Wielebnowski N. 1996. Reassessing the relationship between juvenile mortality and genetic monomorphorism in captive cheetahs. Zoo Biology 15:353-69.

Keywords: 3US/Acinonyx jubatus/captive breeding/captivity/cheetah/genetics/homozygosity/husbandry/juvenile mortality/litter size/mortality rate/research

Abstract: Low levels of genetic heterozygosity are commonly considered a major threat to the survival of wild and captive populations. However, intense focus on genetic issues may obscure the importance of extrinsic factors influencing species' survival in wild and captive environments. A key example for this is the cheetah (*Acinonyx jubatus*), which is frequently cited as suffering from unusually high juvenile mortality and decreased fecundity in captivity due to genetic monomorphism at the species level. It has also been suggested that as a consequence of such extreme homozygosity, juvenile mortality rates of young from related vs. unrelated parents would not be expected to differ significantly. However, examination of current studbook data and breeding records of the North American captive population showed that juvenile mortality of young from related parents was significantly higher than that of young from unrelated parents, largely as a result of intrinsic causes, such as stillbirths and congenital defects, that may have a genetic basis. This indicates that in spite of the cheetah's homozygosity, effects of further inbreeding depression may still occur in the captive population, and deleterious recessive alleles are being segregated. Furthermore, juvenile mortality has declined over time and differs significantly among facilities, even when only young from unrelated parents are considered, suggesting that differences in management practices may be largely responsible for observed changes in mortality rate. Contrary to previous reports, cheetah juvenile mortality is not unusually high when compared to other captive-bred felids. In addition, cheetahs were found to have consistently higher litter sizes and the highest average number of surviving cubs per litter when compared to other captive-bred felid species. These findings cast doubt on the significance of overall homozygosity in this species for its juvenile survival and breeding performance and emphasize the key role of management practice in promoting breeding of endangered species.

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Zoo Biology 15:353–369 (1996)

RESEARCH ARTICLES

Reassessing the Relationship Between Juvenile Mortality and Genetic Monomorphism in Captive Cheetahs

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Low levels of genetic heterozygosity are commonly considered a major threat to the survival of wild and captive populations. However, intense focus on genetic issues may obscure the importance of extrinsic factors influencing species' survival in wild and captive environments. A key example for this is the cheetah (*Acinonyx jubatus*), which is frequently cited as suffering from unusually high juvenile mortality and decreased fecundity in captivity due to genetic monomorphism at the species level. It has also been suggested that as a consequence of such extreme homozygosity, juvenile mortality rates of young from related vs. unrelated parents would not be expected to differ significantly. However, examination of current studbook data and breeding records of the North American captive population showed that juvenile mortality of young from related parents was significantly higher than that of young from unrelated parents, largely as a result of intrinsic causes, such as stillbirths and congenital defects, that may have a genetic basis. This indicates that in spite of the cheetah's homozygosity, effects of further inbreeding depression may still occur in the captive population, and deleterious recessive alleles are being segregated. Furthermore, juvenile mortality has declined over time and differs significantly among facilities, even when only young from unrelated parents are considered, suggesting that differences in management practices may be largely responsible for observed changes in mortality rate. Contrary to previous reports, cheetah juvenile mortality is not unusually high when compared to other captive-bred felids. In addition, cheetahs were found to have consistently higher litter sizes and the highest average number of surviving cubs per litter when compared to other captive-bred felid species. These findings cast doubt on the significance of overall homozygosity in this species for its juvenile survival and breeding performance and emphasize the key role of management practice in promoting breeding of endangered species.

Key words: homozygosity, felids, husbandry

Received for publication July 21, 1995; revision accepted April 11, 1996.

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INTRODUCTION

Loss of heterozygosity has been shown to have a negative impact on components of fitness in many species [Frankel and Soulé, 1981; Allendorf and Leary, 1986; Ledig, 1986; Mitton, 1993]. In particular, studies have provided evidence that within a species more heterozygous individuals show higher levels of fitness than individuals that are less heterozygous [Schaal and Levin, 1976; Allendorf and Leary, 1986; Ledig, 1986; Danzman et al., 1988; Keller et al., 1994]. There is, however, very little evidence that individuals of one species with a higher level of average heterozygosity are more fit than those of another species with lower average heterozygosity [see Caughley, 1994]. For example, there are some highly homozygous species which show widespread geographical distributions (e.g., red pine (*Pinus resinosa*) [see Ledig, 1986] and several species with low levels of heterozygosity (e.g., Northern elephant seal (*Mirounga angustirostris*) [Bonnell and Selander, 1974] and Arabian oryx (*Oryx leucoryx*) [Woodruff and Ryder, 1986]) have recovered from near extinction [Hofman and Bonner, 1985; Stanley Price, 1989]. Conversely, there are rare or endangered species with high levels of heterozygosity (e.g., the greater one-horned rhinoceros (*Rhinocerus unicornis*) [Dinerstein and McCracken, 1990]). Although these empirical findings are clearly equivocal, it is often assumed on the basis of theory that, in rare or endangered species, lack of heterozygosity is responsible for a reduction in overall fitness of the species [Allendorf and Leary, 1986]. Preservation of genetic diversity has therefore become a top priority in conservation management plans for wild and captive populations [Chesser et al., 1980; Schonewald-Cox et al., 1983; Soulé, 1987; Lande, 1988; Woodruff, 1989].

