

Research Article

Reproductive Life History of South African Cheetahs (*Acynonyx jubatus jubatus*) at the San Diego Zoo Wild Animal Park, 1970–2005

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We analyzed 35 years of data from a captive breeding program of cheetahs to determine basic reproductive life history characteristics of females. Breeding females ranged in age from 2.7–10.5 years. Sixteen females and over 13 males produced 129 cubs in 36 litters, with an average litter size of 3.6. Older females produced significantly fewer cubs per litter than younger females, but cub survivorship was comparable across female ages. Sex ratio was balanced at birth and 71% of infants survived the weaning period. Given that the reproductive output of captive cheetahs in our study is similar to that in other zoologic institutions and to cheetahs in the wild, we suggest that reproductive deficits in captive cheetahs arise from the inability of some pairs to breed, due to a lack of mating preference, rather than from a species-wide problem. *Zoo Biol* 25:383–390, 2006. © 2006 Wiley-Liss, Inc.

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INTRODUCTION

Monitoring the reproductive performance of cheetahs in the wild is problematic due to their life history strategy of bearing litters in lairs [Laurenson, 1993; Caro, 1994]. Using lair surveys taken about 2 weeks after birth, coupled with cub counts at emergence, showed an average litter size of 3.5 cubs among Serengeti cheetahs [Caro, 1994; Kelly et al., 1998]. Litter size is fairly consistent across locations, with an average of 3.1 cubs per litter reported for Namibian cheetahs [Marker-Kraus et al., 1996] and 3.5 cubs per litter reported for captive cheetahs [Wack et al., 1991; Marker-Kraus and Grisham, 1993]. The year 2002 was unusual among zoologic institutions because the average litter size (2.7) was lower than in previous years [Marker 2005].

The reproductive success of cheetahs seems to be a function of age, with both litter size and survivorship prospects greatest among five to seven year old females [Kelly et al., 1998]. In general, reproduction commences when cheetahs are about 3 years of age and most cheetah females do not live beyond 7 or 8 years of age in the wild [Kelly et al., 1998]. Most successful breeding in captivity occurs when cheetahs are between 3–10 years of age [Marker-Kraus et al., 1996]. Sex ratio within litters has not been subjected to systematic analysis. The overall sex ratio across litters in captivity is not sex-biased [Marker-Kraus and Grisham, 1993], although the year 2002 witnessed a preponderance of male cubs (63%) [Marker 2005]. In general, about 70–75% of cubs born in captivity survive their first 6 months of life compared to about 30–60% survivorship of cubs in the Serengeti [Caro, 1994; Kelly et al., 1998].

We examine the reproductive performance of captive South African cheetahs over a 35-year period. Our retrospective analysis was aimed at evaluating the outcome of a long-term cheetah breeding program in an effort to guide future breeding plans.

MATERIALS AND METHODS

Study Site and Subjects

The San Diego Zoo Wild Animal Park (SDWAP) was opened to the public in May 1972. However, exotic animals had been maintained in the area for breeding before that date, so the South African cheetah breeding records extend to 1970. The SDWAP has only maintained South African cheetahs (*Acynonyx jubatus jubatus*) in the breeding program. The breeding cheetah population is kept in an off-exhibit area, now known as the Behavioral Biology Research Station, adjacent to the main park. The facility is located on the edge of natural chaparral habitat. Cheetahs live in outdoor, cyclone fence enclosures, each measuring approximately 16 m² and containing natural vegetation, such as grass, shade trees, bushes, etc., as well as shelter areas. The pens are adjacent to each other and connected by a cyclone fence walkway that facilitates animal introductions for breeding and capture for husbandry and maintenance. All females live alone, but have visual, auditory, and olfactory contact with other cheetahs. The keeper staff services the cheetahs by entering the pen to feed, clean, mow, and do pen maintenance while the cheetahs remain in the pen.

Protocol for the Breeding Program

A systematic breeding protocol was implemented in 1985. Before that time period, behavioral data were not regularly recorded and matings were more opportunistic. In some cases, both sexes of cheetahs were enclosed together, so only some sires are known. Beginning in 1985, systematic efforts were undertaken to obtain reliable information on cheetah breeding activity. We have accurate data from 29 females and 24 males housed at the SDWAP during the study period.

