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Keywords: 3NAm/Acinonyx jubatus/breeding/captive breeding/cheetah/pedigree analysis/Studbook/zoo

Abstract: From 1987 to 1991, the North American captive cheetah population increased by 38% (to 266 animals), due to importation and captive breeding. This population constitutes 26% of the world's captive cheetahs and 36% of all reproductively successful animals. Since 1956, 33% of all cubs born in North America occurred during this 5-year period. Because of importation of animals from breeding programs abroad, East African *(A. jubatus raineyi)* genes have been introduced into the North American cheetah population, and 39% of all cubs born during 1987- 1991 were South African/East African hybrids. Also during this time, the breeding population and effective breeding population increased by 86% and 72.6%, respectively. The incidence of infant mortality decreased from 37% (last recorded for the years 1956 to 1986) to 28% (averaged over 5 years), although infant mortality during the latter period ranged from 15% (for unrelated parents) to 41 % (for related parents). Management recommendations implemented to increase fecundity and population size appear to be successful, although the founder base of the population still has only been increased from 52 cheetahs in 1986 to 72 animals in 1991.

All of these factors, combined with a universal frustration to generate a self-sustaining captive population, motivated the Cheetah SSP Propagation Committee to make a rather revolutionary decision in 1988. At its mid-year meeting in Kansas City, the SSP Committee mandated that all cheetahs in North America be designated as a research population. The SSP objectives changed. No longer would primary emphasis be placed upon the traditional goal of producing a self-sustaining, viable population. Rather, the SSP decided to implement and manage a systematic research program focusing upon basic reproduction, genetics, behavior, nutrition, and disease. The logic was simple—the cheetah is a highly specialized species with unique genetic, reproductive, and perhaps other, as yet undefined traits. Initiate research to understand the fundamental biology of the cheetah, and the key(s) to better management will be found.

The program was started with no illusions—the SSP understood (and continues to believe) that it will require years of longitudinal and multidisciplinary studies to answer the obvious questions. Nevertheless, the SSP took this important and precedent-setting first step. The development of an individual species-oriented research program, organized across disciplines and among diverse institutions, has produced an impressive data set, as this *Zoo Biology* issue attests. Papers address the demographics, health, and reproductive status of the North American cheetah population; new discoveries in basic cheetah biology; the latest information on disease prevalence; nutritional considerations; and factors related to reproductive success in free-living cheetahs. The information contained within these first manuscripts was generated in a relatively short time, illustrating the potential power of a coordinated SSP effort to systematically create excellent science while solving practical problems. The completed answer as to why cheetahs are reproductively inefficient in zoos will not be found in this issue. But the information contained herein is an important first step, and attends to what recently has been termed "reality-based conservation," the collection and assimilation of any and all information ultimately useful for enhancing the preservation of a species [Wildt et al., 1992]. Lastly, we hope that this effort will serve as a useful model for other SSP programs facing similar challenges.

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RESEARCH ARTICLES

Captive Breeding of Cheetahs in North American Zoos: 1987–1991

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From 1987 to 1991, the North American captive cheetah population increased by 38% (to 266 animals), due to importation and captive breeding. This population constitutes 26% of the world's captive cheetahs and 36% of all reproductively successful animals. Since 1956, 33% of all cubs born in North America occurred during this 5-year period. Because of importation of animals from breeding programs abroad, East African (*A. jubatus raineyi*) genes have been introduced into the North American cheetah population, and 39% of all cubs born during 1987–1991 were South African/East African hybrids. Also during this time, the breeding population and effective breeding population increased by 86% and 72.6%, respectively. The incidence of infant mortality decreased from 37% (last recorded for the years 1956 to 1986) to 28% (averaged over 5 years), although infant mortality during the latter period ranged from 15% (for unrelated parents) to 41% (for related parents). Management recommendations implemented to increase fecundity and population size appear to be successful, although the founder base of the population still has only been increased from 52 cheetahs in 1986 to 72 animals in 1991.

Key words: studbook, pedigree analysis, *Acinonyx jubatus*

INTRODUCTION

Once widely distributed throughout western Asia and Africa, the free-living cheetah population was estimated to be 100,000 animals in 1900 [Myers, 1975]. Today between 9,000 and 12,000 free-ranging cheetahs remain, according to anecdotal estimates, with the largest concentration in southern Africa and fewer than 200 individuals in Iran. Although cheetahs inhabit a broad section of Africa (including parts of North Africa, Sahel, and eastern and southern Africa), the overall continental

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population continues to decline because of habitat fragmentation [Marker-Kraus and Kraus, 1991].

