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Abstract: Since 1829 the African Cheetah *Acinonyx jubatus* has been exhibited in over 373 zoological facilities. As at 31 December 1994 the international captive population was 1218 animals of which 880 (72%) were captive-bred and 318 (28%) were wild-caught. The steady increase in the captive population is a result of captive breeding, co-operative captive-management programmes and importation from the wild. Of facilities holding Cheetah 26% (96) have bred the species, 15% of which have bred continuously producing 63% (n = 1580) of all cubs born in captivity. Although the number of facilities breeding Cheetah has increased, in 1994 only 10% of them reported successful reproduction. The number has increased gradually and in 1994 was equivalent to 17% of the captive population. Of 1564 animals that have been imported, c. 20% (n = 308) have reproduced and in 1994 155 have living descendants in the captive population. Except for a few East African Cheetah *Acinonyx jubatus raineyi* all of the imported animals are the southern African subspecies *Acinonyx jubatus jubatus*. There has been an increase in the number of subspecific hybrids in the captive population and between 1990 and 1994 28 hybrids produced 24% (190) of cubs. The captive population is not yet self-sustaining and is maintained by the importation of wild-caught animals. Continued progress can be achieved by implication of a co-ordinated global management programme.

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## History of the Cheetah

*Acinonyx jubatus*

### in zoos 1829–1994

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Since 1829 the African Cheetah *Acinonyx jubatus* has been exhibited in over 373 zoological facilities. As at 31 December 1994 the international captive population was 1218 animals of which 880 (72%) were captive-bred and 338 (28%) were wild-caught. The steady increase in the captive population is a result of captive breeding, co-operative captive-management programmes and importation from the wild. Of facilities holding Cheetah 26% (96) have bred the species, 15% of which have bred continuously producing 63% ( $n=1580$ ) of all cubs born in captivity. Although the number of facilities breeding Cheetah has increased, in 1994 only 10% of them reported successful reproduction. The  $N_e$  has increased gradually and in 1994 was equivalent to 17% of the captive population. Of 1564 animals that have been imported, c. 20% ( $n=308$ ) have reproduced and in 1994 155 have living descendants in the captive population. Except for a few East African Cheetah *Acinonyx jubatus raineyi* all of the imported animals are the southern African subspecies *Acinonyx jubatus jubatus*. There has been an increase in the number of subspecific hybrids in the captive population and

between 1990 and 1994 28 hybrids produced 24% (190) of cubs. The captive population is not yet self-sustaining and is maintained by the importation of wild-caught animals. Continued progress can be achieved by implication of a co-ordinated global management programme.

*Key-words:* captive history, captive-management plans, cheetah, pedigree analysis, registry, reproduction, studbook, zoos

The Cheetah *Acinonyx jubatus* is markedly different in both anatomy and behaviour from the other 36 felid species. It is the only species in the genus *Acinonyx* and the fastest land mammal.

Cheetahs were widely distributed throughout western Asia and Africa and in 1900 the wild population was estimated to be 100 000 animals (Myers, 1975). Today c. 12 000 live in 23 African coun-

tries, with the largest concentration in southern Africa. Less than 200 Cheetahs live in Iran (Kraus & Marker-Kraus, 1992). Although Cheetahs are widely distributed in Africa, including parts of North Africa, Sahel and eastern and southern Africa, the population continues to decline because of habitat fragmentation (Kraus & Marker-Kraus, 1992). The Cheetah is classified as Vulnerable or Endangered throughout its range and is on CITES Appendix I (CITES, 1984, 1992; Jackson, this volume).

Wild Cheetahs are threatened by loss of habitat resulting from increased agriculture and a decline in numbers of prey species (Wrogemann, 1975; Hamilton, 1986; Myers, 1986; Morsbach, 1987; Wilson, 1987; Marker-Kraus & Kraus, 1990, this volume). The availability of firearms has resulted in increased poaching of Cheetah and their prey (Kraus & Marker-Kraus, 1992). Most Cheetahs are found outside reserves because in protected areas they are in competition with larger predators such as Lions *Panthera leo* and Hyenas *Parahyaena brunnea* (Caro, 1987; Morsbach, 1987; Laurenson, 1991; Mills, 1991; Kraus & Marker-Kraus, 1992; Marker-Kraus & Kraus, this volume). Namibia has the largest remaining population of free-ranging Cheetahs, estimated at 2500 animals (Morsbach, 1987; Kraus & Marker-Kraus, 1992; Marker-Kraus *et al.*, 1996; Marker-Kraus & Kraus, this volume).

The decline in wild Cheetah populations means that the animals which do survive originate from a less diverse gene pool. The genetic structure of Cheetah populations, compared to other felids, is markedly depleted in genetic variability (O'Brien *et al.*, 1983, 1985, 1987; Menotti-Raymond & O'Brien, 1993). Genetic uniformity may affect reproductive efficiency, infant mortality and disease susceptibility (O'Brien *et al.*, 1983, 1985, 1987; Wildt *et al.*, 1983, 1987, 1993; Evermann *et al.*, 1988; Marker & O'Brien, 1989; Heeney *et*

*al.*, 1990; Junge *et al.*, 1991; Marker-Kraus & Grisham, 1993).

#### HISTORY WITH HUMANS

The Cheetah, also called the 'hunting leopard', has the longest hunting association with humans of any animal, with the exception of the dog. The earliest record is from the Sumerians in c. 3000 BC where a leashed Cheetah, possibly with a hood on its head, is depicted on an official seal. The Cheetah was considered to be a goddess in early lower Egypt (Westendorf, 1966).