A key example in this argument has been the African cheetah (*Acinonyx jubatus*), a species which is frequently used to illustrate the perils of loss of genetic diversity to the scientific and popular community [Allendorf and Leary, 1986; Steinhart, 1992; Sunquist, 1992; but see Caro and Laurenson, 1994]. When it was discovered in the early 1980s that cheetahs exhibit much lower levels of average heterozygosity than other felid and mammal species [O'Brien et al., 1983, 1985, 1986], evidence, mainly from the captive population, was presented to demonstrate the hypothesized deleterious effects of such low genetic diversity on overall fitness [O'Brien et al., 1985]. In particular, high juvenile mortality, low fecundity, and poor breeding success in the captive population were among the evidence advanced to support the idea that genetic impoverishment in the cheetah caused a decline in its overall fitness as a species. It was further argued that no additional inbreeding depression (i.e., no significant difference between juvenile mortality of young from related vs. unrelated parents) might be expected in the captive population because of the already highly inbred state of this species. In short, genetic monomorphism was interpreted as being largely responsible for the cheetah's problems in captivity as well as in the wild [O'Brien et al., 1985; O'Brien, 1994a,b].

Recently, various aspects of the cheetah example have come under critical review [Hedrick, 1992; Caro and Laurenson, 1994; Caughley, 1994; Merola, 1994], and it has been suggested that the strong emphasis on the issue of homozygosity maybe distracting from more immediate threats to the survival of this species [Caro and Laurenson, 1994; Merola, 1994]. In the past, captive management of endangered species has primarily focused on genetic and demographic considerations [Mellen, 1994], and analyses of behavioral and husbandry factors relevant for captive propagation are still rarely mentioned as part of North American zoo breeding programs [Lindburg and Fitch-Snyder, 1994]. This may have lead to the oversight of some important extrinsic factors contributing to species survival and breeding success in captivity.

Since the first publication on genetic monomorphism in cheetahs and the hypothesized consequences of such low levels of genetic diversity, a considerable amount of studbook data on the captive population has accumulated [Marker, 1983–1986; Marker-Kraus, 1988–1992].

In addition, similar studbook information is now available for other felid species, which allows us to compare the cheetah in some aspects of breeding performance to other captive-bred felids for the first time. Previous comparisons of cheetah juvenile mortality rates to other captive-bred species were based on ungulate and rodent juvenile mortality data, and no comparison of breeding performance was provided [O'Brien et al., 1985]. The focus of this paper is to reexamine juvenile mortality rates and breeding performance of the captive North American cheetah population in light of this new evidence and to reevaluate the relative impact of overall homozygosity in this species.

METHODS

Inbred and Noninbred Juvenile Mortality Rates

Juvenile mortality rates and inbreeding coefficients (F) for the North American cheetah population were obtained from studbooks [Marker, 1983–1986; Marker-Kraus, 1988–1992] and other published data [Marker and O'Brien, 1989; Marker-Kraus and Grisham, 1993]. Inbreeding coefficients had been calculated with the computer program SPARKS [ISIS, 1994]. Some limitations of this program are that individuals listed in the studbook as "wild caught" are considered to be unrelated; any unknown sires are also treated as unrelated, and multiple sires are considered as unknowns. This may lead to an underestimate of inbreeding in the population. However, a conservative definition of inbreeding was employed since any offspring with inbreeding coefficients larger than zero were considered inbred.

A subsample from the five most successful breeding facilities in North America (Columbus Zoo, OH; Fossil Rim Wildlife Center, TX; San Diego Wild Animal Park, CA; White Oak Conservation Center, FL; Wildlife Safari, OR) was chosen to further examine the effects of inbreeding. In this sample the parentage of all offspring was known, and accuracy of inbreeding coefficients could be ascertained. Data on juvenile mortality rates and inbreeding were obtained from facility records and studbook information. Offspring born after 1992, the year for which the most recent studbook is available, were included in the analysis only if they originated from a pair of cheetahs that had produced offspring previously. Inbreeding coefficients could then be inferred from the full siblings born prior to 1992.

Causes of Juvenile Mortality

Detailed data on causes of cheetah juvenile mortality were obtained from facility records at Wildlife Safari, Columbus Zoo, Fossil Rim Wildlife Center, and White Oak Conservation Center; causes of juvenile mortality at San Diego Wild Animal Park were obtained from studbook data. All five facilities have kept detailed records and employ staff veterinarians who identified causes of death. Causes were placed into three main categories: 1) *Extrinsic:* fatal injury, husbandry, and maternal problems. Fatal injury refers to accidental mortalities that were either caused by cage mates other than the mother or by an unknown perpetrator was unknown. Common fatal injuries included fractures, ruptures, bite wounds, and cannibalism. Husbandry refers to deaths which resulted from management-related accidents (i.e., anesthesia, premature cesarean delivery, or complications during hand raising other than disease). Maternal problems included cases of maternal neglect and subsequent death as well as being fatally injured or eaten by the mother. 2) *Intrinsic:* stillbirth, neonatal mortalities, premature birth, and congenital deformities. 3) *Other:* viral and bacterial infections (i.e., pneumonia, septicemia, *Escherichia coli,* salmonellosis, clostridium, and unspecified infection and various other causes of disease and organ malfunction (i.e., heart failure, kidney failure, anemia, enteritis of unspecified origin).

