

RESEARCH ARTICLES

Captive Breeding of the Cheetah (*Acinonyx jubatus*) in North American Zoos (1871-1986)

Laurie Marker and Stephen J. O'Brien

Wildlife Safari, Winston, Oregon (L.M.), and Laboratory of Viral Carcinogenesis, National Cancer Institute, Frederick, Maryland (S.J.O.)

The African cheetah has been bred in North American zoological facilities since 1956. The captive population has since grown to around 200 animals because of a combined increase in importation plus captive births. From 1982 to 1986, the captive birth rate declined by 50%, primarily because of a low frequency of breeding individuals in the population. The 1986 population had an effective breeding size of 28.1 in a total population of over 193 cheetahs. The incidence of infant mortality has been high (36.7%) relative to other zoo-bred species, perhaps as a consequence of the previously observed genetic impoverishment of the species. The combination of low fecundity, high infant mortality, and population dynamics indicates that the North American captive cheetah population is neither a self-sustaining nor a theoretically "viable population" as defined by Soule et al. [ZOO BIOLOGY 5:101-114, 1986]. Possible recommendations for improving captive cheetah propagation are discussed.

Key words: studbook, pedigree analysis

INTRODUCTION

The cheetah (*Acinonyx jubatus*) is the single surviving species of an holarctic Pleistocene genus *Acinonyx* and is considered to be markedly divergent in both anatomy and behavior from the other genera of Felidae. Cheetahs have a number of morphological and physiological characteristics that are related to their ability to sprint at high speeds (>70 miles per h) in pursuit of prey [Wrogemann, 1975; Kingdon, 1977]. Because of their swift and elusive character, demographic estimates of wild cheetahs vary considerably, from 1,500 to 25,000 animals [Frame and Frame,

Received for publication September 5, 1987; accepted December 10, 1987.

Laurie Marker's present address is NOAHS Center, National Zoological Park, Smithsonian Institute, Washington, D.C. 20560.

Address reprint requests to Stephen J. O'Brien, Laboratory of Viral Carcinogenesis, National Cancer Institute, Building 560, Room 21-105, Frederick, MD 21701-1013.

1981; Myers, 1975, 1986; Joubert and Mostert, 1975; Eaton, 1974; Hamilton, 1986]. Free-ranging cheetahs presently inhabit a broad section of central, eastern, and southern Africa. Although the area of the cheetah's range is vast, population density estimates are rather low (estimated at less than one animal per 6 km²), which has raised the possibility that cheetah density in certain areas is lower than the ecosystem could support [Frame and Frame, 1981; Myers, 1975]. The species has been classified as endangered by the U.S. Fish and Wildlife Service and is listed as appendix I of the Convention on International Trade on Endangered Species [CITES, 1984].

In light of the cheetah's endangered status, as well as its aesthetic appeal to humankind, the species has historically been the object of multiple attempts to propagate in captivity. For reasons that were unclear until recently, however, the cheetah has not been easy to breed. Despite the widespread capture and training of wild cheetahs by Eurasian rulers for several thousand years, there is but a single report of a captive litter (in the palace of Akbar, a fifteenth century Mogul emperor) until the 1950s [Guggisberg, 1975]. The difficulty in breeding cheetahs prompted several conservation initiatives including: 1) the development of the *North American Regional Cheetah Studbook* in 1983 [Marker, 1983], now in its fourth edition; 2) the inclusion of the species as a target animal of the Species Survival Plan (SSP) of the American Association of Zoological Parks and Aquariums (AAZPA) in 1984; and 3) the establishment of a multidisciplinary research program to provide a biological explanation for the relative difficulty in breeding cheetahs as compared to other felids (lions, tigers, pumas, etc.). Results of these studies have established the species as a paradigm for understanding the interaction of genetic, reproductive, and epidemiological factors in conservation management of threatened and endangered species [O'Brien et al., 1983; Wildt et al., 1983, 1984a,b; O'Brien et al., 1985; Wayne et al., 1986; O'Brien et al., 1986, 1987; Wildt et al., 1987].

An important aspect of the description of a species conservation program is the development of a demographic and genetic profile of the captive-bred population. Toward this end, a cheetah studbook for North American zoos was published in 1983 and is updated annually by one of us (L.M.) [Marker, 1983, 1984, 1985a, 1986]. In 1988, an international studbook of the cheetah will be compiled as well. We present here a report on of the progress of acquisition, breeding, and mortality of the captive cheetah in North American facilities from 1871 to 1986. The results suggest that the cheetah breeding program is in a precarious position due to several factors that we believe can be reversed by implementation of a number of coordinate management decisions.

STATUS OF THE CAPTIVE POPULATION

The earliest records of importation and public display of cheetahs date back to 1871 [Marker, 1984]. A summary of the numbers of imports and captive births since that date is presented in Table 1. In total, 470 cheetahs have been imported into North America and there have been 417 captive births from 113 litters in over 57 zoological facilities. The first captive birth occurred at the Philadelphia Zoo in 1956. Before then, 85 animals had been imported; after that (1956–1986), a total of 385 imports occurred. The following description refers to the breeding period from 1956 to 1986 (Table 2).