Breeding introductions occurred when either a male or a female acted in a manner indicating sexual arousal. Male behaviors, such as “stutter-barking” [Wielebnowski and Brown, 1998], that could indicate the presence of a receptive female were used as cues to female reproductive state. In addition, when females displayed activities that indicated probable estrus, e.g., rolling, rubbing, sniffing, urine spraying, vocalizing (e.g., “meow-chirp,” “growl”), approaching a male at a fence line [Wielebnowski and Brown, 1998], they were placed into the breeding protocol. Breeding protocol involved moving the target female from her pen into an empty pen. The first of multiple possible partners was then given access to her unoccupied pen for 15 min to enable him to olfactory investigate and scent mark the area. If the male subject developed an erection, or emitted a stutter bark, then he would be introduced to the female. They would be paired for up to 30 min, at which time they would be separated if no breeding occurred. If breeding did occur, then the pair would be separated and returned to their own pens. No further breeding using the female would be attempted for at least 3 months to establish paternal certainty. If the male displayed no sign of sexual arousal after pairing with the female, then he would be returned to his pen and a second male subject would then be brought to the female’s original pen. The procedure would continue until all available males had been given an opportunity to breed. Females would be placed with up to three consecutive breeding partners per protocol. If none of the breeding protocols were successful, then the female would resume breeding protocol either when she was next observed in a possible state of estrus or when a male indicated sexual interest in her. Descriptive statistics regarding the number of partners per breeding attempt and the number of estrous cycles per pregnancy cannot be calculated using currently available data.

Database and Statistical Analyses

We considered a breeding to be successful if a litter was produced. In some cases, the cubs were stillborn, but because the gestation went to term, or near term, we classified the breeding as a successful production of cubs. We adopted 4 months of age as a criterion for successful survivorship of cubs because cubs of this age are primarily foraging on meat in the wild [Caro, 1994]. We examined seasonal effects on reproductive output by partitioning the calendar year into four seasonal blocks. Although cheetahs have been breeding at the SDWAP since the early 1970s, analysis of male attributes that might influence reproductive output were reliably available only for the time window from 1985–2005. We analyzed potential sire effects on reproductive output only for the latter time period. All descriptive statistics and analytical procedures were conducted using SPSS 11.0 for Windows (SPSS Inc., Chicago, IL). Kolmogorov-Smirnoff tests were used to check for normality before carrying out parametric statistical tests. Measures of central tendency report the

mean \pm standard deviation (SD), as well as the sample size. We considered findings to be statistically significant when $P < 0.05$ and used two-tailed tests throughout the text.

RESULTS

Of 29 adult females in the breeding program at the SDWAP since 1988, seven (28%) were given the opportunity to breed, but failed to do so, five (17%) bred with males, but failed to produce a litter, and 16 (55%) bred successfully. Of 24 adult males in the breeding program at the SDWAP since 1988, nine (38%) were given the opportunity to breed, but failed to do so, no males bred with females, but failed to produce a litter, two (8%) were possible sires, and 13 (54%) bred successfully. The youngest female to successfully breed was 2.7 years of age, whereas the oldest female to successfully produce a litter was 10.5 years of age. For that time period during which we have accurate data on male mates, the youngest sire was 2.1 years of age, and the oldest male to produce a litter was 11.1 years of age.

The 16 breeding females produced an average of 2.3 (± 1.0) litters each, with 44% of them producing three litters. Of 129 cubs produced, 61 were males, 63 were females, and five were of unknown gender. Sex ratio was evenly distributed within litters (Fig. 1), but two litters were all male, and three litters were all female. Survivorship of cubs was unaffected by sex, with 72% of males and 75% of females surviving past 4 months of age, for an overall cub survivorship rate of 71% ($N = 91/129$). Within litters, males and females had comparable survival rates (Wilcoxon signed-rank test: $Z = -0.424$, $P = 0.671$). Survivorship of cubs was independent of dam age ($r_s = 0.199$, $N = 36$, $P = 0.245$), as well as litter size ($r_s = 0.235$, $N = 36$, $P = 0.168$). Finally, cub survivorship did not depend upon season of the year (Kruskal-Wallis: $H = 2.068$, $P = 0.558$).