Cheetah Juvenile Mortality Over Time

Data on yearly juvenile mortality rates in cheetahs were compiled from studbook records and published studbook information [Marker, 1983–1986; Marker-Kraus, 1988–1992; Marker and O'Brien, 1989; Marker-Kraus and Grisham, 1993] as well as from the Annual Report on Conservation and Science [Grisham and Marker-Kraus, 1994]. Juvenile mortality was defined as death prior to or at 6 months of age [Ralls et al., 1979; Ralls and Ballou, 1982a,b; Shoemaker, 1983; O'Brien et al., 1985; Marker and O'Brien, 1989; Marker-Kraus and Grisham, 1993]. The number of births and deaths and the juvenile mortality rate were calculated over three time intervals. The first interval covers a time period from 1956, the occurrence of the first cheetah birth in North America, to 1971. The second and third intervals cover 11-year periods from 1972 through 1982 and 1983 through 1993, respectively. These intervals reflect changes in intensity of breeding efforts and overall management of the captive population. Furthermore, the number of inbred young born is presented for each time period, and juvenile mortality rates for both inbred and noninbred young were calculated for the three time intervals. This allows for a concurrent examination of the amount of inbreeding and the severity of the inbreeding effect on juvenile mortality over time in the captive population. Information on inbreeding coefficients, however, could only be obtained up to 1992 for the entire North American population [Marker-Kraus, 1988–1992; Marker and O'Brien, 1989; Marker-Kraus and Grisham, 1993].

Variation in Cheetah Juvenile Mortality Rates Among Facilities

Overall juvenile mortality rates as well as inbred and noninbred mortality rates are presented for the five previously mentioned breeding facilities. Together these facilities have produced the majority (~60%) of offspring in the North American captive cheetah population. Three of these facilities started breeding cheetahs in the 1970s (Columbus Zoo, San Diego Wild Animal Park, Wildlife Safari), whereas two started in 1986 (Fossil Rim Wildlife Center, White Oak Conservation Center). Columbus Zoo stopped breeding cheetahs in 1989 due to disease-related problems [Bill Cupps, personal communication].

Juvenile Mortality, Litter Size, and Average Productivity of North American Captive-Bred Felids

Published studbooks and unpublished records and data obtained from studbook keepers were used to calculate overall juvenile mortality rates and litter sizes for ten other felid species [Brady, 1993; Bragin, 1994; Evans, 1994; Fletchall, 1994; Fouraker, 1992, 1993; McMillan, 1994; Sausman, 1994; Shoemaker, 1994; Wharton, 1994; White, 1994; Versteeg, unpublished records]. Data on litter sizes of cheetahs were obtained from published studbooks [Marker, 1983–1986; Marker-Kraus, 1988–1992]. All inbreeding coefficients were calculated using the computer program SPARKS [ISIS, 1994]. In some cases calculated inbreeding coefficients were already available from published studbooks (e.g., cheetah [Marker-Kraus, 1988–1992]. For other species, inbreeding coefficients were calculated from studbook information available on computer disc (e.g., snow leopard (*Panthera uncia*), clouded leopard (*Neofelis nebulosa*), Sumatran tiger [*Panthera tigris sumatrae*]). Again, offspring with inbreeding coefficients larger than zero were considered inbred. Some of the limitations of the use of SPARKS [ISIS, 1994] have been mentioned earlier. In addition, it needs to be noted that standardized systems for record and studbook keeping (i.e., SPARKS) have been a fairly recent development. Earlier record keeping frequently varied widely for different studbooks and still varies today among facilities and countries. Data in today's studbooks, especially for earlier years, are only as reliable as the underlying facility records.

In an attempt to equalize some of the effects of variation in record keeping across facilities, countries, continents, and time, only North American studbooks were used in the analysis. Furthermore, records for each species had to include more than 30 birth events, at least 15 years of breeding records, and breedings at more than four institutions. Only births from individuals with known ancestry (i.e., both dam and sire were listed) were included in the analysis.

Several studbooks exist for subspecies of leopards (*Panthera pardus*), lions (*Panthera leo*), and tigers (*Panthera tigris*). Data on four subspecies of leopards (Chinese leopard (*Panthera pardus japonensis*) Persian leopard (*Panthera pardus saxicolor*) Amur Leopard (*Panthera pardus orientalis*) and Ceylon leopard [*Panthera pardus kotiya*]) were available and were combined to form a compound juvenile mortality rate and litter size [for a previous detailed analysis of leopard studbook data see Shoemaker, 1983]. For the lion, only studbook records on African and hybrid lions (representing hybrids between the Asian (*Panthera leo persica*) and African (*Panthera leo leo*) subspecies) were included. Data on the Asian lion were excluded since they consisted of only 27 offspring from one breeding pair at one facility in North America. For the tiger, studbook data on one subspecies, the Sumatran tiger, could be obtained. Inbreeding coefficients could be obtained only for the clouded leopard, snow leopard, leopard, and tiger.

In an attempt to compare reproductive performance of captive cheetahs with other captive felids, I used the mean number of cubs surviving per litter as a crude measure of average productivity. This number was calculated by multiplying the average litter size of the captive population by the probability of juvenile survivorship (to 6 months) [Robinson and Cox, 1970].

Levels of average heterozygosity have been published previously for 6 of the 11 examined species [Newman et al., 1985; O'Brien et al., 1985, 1987] and are presented for comparison. A Spearman rank-order correlation coefficient [Siegel and Castellan, 1988] was used to test for covariation of the level of average heterozygosity with juvenile mortality, litter size, and productivity (average number of cubs surviving per litter).