Throughout their native range, free-living cheetahs are threatened by loss of habitat due primarily to increased agriculture [Wrogemann, 1975; Hamilton, 1986; Myers, 1986; Morsbach, 1987; Wilson, 1987; Marker-Kraus and Kraus, 1990], declining numbers of prey species, and increased poaching on cheetahs and prey species due to the ready availability of firearms [Marker-Kraus and Kraus, 1991]. Also, cheetahs do not necessarily thrive in protected areas because of increased competition with larger predators such as lions and hyenas [Morsbach, 1987; Mills, 1991]; therefore, the largest percentage of the remaining cheetahs in southern Africa is outside of protected reserves or conservation areas [Marker-Kraus and Kraus, 1991].

Namibia has the largest remaining population of free-ranging cheetahs in the world, estimated at 2,500 animals [Morsbach, 1987; Marker-Kraus and Kraus, 1991]. However, 95% of this population lives on farmland outside of conservation areas where they are in direct conflict with livestock and game farmers. From 1980 to 1991, the Namibian cheetah population is known to have decreased by at least 6,782 animals, and 5,860 of these were killed, whereas only 922 were exported [CITES, 1992]. Nonetheless, because of low reproductive efficiency in zoos, the world's captive population is not self-supporting but rather is maintained through continued import of free-ranging cheetahs, usually from Namibia [Marker-Kraus, 1990]. For example, in December 1991, 30% (299 animals) of the global captive cheetah population (1,014 animals) was wild-caught from Namibian stock [Marker-Kraus, 1992].

The overall decline in cheetah population sizes means that those animals that do survive originate from an ever-decreasing, less diverse gene pool. The genetic structure of cheetah populations, relative to other felids, is markedly depleted in genetic variability [O'Brien et al., 1983, 1985, 1987]. The consequences of genetic uniformity are theorized to contribute, at least in part, to the cheetah's overall low reproductive efficiency and high infant mortality and disease susceptibility [O'Brien et al., 1983, 1985, 1987; Wildt et al., 1983, 1987; Wayne et al., 1986; Marker and O'Brien, 1989; Heeney et al., 1990; Junge et al., 1991].

Historic problems related to propagating cheetahs for thousands of years, first by Eurasian rulers as well as the world's zoos since 1821 [Marker-Kraus, 1989], have prompted a number of initiatives to better understand the species management. These have included: 1) developing a North American cheetah studbook [Marker, 1983, 1984, 1985, 1986] and an international cheetah studbook [Marker-Kraus, 1988, 1989, 1990, 1991, 1992]; 2) including the species as a target animal in the Species Survival Plan (SSP) of the American Association of Zoological Parks and Aquariums (AAZPA); 3) implementing a multidisciplinary research program to provide biological explanations for the relatively poor propagation efficiency in captivity [O'Brien et al., 1983, 1986, 1987; Wildt et al., 1983, 1984a,b, 1987; Wayne et al., 1986]; and 4) formulating an SSP Research Master Plan [Grisham and Lindburg, 1989], which included an even more rigorous multidisciplinary research plan for the species (see other papers in this issue for specific examples of ongoing research).

The current status of acquiring, breeding, and mortality of cheetahs from 1871–1986 was presented in 1989 [Marker and O'Brien]. Several recommendations were made to improve demographic patterns including to: 1) outbreed within the present

TABLE 1. History of captive cheetahs in North America

	1871–1986	1987–1991	Total
No. importations	470	54	524
No. births	417	201	618
No. deaths	556	165	798
No. zoological facilities	39	36	
No. alive at end of period	193	266	

captive population by introducing individuals of different genetic lineages, particularly those from East Africa; 2) increase the breeding population size to augment effective breeding size (N_e) and to reverse the decline of inherent genetic impoverishment; 3) expand the managed captive population to an international studbook and begin managing all cheetahs in captivity; and 4) increase research in the fields of cheetah behavior, reproduction, nutrition, genetics, and diseases. Many of these recommendations have been implemented during the past five years.

We present here the progress achieved in acquisitions and breeding as well as the incidence of mortality for the North American captive cheetah population from 1987 to 1991, when an active population and SSP Research Master Plan was initiated. Results suggest that the captive population has increased significantly due to implementation of the coordinated management and research program and the recommendations made in an earlier report [Marker and O'Brien, 1989].