Cheetahs are the most easily tamed of all the big cats and, in the past, adults were caught, tamed and trained within a few weeks. Emperors kept hundreds of the animals in their stables at any one time. In the 5th century hunting with Cheetahs for sport, or coursing, occurred in Italy. In the 11th and 12th centuries Russian princes hunted with Cheetahs and Crusaders saw the species being used to hunt gazelles *Gazella* spp in Syria and Palestine. Marco Polo reported that hundreds of Cheetahs were kept by Kublai Kahn. Almost all Italian Renaissance courts had Cheetahs as did many of the French courts. Cheetahs were kept by royalty from Ethiopia to China in the 14th, 15th and 16th centuries (Guggisberg, 1975). Prior to the 1950s there is only one report of a litter born in captivity and that was in the 15th century at the Palace of Akbar, a Mogul emperor (Guggisberg, 1975).

Because of the continuous drain on wild populations Cheetahs declined throughout Asia. In the early 1900s India and Iran began to import Cheetahs from Africa for hunting purposes (Divyabhanusinh, unpubl.).

By the end of the 19th century Cheetahs were rare in Asia Minor and Arabia. In 1952 the species was declared extinct in India and in 1956 the last Cheetah was reported in Israel (Kraus & Marker-Kraus, 1992). The only confirmed reports of Asian Cheetahs are from Iran where up

to 200 occur in small isolated populations. Because of the disappearance of larger prey species these animals prey on rabbits (Kraus & Marker-Kraus, 1992).

#### CONSERVATION INITIATIVE FOR CAPTIVE CHEETAH

During the 1980s several conservation initiatives for Cheetah were established including: (1) the development of regional studbooks in North America (Marker, 1983), Japan (Hayashi, 1986) and Great Britain (McKeown, 1992); (2) the development of an international studbook in 1988 (Marker-Kraus, 1990a); (3) the inclusion of the species as a target animal of (a) the Species Survival Plan (SSP) of the American Zoo and Aquarium Association (AZA; formerly AAZPA) in 1984, (b) the European Endangered Species Programme (EEP) of the European Association of Zoos and Aquaria (EAZA), (c) the Australian Species Management Program (AMSP) of the Australasian Regional Association of Zoological Parks and Aquaria (ARAZPA), (d) the Species Survival Committee of the Japanese Association of Zoological Gardens and Aquariums (JAZGA) and (e) the African Preservation Programme (APP) of the Pan African Association of Zoological Gardens, Aquaria and Botanical Gardens (PAAZAB); (4) a Cheetah SSP Research Master Plan which involved implementing a multidisciplinary research programme, to provide a biological explanation for the relatively poor captive breeding (Grisham & Lindburg, 1988), including research in genetics, captive behaviour and husbandry, reproductive physiology, disease and nutrition (Howard *et al.*, 1992, 1993; Brown *et al.*, 1993; Caro, 1993; Dierenfeld, 1993; Evermann *et al.*, 1993; Laurenson, 1993; Lindburg *et al.*, 1993; Marker-Kraus & Grisham, 1993; Munson, 1993; Wildt & Grisham, 1993; Wildt *et al.*, 1993; O'Brien, 1994). These programmes, in conjunction with the IUCN's Conservation Breeding Specialist

Group (CBSG), are working to manage the captive population.

An important aspect of a species conservation programme is the development of a demographic and genetic profile of the captive population. The international studbook, first published in 1989 and updated annually (Marker-Kraus, 1990a,b, 1991, 1992, 1993, 1995, 1996), contains detailed records of all captive Cheetahs. Much of the historic information was collected by M. Jones who between 1951 and 1982 visited zoos world-wide and recorded information on Cheetah and other species (McKeever, 1994). This information, with data submitted by zoos and ISIS, has allowed for detailed analysis of the captive population. There are 3381 Cheetahs registered in the international studbook and 673 other animals known from historical records.

Between 1829 and 1994 over 1567 Cheetahs were imported from the wild and exhibited at more than 373 facilities. There were 2517 captive births and 3472 deaths during this time.

#### THE CAPTIVE CHEETAH POPULATION 1829–1954

The earliest record of a Cheetah in a zoological collection is in 1829 at The Zoological Society of London (Marker-Kraus, 1990a). This animal lived less than 1 year. Cheetahs were not exhibited again until 1851 at Antwerp, 1852 at Berlin ZG, 1860 at Frankfurt and 1863 at Hamburg. In 1871 Cheetahs were first exhibited in North America at Central Park Zoo, New York. Between 1851 and 1900 only 14 zoos exhibited Cheetahs. Other early facilities holding Cheetah include Cairo in 1900, Basel Zoo in 1910, National Zoo in Washington in 1913, Chicago Lincoln Park in 1914 and St Louis Zoo in 1929.

Between 1829 and 1954 139 wild-caught Cheetahs were exhibited at 47 facilities (Table 1). Most of these animals only survived for up to 1 year and in this period there were 115 deaths and no births.

	1829– 1854	1855– 1879	1880– 1904	1905– 1929	1930– 1954
Imports	5	1	19	25	89
Deaths	2	1	10	29	73
Animals at start/end of period <sup>1</sup>	1				32

<sup>1</sup>In 1829 one Cheetah was kept at London Zoo and in 1954 32 Cheetahs were held at 18 institutions.

**Table 1. Number of importations and deaths in the captive Cheetah *Acinonyx jubatus* population between 1829 and 1954; data are as at 31 December for each period.**

Although several European zoos began exhibiting Cheetah in the late 1800s and early 1900s the species was rarely seen in North American zoos until the 1950s, after which they became one of the major animal exhibits in both Europe and North America (Marker-Kraus, 1990a). As at 31 December 1954 32 Cheetahs were exhibited at 18 facilities.

#### THE CAPTIVE CHEETAH POPULATION 1955–1994

Between 1955 and 1994 1440 Cheetahs were imported to zoological collections (Table 2). Cheetahs were exported from East Africa, Kenya and Somalia until the late 1960s when they became scarce in these areas (Marker-Kraus, 1990a). Since the 1960s Cheetah have been exported primarily from Namibia (Marker-Kraus, 1990a). The captive population increased from 33 animals in 1955 to 1218 in 1994 (Fig. 1; Table 2). During this time there were 3436 deaths.