TABLE 1. History of captive cheetahs in North America

	1871–1913	1914–1925	1926–1955	1956–1986
No. imported	14	0	71	385
No. births	0	0	0	417
No. deaths	9	4	54	566
No. zoological facilities	4	1	13	39
No. alive at end of period	5	1	19	193

The increase in the total number of animals in North American facilities during this period is illustrated in Figure 1. The total number of captive animals gradually increased to a maximum of 212 in 1975. The number dropped gradually after this time to a low of 165 in 1980 and increased again to 193 by the end of 1986.

The population growth presented in Figure 1 consists of at least three parameters: imports, captive births, and death. The changes in these three characters of the population are shown as a function of time in Figure 2. Examination of this figure shows that the majority of the increase in the captive cheetah population before 1972, when the numbers reached 167, can be attributed to imports. During the 1956–1972 period, there were 305 wild-caught imports and only a few captive births ($N = 21$). Importation of cheetahs was terminated by the passage of the Endangered Species Act in 1973 (see Fig. 2). At about the same time, the captive reproduction of cheetahs increased to a peak of 37 births in 1975, followed by a temporary decline until 1980, after which a high of 41 births in 10 captive litters occurred in 1981. From 1982 to 1985, the number of births decreased continuously. The apparent plateau in cheetah numbers from 1983 to 1986 (Fig. 1) is actually the result of increased imports offset by a steady decline in captive births (Fig. 2). As of December 31, 1986, the captive cheetah population in North America consisted of 18 wild-caught animals (9%) and 176 (91%) captive-bred animals.

CAPTIVE REPRODUCTION

During the last three decades, the success in breeding of the imported wild-caught cheetahs has been relatively poor. Of the 385 animals that were imported, 349 were wild-caught and 36 were captive-born in facilities outside of North America. Of the wild-caught animals, 52 (15%) have successfully reproduced. On a facility basis, 22 of the over 50 (44%) zoological parks that have attempted to breed cheetahs have succeeded. A breakdown of cheetah breeding at individual facilities is presented in Table 3. This table indicates that a high proportion of the cheetah propagation has occurred at a handful of zoos, with more than half of the contributing institutions having limited success over a brief time period with a single breeding male or female or both.

The age distribution of successful cheetah breeders is presented in Figure 3. Successful parentage has been reported with cheetahs as young as 2 years old or as old as 12 years of age, while the majority of successful breeding for both sexes occur between 3 and 9 years of age. These data are relevant in assessing the age structure of the 1986 population (Fig. 4). The present population includes 49 (25.4%) animals

TABLE 2. Breeding activity 1956–1986

Year	No. im-ports	No. litters	No. births	Deaths			Infant mortality ≤ 6 (%)	No. success-fully bred during the year		No. proven breeders alive at end of year		No. live animals	No. facilities
				Total	≤ 1 mo	1–6 mo		δ	η	δ	η		
1956	3	1	3	4	3	—	100	1	1	1	1	19	14
1957	3	1	2	5	—	2	100	1	1	1	1	21	15
1958	5	—	—	2	—	—	—	—	—	—	—	21	15
1959	10	—	—	7	—	—	—	—	—	—	—	26	19
1960	10	—	—	6	—	—	—	—	—	—	—	30	22
1961	8	—	—	5	—	—	—	—	—	—	—	33	21
1962	18	2	5	11	5	—	100	1	1	1	1	46	27
1963	7	—	—	5	—	—	—	—	—	—	—	48	27
1964	28	—	—	7	—	—	—	—	—	—	—	79	34
1965	14	—	—	5	—	—	—	—	—	—	—	83	36
1966	27	—	—	8	—	—	—	—	—	—	—	105	38
1967	15	—	—	23	—	—	—	—	—	—	—	104	40
1968	33	—	—	20	—	—	—	—	—	—	—	107	39
1969	10	—	—	10	—	—	—	—	—	—	—	107	36
1970	63	1	3	17	2	—	67	1	1	1	1	146	37
1971	24	2	5	18	1	—	20	2	2	3	3	142	38
1972	26	1	3	11	—	—	0	1	1	3	3	167	41
1973	23	7	25	24	9	—	36	5	5	5	7	187	41
1974	12	10	41	10	15	0	37	7	9	13	15	208	40
1975	—	8	37	24	6	—	16	6	8	12	15	212	40
1976	1	8	35	20	9	1	28	7	8	13	16	207	37
1977	—	4	16	21	4	—	25	4	4	11	10	201	37
1978	—	7	25	20	12	—	48	6	7	11	12	204	35
1979	—	5	15	28	6	1	47	5	5	13	12	182	33
1980	—	7	18	29	7	1	44	5	7	13	15	165	29
1981	—	10	41	35	14	2	39	6	8	14	15	187	21
1982	—	8	33	40	9	4	39	4	7	13	19	172	32
1983	—	8	30	41	9	2	37	5	6	9	16	163	33
1984	13	9	27	29	3	2	19	6	9	10	18	205	39
1985	25	5	18	34	7	1	44	5	5	9	14	202	40
1986	7	9	35	47	15	1	46	6	8	12	17	193	38
Total	385	113	417	566	136	17	Ave.37						

over the usual reproductive age (≥ 10 years old), 92 (47.6%) animals between 3 and 9, and 53 (27.4%) subadults (0–2 years old). Among the 193 animals alive in 1986, only 12 males and 17 females are proven breeders; that is, they have bred successfully at least once. This number permits the computation of the effective breeding size (N_e) for the 1986 population using the formula

$$N_e = \frac{4 \times M \times F}{M + F} = 28.1,$$

where M is the number of breeding males and F is the number of breeding females. This value (N_e) is equivalent to 14.5% of the captive population. Over the past 30 years, N_e was seldom higher (see Table 2). When combined with the observation that

