of studies on widely varying taxa have demonstrated a positive relationship between heterozygosity and parameters of fitness. such as increased longevity, growth rates, fecundity, metabolic efficiency. and overall developmental stability (see Mitton 1978; Garton 1984: Koehn & Gaffney 1984; Mitton & Grant 1984). The deleterious effects of inbreeding manifested in terms of increased infant mortality, decreased litter size. infertility. and susceptibility to disease are likewise well documented (Lerner 1954; Wright 1977; Falconer 1951; Ralls & Ballou 1983). Genetic diversity has thus come to be viewed as contributing to the fitness of the individuals comprising a species as well as to the evolutionary potential of a species as a n-hole.

This emphasis on the importance of genetic diversity stems in part from Lerner's (1954) suggestion of heterozygote superiority. the superior "buffering capacity" of relatively heterozygous individuals that enables the organism to overcome environmental perturbations and develop more closely to the phenotypic optimum for the species. termed developmental homeostasis. Developmental homeostasis is reflected in the organism in the degree of symmetry between bilaterally paired traits. The level of genetic variability that corresponds with homeostasis has been demonstrated to vary between species: that is. the level at which a species attains ho-

meostasis is specific to that species (tit 1982). Average levels of polymorphism and heterozygosity are known to vary dramatically between species (Selander & Kauffman 1973; Powell 1975; Nevo 1978: Baccus et al. 1983) (Fig. 1).

Alternative Interpretations of Genetic Invariability in the Cheetah

The cheetah, *Acinonyx jubatus*, exhibits relatively low levels of genetic variability: $P = 0.02$ and $H = 0.0004$ in the South African subspecies *A. j. jubatus*, $P = 0.0\text{-}i$ and $H = 0.014$ in the East African subspecies *A. j. raineyi* (O'Brien et al. 1983. 1987). Cheetahs also exhibit an unusually high degree of uniformity at the major histocompatibility complex (MHC), normally the most polymorphic cluster of genes in the mammalian genome (O'Brien et al. 1985: Yuhki & O'Brien 1990). O'Brien and colleagues point out that cheetahs exhibit far less genetic variability than most mammals and suggest that the cheetah is "depauperate" in genetic variation (O'Brien et al. 1983). They propose that the cheetah has passed through one or more population bottlenecks, fol-

lowed by a high level of inbreeding, and. as a consequence. the species has lost a good deal of its presumed former genetic variability (O'Brien et al. 1987; O'Brien & Evermann 1988). Problems encountered in captive breeding of cheetahs are largely attributed to this hypothetical loss of genetic diversity in the species (see O'Brien et al. 1985; Wayne et al. 1986a; Yuhki & O'Brien 1990).