Before 1973 the increase in the captive population was primarily the result of importation (Fig. 2); between 1955 and 1973 there were 549 imports but only 108 births (Table 2). In 1974 84 Cheetahs were imported which represented 21% of the total captive population for that year (Fig. 2; Table 2). This was the last large importation of wild-caught Cheetahs because in 1975 CITES legislation resulted in a reduction in the number of imports allowed (CITES, 1984).

From 1973 the number of captive births steadily increased with the exception of two temporary declines in 1977 and 1987 (Fig. 2; Table 2). From 1980 to 1994 (not including 1987) 30 or more litters were born per year. Between 1955 and 1994 2517 cubs were born in 759 litters at 96 facilities (Table 2).

The increase in the captive population was a result of captive breeding, co-operative management programmes and importation from the wild. As at 31 December 1994 the captive population was 1218 (612,606) of which 880 (72%) were captive-bred and 338 (28%) were wild-caught. These Cheetahs were housed at 211 facilities in 47 countries in eight geographical regions (Table 3).

#### REPRODUCTION

In 1956 the first authenticated captive birth occurred at Philadelphia Zoo and this pair had a second litter in 1957. Births are also recorded in 1960 at Krefeld, 1962 at Oklahoma and 1967 at Whipsnade. Of 373 facilities which have housed Cheetah only 96 (26%) have reported successful reproduction. Captive births increased gradually until 1974 when 15 collections bred the species, representing 19% of the facilities holding Cheetahs at that time. It is possible that the increase in breeding in 1974 and 1975 was a result of the high number of wild-caught animals imported at that time ( $n=128$ ) which represented 30% of the captive population in 1975

YEAR	IMPORTS	LITTERS	NO. BORN	DEATHS			NO. ANIMALS	NO. INSTIT.	NO. INSTIT. WHICH BRED
				TOTAL	≤ 30 DAYS	≥ 1 YEAR			
1955	4			3			33	29	
1956	6	1	3	11	3	3	45	30	1
1957	8	1	2	6		2	52	33	1
1958	10			5			68	43	
1959	13			17			75	48	
1960	11	1	4	12	2	2	91	51	1
1961	6			4			89	53	
1962	37	2	5	19	5	5	153	102	1
1963	17	1	2	23	2	2	165	75	1
1964	30			21			206	92	
1965	36			18			215	87	
1966	40	2	4	31			276	112	1
1967	46	1	3	26		1	260	103	1
1968	27	2	6	38	1	1	156	57	2
1969	39	1	2	10			184	64	1
1970	90	5	11	30	2	2	238	66	4
1971	38	5	14	39	4	5	264	71	5
1972	34	5	16	33	2	2	304	76	5
1973	57	12	36	40	3	7	328	79	9
1974	84	23	86	117	24	48	401	80	15
1975	44	28	102	135	19	31	423	87	16
1976	57	28	106	107	26	33	503	98	14
1977	66	18	58	58	10	11	573	107	11
1978	49	25	80	87	17	22	625	108	14
1979	37	23	66	80	13	20	658	117	13
1980	34	35	113	144	39	51	711	127	16
1981	21	30	96	147	28	38	718	138	18
1982	40	33	111	169	35	58	760	137	19
1983	43	30	115	160	17	39	788	142	15
1984	28	33	120	157	14	46	848	150	21
1985	40	36	97	170	17	36	856	152	19
1986	54	34	112	165	23	33	879	159	17
1987	29	24	79	124	12	17	885	170	14
1988	59	37	120	163	25	36	940	179	15
1989	32	42	136	186	34	39	953	174	23
1990	31	38	128	206	19	29	930	165	24
1991	27	48	172	166	31	43	1040	184	25
1992	31	56	181	208	44	61	1119	192	29
1993	44	56	192	170	32	46	1168	204	32
1994	41	43	139	131	34	37	1218	211	21
TOTAL	1440	759	2517	3436	537	806			

Table 2. Population growth of the captive Cheetah population 1955–1994.

(Table 2). In 1993 16% of facilities bred Cheetah, although by 1994 only 10% reported breeding success.

Most breeding has occurred at a few zoos. Over 45% ( $n=44$ ) of facilities which have bred Cheetah have had limited success over a brief period with a particular

♂ or ♀ or both. Forty facilities (42%) have bred for only 1 or 2 years and since 1990 44 facilities (46%) have not bred and half of these no longer hold the species. Of the facilities which have bred Cheetah 52 (54%) have continued to breed in the

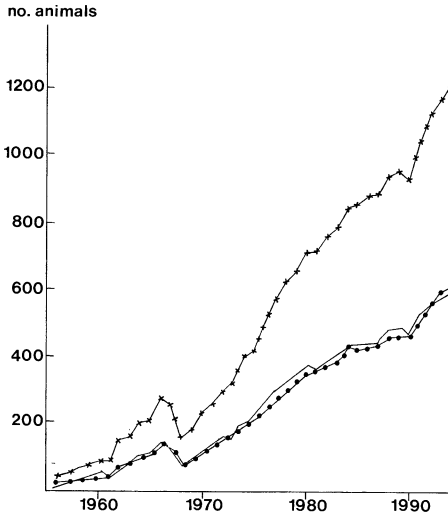


Fig. 1. Number of Cheetahs *Acinonyx jubatus* in 373 facilities from 1955 to 1994; crosses total; dots ♂♂; line ♀♀.

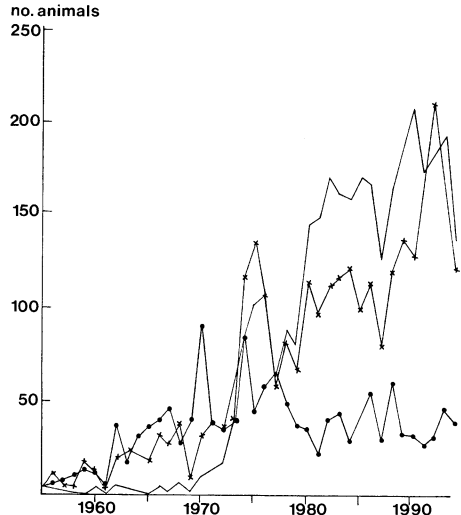


Fig. 2. Time course of dots imports, line captive births and crosses deaths of Cheetahs between 1955 and 1994.