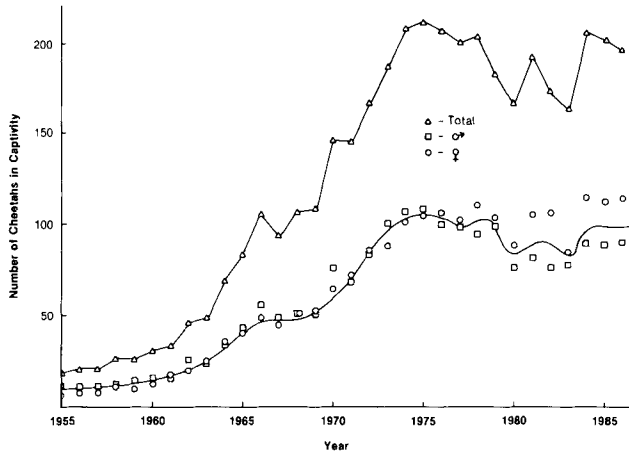


Fig. 1. Total no. cheetahs in 66 North American zoological facilities from 1956 to 1986. Data from Figures 1–6 are documented in Marker [1985a].

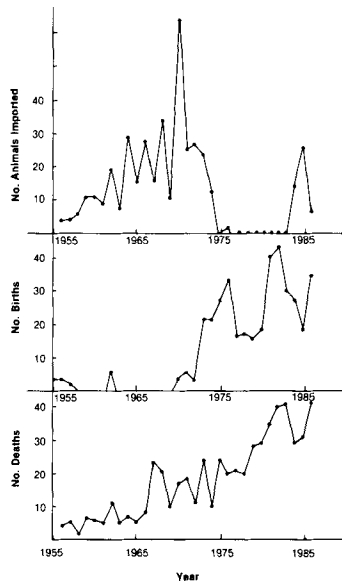


Fig. 2. Time course of cheetah imports, captive births, and deaths in North American zoological facilities 1956–1986.

only 15% of the wild-caught animals have successfully reproduced, the chronically low N_e indicates that the captive population falls well below the accepted definition of a viable population [Soule et al., 1986].

SURVIVORSHIP AND MORTALITY

The growth pattern of a population is actually derived from the combination of both reproduction and relative survival. As shown in Figure 2, cheetah mortality

TABLE 3. Cheetah breeding activity in North American zoos 1956-1986

Facility	No. litters	No. cubs	Infant mortality ≤6 mo (%)	Breeding period	Resident breeding	
					♂	♀
Wildlife Safari, OR	22	97	31	1973-85	5	7
San Diego Wild Animal Park, CA	17	64	34	1970-86	5-8	8
Columbus Zoo, OH	13	48	52	1979-86	5	3
Lion Country Safari, CA	9	35	40	1974-78	2	4
Frank Gilbert, AZ	8	33	24	1974-85	3-4	2
Lion Country Safari, TX	6	21	47	1974-76	2	3
Cincinnati Zoo, OH	7	21	29	1974-81	1-3	2
St. Louis Zoo, MO	6	21	14	1978-84	1	1
Lion Country Safari, GA	3	12	25	1973-75	1	1
Oklahoma City Zoo, OK	3	8	100	1962-74	3	2
Fossil Rim Ranch, TX	2	8	0	1986	1	2
Phoenix Zoo, AZ	3	7	57	1980-81	2	2
Miami Zoo, FL	2	7	0	1975-78	1	1
White Oak Plantation, FL	2	6	33	1986	1	1
Philadelphia Zoo, PA	2	5	100	1956-57	1	1
Albuquerque Zoo, NM	2	3	33	1984-85	1	1
Metro Toronto Zoo Ont., Canada	1	6	67	1976	1-2	1
African Lion Safari Ont., Canada	1	5	100	1978	1	1
B. Lowe, OH	1	4	0	1979	1-2	1
Toledo Zoo, OH	1	4	0	1971	1	1
Salt Lake City, UT	1	1	100	1973	1	1
Milwaukee Zoo, WI	1	1	100	1971	1	1
Total	113	417				

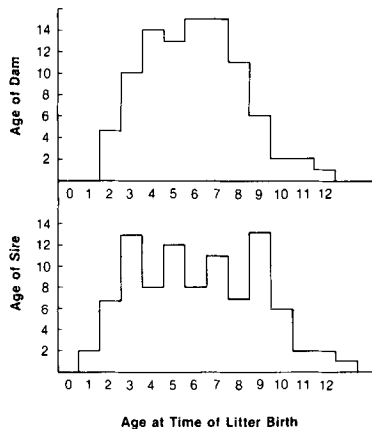


Fig. 3. Age distribution of successfully breeding cheetahs during the study period.

gradually increased over the 30-year breeding period, clearly correlating with population growth (Fig. 1). The timing of death in the cheetah population, however, revealed some marked trends. First, the incidence of infant mortality before age 6 months (Table 2) was 37%, a rather high value compared to other noninbred zoo