STATUS OF THE CAPTIVE NORTH AMERICAN POPULATION

From 1871 to 1986, 470 cheetahs were imported from the wild, 417 captive births in 113 litters were reported, and 566 deaths occurred (Table 1). At the end of 1986, the captive population numbered 193 animals in 39 facilities. From 1987–1991, the captive population increased by 38% (73 animals) to 266 animals in 36 facilities. A total of 54 animals were imported, and there were 201 cub births (58 litters in 13 facilities).

The number of cheetahs in North American facilities increased from 198 in 1988 to 266 by the end of 1991 (Fig. 1). This growth curve is based upon importation, birth, and death rates. The changes in these three parameters as a function of time (Fig. 2) indicate that the increase is equally due to imports and births. All but five (2.3) individuals imported during this period were captive-born in facilities abroad. At the end of 1991, the captive population contained only six wild-born animals (2%), compared to the global captive population of which 30% were wild-born [Marker-Kraus, 1992]. The North American population constituted 26% of the world's captive population at that time (Fig. 3).

REPRODUCTION

From 1987 to 1991, 53 (27.26) animals produced 201 (104.88.9) cubs in 58 litters (Table 2). This represented 33% of all cubs produced since 1956 (Table 1). Overall, the breeding population increased by 86%, and the number of proven breeders alive at the end of 1991 was 66% higher than at the end of 1986. We attributed this change primarily to the rise in imports related to increased international cooperation in captive

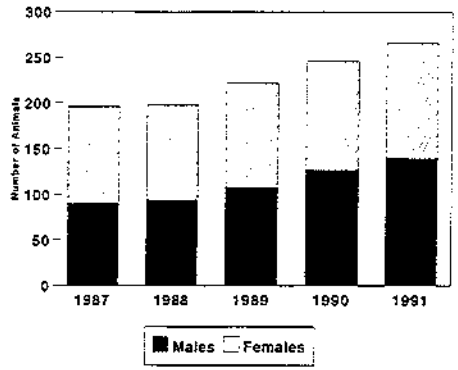

Fig. 1. Total number of cheetahs in 36 North American facilities from 1987–1991. Data from Figures 1–7 are documented in Marker-Kraus [1992].

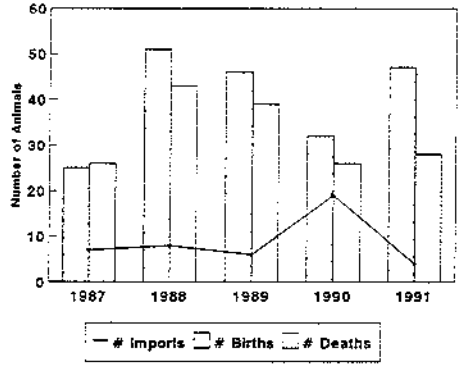

Fig. 2. Time course of cheetah imports, captive births, and deaths in North American facilities 1987–1991.

breeding. For example, from 1976 to 1984, no cheetahs were imported into North America, because of passage of the Endangered Species Act in 1973 [Marker and O'Brien, 1989]. Of 89 animals imported over an 8-year interval, 28% (25 animals) subsequently reproduced during the years 1987–1991. Seventy percent of the breeding animals from 1987 to 1991 were animals imported since 1984, and their reproductive success represented 87% of all cubs born during this period (Table 3).

Of the imported animals that reproduced, five (2.3) were wild-born. One was conceived through the use of artificial insemination (AI) and represented the first successful birth by this method [Howard et al., 1992]. Five (3.2) of the imported breeding animals were subspecific hybrids representing two (1.1) East African founders. During this 5-year period, 46 (24.22) cubs were produced by these hybrids, and six or seven (2/3.4) of their offspring produced 32 (22.9.1) cubs, thus adding additional East African genes into the North American population. Of the 53 breeding

but no analysis of relative fecundity

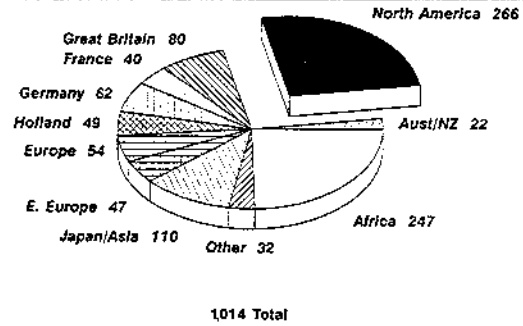

Fig. 3. North American captive cheetah population in relation to the world's captive cheetah population, by region.