The perception of genetic invariability in the cheetah as extreme or unusual is often influenced by the comparison of levels of variation in the cheetah with the averages for other animal groups. which, as demonstrated in Figure 1, vary widely. Given that levels of genetic diversity appear to conform to ecological niches and taxonomic grouping to some degree (Selander & Kauffman 1973; Nevo 1978), rather than comparing the cheetah with all other mammals the more appropriate comparison may be other terrestrial members of the Carnivora. This comparison demonstrates that although the cheetah's level of variability is relatively low, it is not unique among carnivores. Large mammals in general tend to exhibit less generic variability than other mammals (Wooten & Smith 1985; Kilpatrick et al. 1986; Mitton & Raphael 1990; but see Baccus et al. 1983). Ter-
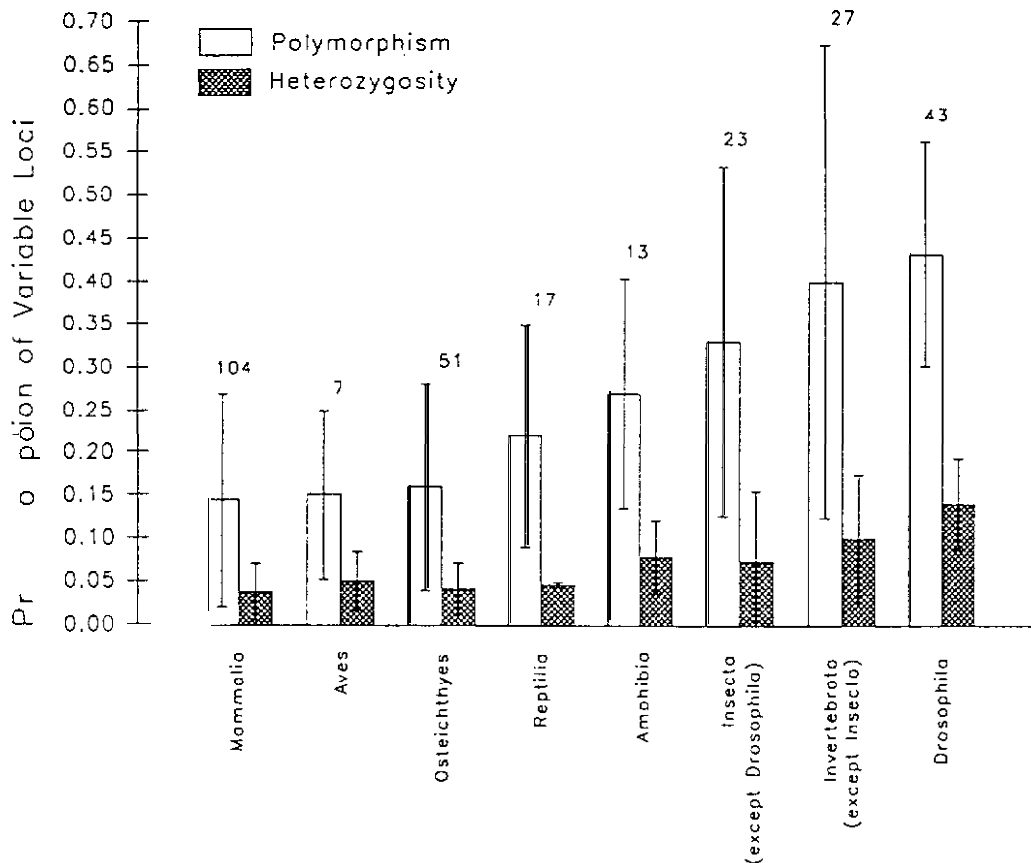

Figure 1. Comparison of levels of genetic variation among different animal groups. Note the high degree of variance both within and between the groups and the low level of genetic diversity displayed by mammals in general (after Nevo 1978. except Mammalia, this study). Sample sizes displayed at top of error bars.

restrial carnivores are characterized by particularly low generic variability, exhibiting significantly lower levels of both polymorphism and heterozygosity than other mammals (Table 1). Of those carnivores for which data are available, more than 30% exhibit levels of genetic diversity lower than that of cheetahs; eight of the carnivores examined show no polymorphism (Fig. 2). Given this phylogenetic context. it is not surprising that a terrestrial carnivore such as the cheetah shows low genetic diversity compared to other mammals. nor can the cheetah's low level of genetic variability be considered an anomaly.

Comparisons of presumptive fitness based on relative levels of heterozygosity are valid only within species: one cannot compare levels of heterozygosity between species and claim that one species is more or less tit than another based on their relative levels of variability. For example. within the Felidae there is a wide range of values for heterozygosity and polymorphism (Fig. 2). The level of heterozygosity in the leopard. *Panthera parldus* (H = 0.029). is less than half that exhibited by *the ocelot, Leopardus parldalus (H = 0.072).* Yet this difference is generally not considered as evidence that *P. parldus* is generically impoverished or inferior to *L parldalus;* rather. an alternative view is that the two species merely exhibit different levels of variability specific to their species. Likewise. the cheetah's low level of variability may accurately reflect its relative position on the lower end of the distribution of genetic diversity within the Felidae. but *it* does not necessarily imply that the cheetah is any less "fit" than other felids.