1990s and 25 only began breeding in the 1990s.

Fourteen facilities (15%) have had continuous breeding success and have produced more than 50 cubs each with multiple sires and dams, producing 63% ( $n = 1580$ ) of all cubs born in captivity. All of these facilities have continued to breed in the 1990s.

Since 1956 594 (298.296) animals have bred successfully, of which 308 (156.152) were wild-caught and 286 (142.144) were captive-born. Analysis of breeding

animals has revealed that: (1) the mean number of litters was 2.67 for each breeding animal (range 1–14); (2) the mean number of cubs per breeding animal was 9.07 (range 1–53) (Table 4). Using a two-tailed *T*-test assuming equal variance is applied, there is no statistically significant difference in these parameters when wild-caught breeding animals, past and present, are compared to captive-born breeding animals.

The age distribution of all breeding animals by sex for first and last litters is

REGION	% CAPTIVE POPULATION	NO. ANIMALS	NO. COUNTRIES	NO. FACILITIES
Southern Africa	28	168.171	4	37
North America	27	174.149	2	48
Europe	23	134.146	17	72
Far East	10	59.61	8	16
United Kingdom	6	37.38	3	15
Central and South America	3	14.21	4	9
North-East Africa, Middle East and India	2	14.16	7	9
Australia and New Zealand	1	12.4	2	5
TOTAL		612.606	47	211

Table 3. Regional distribution of the captive Cheetah population as at 31 December 1994.

given in Fig. 3. Age at first litter for wild-caught and captive-born animals ranges between 18 months and 15 years (Table 4). For both sexes most successful breeding occurs between 3 and 9 years of age (Figs 3 and 4). These data are relevant in assessing the age structure of the captive population (Fig. 5). As at 31 December 1994 179 animals (15%) were over the optimal reproductive age ( $\geq 10$  years old), 765 (63%) were between 3 and 9 years old and 274 (22%) were sub-adults. Of the 203 (102.101) breeding animals alive as at 31 December 1994 29% (59) were over the optimal reproductive age ( $\geq 10$  years) (Fig. 6).

The mean age for first litters was 4.85 years for ♀♀ and 5.18 for ♂♂. The average age at last litter for both ♂♂ and ♀♀ was 6.96 years (Table 4). Using a two-tailed *T*-test assuming equal variance is applied, wild-caught breeding ♂♂ and ♀♀, past and present, were compared to captive-born breeding ♂♂ and ♀♀. A significant difference ( $P \leq 0.05$ ) was found in the age at first litter for ♀♀ and the age of last litter for ♂♂. The mean age at first litter for wild-caught ♀♀ was 5.06 years, compared to 4.64 years for captive-born ♀♀ ( $P = 0.015$ ). Also of significant difference was the age of last litter for wild-caught ♂♂, 7.67 years, compared to 6.38 years for captive-born ♂♂ ( $P = 0.002$ ). These differ-

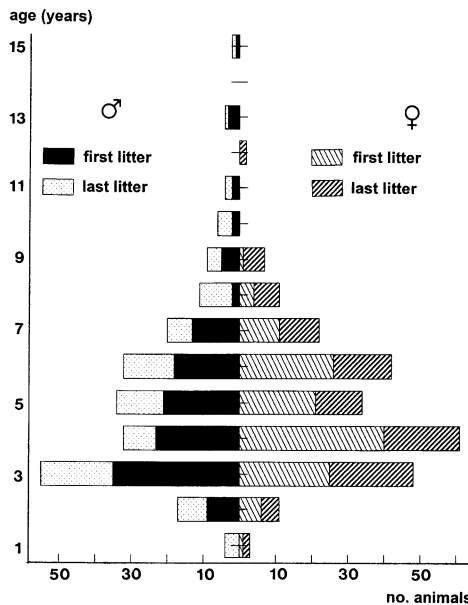


Fig. 3. Age distribution of successfully breeding ♂♂ and ♀♀ Cheetahs at first and last litters.

ences may be the result of the estimated ages of wild-caught animals; because of their living conditions, wild-caught Cheetahs may appear older than captive-born animals of the same age. However, these data may be significant and further investigation is necessary.

In 1994 only 35.39 Cheetahs actually bred although there were 102.101 proven

	WILD ♂	CAPTIVE ♂	WILD ♀	CAPTIVE ♀
Age at first litter				
Range	<2–15	2–15	<2–13	<2–9
Mean	5.33	5.04	5.06	4.64
Age at last litter				
Range	<2–15	1–15	2–13	<2–13
Mean	7.67	6.38	7.16	6.65
No. litters				
Range	1–14	1–13	1–9	1–8
Mean	2.77	2.63	2.62	2.66
No. cubs				
Range	1–53	1–40	1–28	1–32
Mean	9.42	8.92	8.72	9.25

Table 4. Mean age at first and last litter and number of litters and cubs for captive and wild-caught Cheetah 1956–1994.