TABLE 2. Population changes, 1987–1991

Year	No. imports	No. litters	No. births	Deaths Total	Deaths ≤1 mo	Deaths 1–6 mo	Infant mort. ≤6 mo (%)	No. successfully bred during the year M	No. successfully bred during the year F	No. proven breeders alive at end of year M	No. proven breeders alive at end of year F	No. animals	No. facilities
1987	7	7	25	26	4	1	20	5/6	7	9	18	196	38
1988	8	14	51	44	17	2	37	6	11	9	18	198	43
1989	6	13	46	41	8	6	30	10	13	13	22	227	33
1990	19	10	32	26	3	2	16	9	10	18	23	246	35
1991	4	14	47	28	13	—	24	12	14	21	27	266	36
Total	44	58	201	165	45	11	Avg 28						

animals during the 5-year period, 23% were hybrids, and of the 201 cubs born, 78 (39%) were hybrids.

Thirteen of the 36 (30%) zoological facilities in North America, maintaining cheetahs from 1987 to 1991, had reproductive success. However, a high portion of the propagation occurred in a limited number of zoos (Table 4). Fifteen percent of the facilities produced cheetah cubs annually, with 15% producing in both 1990 and 1991, and 25% having produced offspring for the first time in 1991.

The age distribution of breeders during 1987–1991 is presented in Figure 4, and age at first and last litters is shown in Figure 5. These data are relevant for generating the age structure of the population in 1991 (Fig. 6). The population included 26 animals (10%) over the usual reproductive age (>10 years old), 160 animals (60%) between 3 and 9 years, and 80 subadults (30%) that ranged from neonates to 2 years of age. This age structure was closer to a stable age distribution, as described by Foose [1980], than that measured in 1986 [Marker and O'Brien, 1989]. However, the distribution remained unfavorable as evidenced by the low and disproportionate number of females under 2 years old, and the small number of animals in the 6- and 7-year age range.

TABLE 3. Number of animals imported into the North American captive cheetah population between 1984–1991, and the number of animals from each year which reproduced 1987–1991

Year	Number of animals imported	Number of animals reproducing during 1987–1991 period
1984	13	3
1985	25	11
1986	7	5
1987	7	2
1988	8	2
1989	6	1
1990	19	1
1991	4	0
Total	89	25

TABLE 4. Reproduction in North American zoos, 1987–1991

Facility	No. litters	No. cubs	Infant mortality ≤6 mo. (%)	Resident breeding M	Resident breeding F
Columbus Zoo, OH	13	43	35	2	4
Fossil Rim Ranch, TX	12	44	25	3	4
San Diego Wild Animal Park, CA	8	31	23	6	4
White Oak Plantation, FL	6	25	20	4	3
Metro Toronto Zoo, Ont., Canada	4	11	27	2	2
Wildlife Safari, OR	3	11	46	3	2
St. Louis Zoo, MO	3	7	14	2	1
Lincoln Park Zoo, IL	2	10	20	1	1
Toledo Zoo, OH	2	8	0	1	1
Jackson Zoo, MS	2	6	33	1	1
Dickerson Park Zoo, MO	1	1	0	1	1
Caldwell Zoo, TX	1	1	100	1	1
Polar Park Zoo, Alb., Canada	1	2	100	1	1
Total	58	201			

Among the 266 animals alive in 1991, 22 males and 27 females were proven breeders; that is, animals that had successfully produced cubs at least once. These values permitted calculating the effective breeding size (N_e) for the 1991 population using the formula

$$N_e = \frac{4 \times M \times F}{M+F} = 48.5,$$

where M is the number of breeding males and F is the number of breeding females. This value (N_e) was equivalent to 18.2% of the captive population, and was an increase of 72.6% from 28.1% in 1986 [Marker and O'Brien, 1989] to 48.5% in 1991. The current N_e is the highest in the history of the North American captive breeding program (1956–1991).