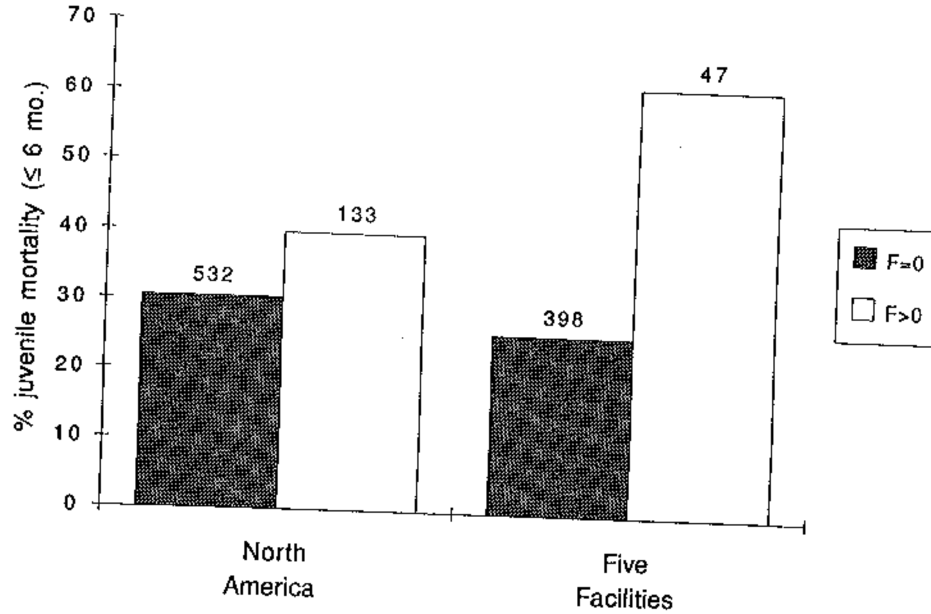

Fig. 1. Inbred (F > 0, where F is the inbreeding coefficient) vs. noninbred (F = 0) juvenile mortality rates in the North American captive cheetah population and in a subsample of five major North American breeding facilities. The number on top of each column presents the number of cubs born.

RESULTS

Inbred and Noninbred Juvenile Mortality Rate

For the North American cheetah population, inbred juvenile mortality was 39.8% (53/133), and noninbred juvenile mortality was 30.5% (162/532) from the years 1956 through 1992 ($\chi^2 = 4.296$, df = 1, $P < 0.05$) (Fig. 1). In the subsample from five facilities, for which more detailed records were available, juvenile mortality was 61.7% (29/47) for inbred offspring and 25.9% (103/398) for noninbred offspring ($\chi^2 = 25.855$, df = 1, $P<0.001$) (Fig. 1).

Causes of Juvenile Mortality

The main causes of mortality differed significantly between inbred and noninbred deaths in this subsample (Table 1). Among inbred cubs, 67.9% died of stillbirth, neonatal problems, or congenital problems (intrinsic causes), whereas only 37.5% of noninbred cubs died from such causes ($\chi^2 = 7.915$, df = 1, $P = 0.005$). A trend in the opposite direction was detected for "other" causes, with 27.3% of noninbred cubs dying from such causes vs. 10.7% of inbred cubs ($\chi^2 = 3.261$, df = 1, $P = 0.071$). However, no significant difference was found for largely extrinsic causes ($\chi^2 = 1.862$, df = 1, $P = 0.172$). Extrinsic and other causes therefore seem to affect noninbred and inbred individuals alike during the first 6 months of life.

Cheetah Juvenile Mortality Over Time

Cheetah juvenile mortality declined over time (Fig. 2). There was a significant difference in juvenile mortality rate before and after 1972 when regular annual breed-

TABLE 1. Comparison of causes of cheetah juvenile mortality in inbred (F > 0) and noninbred (F = 0) cubs at five North American breeding facilities between 1970 and 1994

Causes of juvenile mortality (cheetah)	F[a] = 0 (%)	F > 0 (%)
Extrinsic		
Fatal injury	14.8 (13)[b]	21.4 (6)
Husbandry	12.5 (11)	0
Maternal problems	8.0 (7)	0
Total	35.2 (31)	21.4 (6)
Intrinsic		
Stillbirths	19.3 (17)	35.7 (10)
Neonatal	9.1 (8)	10.7 (3)
Premature	3.4 (3)	0
Congenital	5.7 (5)	21.4 (6)
Total	37.5 (33)	67.9 (19)
Other		
Various infections	20.5 (18)	7.1 (2)
Various other	6.8 (6)	3.6 (1)
Total	27.3 (24)	10.7 (3)
Unknown	15	1
Total died	103	29

[a] F = inbreeding coefficient.
[b] Percentages are based on known causes.

ing had commenced and some of today's large breeding facilities were being established (χ^2 = 10.31, df = 1, P = 0.001). After the first studbook was published in 1983, the decline continued (χ^2 = 3.734, df = 1, P = 0.05) (Fig. 2). Furthermore, Figure 2 shows that 57.4% of all North American cheetah births occurred between the years 1983 and 1993, indicating that the number of births has increased substantially over time.