The most popular explanation for the present low levels of genetic diversity in the cheetah is a population bottleneck (see O'Brien et al. *1987;* O'Brien & Evermann 1988). Using DNA fingerprinting and mitochondrial DNA sequencing techniques. the calculations of Menotti-Raymond and O'Brien (1993) support the hypothesis of an ancient Pleistocene bottleneck that occurred approximately 10.000 years ago. O'Brien et al. (1987) have also proposed that a second, more recent.

population bottleneck may be responsible for the relatively lower variation of the South African cheetah.

Nowhere is there evidence for a high level of genetic diversity in the cheetah prior to the hypothetical bottleneck. One cannot validly assume a reduction in genetic variation based on present low levels of heterozygosity unless the historical degree of variability of a population is known. The case of the eastern barred bandicoot. *Perameles gunnii,* demonstrates the need for discretion in making such assumptions. No polymorphism was detected in an isolated, endangered population of these bandicoots in Australia (Sherwin et al. 1991). Standard interpretation would suggest that a population crash had resulted in a drastic reduction of the bandicoot's genetic diversiry. But subsequent elecrrophoretic studies of a widespread. dense population of *P. gunnii* in Tasmania showed a lack of genetic variability at all of the loci tested. What might easily have been interpreted as a potentially deleterious loss of genetic variability in the Australian population in fact appears to be the normal level in P. *gunnii*

If one assumes that the cheetah had an historically greater level of genetic variability, then the population bottleneck is inadequate as an explanation for the present low level of diversity exhibited by this species. Even an extreme bottleneck, in which the population is reduced to only two individuals, can result in the conservation of 75% of the original genetic variance in the founder population (Frankel & Soulé 1981). If the average individual is highly heterozygous prior to the population reduction, then much of the genetic variability will be retained (Nei et al. 1975; Carson 1990). Populations that have been through documented bottlenecks often retain high levels of variability (see Dinerstein & McCracken 1990); it is even possible for variation to increase following such an event (Carson 1990). For genetic variability to undergo a drastic reduction. the bottleneck must be maintained over several generations (Lande 1988) or the population must undergo a series of bottlenecks (O'Brien et al. 1987).

Table 1.   Comparison of genetic variation[a] in the order Carnivora with other members of the class Mammalia.

	n^d	*Polymorphism*[b]			*Heterozygosity*[c]		
		mean	*median*	*SE*	*mean*	*median*	*SE*
Carnivora[e]	26 (P)	0.089	0.088	0.088	0.028	0.022	0.037
	26 (H)						
Mammalia[f]	78 (P)	0.163	0.125	0.129	0.042	0.038	0.030
	81 (H)						

[a] *All values of polymorphism and heterozygosity compiled from Fisher et al. 1976; Manlove et al. 1977; Nevo 1978; Allendorf et al. 1979; Deu & Kennedy 1980; O'Brien 1980; Simonsen 1982; Simonsen et al. 1982. O'Brien et al. 1983, 1985, 198ˉ; Newman et al. 1985; Sage & Wolff 1986; Mitton & Raphael 1990; Sherwin et al. 1991.*
[b] *Difference in levels of polymorphism significant, p = 0.006-i. Wilcoxon rank sum test.*
[c] *Difference in levels of heterozygosity significant, p = 0.000ˉ5. Wilcoxon rank sum test.*
[d] P *denotes sample size for calculation of polymorphism values. H denotes sample size for calculation of heterozygosity values.*
[e] *Terrestrial carnivores only; species that have experienced documented population bottlenecks (such as Mustela nigripes. Panthera leo persica) were not included in the analysis.*
[f] *Mammals, excluding terrestrial carnivores.*