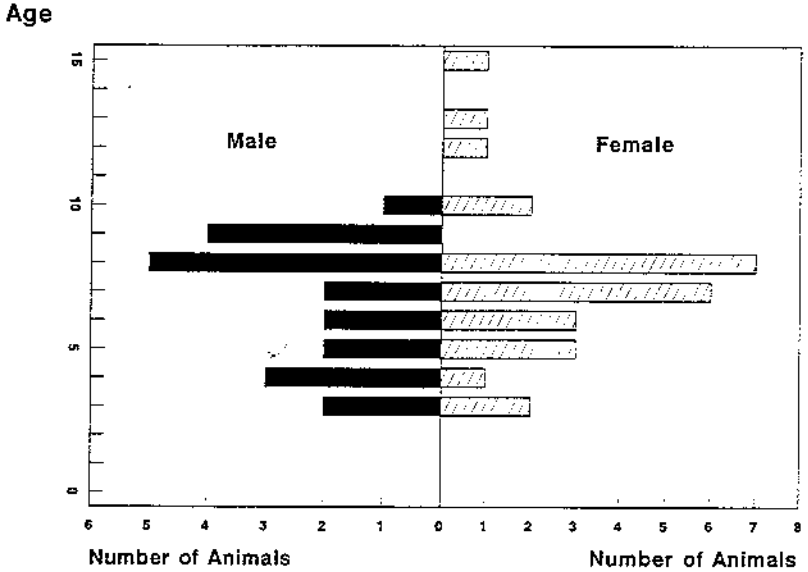

Fig. 4. Age distribution of proven breeders alive in North American captive cheetah population as of December 1991.

SURVIVORSHIP AND MORTALITY

The growth pattern of a population is derived from a combination of reproduction and survival. As illustrated in Figure 2, in 1987, the number of deaths and births were nearly equal. However, in each of the last four years in this period, the birth rate exceeded the death rate, and in 1991, the excess of births over deaths had reached a high point of 19 individuals.

The age at death in the cheetah population over the past 5 years revealed some important trends. First, the incidence of infant mortality before 6 months of age (Table 2) averaged 28%, less than the overall mean for the previous 30 years, but still a rather high value compared to other zoo species known to be genetically diverse [Ralls et al., 1979; O'Brien et al., 1985; Ralls and Ballou, 1982a,b]. The extent of infant mortality varied widely among the 13 institutions having reproductive success during the past 5 years (0–100%; Tables 2 and 4). Of particular importance, when the incidence of infant mortality was computed for those cubs born to related parents (inbred) of southern African origin, the frequency was 14 of 34, or 41%. By comparison, the mortality frequency for cubs born to related parents of East/southern African hybrid parents was 15 of 37, or 41%. By contrast, the frequency for cubs born to unrelated parents (non-inbred) from southern African origin was 22 of 89, or 25%, and for cubs born from unrelated hybrid parents of East/southern African origin, 6 of 41, or 15%. Overall, using a simple Chi-square statistical analysis, there was a higher ($P < 0.05$) rate of infant mortality in offspring born to related compared to unrelated parents. The low infant mortality rates from east/southern subspecies

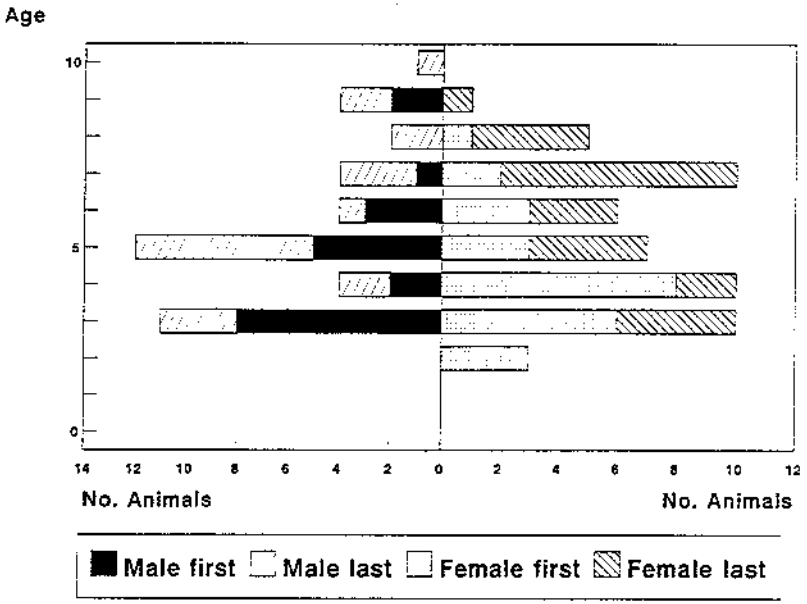

Fig. 5. Age at first and last litters of proven breeders alive in North American captive cheetah population as of December 1991.

hybrids appeared to affirm the trends reported earlier by O'Brien et al. [1985] and Marker and O'Brien [1989], who observed the lowest infant mortality among hybrids from the Whipsnade breeding facility.