The amount of inbreeding in the captive population also increased over time, from 0% in the first time interval to 12% in the second and 28% in the third interval (Table 2). The severity of the inbreeding effect on juvenile mortality, however, remained almost constant over the presented time intervals, with 41% and 39%, respectively (χ^2 = 0.034, df = 1, P = 0.855) (Table 2). Noninbred juvenile mortality alone declined significantly over time (χ^2 = 20.711, df = 2, $P < 0.001$) (Table 2).

Variation of Juvenile Mortality Rates Among Facilities

Overall juvenile mortality rates varied significantly among the five most successful breeding facilities in the country (range: 17–44%; χ^2 = 18.672, df = 4, $P < 0.001$) (Table 3). When only the three facilities which started breeding in the 1970s were examined (Wildlife Safari, Columbus Zoo, San Diego Wild Animal Park), variation in mortality rates was still found to be significant (range: 27–44%; χ^2 = 6.067, df = 2, P = 0.05). The occurrence of inbreeding varied substantially among facilities, with the two most recently established facilities showing no inbreeding at all (Table 3). However, inbred juvenile mortality rates did not vary significantly among the three older facilities (χ^2 = 3.905, df = 2, P = 0.142), whereas noninbred

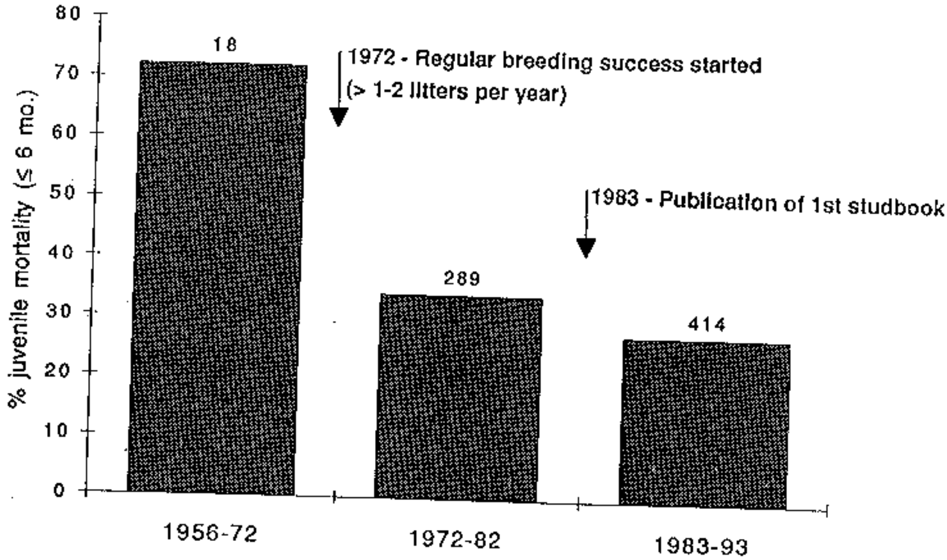

Fig. 2. Changes in juvenile mortality rate of the North American captive cheetah population over time (1956–1993), examined in combination with changes in breeding and management. The number on top of each column presents the number of cubs born.

TABLE 2. Noninbred, inbred, and overall juvenile mortality rates (≤ 6 months) for the North American cheetah population presented over three time intervals from 1956–1992

Time interval	Total juvenile mortality (%) (number born/ number died)	Noninbred juvenile mortality (%) (number born/ number died)	Inbred juvenile mortality (%) (number born/ number died)	Average level of inbreeding (%) (number born/ number inbred)
1956–1971	72.2 (18/13)	72.2 (18/13)	No inbreeding	0 (18/0)
1972–1982	34.6 (289/100)	33.7 (255/86)	41.2 (34/14)	11.8 (289/34)
1983–1992	28.5 (358/102)	24.3 (259/63)	39.4 (99/39)	27.7 (358/99)
1956–1992	32.3 (665/215)	30.5 (532/162)	39.8 (133/53)	20 (665/133)

juvenile mortalities alone did show significant variation (χ^2 = 13.291, df = 2, P = 0.001) (Table 3). This indicates that there are major interfacility differences in juvenile mortality rates which cannot be explained by inbreeding. Furthermore, when only noninbred juvenile mortality rates were compared across all five facilities, the interfacility variation also remained highly significant (Range: 17–42%; χ^2 = 21.026, df = 4, $P < 0.001$) (Table 3).

Juvenile Mortality, Litter Size, and Average Productivity of North American Captive-Bred Felids

Cheetah juvenile mortality was found to be lower than juvenile mortality of six other felids and higher than four species (Table 4). When only noninbred juvenile mortality rates were compared, the results were similar, with the cheetah showing a lower mortality rate in three cases out of six (Table 4). In addition, the cheetah

TABLE 3. Noninbred, inbred, and overall juvenile mortality rates (≤6 months) of cheetahs at five North American breeding facilities