Species

Vulpes vulpes	282
Mustela erminea	39
Martes foina	121
Mustela putorius	24
Mustela nivalis	13
Meles meles	5
Martes martes	2
Ursus maritimus	52
Acinonyx jubatus jubatus *	98
Acinonyx jubatus raineyi *	30
Canis familiaris dingo	6
Neofelis nebulosa *	25
Panthera pardus *	18
Ursus americanus	207
Panthera tigris *	40
Felis caracal *	16
Canis lupus	12
Panthera leo *	20
Leptailurus serval *	16
Canis latrans	6
Procyon lotor	451
Leopardus wiedii *	11
Leopardus pardalis *	6
Felis catus *	56
Herpestes auropunctatus	45
Martes americana	10

☐ Polymorphism
▨ Heterozygosity

0.00 0.05 0.10 0.15 0.20 0.25 0.30 0.35
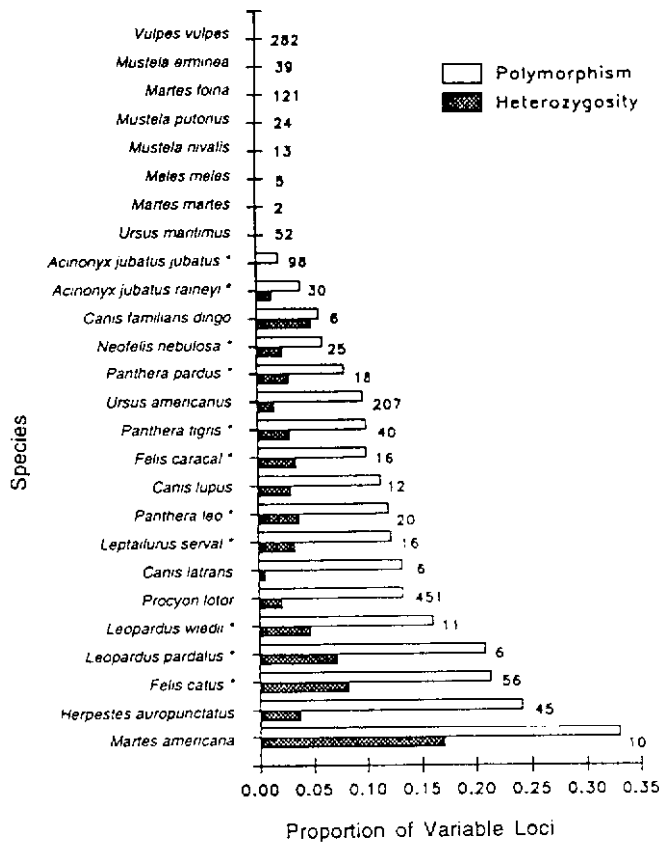
Proportion of Variable Loci

Figure 2. Levels of genetic variation for terrestrial carnivores. The first eight species listed, of the 26 for which data are available, exhibit less genetic variability than either subspecies of cheetah (Acinonyx jubatus jubatus and A.j. raineyi); none of these species are considered endangered. Asterisks (*) indicate members of the Felidae. Carnivores that have experienced documented population bottlenecks (such as Mustela nigripes, Panthera leo persica) were not included in the analysis. Sample sizes displayed at end of bars. (Values of polymorphism and heterozygosity compiled from Fisher et al. 1976; Allendorf et al. 1979; Dew & Kennedy 1980; O'Brien 1980; Simonsen 1982; Newman et al. 1985; Kilpatrick et al. 1986; O'Brien et al. 1987; Manlove et al. 1990; Mitton & Raphael 1990).