YEAR	NO. CHEETAHS WHICH BRED SUCCESSFULLY DURING YEAR	NO. PROVEN BREEDERS ALIVE AT END OF YEAR	$N_e$ (%)
1955			
1956	1.1	1.1	4
1957	1.1	1.1	4
1958		1.1	3
1959		1.1	2
1960	1.1	1.1	2
1961		1.1	2
1962	1.1	2.2	3
1963	1.1	2.2	2
1964		2.2	2
1965		2.2	2
1966	1.1	2.2	1
1967	1.1	2.2	2
1968	2.2	1.2	2
1969	1.1	2.3	3
1970	4.4	2.4	2
1971	5.5	4.5	3
1972	5.5	5.7	4
1973	10.10	12.15	8
1974	19.15	15.19	8
1975	21.20	23.26	12
1976	16.17	27.31	12
1977	16.17	29.21	9
1978	17.21	31.35	11
1979	16.20	32.38	11
1980	25.31	38.49	12
1981	23.26	49.53	14
1982	25.27	43.61	13
1983	27.30	48.65	14
1984	27.33	48.71	14
1985	25.30	48.72	14
1986	24.30	47.68	13
1987	15.19	40.63	11
1988	26.31	39.65	10
1989	32.36	45.71	12
1990	28.35	52.72	13
1991	37.47	64.86	14
1992	45.53	88.102	17
1993	46.45	110.116	19
1994	35.39	105.103	17

**Table 5.** Number of Cheetahs which bred successfully each year and the number of proven breeders alive at the end of each year between 1955 and 1994. Effective breeding size for the population ( $N_e$ ) is given as a percentage of the captive population.

breeding animals alive; that is animals that had successfully produced cubs at least once (Table 5). These values permitted the calculation of an effective breeding size ( $N_e$ ) for the population using the formula:

$$N_e = (4 \times M \times F) \div (M+F) = 202.9$$

where M is the number of breeding ♂♂ and F is the number of breeding ♀♀.  $N_e$  is equivalent to 17% of the captive population. Over the past 40 years, although the number of Cheetah births has risen,  $N_e$  has only increased gradually and was higher in 1993 (110.116 proven breeders,  $N_e = 225.8$ , 19% of total population in 1993,  $n = 1168$ ) (Table 5). The chronically low  $N_e$  indicated that the captive population falls well below the accepted definition of a viable population (Soulé *et al.*, 1986).

#### SURVIVORSHIP AND MORTALITY

The growth pattern of a population is derived from the combination of reproduction and relative survival. Cheetah mortality has increased gradually over the 40 years since captive breeding began and clearly correlates with population growth (Figs 1 and 2). An analysis of age at death indicated that the most vulnerable age was 0–1 month old, (25% of all deaths) (Fig. 7). After the age of 2 years there is a clear demarcation between the age of death for wild-caught animals and captive-bred animals.

The combined incidence of infant mortality in captive-born animals between 1956 and 1994 was 21% at 1 month and 28% at  $\leq 6$  months of age. These are high values compared to other non-inbred zoo species (Ralls & Ballou, 1982; O'Brien *et al.*, 1985). Infant mortality varied widely among institutions (0–100%) and also between years (Table 2). The high incidence of infant mortality may be the result of an ancestral genetic homogenization event that purged large portions of genetic variation from the species (O'Brien *et al.*, 1985, 1987; Menotti-Raymond & O'Brien, 1993) and captive husbandry problems (Lindburg, 1991; Caro, 1993; Laurenson, 1993; Lindburg *et al.*, 1993). In captive-born animals mortality after the first year was almost equally distributed from 2 to 13 years of age. With few exceptions, mortality in wild-caught animals was almost

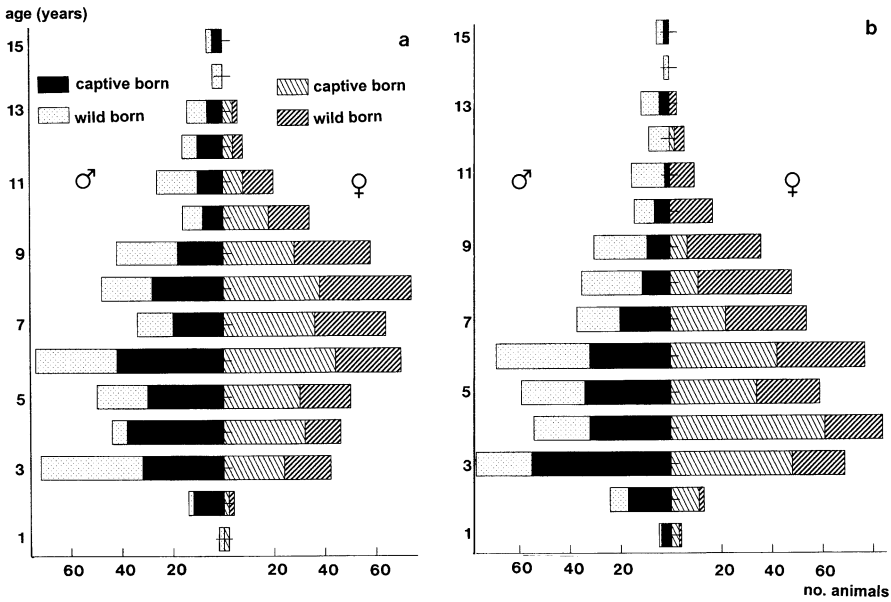


Fig. 4. Age distribution of successfully breeding Cheetahs at a. first litter and b. last litter.

equally distributed from 2 to 17 years of age. This could suggest that once wild Cheetahs survive to an age when they can be brought into captivity they live over 4 years longer than captive-born animals. However, the age of wild-caught animals is seldom known and no allowance has been made any inaccuracies in estimating age. All dates refer to the time between arrival in captivity and the date of death, thus longevity for wild-caught animals only gives a reference of life span in captivity.

Comparing age of death for all animals from 1829 to 1994 (Fig. 7) and age at death in 1994 (Fig. 8) reveals that longevity has increased. The mean age at death calculated for all animals was 6.1 years, with wild-caught animals at 8.2 years and captive-born animals at 4.5 years. Mean age at death calculated for all animals over 1 year of age was 8.3 years, with wild-caught animals at 8.4 years and captive-born animals at 8.0 years. Using a two-tailed *T*-test for both of these parameters there was no statistically significant difference.