Facility	Total juvenile mortality (%) (number born/ number died)	Noninbred juvenile mortality (%) (number born/ number died)	Inbred juvenile mortality (%) (number born/ number died)	Average level of inbreeding (%) (number born/ number inbred)	Years of breeding
Wildlife Safari	33.1 (127/42)	29.8 (104/31)	47.8 (23/11)	18.1 (127/23)	1973–1994
San Diego Wild Animal Park	27.4 (106/29)	17.0 (88/15)	77.8 (18/14)	17.0 (106/18)	1970–1994
Columbus Zoo	44.0 (91/40)	42.4 (85/36)	66.7 (6/4)	6.6 (91/6)	1979–1989
Fossil Rim Wildlife Center	17.3 (75/13)	17.3 (75/13)	No inbreeding	0 (75/0)	1986–1994
White Oak Conservation Center	17.4 (46/8)	17.4 (46/8)	No inbreeding	0 (46/0)	1986–1994
Totals	29.7 (445/132)	25.9 (398/103)	61.7 (47/29)	10.6 (445/47)	1970–1994

showed the highest average litter size and the highest average number of cubs surviving per litter (Table 4), suggesting relatively high levels of productivity when compared to other captive-bred North American felid populations. Four of the six species for which measures of average heterozygosity were available show higher overall juvenile mortality rates and higher levels of heterozygosity than the cheetah; one of the species with higher noninbred juvenile mortality rates shows higher average heterozygosity (Table 4). Furthermore, no correlation could be found between level of average heterozygosity and juvenile mortality rate ($r_s = -0.1$, $n = 6$, $P = 0.823$), and no significant correlation was detected between either average litter size and average level of heterozygosity ($r_s = -0.43$, $n = 6$, $P = 0.338$) or productivity and heterozygosity ($r_s = -0.49$, $n = 6$, $P = 0.277$) (Table 4).

DISCUSSION

Inbred and Noninbred Juvenile Mortality Rates and Causes of Juvenile Mortality

Inbred offspring showed significantly higher juvenile mortality rates than noninbred offspring [see also Hedrick, 1987; Marker-Kraus and Grisham, 1993; Caughley, 1994]. This contradicts the expectation that due to the cheetah's extreme genetic monomorphism juvenile mortality in inbred and noninbred cheetahs would not differ significantly [O'Brien et al., 1985]. In spite of the genetic monomorphism measured for part of their genome, cheetahs appear to have sufficient variation at the loci affecting juvenile survival to cause a significant difference in juvenile mortality rates of inbred and noninbred cubs [see Hedrick, 1992; Caughley, 1994]. The fact that inbred offspring were significantly more likely to die from intrinsic factors, such as stillbirths and congenital defects, than were noninbred offspring further supports this notion. Extrinsic and other causes of death were more evenly distributed between inbred and noninbred young, indicating that inbred cubs were not disproportionately affected by such events.

TABLE 4. Parameters of captive breeding performance and levels of average heterozygosity for eleven felid species bred in North America*

Species	Studbook total: Juvenile mortality (%) (number of births)	Years of breeding	Noninbred juvenile mortality (%) (number of births)	Years for records of inbreeding coefficients	Average litter size (number born/litters)	Average number of cubs surviving per litter	Average[a] hetero zygosity
Acinonyx jubatus (cheetah)	31.8 (723)	1956–1993	30.9 (534)	1956–1992	3.6 (667/185)	2.4	0.014
Panthera pardus (leopard)	39.9 (228)	1965–1994	58.7 (75)	1965–1994	1.8 (228/124)	1.1	0.029
Panthera uncia (snow leopard)	25.2 (432)	1945–1987	25.1 (338)	1945–1987	2.1 (432/208)	1.6	N.A.
Panthera onca (jaguar)	26.7 (677)	1926–1994	N.A.	N.A.	1.6 (677/435)	1.2	N.A.
Panthera tigris (tiger)	23.8 (122)	1942–1993	21.8 (55)	1942–1993	2.1 (122/58)	1.6	0.035
Panthera leo (lion)	35.6 (160)	1975–1994	N.A.	N.A.	2.3 (160/70)	1.5	0.037
Neofelis nebulosa (clouded leopard)	37.7 (471)	1955–1994	33.1 (320)	1955–1994	1.7 (396/228)	1.0	N.A.
Lynx caracal (caracal)	40.3 (129)	1968–1994	N.A.	N.A.	1.8 (129/71)	1.1	0.029
Felis pardalis (ocelot)	34.9 (266)	1901–1994	N.A.	N.A.	1.3 (266/213)	0.8	0.072
Felis nigripes (black footed cat)	29.5 (44)	1966–1994	40.0 (25)	1966–1994	1.6 (44/28)	1.1	N.A.
Felis margarita (sand cat)	50.0 (142)	1969–1994	N.A.	N.A.	2.5 (142/56)	1.3	N.A.

*N.A., no inbreeding.
[a]O'Brien et al., 1985.

Cheetah Juvenile Mortality Over Time

If genetic monomorphism in the cheetah is as severe for other portions of the genome as indicated by a variety of previous measurements [O'Brien et al. 1983, 1985; Yukhi and O'Brien, 1990; Menotti-Raymond and O'Brien, 1993], one would indeed expect no significant effects of further inbreeding in captivity. In addition, if this monomorphism is the major factor influencing juvenile mortality rate and overall fitness in the cheetah, one would not expect a decline in mortality rate and an increase in breeding success over time. However, juvenile mortality rates of inbred vs. noninbred young were found to differ significantly, and juvenile mortality rate and breeding success have improved over time (Fig. 2). The observed decline in mortality rate does not appear to be caused by a decline in inbreeding, since inbreeding levels increased over the presented time intervals and the severity of the inbreeding effect remained constant over time (Table 2). Noninbred juvenile mortality alone shows a significant decline over time, indicating that changes in husbandry techniques were more likely to be the key factor leading to the observed improvement (Table 2).