The case for erosion of generic diversity in the cheetah through repeated bottlenecks has been made by O'Brien and colleagues (1987), but this would potentially apply only to the south African subspecies. A j. jubatus, which is believed to have gone through a second, recent bottleneck due to overhunting at the turn of the century (and which does indeed exhibit lower levels of polymorphism). There is no indication that the east African subspecies. A j. raineyi, has been subjected to repeated population bottlenecks. If the east African

cheetah formerly exhibited a high degree of genetic diversity, then much of this variability should still be present in the species; a formerly polymorphic population is unlikely to be reduced to one of near-monomorphism following a bottleneck (Lande 1988; Pimm et al. 1989). Given the extremely low genetic variability presently seen in cheetahs, it appears unlikely that this species was historically highly polymorphic, regardless of the possible occurrence of a population bottleneck in the Pleistocene. In the absence of evidence for sustained or repeated bottlenecks to explain the genetic homogeneity of the cheetah, I suggest that we consider an alternative scenario. Just as we may infer that cheetahs exhibited greater variability prior to the proposed bottleneck, it is not unreasonable to consider that the cheetah normally exhibits a relatively low level of genetic polymorphism.

If variability is reduced gradually, deleterious recessives are eliminated from the population by selection: the resulting population may be relatively homozygous but with no permanent "inbreeding" effects (Wright 1977; Falconer 1981; Lande 1988). Gilpin (1991) suggests that some species may persist at relatively low levels of heterozygosity due to a metapopulation structure. Additionally, Lande (1988) points out that all levels of generic variation are not necessarily proportional: low levels of polymorphism in soluble proteins does nor necessarily equate to low levels of heritability in quantitative characters, nor is it necessarily indicative of inbreeding. I argue that cheetahs do not appear to suffer any ill effects due to their genetic composition but rather appear to be quite viable in spite of their homozygous constitution. It is worth considering that, rather than representing the remnants of former diversity, the cheetah's present level of genetic variability may be close to the historically normal level for this species. The evidence from fluctuating asymmetry appears to support this hypothesis.

The Evidence from Fluctuating Asymmetry

One method for determining whether genetic variation has been reduced in natural populations is to use the measures of fluctuating asymmetry (FA), defined as small, random deviations from perfect symmetry in bilaterally paired traits (Van Valen 1962), and of morphological variance (the standard deviation from the mean). FA is a measurement on the individual, whereas morphological variation is necessarily a population parameter.

FA has been shown to be a reliable indicator of both environmental and generic stresses across 3 variety of taxa (Wayne et al. 1986a; Leary & Allendorf 1989; Parsons 1990). The loss of genetic variability (increased homozygosity) in a normally variable population is re-

flected by a decrease in homeostasis, which in turn is expressed as a measurable increase in both FA and phenotypic variance (see Lerner 1954; Thoday 1956; Eanes 1978; Mitton 1978; Soulé 1979; Leary et al. 1983, 1985; but see Patterson & Patton 1990). Similarly, both measures increase with inbreeding (Leamy 1984; Leary & Allendorf 1989; Parsons 1990). If the cheetah's present level of genetic diversity represents a reduction of formerly greater variability and/or inbreeding, this loss should be reflected in the form of increased FA and morphological variation.

The first measurements of FA and morphological variance in cheetahs by Wayne et al. (1986b) used 16 characters of the skull and dentition. These measurements were compared with those of leopards (*Panthera pardus*), ocelots (*Leopardus pardalus*), and margays (*Leopardus weidii).* Wayne et al. reported a greater degree of FA in the cheetah than in the other felids; there was no difference in the degree of morphological variance. Willig and Owen (1987) criticized the statistical analyses of Wayne et al. and recalculated their data using a more appropriate statistical test. Their results showed no significant difference in the degree of FA between the cheetah and the leopard. The case for Willig and Owen's interpretation of the data *is* strengthened because neither they nor Wayne et al. found an increase in morphological variation. usually positively correlated with FA (Leary et al. 1985). Finally. Kieser and Groeneveld (1991) measured FA in cheetahs using a series of seven dental measurements; FA was compared with that in the African wildcat. *Felis lybica,* and caracal, *Felis caracal* Their study found no significant difference in either FA or morphological variance between the three species.