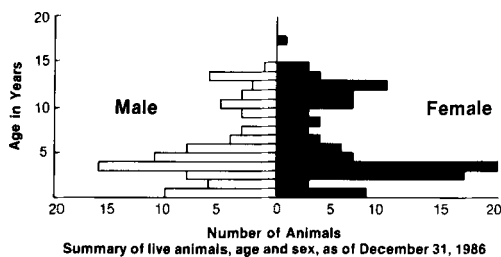


Fig. 4. Age distribution of 1986 populations of cheetahs in North American zoos.

species [O'Brien et al., 1985; Ralls and Ballou, 1982a,b; Ralls et al., 1979]. The extent of infant mortality varied widely among institutions (0–100%; Table 3) and also between years (Table 2). When the frequency of infant mortality is computed for those cubs born to related parents (inbred), the frequency is $23/56 = 41\%$. The frequency for cubs born from unrelated parents (noninbred) was $130/361 = 36\%$. Although the frequency of inbred infant mortality was slightly higher, this difference is not statistically significant ($\chi^2 = 0.53$; $P \geq 0.1$). We have interpreted the apparent equivalence of survivorship among inbred vs. outbred cheetah litters as a reflection of an ancestral genetic homogenization event that purged large portions of genetic variation from the species [O'Brien et al. 1985, 1987].

The age of death of cheetahs recorded in the *North American Regional Cheetah Studbook* is presented in Figure 5. Two points are evident from analysis of these data. First, the most vulnerable age is infancy (0–1 month) when the mortality is 10 times the frequency than at any other age. Second, there is a clear demarcation between time of death for wild-caught animals vs. captive-bred animals. The captive-born animals died almost equivalently from age 2 to 10 years if they survived the first 6 months. With few exceptions, wild-caught animals lived to be 12–16 years of age. At face value, this distribution would suggest that once wild cheetahs survive in the field to an age where they can be captured and shipped to the United States, their survivorship is extended nearly 5 years longer than their captive-bred counterparts in U.S. zoos. This interpretation, however, should be considered as tentative at best since most captive-bred animals in this study are young (≤ 13 years old) and have not yet lived long enough to die at older ages.

The cause of death among captive cheetahs was determined by examination of 214 necropsy reports of specimens that died in captivity (Table 4). As expected, most deaths were attributable to infant mortalities resulting from stillbirths, premature births, congenital defects, infection, mother neglect, or cannibalism ($N = 79$ individuals; 36.9%). The second most predominant killer was feline infectious peritonitis (FIP), a fatal coronavirus disease that killed 39 animals (18.2%). All of the FIP diagnoses involved animals that died after 1982 when a major clinical epizootic occurred at Wildlife Safari Park in Oregon [O'Brien et al., 1985; Pfeifer et al., 1983; Evermann et al., 1986]. Although FIP had been reported in other cheetah facilities earlier than 1982 [Van Rensburg and Silkstone, 1984; Horzinek and Osterhaus, 1979; Worley, 1986], the extent of documentation of the Oregon epizootic alerted the U.S. wildlife veterinary community to the extremes of morbidity that this disease can cause in cheetahs. It is possible that the FIP virus was present earlier in cheetah colonies,



Fig. 5. No. cheetahs dying at different ages: 1969–1986.

but was not recognized before 1982 since the disease is difficult to diagnose. For example, a common complication of FIP is kidney and/or liver complications, which are listed as the next most common cause of mortality in captive cheetahs (combined total of 41 animals [19%]). It may be significant, however, that many cheetahs that have died of kidney and liver damage are not associated with coronavirus infection [M. Worley, personal communication]. The remainder of causes of death included a number of different, less common diagnoses.

FOUNDERS AND PRESENT GENETIC STRUCTURE

The pedigree of the 194 living cheetahs in North America by the end of 1986 is presented in Figure 6. All but one of the 52 founder animals were originally derived from the South African subspecies *A. jubatus jubatus* from Southwest Africa/Namibia. Of the 349 wild-caught cheetahs that were imported, 52 (14.8%) reproduced and 33 of these have living descendants (presented in Fig. 6). Among the 417 captive-bred offspring, 257 survived to reproductive age. Of this latter group, 35 (13.6%) have successfully bred. The equivalence in the breeding frequency of captive-bred (13.6%) vs. wild-caught parentage (14.8%) suggests the equivalent potential of these two groups for captive propagation. This indicates that subsequent generations of captive-bred cheetahs should breed as well if not better than their wild-caught progenitors.

Despite the large number of founders compared to other SSP programs animals (e.g., Asiatic lion, golden lion tamarin, Sumatran tiger), relatively few have made a disproportionately large contribution to the 1986 populations' gene pool. For example, from 1981 to 1985, 27 cheetahs reproduced, but 10 of these animals produced two-thirds of the offspring. These 27 animals have produced a total of 149 cubs that represent 39% of cubs born over the entire 30-year study period. Further, the actual number of offspring produced declined steadily from 1981 to 1985 (Fig. 2). In 1986, there was a modest increase in new births. It may be significant that 8 of the 12 new breeders in that year were imports.