Average litter size was 3.6 (± 1.4 ; $N = 36$) cubs, with a mode of four cubs per litter. Litter size over the 35-year period varied from one to eight offspring. In two cases, dams produced a single cub, both of which were females. Neither daughter survived. One died on the first day of life, whereas the other survived for 2 months. Births occurred throughout the year, but exhibited a distinct bimodal pattern, with 39% of litters produced during the spring and 36% of cubs born in the autumn

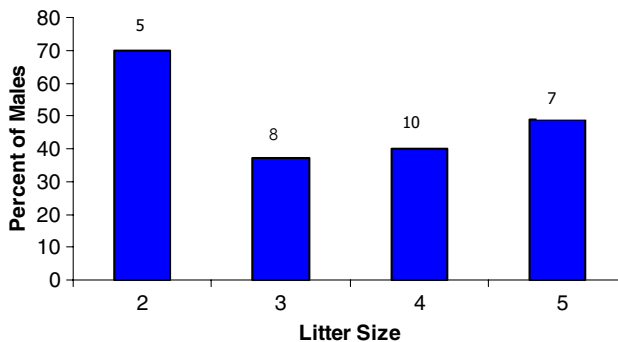


Fig. 1. Sex ratio of cheetah litters during this study. Sample size is indicated above the histogram bars. Sample sizes were too small for litters ≥ 5 .

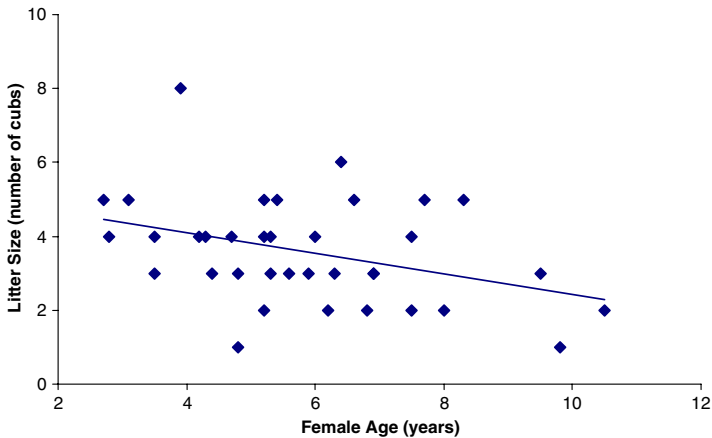


Fig. 2. The effect of female age at conception on litter size ($r = -0.373$, $N = 36$, $P = 0.025$; $Y = 5.223 - 0.280X$). Each diamond represents one litter.

($\chi^2 = 9.56$, $df = 3$, $P < 0.025$). Chronologic age of the dam had a significant negative relationship to the number of cubs born in a litter (Fig. 2), whereas male age had no effect on litter size ($r = 0.022$, $N = 22$, $P = 0.923$). The age difference between the mating dyad did not influence litter size ($r = 0.290$, $N = 22$, $P = 0.190$).

DISCUSSION

An earlier report [Marker-Kraus and Grisham 1993], based upon eight litters produced at the SDWAP between 1987–1991, found that average litter size was 3.9. Although the fraction of non-breeding cheetahs is probably lower in the wild than in captivity, the litter size of breeding cheetahs shows little variance across locations and conditions. For example, in Namibia, the Cheetah Conservation Fund reported an average litter size of 3.1 cubs compared to a survey of Namibian farmers reported an average of 3.4 cubs per litter [Marker-Kraus et al., 1996]. Records from zoologic institutions around the world indicate an average litter size of 3.4–3.5 cubs, with a range from one to eight [Wack et al., 1991; Marker-Kraus and Grisham, 1993; Marker-Kraus et al., 1996], except for the year 2002 [Marker 2005]. The reproductive life history patterns of cheetahs at the SDWAP over a 35-year-period showed an average litter size of 3.6 cubs.

Given that the range, mean, and modal litter size are nearly identical across all localities, we suggest that stabilizing selection [Futuyma, 1998] has had a strong impact on regulating litter size in cheetahs. Stabilizing selection will establish an evolutionary equilibrium over time when the two extremes of a distribution are less advantageous than the optimum value. For example, birth weight among people exhibits a pattern of stabilizing selection because both very light and very heavy babies have a reduced probability of survivorship [Futuyma, 1998]. Among the cheetahs of the Serengeti, reproductive output was relatively independent of prey abundance [Kelly et al., 1998], so food availability in captivity is not likely to increase litter size when progeny production is essentially independent of resource availability. The solitary lifestyle of cheetah females in the wild has probably resulted

in evolutionary pressures that maximize reproductive success when litter size is three to four cubs.

In both captive and wild environments, cheetahs reproduce throughout the year, although seasonal peaks are reported [Marker-Kruas et al., 1996; Kelly et al., 1998]. At the San Diego Zoo Wild Animal Park, seasonal effects on semen traits in cheetahs are absent [Durrant et al., 2001], but births were more likely to occur during the spring and autumn months. The annual distribution of births might reflect the management program more than seasonal variation in cheetah reproductive biology or behavior. Despite evidence of seasonality in cheetah births at the SDWAP, as well as elsewhere, cheetahs have litters throughout the year, so their reproductive output is not regulated by seasonal factors.