In short, much of the evidence to date does not indicate increased FA or morphological variability in the cheetah. and the increased FA reported by Wayne et al. (1986b) is questionable. This suggests that cheetahs have not suffered depletion of their genetic diversity but that cheetahs exhibit developmental stability at their present level of variability. The absence of increased FA and morphological variance, indicating homeostasis, also contradicts the generally accepted notion that cheetahs are seriously inbred.

Inbreeding Depression as an Artifact of Captivity

The suggestion that cheetahs exhibit "classic" signs of inbreeding depression is often cited as further evidence for a loss of genetic variation in the species. Homozygosity is not necessarily indicative of a history of inbreeding, however (Ralls et al. 1986; Lande 1988). and many of the problems attributed to inbreeding depression in cheetahs may be due to maintenance of these animals in captivity. as recognized by O'Brien et al.

(1987). The recent findings of Wildt et al. (1993) support the suggestion that captive breeding problems are more managerial than biological. Despite similarities in ejaculate quality, ovarian activity, and hormonal patterns in cheetahs at various institutions, reproductive success varies dramatically between captive breeding facilities. The authors point to the striking differences in management schemes utilized at each of these institutions as the most likely explanation for this disparity.

Captive breeding of cheetahs is notoriously difficult (see O'Brien et al. 1985). If the genetic composition of the cheetah is the basis for problems in captive breeding, then all breeding programs should experience similar difficulties. A comparison of the success in captive breeding programs indicates that the problems are not inherent to the cheetah Over a five-year period. only 9–12% of sexually mature females in North American zoos produced live cubs, as compared to 60–80% of the females at a South African research center (Brand 1980; Marker 1983). The North American record has improved recently. primarily due to changes in husbandry of the captive populations (Marker-Kraus & Grisham 1993).

Some of the problems that have bee" attributed to genetics in the captive breeding of cheetahs are more likely related to diet. Cheetahs at the South African center are fed whole animal carcasses, whereas cheetahs in North American zoos are fed a commercially prepared feline diet. The prepared diet is high in phytoestrogens. believed to be responsible for an irregular estrus cycle and even infertility in the cheetahs (Setchell et al. 1987). The prepared diet has also been linked with liver disease, long recognized as the leading cause of death for adult cheetahs in North American zoos (van der Werken 1967; Munson 1993). In addition, several of the commercial feline zoo diets contain toxic levels of vitamin A (Gosselin et al. 1989). A change in diet of female cheetahs at North American facilities led to the resumption of a normal estrus cycle and a marked reduction in liver pathologies (Setchell et al 1987).

The fertility of female cheetahs has a behavioral component as well. In the wild, males and females associate only during the brief courtship period when the female comes into estrus. The practice of keeping males and females together in captivity year-round actually leads to the suppression of estrus in the female (Kitchener 1991). This is consistent with the speculation that the cheetah is an induced ovulator, suggesting that cheetahs will ovulate only under the correct conditions (Wildt et al. 1993). In addition. Eaton (1973) proposes that the confines of captivity prevent the performance of the cheetah's ritual courtship chases, contributing further to the cheetah's reluctance to breed. It is possible that the absence of male courtship groups—characteristic of nature courtship behavior-and the consequent lack of male-male competition and aggressive behavior may

contribute to the low levels of testosterone found by Wildt et al. (1993) in captive male cheetahs: the authors speculate that consistently low testosterone levels may negatively affect ejaculate quality. The fundamental importance of such behavioral factors to the success of the captive breeding of cheetahs is drawing increased notice as researchers strive to improve management programs (see Caro 1993; Laurenson 1993).