At London Zoo between 1930 and 1960 45% of all Cheetahs survived less than 1 year. Mean longevity for Cheetahs which survived the first year was 3 years and 9 months. Maximum life span for a Cheetah at this time was 8.5 years. In 1976 a survey conducted by Amsterdam Zoo revealed that longevity in captivity had increased. Between 1947 and 1966, 74% of Cheetahs died before 5 years of age whereas between 1967 and 1974, only 44% died before 5 years of age. Although this suggests that longevity had increased between 1967 and 1974 only 21% of the captive Cheetah lived for 10 years. Between 1829 and 1994 931 animals (23%) of the registered and known Cheetahs in captivity ( $n = 4054$ ) lived over 10 years. At time of writing the longevity record for a captive Cheetah is 21 years of age and 56 animals have lived over 17 years.

Post-mortem reports and information from individual institutions reported causes of death for 1630 animals of which 364 (22%) represented mortality in animals under 6 months old. In cubs under 1 month old the main causes of

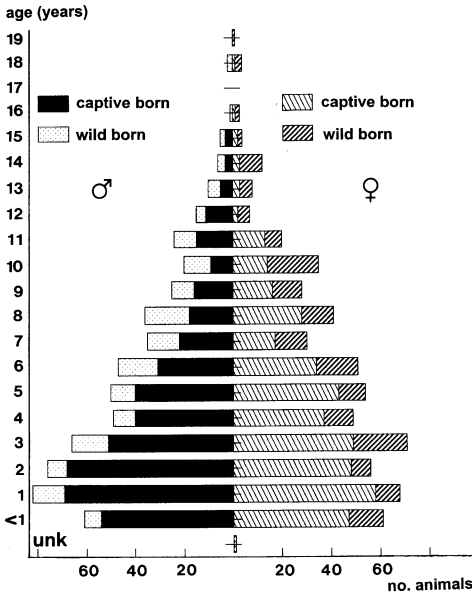


Fig. 5. Age distribution of the captive population of Cheetahs as at 31 December 1994.

death were undetermined or miscellaneous (24%), and still births (20%) (Table 6).

The predominant causes of death in animals over 6 months old ( $n = 1266$ ) were kidney disease (15%) and gastro-intestinal disorders, including enteritis, *Escherichia coli* and colitis (9%), which have only recently been identified as major problems in captive Cheetah (Munson, 1993) (Table 7). Feline infectious peritonitis (FIP), a fatal coronavirus disease, was responsible for 6% of deaths. FIP is difficult to diagnose and, although it may have been present earlier, it was not recognized until 1982 (Pfeifer *et al.*, 1983, O'Brien *et al.*, 1985; Evermann *et al.*, 1988). A common symptom of FIP is kidney and/or liver disease which account for 21% of mortality in captive Cheetah. Surveillance of this virus has continued and the number of sero-positive Cheetah in the North American population has increased from 35% in 1989 to 60% in 1990 (Evermann & McKeirnan, 1991; Grisham & Killmar, this volume).

FOUNDERS AND PRESENT GENETIC STRUCTURE

Of the 1579 wild-caught Cheetahs that were imported between 1829 and 1994, 308 (20%) reproduced and 155 of these have living descendants. Of 2517 captive-born animals, 1208 reached reproductive age and 286 (24%) of these have bred. The breeding frequency of captive-bred animals (24%) versus wild-caught (20%) animals suggests that subsequent generations of captive-bred Cheetahs should breed as well if not better than their wild-caught progenitors.

All founders in the current captive population are from the southern African subspecies *Acinonyx jubatus jubatus*, except 3.4 East African Cheetahs *Acinonyx raineyi*. Two East African founders have not contributed to the captive population because none of their offspring have survived. The other five have bred and in 1994 there were numerous hybrids in the population. Over the last few years the representation of two of the East African founders, stdbk no. 333 and stdbk

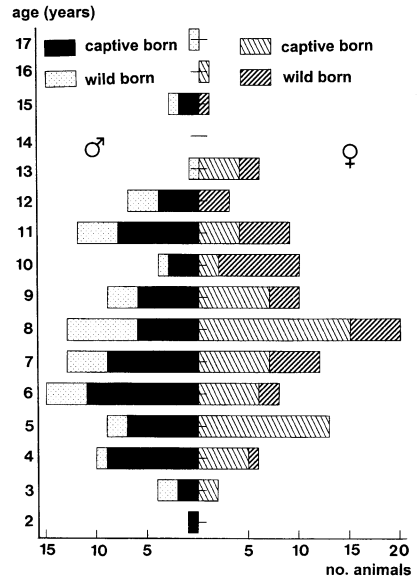


Fig. 6. Age distribution of proven breeding Cheetahs living as at 31 December 1994.

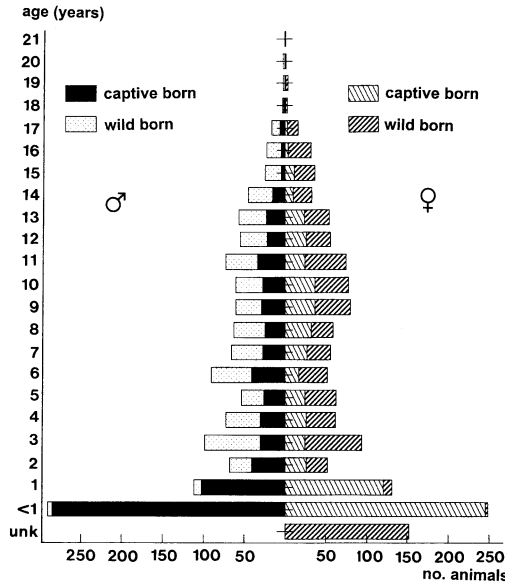


Fig. 7. Age distribution of mortality in cheetahs between 1829 and 1994.

no. 353, has increased in Europe and North America.

Between 1990 and 1994 27 (10.17) hybrids produced 190 cubs, 24% of births for that period. Hybrids represent 13% of the breeding population. Using a two-tailed *T*-test to compare the reproductive success between hybrids and the southern African subspecies revealed a significant difference between the total number of cubs born to hybrids ( $P \leq 0.009$ ) although there was no significant difference in rates of infant mortality.