The age at death of cheetahs is presented in Figure 7. The most vulnerable age group was infancy (<1 mo.), when mortality was three times the frequency of any other age.

Overall, most deaths (34%) were attributed to infants (N = 56), and resulted from infections (N = 9), stillbirths (N = 7), cannibalism (N = 4), congenital defects (N = 4), hypothermia (N = 4), premature birth (N = 3), maternal neglect (N = 3), unknown (N = 18), or other causes (N = 4) (Table 5). The second most predominant cause of death in all age classes was kidney disease (N = 25) (15%), followed by liver disease being responsible for 10 additional deaths (6%). Kidney and liver disease combined was diagnosed to contribute to eight additional deaths (4%); therefore, 25% of the total deaths were due to kidney and/or liver disease. The incidence of reported deaths caused by Feline Infectious Peritonitis (FIP) was low (three animals) during the 5-year period. Surveillance of this virus has continued (see this issue), and the number of seropositive cheetahs in the population has increased from 35% in 1989 to 60% in 1990 [Evermann and McKerinan, 1991].

FOUNDERS AND PRESENT GENETIC STRUCTURE

The 1991 population contained a large number of founders compared to other SSP programs (N = 72), and had 20 more individuals than were available in the 1986

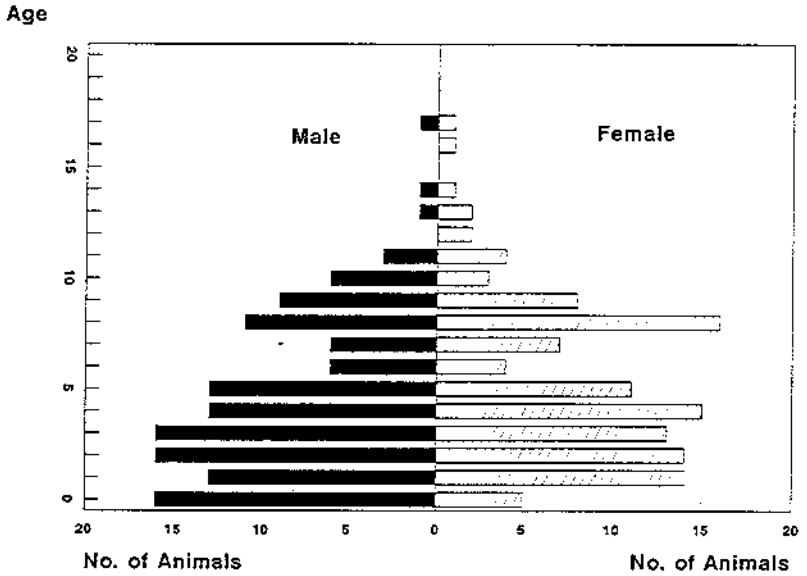

Fig. 6. Age distribution of 1991 population of cheetahs in North American facilities.

population [Marker and O'Brien, 1989]. All but two of the founders were originally derived from the southern African subspecies *Acinonyx j. jubatus* from Namibia/South West Africa and the Northern Transvaal in South Africa; two of the founder animals were from East Africa. Of the 52 founders in the 1986 population [Marker and O'Brien, 1989], only 26 were still alive at the end of 1991. However, there were 46 new founders in the North American population due primarily to importations from the Republic of South Africa.

Despite the large number of founders and breeding animals in the population, a relatively small number of cheetahs made a disproportionately large contribution to the 1991 population gene pool. For example, of the 201 cubs born, 50% were sired by a total of five males, two of which produced 32% of all offspring during the 5-year period.

CAPTIVE BREEDING COMPARISONS FOR CHEETAHS WITHIN AND OUTSIDE NORTH AMERICA

From 1987 to 1991, 613 cheetahs were born at 36 facilities in 14 countries [Marker-Kraus, 1992]. North American facilities represented 36% of all breeding institutions and produced 33% of all cubs. During this time, four facilities outside of North America contributed a total of 231 cubs or 37% of the world's total births. These institutions included the DeWildt Cheetah Breeding Center in the Republic of South Africa (N = 102 cubs), Fota Wildlife Park in Ireland (N = 51 cubs), Wassenaar Breeding Center in the Netherlands (N = 40 cubs), and Himeji Central Park