Small litter sizes in captive cheetahs (mean 1.5) have been cited as evidence of inbreeding (see Falconer 1981), because inbreeding is most often associated with a lowering of reproductive capacity. Litter sizes for cheetahs in the wild, however. range from estimates of three to four offspring (Eaton 1974) to as many as five and six young (Myers 1975). Using measures of mean litter size, number of litters per year, and age at first conception, the reproductive capacity of the cheetah is equal to, if not greater than, that of the other large felids. despite the differences in generic diversity between the species (Table 2). There is no evidence that the reproductive capacity of free-living cheetahs has diminished. Caro and Laurenson (1994) note high fecundity and rapid rates of litter production in wild cheetahs. with no apparent ill effects of genetic monomorphism on reproductive behavior or physiology. Of 48 cub deaths observed, these researchers report that fewer than 0.5% could possibly have been attributable to genetic defects.

The high levels of spermatozoal abnormalities that characterize the ejaculate of cheetah (70.9–78.7%) (O'Brien et al. 1987; Wildt et al. 1993) have also been attributed to inbreeding. Such levels are usually associated with extremely inbred livestock and mice (see O'Brien et al. 1987: Yuhki & O'Brien 1990), which are considered infertile at this level of spermatozoal abnormalities (Leamy 1984). The cheetah's fertility appears relatively unimpaired. however. Despite the high levels of structurally abnormal sperm. 83.3% of male cheetahs tested by Lindburg et al. (1993) were capable of producing pregnancies; 89.5% of these pregnancies were achieved during a single estrus. The relatively high reproductive potential of male cheetahs led the authors to suggest again that the management of cheetahs in captive breeding programs rather than physiology may be the critical factor affecting reproductive success. In addition, high levels of abnormal sperm may not be par-

ticularly aberrant in large felids. Analyses of sperm samples from five species of great cats showed relatively high percentages of sperm abnormalities in all of them, including a count of 50% in the American cougar, *Felis concolor* (Rasch 1989, 1990).

The evidence for increased susceptibility to disease may also be confounded by the use of information from captive populations. Most frequently cited is an outbreak of feline infectious peritonitis in an Oregon wild animal park in 1782 and 1983 (O'Brien et al. 1985). This corona virus has a mortality rare in domestic cats of from 1 to 10%; in the captive cheetah population. the mortality rate was from 50 to 60%. These cheetahs were in an unnaturally dense population. In the wild. social groups of males maintain a territory of 12-36 km"; solitary females may cover home ranges anywhere from 60 to 800 km' in size (Schaller 1972). Furthermore, cheetahs scrupulously avoid contact with conspecifics (Eaton 1974). Under natural conditions, the opportunity for conspecific contact and hence disease transmission is low. By contrast, in the wild animal park. the density of cheetahs was 24 individuals in a 3.5.acre area. Clearly the opportunity for rapid disease transmission is greatly elevated under these conditions. This may be especially detrimental for a species that has not developed an immune system in an evolutionary context of high population density and conspecific contact.

The naturally low population densities of the cheetah and its behavioral tendency to avoid conspecifics may compensate to some degree for the lack of genetic variability at the major histocompatibility complex (MHC). Variability at the MHC, a vital component of the immune system. is a critical defense against pathogens. O'Brien et al. (1985) found that cheetahs are extremely slow to reject skin grafts from conspecifics, indicating an unusually high degree of compatibility between individuals at the MHC complex. *This* does not mean that cheetahs are incapable of immune defenses: half of the cheetahs exposed to feline infectious peritonitis in the wild animal park survived the virus. In addition. Caro and Laurenson (1994) report that wild cheetahs tested seropositive to a variety of pathogens and parasites. There is no evidence of elevated susceptibility to disease in wild populations of cheetahs *similar to that* observed under captive conditions: for example. despite the known

Table 2. Comparative reproductive capacity and levels of genetic variability for cheetahs, lions. and leopards in the wild.