TABLE 4. Reported cause of death in captive cheetahs

Cause of death	No. animals	Studbook no.
Juvenile mortality	79	86, 87, 117, 118, 119, 120, 148, 180, 181, 182, 183, 188, 192, 193, 194, 199, 200, 201, 202, 224, 227, 228, 229, 236, 237, 241, 242, 243, 246, 251, 252, 256, 257, 263, 274, 279, 284, 285, 286, 287, 288, 289, 290, 292, 298, 321, 322, 323, 324, 325, 326, 327, 377, 382, 389, 401, 402, 413, 438, 440, 441, 442, 443, 473, 474, 475, 476, 477, 478, 479, 480, 481, 485, 496, 497, 498, 499, 500, 509
FIP	39	10, 35, 80, 125, 127, 139, 146, 187, 195, 275, 293, 294, 295, 296, 297, 306, 309, 310, 311, 312, 315, 316, 317, 318, 320, 329, 381, 425, 427, 428, 435, 151, 258, 259, 264, 378, 379, 392, 396
Kidney disease	19	1, 15, 26, 54, 55, 56, 57, 112, 130, 142, 164, 198, 226, 112, 133, 137, 163, 175, 37
Liver disease	14	27, 52, 82, 83, 95, 159, 171, 189, 207, 216, 67, 176, 189, 24
Kidney and liver	8	11, 29, 70, 79, 84, 135, 168, 388
Euthanasia (old age)	11	5, 6, 16, 18, 32, 33, 58, 90, 34, 53, 64
Aggression (accident)	8	8, 17, 49, 50, 65, 123, 269, 250
Pneumonia	8	77, 102, 121, 124, 147, 307, 446, 452
Neoplasia	4	19, 61, 92, 109
Anesthesia	4	4, 267, 276, 328
Pancreatitis	2	47, 211
Distemper	1	60
Heart failure	1	105
Hypothermia	1	375
Miscellaneous bacterial and parasitic infections (septicemia, valley fever, toxoplasmosis)	15	46, 59, 100, 113, 145, 179, 185, 222, 233, 253, 284, 331, 400, 122, 232

COMPARISON OF BREEDING OF CHEETAHS WITHIN AND OUTSIDE OF NORTH AMERICA

Two facilities outside the United States, Whipsnade Park (London Zoological Society) and DeWildt Cheetah Breeding and Research Centre (National Zoological Gardens of South Africa), have also developed successful cheetah breeding programs over the last two decades [Brand, 1980; Bertschinger et al., 1984; Manton, 1970; Marker, 1984]. A summary of these programs over the last two decades is presented in Table 5. A significant difference in infant mortality is apparent between the De Wildt vs. Whipsnade programs ($\chi^2 = 9.68$; $P < .01$). The lower infant mortality at Whipsnade may be due to the hybrid matings between southern (*A. jubatus jubatus*) and East African cheetahs (*A. jubatus raineyi*) in their breeding program in contrast to De Wildt where all the animals were derived exclusively from the southern African

Pedigree Chart of Captive Born Cheetahs in North America (31 December, 1986)