In the early 1970s, breeding success increased, and breeding began to occur on an annual basis. In addition, juvenile mortality declined when compared to early breeding efforts. Concurrently, interest in breeding cheetahs seemed to increase, and two of the most successful breeding facilities, Wildlife Safari (1973) and San Diego Wild Animal Park (1970), were established. In the early 1980s, extreme genetic monomorphism was detected in the cheetah, and an investigation of potentially associated problems commenced [O'Brien et al., 1983, 1985]. The first studbook for the North American cheetah population was published in 1983, and a crisis state was pronounced for the population. Regular meetings were instigated to assess the state of the captive population, and interfacility communication increased through these efforts. A further decline in juvenile mortality rate and an increase in number of births occurred subsequently. Today, according to the most recently published annual report of the Cheetah Species Survival Plan [Grisham and Marker-Kraus, 1994], the North American cheetah population is regarded as stabilizing, self-sustaining, and no longer in demographic crisis.

Such improvements of breeding success and juvenile survivorship over time are not unusual and have been witnessed in other captive-bred species. For example, the snow leopard and tiger, two felid species now perceived as showing good breeding success in captivity, were in the past seen as difficult to breed and showed high rates of juvenile mortality in the 1960s [Marma and Yunchis, 1968; Van Bemmel, 1968; Zhi-yen, 1988]. Considerable effort was undertaken to improve breeding of both species. Symposia were held, studbooks developed, research efforts increased [i.e., Blomquist, 1984, 1988a,b,c; Freeman, 1988; Tilson and Seal, 1987], and communication between facilities and countries was coordinated and encouraged. Several other species—the elephant shrew (*Elephantulus* sp.), the golden lion tamarin (*Leontopithecus rosalia*), and the lion-tail macaque (*Macaca silenus*)—each have benefitted substantially from improvements in husbandry techniques as a result of increased knowledge about the species sociobiology and reproductive behavior [Lindburg and Gledhill, 1992; Kleiman, 1994].

In summary, poor breeding success and high juvenile mortality in captivity appear to offer little indication of a more general fitness problem in any species [see Lindburg and Fitch-Snyder, 1994]. These parameters often vary with changes in husbandry techniques and frequently improve over time with accumulated knowledge about species requirements. The use of captive breeding performance and juvenile mortality as indicators of potential consequences of genetic homozygosity is therefore in question.

Variation in Cheetah Juvenile Mortality Rates Among Facilities

Variation in juvenile mortality rates among facilities, countries, and continents has been observed in many captive-bred exotic and domestic species [Robinson and Cox, 1970; Shoemaker, 1983; Ballou and Seidensticker, 1987; Bangjie and Yanfa, 1988; Blomquist, 1988a,b]. It has commonly been attributed to differences in management style and other extrinsic factors [Bangjie and Yanfa, 1988; Blomquist 1988a,b], and successful breeding of an exotic species in captivity has been regarded as an indicator of our understanding of the husbandry requirements and biology of the species [Hediger, 1950].

Juvenile mortality rates of captive cheetahs were found to vary significantly among facilities. Since husbandry styles are known to vary substantially among facilities, this appears to be an important possible source of the observed variation and should warrant further investigation. Previous reports of unusually high juvenile mortality rates in captive cheetah, however, have focused only on an average mortality rate for the North American captive population [O'Brien et al., 1985, 1987; O'Brien, 1994b].

Since the effect of inbreeding on juvenile mortality was significant for the captive cheetah population (Fig. 1) [see also Hedrick, 1992; Marker-Kraus and Grisham, 1993; Caughley, 1994], some of the observed variation among facilities may be attributed to varying levels of inbreeding. The two newest breeding facilities, which had no inbreeding, indeed show the lowest mortality rates (17%). However, comparison of only noninbred juvenile mortality rates across facilities still revealed highly significant interfacility variation. These results again point to husbandry style and management techniques as key factors influencing juvenile mortality.

Furthermore, although an average of about 35 facilities per year have tried to breed cheetahs since the early 1970s, only the five facilities presented here have been highly successful and have produced the majority of offspring in the North American population. Variation in breeding success therefore is substantial and is also likely to be the result of differences in management styles and other external factors.

In the cheetah, surveys of reproductive physiology of wild and captive cheetahs revealed no significant difference in semen characteristics between wild and captive populations [Wildt et al., 1987] or within the North American captive population [Wildt et al., 1993]. In addition, no marked differences in reproductive and endocrine characteristics of proven and unproven breeders could be detected in a survey of 128 cheetahs at 18 North American institutions [Wildt et al., 1993]. Significant interfacility variation in breeding success and juvenile mortality rates therefore strongly suggests differences in husbandry techniques as the main factor in the successful captive propagation of the cheetah [see also Merola, 1994].

Juvenile Mortality, Litter Size, and Average Productivity of Captive-Bred Felids

The cheetah has been reported as showing higher juvenile mortality rates in captivity when compared to other captive-bred species, and this was hypothesized to be a result of its low genetic variation [O'Brien et al., 1985; O'Brien, 1994a,b]. The original comparison was based on data from ungulate and rodent species [O'Brien et al., 1985]. Rates of juvenile mortality, however, can be expected to vary widely with respect to life history strategies and among different taxa. For example, a survey of neonatal mortality in 52 zoo species found lower average juvenile mortality in ungulates (~16%) than in carnivores (~33%) [Loudon, 1985]. Furthermore, juvenile mortality is not necessarily a measure of fitness; the relationship of fecundity rate and juvenile mortality rate needs to be examined to investigate fitness [Caughley, 1994]. Ideally, lifetime reproductive success should be assessed. However, this measure cannot be applied well to the captive situation since the amount of breeding is controlled by management decisions rather than by an individual's reproductive potential.