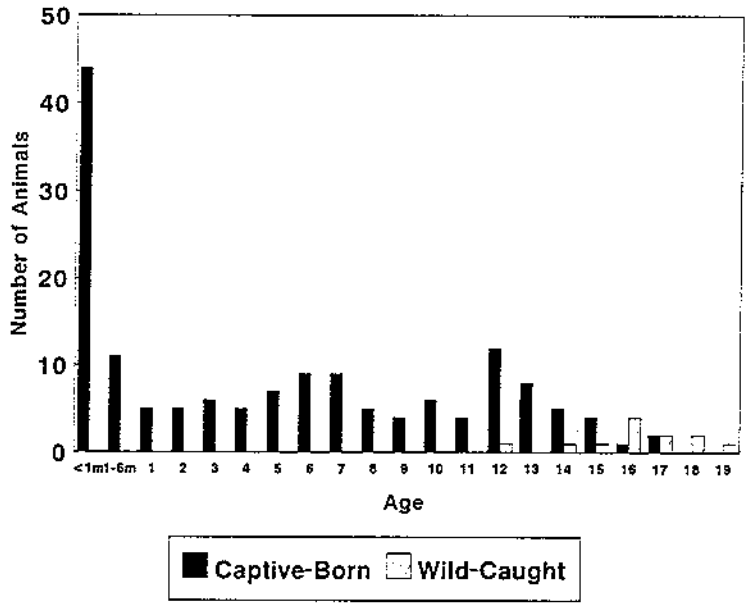

Fig. 7. Number of cheetahs dying at different ages: 1987–1991.

Zoo in Japan (N = 38 cubs). Of the large population maintained at DeWildt (87 animals in 1991), 21 males and 35 females have reproduced since 1975. Forty-six percent of the reproductively successful females were wild-caught, and, of the captive-born females reproducing, 75% were descendants from one founding pair. Fifty-two percent of the breeding males have produced one or two litters and 29% have produced more than nine litters. Two males produced more than 15 litters, primarily for the purpose of generating cubs with the coat color mutation consistent with the "King" cheetah trait [Skinner, personal communication, 1992].

In 1991, the North American captive population represented 26% of the world's population of captive cheetahs (Fig. 3), and 36% of all reproductively successful animals. In this same year, 45 litters were born in captivity throughout the world, producing 167 cubs, of which 28% (47 cubs) were born in North America [Marker-Kraus, 1992].

DISCUSSION

Because of an overall increased population and effective population size, the North American cheetah population is now in a position to be demographically and genetically managed. Critical components of this scheme will require equalizing founder representation by equalizing breeding success, stabilizing the age/sex distribution, and minimizing inbreeding within the population.

TABLE 5. Reported cause of death in captive cheetahs, 1987–1991

Cause of death	Number of animals	Studbook number
Juvenile mortality	56	532, 534, 535, 540, 547, 551, 552, 553, 557, 558, 564, 566, 571, 578, 579, 580, 596, 597, 598, 599, 603, 608, 609, 610, 1887, 1911, 1912, 1913, 1914, 1950, 1951, 1952, 1953, 1954, 1971, 1972, 1973, 1974, 2202, 2221, 2230, 2244, 2254, 2538, 2449, 2470, 2471, 2514, 2563, 2564, 2565, 2568, 2657, 2658, 2671, 2672
Kidney disease	25	28, 62, 76, 78, 98, 101, 104, 131, 134, 138, 140, 153, 158, 167, 170, 178, 186, 191, 231, 260, 281, 319, 350, 376, 456
Liver disease	10	89, 106, 107, 128, 154, 209, 222, 234, 367, 383
Old age	10	38, 66, 73, 81, 114, 162, 166, 360, 423
Kidney and liver	8	115, 165, 272, 282, 366, 319, 372, 393
Aggression	5	235, 529, 538, 549, 577
Feline Infectious Peritonitis	3	196, 361, 517
Central nervous system	3	36, 39, 99
Pneumonia	3	126, 230, 520
Neoplasia	2	408, 453
Pancreatitis	2	152, 240
Heart problems	2	132, 173
Intestinal problems	2	544, 593
Accidental	2	424, 561
Distemper	1	587
Chronic herpes	1	399
Calcium deficiency	1	2239
Miscellaneous health problems	13	51, 74, 127, 157, 184, 197, 350, 394, 434, 470, 482, 514, 516
Unknown	12	177, 190, 208, 236, 261, 416, 421, 450, 515, 523, 563, 581

We suggest that there has been a gradual improvement in management of cheetahs, that has allowed more facilities to be successful (30% in 1991 compared to 14% in 1986). However, it must be noted that four institutions produced 71% of the cubs born from 1987 to 1991, causing a disproportionate number of offspring to be produced by a disproportionate number of founders. Therefore, there is a substantial need to continue enhancing management to ensure optimal captive breeding.