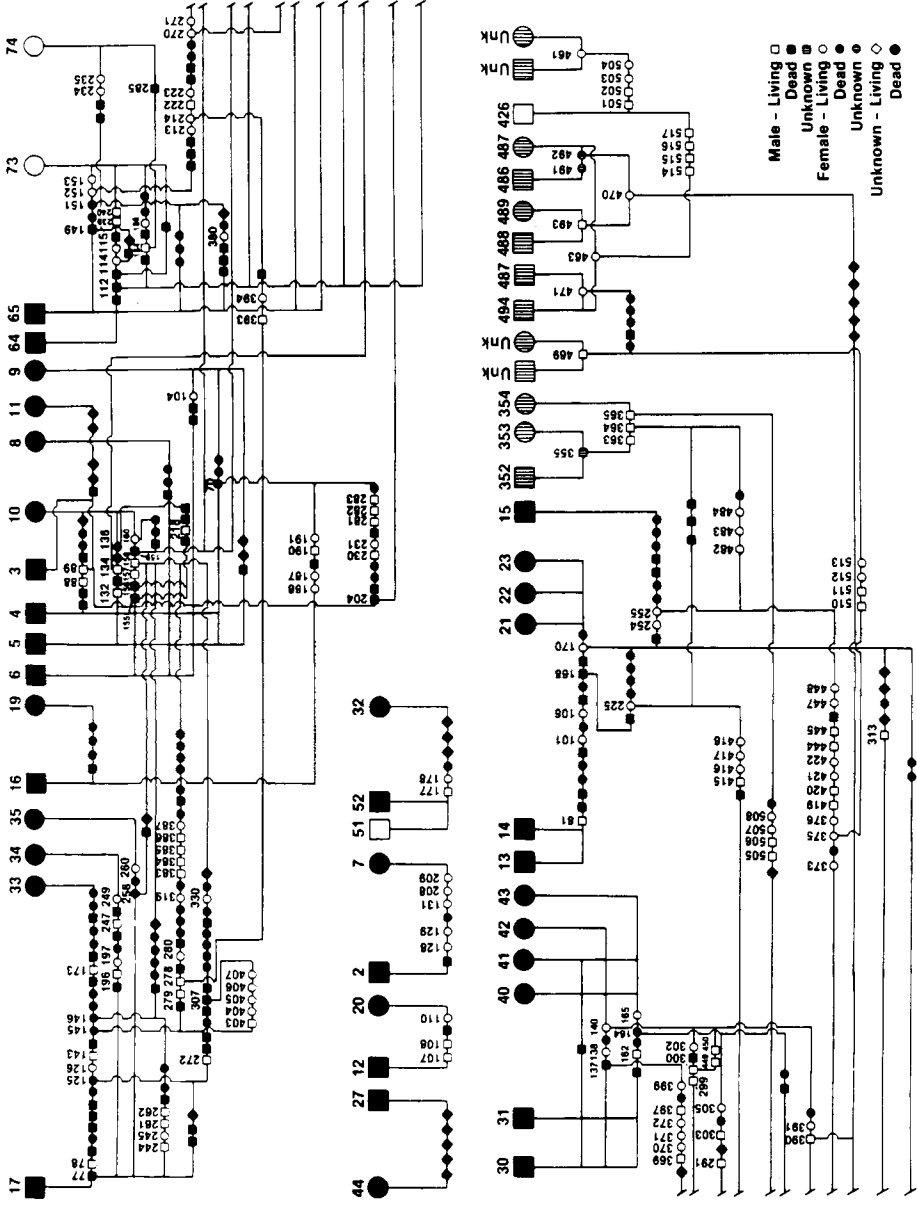


Fig. 6. Pedigree of North American captive-born cheetahs in U.S. zoos in 1986. Not included are 10 successful breeders that have no living descendants. Solid figures are deceased. Nos. are *North American Regional Cheetah Studbook* nos. [Marker, 1986]. (□) ♂; (○) ♀.

TABLE 5. Comparison with other cheetah breeding programs*

Breeding facility	Period	No. litters	No. births	No. Deaths ≤ 6 mo	Infant mortality (%)	Inbred offspring (%)
De Wildt Republic of South Africa	1975–1983	68	230	104	45.2	0
Whipsnade Great Britain	1964–1984	31	106	29	27.4	44
North America	1956–1986	113	417	153	36.7	13

*Data derived from Bertchinger et al. [1984], Marker [1985a], and O'Brien et al. [1985].

subspecies. This is especially true when one considers that the South African subspecies is particularly diminished in endemic genic variation, but is slightly differentiated genetically from the East African subspecies [O'Brien et al., 1986, 1987]. It is also possible that differences in captive management procedures may impact on these values as well.

DISCUSSION

The experience of North American zoological facilities has reaffirmed the traditional difficulty in captive propagation of the cheetah. Despite the capturing, rearing, and public display of cheetahs for thousands of years, the first documented captive breeding of cheetahs did not occur until 1956. By 1974, a population of over 200 animals had been achieved and is currently maintained by a combination of imports and captive breeding. The breeding program, however, is not self-sustaining, and has shown a marked decline from 1982 to 1985 (Fig. 2). The captive population has traditionally had a low effective breeding size (less than 15% of the total), and the 1986 population of 193 animals has an N_e of 28 animals. The fecundity of wild-caught vs. captive-born animals is equivalent and low (13.6% to 14.8%). In the absence of further imports, the size of the captive population would be expected to decline further.

The present population has a large number of founders relative to other SSP programs ($N = 52$). However, because of the limited number of breeding animals, relatively few individuals have made a disproportionately large genetic contribution to the living animal gene pool. The potential for improvement of the breeding program by improving management is suggested by the observation that 7 of the 22 facilities that have bred cheetahs have produced 70% of all the cheetahs born in North America. Specific SSP recommendations for cheetah breeding based on empirical observations of these facilities are now being developed for participating institutions.

The difficulty in captive breeding of the cheetah prompted a rather extensive genetic and physiological analysis of both captive and free-ranging cheetahs [reviewed in O'Brien et al., 1985, 1986]. The cheetah appears to be unique among felids and other mammals in having an extreme paucity of genetic variation as estimated by electrophoretic surveys of allozymes and cell proteins resolved by two-dimensional gels [O'Brien et al., 1983]. More unusual was the observation of allogeneic skin graft acceptance among unrelated cheetahs, revealing genetic monomorphism at the major histocompatibility complex, an abundantly polymorphic locus in nearly all mammals

[O'Brien et al., 1985]. A comparative analysis of cheetah ejaculates revealed a sperm count one-tenth of that observed in domestic cats and an extremely high frequency (71%) of morphological spermatozoal abnormalities [Wildt et al., 1983, 1987]. In addition to these phenotypic observations, patterns of skeletal variation also show significant asymmetry of bilateral characters, a phenomenon generally common in inbred animals [Wayne et al., 1986]. The combined genetic, reproductive, and morphological data placed the cheetah in a status reminiscent of deliberately inbred mice or livestock and prompted us to hypothesize that in its recent history the species had probably suffered a demographic contraction or population bottleneck necessarily followed by inbreeding [O'Brien et al., 1987]. Based on the genetic and physiological similarities of the southern and eastern African subspecies, we concluded that the proposed bottleneck was an ancient one, perhaps dating back to the global mammalian extinctions near the end of the Pleistocene over 10,000 years ago.

Considering the combined results of the genetics, physiology, structure, and natural history of the captive cheetah populations, there are several recommendations that seem important to improve the demographic patterns. First, outbreeding individuals within the present captive population should be optimized primarily to mask the potentially deleterious physiological effects of inbreeding among cheetahs. This strategy could be extended by the introduction of new animals of different genetic lineages. A particular advantage may be achieved by the inclusion of East African animals into the program, an approach that was apparently successful at Whipsnade (Table 5). The probability of outbreeding depression [Shields, 1982] is miniscule because the genetic distance between the two subspecies is trivial, 10 times less, for example, than the genetic distance between human racial groups [O'Brien et al., 1987].