Between 1990 and 1994 32% of cheetahs which bred were wild-caught. During this period 174 wild-caught animals were imported of which 71 (41%) have bred which indicates that the animals imported more recently have bred more successfully than those imported earlier.

Of the 308 wild-caught animals that have bred only 155 were represented in the 1994 population. Although the 1994 captive cheetah population contained a large number of founders ( $n = 424$ ), 269 of these are wild-caught animals that are alive and have not yet produced offspring.

Of 338 wild-caught animals alive in the captive population in 1994 only 69 (20%) are proven breeders.

Between 1990 and 1994 812 cubs were born which represents 32% of total births between 1956 and 1994 (Table 2). A relatively small number of cheetahs have made a disproportionately large contribution to the 1994 population gene pool: of the 812 young born eight ♂♂ sired 173 (21%) and 12 ♀♀ produced 195 (24%) of the cubs.

#### REGIONAL CAPTIVE BREEDING

Southern Africa and North America have both produced about 30% of cubs while Australia and New Zealand, and North Africa (Morocco) only produced 2% collectively (Table 8). Regional breeding success is important in relation to the number of animals actually living in the population (Table 3). In 1994 28% of the captive population was in southern Africa, most of which were wild-caught. North America maintained 27% of the population, 98% of which was captive-born. The higher breeding success in North

America may be attributed in part to the SSP co-operative management programme which was developed in 1984 (Grisham, this volume).

Within each region there has been at least one facility that has had particular breeding success. In southern Africa, the DeWildt Cheetah Breeding and Research Centre has produced the most cubs ( $n=395$ ) 16% of all births and 57% of cubs born in the region (Table 9). The success of particular facilities could be related to the large enclosures provided for animals which may reduce stress levels and increase the chances for successful breeding (see also Beekman *et al.*, this volume; Bircher & Noble, this volume). These facilities also hold large numbers of animals, which may allow for more opportunity for mate choice and other social factors which influence breeding (Table 9).

Regional breeding success should be monitored to facilitate co-operation between institutions and the transfer of animals within regions. One region may have greater founder representation than

CAUSE OF DEATH	NO. ANIMALS	% TOTAL MORTALITY
Mortality < 30 days	89	24
Stillborn	72	20
Eaten by adult	68	19
Maternal neglect	60	17
Nutritional deficiency	25	7
Congenital defect	19	5
Exposure	14	4
Aggression	9	2
Trauma	8	2

Table 6. Reported cause of death in captive Cheetah < 6 months of age ( $n=364$ ) between 1829–1994.

another and over-represented animals in one region may be extremely important in others.

Outbreeding within the present population should be optimized in order to mask the potential deleterious physiological effects of inherent inbreeding (Marker & O'Brien, 1989). This strategy could be extended by the introduction of new animals of different genetic lineages, preferably from the present captive population.

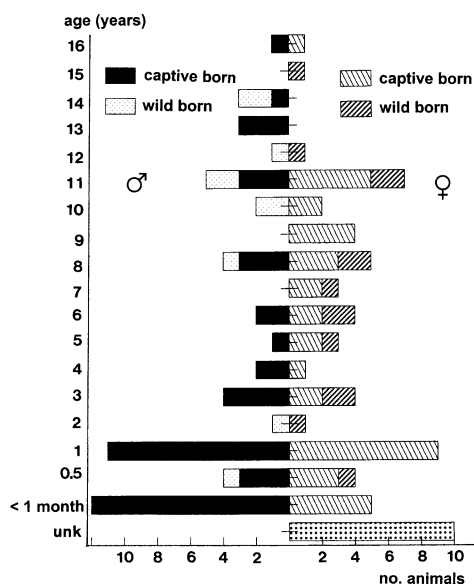


Fig. 8. Age distribution of mortality in Cheetahs in 1994.

## DISCUSSION

Despite an overall increase in the captive Cheetah population the age/sex distribution is not stable and the effective population size ( $N_e$ ) is low. The captive population is in need of a global-demographic and genetic-management programme. The critical objectives of this programme are equalizing founder representation and stabilizing the age/sex distribution within the captive population which, without a stable age distribution, could fluctuate detrimentally (Foose, 1980, 1983).

Although management of Cheetahs has improved and captive breeding has increased in 1994 only 10% of facilities bred the species, compared with 14% in 1984. Because 14 institutions have produced 63% of all cubs a disproportionate number of founders are represented. Therefore, there is a substantial need to

CAUSE OF DEATH	NO. ANIMALS	% TOTAL MORTALITY
Kidney disease	184	14
Gastro-intestinal (incl. enteritis, <i>Escherichia coli</i> , colitis)	109	9
Trauma (incl. accidents, ruptures)	98	8
Respiratory (incl. pneumonia, lung diseases)	95	7
Liver (incl. hepatitis, veno-occlusive disease)	78	6
Feline infectious peritonitis	74	6
Miscellaneous	69	5
Infection	67	5
Senescence	52	4
Panleucopaenia	48	4
Euthanasia/unknown	47	4
Unknown	46	4
Aggression	41	3
Heart	30	2
Muscular/skeletal	28	2
Liver/kidney disease	26	2
Cancer	26	2
Peritonitis	21	2
Poison/toxin	21	2
Nutritional deficiency	18	1
Pancreatitis	16	1
Parasites	15	1
Central nervous system	12	1
Tuberculosis	12	1
Spleen	9	1
Tumour	9	1
Haemorrhage	8	1
Anaemia	7	1

**Table 7. Reported cause of death for captive Cheetah > 6 months of age ( $n = 1266$ ) between 1829-1994.**

continue enhancing management to ensure optimal captive breeding.