The primary difference in reproductive success between captive and wild populations is that cub survivorship is lower in the wild. About 70% of cheetahs survive to independence in captive environments [Marker-Kraus and Grisham, 1993; Marker 2005]. On the other hand, predation on cheetah cubs in the wild is so intense that only about 30–60% of cubs survive to independence [Caro, 1994; Kelly et al., 1998]. Our data suggest that experience among dams is probably not a major factor affecting cub survivorship because success in rearing a litter was independent of maternal age. Similarly, among cheetahs in the Serengeti, Laurenson [1993] found that cub survivorship was comparable between primiparous and multiparous females. In brief, neither season of the year, sex of the cub, or age of the dam seems to affect probability of cub survivorship in either captivity or the wild.

Cheetah females in the SDWAP breeding program could be partitioned into two subsets: breeders (55%) and non-breeders (45%). The two sets were of similar age and genetic stock. Wildt et al. [1993] conducted an extensive inter-institutional survey of cheetah reproductive biology and uncovered no significant differences in key endocrine, physiologic, or morphologic characteristics between breeders and non-breeders. Of 43 female cheetahs presented with a breeding opportunity in a variety of zoologic institutions, Wildt et al. [1993] found that about 67% of them were non-breeders. Our results conform to their conclusions that the central problem for captive management is determining why some cheetahs breed, whereas others do not.

They suggest that “behavioral inadequacy or libido dysfunction” [Wildt et al., 1993] are likely contributions to cheetah non-breeding status. We suggest that failure to breed could result more from pair incompatibility than from traits linked to one sex or the other. In 1868, Charles Darwin remarked [Darwin, 1868] that “It is by no means rare to find certain males and females which will not breed together, though both are known to be perfectly fertile with other males and females... The cause lies in an innate sexual incompatibility of the pair.” When rhesus monkeys (*Macaca mulatta*) are placed in mating trials with female reproductive state modified to be consistent across trials, differences in breeding activity arise from partner preferences, not lack of libido or behavioral problems [Goy, 1979]. Factors facilitating mate choice among cheetahs are unknown, but we propose that the reproductive failure of some pairs results from lack of mate preference.

The tendency to produce fewer cubs with age is contrary to the expectation that females maximize reproductive effort as a function of age [Williams, 1966; Pianka and Parker, 1975; Clutton-Brock, 1991]. If body condition declines with age among cheetahs, however, then the relative reproductive output of older females might be constrained by physiologic limits not encountered by younger females,

which results in a lower net output per litter. Aging compromises female ability to reproduce as a result of a cascade of changes in the hypothalamic–pituitary–gonadal axis coupled with reductions in oocyte quality [vom Saal et al., 1994]. Among captive chimpanzees (*Pan troglodytes*), maternal age is more responsible for negative reproductive outcomes than is parity [Roof et al., 2005]. However, despite the significant reduction in average litter size with age, the optimum litter size seems to be three to four cubs regardless of age.

Our results have at least two major implications for the future of captive breeding programs. First, the findings dovetail with those of Wildt et al. [1993] showing that the fundamental problem in the captive breeding program is the failure of some animals to reproduce. Whether this failure is due to behavioral problems, as they suggest, or to pair incompatibility, as we suggest, can only be resolved by undertaking a sustained research program that involves more frequent shifting of potential partners, combined with more precise and systematic behavioral data collection. Second, the reproductive output of cheetahs is remarkably constrained across a variety of conditions. On average, breeding cheetahs produce litters with three to four cubs, evenly divided between the sexes, with about 70% surviving in captivity. An extensive multi-institutional survey over a 5-year period showed that 33% of females given the opportunity to breed successfully produced a litter, whereas our extensive survey over a 35-year-period from a single institution showed that 55% of females given the opportunity to breed will produce a litter. Circumstantial evidence indicates that only about one-third to one-half of the cheetahs placed into a captive breeding situation are predicted to produce cubs.

CONCLUSIONS

Sixteen dams produced 129 cubs in 36 litters over a 35-year-period, with an average of 3.6 cubs per litter. Sex ratio within litters was unbiased. Cub survivorship was similar for males and females, as well as independent of female age. About 71% of cubs survived. Births occurred throughout the year and older females had fewer offspring per litter than younger females. We suggest that mating partner preference is probably a key factor influencing reproductive success in cheetahs.

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