Second, because the N_e may be typically low because of inherent genetic impoverishment, the only way to reverse decline may be to increase the size of the breeding population. Soule et al. [1986] have estimated that in order to have a viable population, a principal aim would be to retain 90% of the endemic genetic variation for over 200 years. Experience with domestic animal breeding has determined that inbreeding depression can be avoided if the rate of inbreeding per generation remains below 1%. This translates into an effective breeding size (N_e) of at least 50 animals. If the cheetah's present N_e (14.5%) cannot be improved by husbandry, a total population of 340 animals would be required to maintain an effective breeding size of 50. Increasing the captive population could be achieved in some ways that would not impact on the remaining free-ranging populations. The first is to expand the managed captive population to an international studbook, a process actually begun in 1987 with L.M. designated as International Studbook Keeper. Second, inclusion of all captive cheetahs in studbook management should be implemented as well as consideration of recently acquired animals being captured in habitats where cheetahs are legally hunted and trapped, as is the case in Southwest Africa/Namibia [Morsbach, 1987].

Finally, increased research on physiology, reproduction, nutrition, genetics, and behavior of captive cheetahs should be encouraged. Although we know much about the cheetah compared to other threatened species, there are many unanswered but approachable questions. A recently drafted master plan developed by the cheetah propagation group of the Species Survival Plan of the AAZPA has listed basic research in reproduction as a primary end of the SSP. This plan has defined research goals in the related fields of reproduction, nutrition [Setchell et al., 1987], behavior,

genetics, husbandry [Grisham, 1988], pathology [Gosselin et al., 1988], and epidemiology. The anticipated results may provide the key to stabilization of the worldwide captive population with the ultimate end of release of captive-bred animals to suitable natural habitats.

ACKNOWLEDGMENTS

The authors are grateful to the species coordinators at the indicated zoological facilities listed in Table 3; to Ann van Dyke and Victor Manton for providing extensive breeding records for Whipsnade and De Wildt facilities, respectively; to Drs. U.S. Seal, Tom Foose, and Don Brunning for discussion; and to Drs. Alan Shoemaker, John Ballou, Pat Johnson, Lisa Forman, and David Wildt for critical reading of this manuscript.

REFERENCES

- Bertschinger, H.J.; Meltzer, D.G.A.; van Dijk, A.; Courbroughl, R.I.; Soley, J.T.; Collett, F.A. Cheetah life line. *NUCLEAR ACTIVE* 30:2-7, 1984.
- Brand, D.J. Captive propagation at the National Zoological Gardens of South Africa. *INTERNATIONAL ZOOLOGICAL YEARBOOK* 20:107-112, 1980.
- CITES. Convention on International Trade in Endangered Species of Wild Flora and Fauna, Part of the Endangered Species Act. *CODE FEDERAL REGISTER*, Part 23, 1984.
- Eaton, R.L. *THE CHEETAH. THE BIOLOGY, ECOLOGY AND BEHAVIOR OF AN ENDANGERED SPECIES*. New York, Van Nostrand Reinhold, 1974.
- Evermann, J.F.; Roelke, M.E.; Briggs, M.B. Feline coronavirus infections of cheetah. *FELINE PRACTICE* 16:21-30, 1986.
- Frame, G.W.; Frame, L. *SWIFT AND ENDURING, CHEETAHS AND WILD DOGS OF THE SERENGETI*. New York, E.P. Dutton, 1981.
- Gosselin, S.J.; Loudy, D.L.; Tarr, J.J.; Balistreri, W.F.; Setchell, K.D.R.; Johnston, J.O.; Kramer, L.W.; Dresser, B.L. Veno-occlusive disease of the liver in captive cheetah. *VETERINARY PATHOLOGY* 25:48-57, 1988.
- Grisham, J. AAZPA Species Survival Plan Program. Husbandry and reproduction of cheetah: Proposed guidelines in cheetah master plan produced by Special Survival Plan (SSP), April 1988.
- Guggisberg, C.A.W. *WILD CATS OF THE WORLD*. New York, Taplinger, 1975.
- Hamilton, Ph.H. Status of the cheetah in sub-Kenya, with reference to sub-Saharan Africa. In *CATS OF THE WORLD: BIOLOGY CONSERVATION AND MANAGEMENT*. S.D. Miller; D.D. Everett, eds. Washington, DC, National Wildlife Federation, 1986.
- Horzinek, M.C.; Osterhaus, A.D.M.E. Feline infectious peritonitis: A worldwide serosurvey. *AMERICAN JOURNAL OF VETERINARY RESEARCH* 40:1487-1492, 1979.
- Joubert, E.; Mostert, P.K.N. Distribution patterns and status of some mammals in South West Africa. *MADOQUA* 9:6-44, 1975.
- Kingdon, J. *EAST AFRICAN MAMMALS, AN ATLAS OF EVOLUTION IN AFRICA*, Vol. 3. New York, Academic Press, 1977.
- Manton, V.J.A. Breeding cheetah at Whipsnade Park. *INTERNATIONAL ZOO YEARBOOK* 10:85-86, 1970.
- Marker, L. *NORTH AMERICAN REGIONAL CHEETAH STUDBOOK*. Winston, Wildlife Safari Publ., 1983, 1984, 1985a, 1986.
- Marker, L. *CHEETAH STUDBOOK QUESTIONNAIRE SURVEY*. Winston, Wildlife Safari Publ., 1985b.
- Morsbach, D. Cheetahs in Namibia. *CAT NEWS* 6:25-26, 1987.
- Myers, N. The cheetah, *Acinonyx jubatus* in Africa. I.U.C.N. MONOGRAPH 4. Morges, Switzerland, International Union for Conservation of Nature and Natural Resources, 1975.
- Myers, N. Conservation of Africa's cats: Problems and opportunities. In *CATS OF THE WORLD: BIOLOGY CONSERVATION AND MANAGEMENT*. S.D. Miller; D.D. Everett, eds. Washington, DC, National Wildlife Federation, 1986.
- O'Brien, S.J.; Wildt, D.E.; Goldman, D.; Merrill, C.R.; Bush, M. The cheetah is depauperate in biochemical genetic variation. *SCIENCE* 221:459-462, 1983.
- O'Brien, S.J.; Roelke, M.E.; Marker, L.; Newman, A.; Winkler, C.A.; Meltzer, D.; Colly, L.; Evermann, J.F.; Bush, M.; Wildt, D.E. Genetic basis for species vulnerability in the cheetah. *SCIENCE* 227:1428-1434, 1985.
- O'Brien, S.J.; Wildt, D.E.; Bush, M. The cheetah in genetic peril. *SCIENTIFIC AMERICAN* 254:84-92, 1986.
- O'Brien, S.J.; Wildt, D.E.; Bush, M.; Caro, T.;