Although half of the founders or their respective offspring existing in the 1986 population have died, overall founder numbers have increased by 42 animals. This large number, with a wide range of genetic backgrounds (Namibia, Republic of South Africa, East Africa), has the potential of contributing a maximum amount of the existing genetic diversity to future offspring. However, equalizing founder representation is critical for optimal genetic management. It is apparent that certain cheetahs are disproportionately represented, and it is crucial that the management plan dictate that the more prolific cheetahs be replaced with previously unrepresented lineages. Such replacements should occur only after a systematic and thorough analysis of the objectives and realities of genetic population management, a process that is now ongoing.

Without a stable age distribution, a captive population can behave erratically,

oscillating drastically and detrimentally [Foose, 1983]. The age/sex distribution of the 1991 population still has not achieved optimal stability, a problem that may be solved by coordinating importations from other facilities abroad.

Despite the attention given to the genetic impoverishment of the cheetah [O'Brien et al., 1983, 1985], inbreeding is still occurring in the North American population. From 1987–1991, 71 cubs were born from matings between related parents which may have been related to a coincidental and markedly elevated incidence of infant mortality. Although some inbreeding may be required to maximize founder representation, as a general practice it should be rigorously avoided. The world's captive cheetah population is grouped into small subpopulations among different countries. It is possible and highly preferable to outbreed with these other populations to reduce the possibility of inbreeding. In recent years, Great Britain, the Netherlands, and the Republic of South Africa have served as the primary resources for importations. We now suggest that considerable care be taken in the selection of cheetahs from these countries and that more emphasis be placed on importing founders from other captive breeding sources abroad.

The gradually increasing success in North America over recent years suggests that greater reproductive success can be achieved through a cooperative management program involving not only North American zoos but also institutions abroad. It is important that all institutions continue to collaborate in the managed reproduction of animals and animal transfers that facilitate breeding priorities.

Specific SSP management guidelines and husbandry recommendations for cheetah breeding, based upon empirical observations from many facility managers, have recently been published [Grisham, 1992] and will assist worldwide captive management of the cheetah. Additionally, recent successes in assisted reproduction in the cheetah [Howard et al., 1992] and other felid species [Howard and Wildt, pers. comm.] suggest that techniques like AI and the movement of germ plasm rather than living animals will offer tremendous advantages to both practical and genetic management. In the future, and in the absence of further imports from the wild, the size of the world's captive population could be expected to decline, unless there is continued improvement in captive breeding efficiency. But with our gradually expanding data base on husbandry and genetic management combined with an in-progress, aggressive research Master Plan, the future of the North American breeding program appears promising. Our eventual goals should include not only a stable captive population, but eventually the production of animals useful for dispersal to the world's zoos or for reintroduction into the wild.

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Behavioral Solutions to Breeding Cheetahs in Captivity: Insights From the Wild

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Knowledge of cheetahs' behavior is increasingly seen as the key to solving the mystery of cheetahs' poor breeding performance in captivity. In the absence of zoos' maintaining systematic records of individuals' behavior during introductions, behavior of free-living animals can be informative. In the wild, most female cheetahs probably mate with males living in small groups or coalitions; thus, zoos may benefit from replicating these social conditions, provided injuries can be minimized. Relations between free-living coalition members are amicable, and escalated aggression was never witnessed during 4 years of observation. Some antagonism was seen in newly formed trios, although this had disappeared in longer established coalitions. Minor aggression occurred over carcasses, being greater at small and intermediate sized kills than at large ones. In the presence of females, mild intramale aggression was only seen within 1 of 7 coalitions. Free-living females showed similar rates of behavior in the presence of different numbers of males, aside from more frequent growling at large groups. These findings suggest that captive institutions should be less nervous about housing male cheetahs together and introducing females to groups of males for purposes of breeding.

Key words: ***Acinonyx jubatus*, behavioral interactions, coalition, free-living, reproduction**

INTRODUCTION

Cheetah (*Acinonyx jubatus*) numbers are thought to be declining across the African continent [Myers, 1975], because their gazelle prey are being exterminated from the Sahel zone [Newby, 1992] and because they are shot as vermin in southern Africa. In addition, and in common with most large predators in Africa [e.g., Fanshawe et al., 1991], the range of the species is almost certainly diminishing due to agricultural encroachment. Nevertheless, the wild cheetah population stands at be-

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