Species	Mean Litter Size[a]	Number of Litters per Year[a]	Age at First Reproduction[a] (years)	P	H
Acinonyx jubatus	3.5	0.5	2	0.04[b]	0.014[b]
Panthera leo	3.5	0.5	2	0.11[c]	0.038[c]
Panthera pardus	2.5	0.5	2	0.08[d]	0.029[d]

[a] Eisenberg 1986.
[b] A.j. raineyi: O'Brien et al. 1987.
[c] Yuhki & O'Brien 1990.
[d] Newman et al. 1985.

presence of a fatal virus, feline infectious enteritis (Schaller 1972). cheetahs in the wild did not suffer the devastating level of mortality seen in the population of the wild animal park. Although apparently not affected in the wild, disease transmission between cheetahs does appear to be exacerbated under the conditions of captivity. This is an important point to consider in conservation efforts, because the cheetah's great similarity at the MHC may be a real liability as the species is increasingly relegated to populations of artificially high density in game reserves and captive-breeding programs.

The Decline of Wild Cheetah Populations

The cheetah's rapid decline, by as much as 50% in the wild between *1960* and 1975 (Myers 1975), is more likely due to loss of native habitat and agricultural expansion than to its genetic composition. Cheetahs are increasingly restricted to high-density populations in small islands of habitat: one cheetah per 6 km' in preserves, as opposed to the normal one per 100 km^2 (Myers 1975). These high densities contribute not only to enhanced disease transmission but to increased predation. As cheetahs are forced into small preserves. so too are their primary predators. Predation by lions (*Panthera leo*), leopards (*Panthera pardus*). and hyenas (*Crocuta crocuta*), is rhe primary cause of death of cheetahs in the wild (Eaton 1974). Caro and Laurenson *(1994)* report that 73% of observed cheetah cub deaths were due to predation; this problem is exacerbated in wildlife reserves, where predator density is high and prey relatively scarce (Caro et al. 1987). Outside reserves, rangelands for native ungulates are being depleted by the growth of cattle ranching, further reducing prey species. Cheetahs are also hunted as a precaution against the taking of livestock, hunted for the international fur trade. and trapped for the live market (Myers 1975). Significantly. no factor that has been identified as contributing to the drastic decline in the wild cheetah population has any genetic basis.

Conclusion

The genetic invariability of the cheetah raises some intriguing questions regarding our assumptions about homozygosity, inbreeding and "normal" levels of genetic diversity in natural populations. Is it possible for a species to exist at what we have traditionally considered a perilous level of genetic uniformity? The reproductive viability of the cheetah and the survival of the species at such a low level of variability suggests that homozygosity may not be a universally deleterious characteristic. Measures of fluctuating asymmetry indicate that the cheetah is not suffering from genetic stress. Comparison of rhe cheetah's level of genetic diversity with that of other terrestrial carnivores demonstrates that the genetic uniformity of this species is not unique, nor is such a level of genetic variation unknown in viable populations. Finally, the reproductive performance of wild cheetahs is unimpaired despite their genetic monomorphism, strongly suggesting that problems formerly attributed to inbreeding in captive cheetahs may be more properly characterized as behavioral and physiological consequences of the captive environment. In short, the level of genetic diversity in wild cheetahs does not appear to compromise either their reproduction or survival.

Cheetah populations have survived at relatively low levels of genetic variation for thousands of years. Only in the last century has there been a marked decline in the species, strongly suggesting that human development and habitat loss have a greater impact on the cheetah's welfare than its level of genetic diversity. In setting priorities for the conservation of this species, we should consider that our concern over the cheetah's level of genetic variation and its effect on the short-term survival of the species in the wild may be unwarranted. In addition. the emphasis on the cheetah's homozygosity may be distracting conservation biologists from a very real issue. the loss of the cheetah's natural habitat and the consequent relegation of the species to parks and zoological institutions. Should the conservation emphasis shift to captive propagation, experience shows that the cheetah's genetic composition and behavioral characteristics may be detrimental under these artificial conditions. The long-term question of the possible effects of the cheetah's genetic uniformity on its evolutionary future as a natural population most likely will remain unanswered. Unless conservation priorities shift to the protection of adequate habitat for this species in the wild, it is almost certainly human impact and habitat loss, not homozygosity, that will lead the cheetah to extinction.

Acknowledgments

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