- Fitzgibbon, C.; Leakey, R. East African cheetahs: Evidence for two bottlenecks? PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA 84:508-511, 1987.
- Pfeifer, M.L.; Evermann, J.F.; Roelke, M.E.; Gallina, A.M.; Ott, R.L.; McKeirnan, A.J. Feline infectious peritonitis in a captive cheetah. JOURNAL OF THE AMERICAN VETERINARY MEDICAL ASSOCIATION 183:1317-1319, 1983.
- Ralls, K.; Ballou, J. Effects of inbreeding on infant mortality in captive primates. INTERNATIONAL JOURNAL OF PRIMATOLOGY 3: 491-505, 1982a.
- Ralls, K.; Ballou, J. Effects of inbreeding on juvenile mortality in some small mammal species. JOURNAL OF LABORATORY ANIMALS 16:159-166, 1982b.
- Ralls, K.; Brugger, K.; Ballou, J. Inbreeding and juvenile mortality in small populations of ungulates. SCIENCE 206:1101-1103, 1979.
- Setchell, K.D.R.; Gosselin, S.J.; Welsh, M.B.; Johnston, J.O.; Balistreri, W.F.; Kramer, L.W.; Dresser, B.L.; Tarr, M.J. Dietary estrogens—A probable cause of infertility and liver disease in captive cheetahs. GASTROENTEROLOGY 93: 225-235, 1987.
- Shields, W.M. PHILOPATRY, INBREEDING, AND THE EVOLUTION OF SEX. Albany, State University of New York Press, 1982.
- Soule, M.; Gilpin, M.; Conway, W.; Foose, T. The millenium ark: How long a voyage, how many staterooms, how many passengers? ZOO BIOLOGY 5:101-114, 1986.
- Van Rensburg, I.B.J.; Silkstone, M.A. Concomitant feline infectious peritonitis and toxoplasmosis in a cheetah. JOURNAL OF SOUTH AFRICAN VETERINARY ASSOCIATION Dec.:205-207, 1984.
- Wayne, R.K.; Modi, W.S.; O'Brien, S.J. Morphological variability and asymmetry in the cheetah (*Acinonyx jubatus*), a genetically uniform species. EVOLUTION 40:78-85, 1986.
- Wildt, D.E.; Bush, M.; Howard, J.G.; O'Brien, S.J.; Meltzer, D.; van Dyk, A.; Ebedes, H.; Brand, D.J. Unique seminal quality in the South African cheetah and a comparative evaluation in the domestic cat. BIOLOGY OF REPRODUCTION 29:1019-1025, 1983.
- Wildt, D.E.; Chakraborty, P.K.; Meltzer, D.; Bush, M. Pituitary and gonadal response to luteinizing hormone releasing hormone administration in the female and male cheetah. JOURNAL OF ENDOCRINOLOGY 101:51-56, 1984a.
- Wildt, D.E.; Meltzer, D.; Chakraborty, P.K.; Bush, M. Adrenal testicular-pituitary relationships in the cheetah subjected to anesthesia/electroejaculation. BIOLOGY OF REPRODUCTION 30:665-672, 1984b.
- Wildt, D.E.; O'Brien, S.J.; Howard, J.G.; Caro, T.M.; Roelke, M.E.; Brown, J.L.; Bush, M. Similarity in ejaculate-endocrine characteristics in captive versus free-ranging cheetahs of two subspecies. BIOLOGY OF REPRODUCTION 36:351-360, 1987.
- Worley, M. Viral diseases and exotic cats. ZOONOZ 10:16, 1986.
- Wrogemann, N. CHEETAH UNDER THE SUN. New York, McGraw-Hill, 1975.