In this paper only felid species were used for comparison with the cheetah, and a crude measure of productivity was calculated to provide a reference point for fecundity. Data indicate that the North American captive cheetah population shows a low to average juvenile mortality rate with regard to other captive-bred felids, even when only noninbred mortalities are considered, and the cheetah has larger average litter sizes than other felids. In addition, the cheetah shows the highest average productivity when compared to ten other felids.

Reportedly, cheetahs exhibit much lower levels of average heterozygosity than other felid species [O'Brien et al., 1985, 1987]; and higher juvenile mortality rates and lower fecundity in captivity compared to other felids were seen as a consequence of this genetic depletion [O'Brien et al., 1987; O'Brien, 1994b]. Following this line of argument, a relationship should exist between species' average levels of heterozygosity and their rate of juvenile mortality and fecundity. However, there appears to be no significant correlation between average heterozygosity of a given species and its juvenile mortality, average litter size, or productivity based on the underlying data set.

A survey of litter sizes in felids also ranked the cheetah, with an average of 3.6 cubs per litter, higher than all but 2 of 29 species examined [Caro, 1994]. In combination with relatively low neonate and litter birth weight, large litter size may therefore represent a life history adaptation to counter high extrinsic juvenile mortality due to predation by lions and hyenas [Caro, 1994; Laurenson, 1994]. In captivity, however, juvenile mortality rate cannot be considered unusually high, and high levels of average productivity per breeding cheetah are the result of the large litter sizes found in this species.

Any case for low fecundity in captive cheetah [O'Brien et al., 1985; O'Brien, 1994b] would have to be based on a relatively small proportion of breeding individuals in the population. In a recent analysis of the North American cheetah population, 18.2% of individuals were reported as breeders [Marker-Kraus and Grisham, 1993]. A relatively small number of individuals at few institutions are therefore producing a disproportionate number of offspring. However, if breeding problems were largely a consequence of the low levels of genetic diversity observed in cheetahs, one might expect a more uniform distribution of the problem throughout the population.

Since the survey conducted on reproductive physiology of the North American population could detect no significant physiological differences between breeders and nonbreeders [Wildt et al., 1993], the differences in breeding performance may be largely caused by external and ultimately husbandry related factors. There is no evidence today that the low proportion of breeding individuals in the captive population is a result of low levels of genetic diversity measured in the cheetah [see Lindburg et al., 1993; Caughley, 1994].

Small numbers of breeding individuals in captive populations have been observed for other species (e.g., clouded leopard and giant panda, *Ailuropoda melanoleuca*), and breeding success may improve over time with changes in husbandry practices. Providing the appropriate environment for successful captive propagation therefore should be expected to require a thorough understanding of breeding and social behavior, reproductive physiology, and other important aspects of a species' biological and ecological requirements [see Lindburg and Fitch-Snyder, 1994; Kleiman, 1994].

CONCLUSIONS

1. There appears to be no evidence for a significant effect of the extreme level of genetic monomorphism measured for part of the cheetah's genome on the juvenile mortality rate and reproductive performance of this species in captivity. This finding therefore questions the continued use of the cheetah as a textbook example for supporting the importance of genetic factors in conservation.

2. There is, however, evidence for a significant effect of inbreeding on juvenile mortality within the North American cheetah population, suggesting that there may be more variation for certain loci than originally assumed, based on earlier measurements of genetic diversity.

3. Although genetic factors appear to be largely responsible for a higher incidence in juvenile mortality among inbred young in the captive population, they fail to account for variation in noninbred mortality rates between facilities and for the observed decline of juvenile mortality and improvement in breeding success over time.

4. Differences in husbandry and management techniques are suggested as the main factors causing variation in captive cheetah juvenile mortality and breeding performance over time and among facilities; since such extrinsic factors are key to successful propagation of most species, their investigation should be emphasized and become a more important element in the development of captive management plans.

ACKNOWLEDGMENTS

I thank Penny Andrews, Gerald Brady, Nanette Bragin, Robert Evans, Norah Fletchall, Michael Fouraker, Jack Grisham, Kathy Traylor-Holzer, Greta McMillan, Karen Sausman, Alan Shoemaker, Diane Versteeg, Tarren Wagener, Dan Wharton, Sue Ellen White, Alan Varsik, and Karen Ziegler-Hughes, who have made their records available to me and provided helpful comments. Further, I thank the Fossil Rim Wildlife Center, TX, White Oak Conservation Center, Plantation, FL, Wildlife Safari, OR, and Columbus Zoo, OH, for permitting me to view their records on cheetahs and causes of mortality. The Sacramento Zoo was kind enough to allow me the use of its computers to run SPARKS. In particular, two local studbook keepers, Susan Healy and Leslie Field, patiently offered several hours of their time to help with SPARKS and extract all necessary information.

I am grateful to Paule Gros, Marcella Kelly, Rebecca Lewison, Don Lindburg, Peter Marler, Alessia Ortolani, Joel Pagel, Kyle Summers, Dirk Van Vuren, Bob

Wiese, Kevin Willis, and three anonymous reviewers for providing helpful comments, discussions, and information; Don Lindburg for providing pertinent literature and some data on the cheetah population at the San Diego Wild Animal Park; Lien Luong for hours of sifting through breeding records; and Tim Caro for advice and for reviewing the manuscript.

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