Inherent genetic impoverishment and husbandry problems contribute to the low  $N_e$  (17%) in the captive population. The only way to improve the  $N_e$  is to increase the size of the breeding population. This should not affect the remaining free-ranging populations and it is recommended that new blood lines are obtained from captive-born animals instead of from the wild. Breeding facilities should cooperate to assist the movement of animals internationally.

Since the first captive birth in 1956, half the breeding founders or their offspring have died, but because of the importation of wild-caught animals potential founder numbers have increased by 116 animals in the 1994 population. These potential founders have a wide genetic background (Namibia, South Africa, East Africa and Zimbabwe) and could contribute a maximum amount of the existing genetic diversity to future offspring. However, equalizing founder representation is critical for optimal genetic management. Certain Cheetahs are disproportionately represented and a management plan should recommend that the more prolific Cheetahs be replaced with previously unrepresented lineages. The captive Cheetah population is grouped into small sub-populations in different countries. It is possible and highly preferable to out-breed with these other populations to reduce the possibility of inbreeding. This may be achieved by co-ordinated transfers between regions or by using artificial reproduction strategies (Caldwell & Howard 1991; Howard *et al.*, 1992; Grisham, this volume; Wildt & Roth, this volume). Such recommendations can only be made after a systematic and thorough analysis of the objectives and realities of an international co-operative genetic-management programme.

In recent years, Great Britain, the Netherlands and South Africa have been the primary importers of wild Cheetahs. More emphasis should be placed on transferring potential founders between regions; for example, Cheetahs in the North American population could be exported to other regions which may create new bloodlines. If institutions collaborate in (1) the managed reproduction of Cheetahs and (2) animal transfers that facilitate breeding priorities, then greater reproductive success may be achieved.

Although a few facilities have had significant breeding success the captive population is not self-sustaining and is being maintained through importation of

REGION	NO. CUBS	NO. LITTERS	NO. FACILITIES	YEARS BREEDING
North America	753	224	32	1956-1994
Southern Africa	696	232	13	1970-1994
Europe	528	149	29	1960-1994
United Kingdom	321	86	10	1967-1994
Far East	181	61	7	1980-1994
Australia/New Zealand	23	10	3	1976-1993
N.E. Africa/Middle East/ India	15	5	2	1976-1983

**Table 8. Regional breeding success of captive Cheetah between 1956 and 1994.**

wild-caught animals, which goes against the current goals of zoological institutions and zoo associations. The number of cubs born cannot be used as the sole measure of reproductive success and the reproduction of those offspring must also be considered.

Captive-management guidelines and husbandry recommendations for breeding Cheetah, based on empirical observations from many facility managers, have been developed (Grisham, 1992). Additionally, recent success in assisted reproduction in Cheetahs suggests that techniques such as artificial insemination and the utilization of germ plasm rather than the transfer of living animals will be of great benefit to both practical and genetic management (Howard *et al.*, 1992; Wildt & Roth, this volume).

Reviewing the management strategies at facilities that report breeding may assist

reproductive success at other facilities. Larger enclosures and a higher number of animals held at a collection may contribute to breeding success. Institutions that do not have the space or resources to meet these criteria could exhibit animals that are not suitable for breeding purposes, such as those which are too old or too young for breeding, over-represented animals and ♂ groups which should be kept together for breeding purposes in the future. Genetically valuable animals should be moved to proven breeding facilities thus allowing greater opportunity for reproductive success.

As the free-ranging Cheetah population continues to decline and as genetic diversity of the remaining population diminishes, the captive and wild populations should be co-operatively managed. In the absence of further importations from the wild, the size of the captive population

REGION (NO. FACILITIES)	TOTAL NO. CUBS BORN IN REGION	FACILITY	NO. CUBS BORN AT FACILITY	%	
				TOTAL BIRTHS	CUBS BORN IN REGION
Southern Africa (13)	696	DeWildt SA	395	16	57
		Winston USA	127	5	17
North America (32)	753	San Diego WAP USA	106	4	14
		Whipsnade GB	132	5	41
United Kingdom (10)	321	Fota Ire	104	4	33
		Wakayamaken Jap	79	3	43
Far East (7)	181	Himeji Jap	78	3	43

**Table 9. Specific breeding success of Cheetah at particular facilities on a regional basis between 1956 and 1994.**

could be expected to decline unless there is further improvement in captive breeding. This trend, coupled with the continuing decline of the wild population, leaves the species extremely vulnerable. With the expanding database on husbandry and genetic management combined with international co-operation, the future of the captive population appears promising. A global-management programme will be a critical component for the long-term survival of the species.

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## Breeding and observations on the behaviour of Cheetah *Acinonyx jubatus* at Wassenaar Wildlife Breeding Centre

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The Wassenaar Wildlife Breeding Centre was formerly a part of Wassenaar Zoo but has been an independent institution since 1984. The Centre, which is not open to the public, has established a breeding protocol for Cheetah *Acinonyx jubatus* which has resulted in 58.54 births since 1980. This paper describes the husbandry and breeding of Cheetahs and the development of cubs. Behavioural comparisons on Cheetahs at Wassenaar and five other institutions, and observations on the behaviour of two ♀♀ and the breeding behaviour of one ♂ are also described.

*Key-words*: captive felid management, cheetah, feline reproduction

In 1937 the private collection of P. W. Louwman was officially opened to the public as Wassenaar Zoo and in 1983 the Zoo was given semi-governmental status. In 1984 Wassenaar Wildlife Breeding Centre, formerly an off-exhibit part of the

Zoo, became an independent institution. In 1985 the Zoo was closed but the Centre remained unaffected.

The Wassenaar Wildlife Breeding Centre specializes in breeding threatened species, particularly those that need a quiet and undisturbed environment. Because there is no visiting public the visibility of the animals does not need to be considered and enclosures can be designed to provide optimal living conditions. The Centre also provides holding facilities for animals until they can be placed elsewhere.

As an increasing number of species become threatened in the wild, captive breeding, via co-ordinated breeding programmes, has become a valuable conservation tool. Furthermore, some animals which are born in captivity can be rein-