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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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tween 5,000 and 15,000 animals (P. Gros, personal communication), and has not yet reached as critically low a level as several other large mammals in Africa. At present, therefore, the major share of conservation efforts and funding should be targeted toward gazetting secure habitats for wild cheetahs, maintaining an adequate prey base, and recompensating farmers for stock losses. If, however, habitat conservation efforts fail and the wild population declines to very low levels in the next century, the captive population in zoos and breeding institutions could act as a final buffer against extinction and as a source for future reintroductions [Foose 1983].

Unfortunately, the breeding performance of captive cheetahs is poor compared to other large felids [e.g., Ballou and Seidensticker, 1987], and the captive population is not self-sustaining [Marker and O'Brien, 1989]. The principal problem is that the proportion of breeding individuals is very low, although juvenile mortality is also important [Marker-Kraus, 1990]. In the past, zoological institutions have tried a number of behavioral methods to promote successful breeding. Some of these have mimicked this species' unique social organization by housing male littermates or even non-relative males together for long periods and introducing them to a female [see Florio and Spinelli, 1967, 1968; Benzon and Smith, 1974]. Others have tried more ad hoc social manipulations in an attempt to stimulate interest so often lacking in breeding attempts. These have included introducing a male to a female [Manton, 1970], having a teaser male in an adjacent yard [Benzon and Smith, 1975]; placing the male and female in a neutral yard [Marker-Kraus et al., 1990]; or introducing a single male to a group of females [Vallat, 1971]. Still others have been understandably reluctant to keep males, or even females, together since they might attack each other or members of the opposite sex during introductions. Indeed, there are several anecdotal reports of cheetahs killing each other in such circumstances. Despite these ingenious and varied attempts, some of which have been successful, no single method has demonstrated proven success across different institutions. Frustratingly, breeding success is associated with widely different husbandry practices adopted by highly skilled individuals working in relative isolation.

In more recent years, a wave of research has sought to understand the causes of cheetahs' failure to breed in captivity, focusing mainly on reproductive physiology [Wildt et al., 1993], and to a lesser extent on disease [Heeney et al., 1990; Evermann et al., 1993], nutrition [Setchell et al., 1987], and genetics [O'Brien et al., 1985]. Though these approaches held great promise 5 years ago, their findings and those of parallel studies have now turned the spotlight back on behavioral research to solve the mystery of cheetahs' reluctance to breed in captivity. This is because of the following: 1) The key finding to emerge from Wildt et al.'s survey [1993] is that proven and non-proven breeders of both sexes do not differ physiologically, indicating difficulties with breeding probably lie outside the physiological realm. 2) Ninety-five percent of 20 wild females under close observation in Serengeti reproduced and did so rapidly [Laurenson et al., 1992], suggesting husbandry is to blame for poor breeding performance in captivity. 3) Veterinary care is unlikely to be responsible because it is sophisticated and rigorous [Grisham, in prep], and is as well established in cheetahs as in other large cats. 4) Suitable feeding regimes have been honed through a combination of research [Fitch and Fagan, 1982; Bond and Lindburg, 1990] and trial and error, again suggesting that this aspect of husbandry is not responsible for poor breeding performance. 5) Captive cheetahs show a similar degree of genetic monomorphism to their rapidly reproducing free-living counterparts [O'Brien et al., 1987], indicating that lack of genetic variability cannot account for low rates of litter production in captivity.

Unfortunately, however, there are few in-depth studies on the behavior of captive cheetahs [but see King, 1986; Sarri, 1991; see also Caro, in press, for an exhaustive bibliography of cheetah publications] although a number are currently underway [S. Wells, N. Wielebnowski, in progress]. Surprisingly, more systematic behavioral studies have been conducted on free-living cheetahs than on their captive counterparts [e.g., McLaughlin, 1970; Schaller, 1972; Eaton, 1974; Burney, 1980; Frame and Frame, 1981; Laurenson, 1993; Caro, in press]. At the present time, therefore, the behavior of free-living cheetahs may be the best available model for evaluating the social conditions under which cheetahs should be maintained and bred in captivity, given certain provisos.

Whereas female cheetahs live alone in the wild, males are also found living in coalitions of two or three animals that last the duration of their lifetime [Caro and Collins, 1987; Caro, 1991]. For example, of 110 males living on the Serengeti Plains of Tanzania between 1980 and 1984, 19.1% lived in permanent trios, 40.0% in pairs, and 40.9% lived alone [Caro and Collins, 1986]. The majority of pairs consisted of brothers from the same litter (91.6%, N = 24 pairs), while the majority of trios included one non-relative that had joined two littermates (80.0%, N = 10 trios) [Caro, 1990], usually at the time they were adolescents [Caro, in press].

Coalitions have a greater probability of taking over a territory and holding it for longer than single males; significantly more females collect on territories held by males than elsewhere; and territorial males encounter a greater number of females than do non-territorial males [Caro, in press]. Since free-living female cheetahs are more likely to meet up with groups of males than with singletons, they are, by extension, more likely to mate with a coalition member than a singleton, although no matings have been observed in our Serengeti study.

To investigate the practicality of mimicking the social structure of free-living cheetahs in captivity, this paper first describes the behavior of free-living males in coalitions, then attempts to determine whether groups of wild males pose a danger to females that they encounter, and finally examines whether females show differential interest in coalitions of varying size.

MATERIALS AND METHODS

Behavioral observations of free-living cheetahs were made in the Serengeti National Park, Tanzania, between March 1980 and December 1983. Methods of locating, identifying, and observing cheetahs are given elsewhere [Caro, 1987; Caro and Collins, 1987]. Observations of males were made during daylight hours only (121 days in total), focusing, in particular, on behavioral interactions at kills and in the presence of female cheetahs. In addition, during the middle of the day (09.30–17.00 hours), outside the main hunting periods, male coalitions were repeatedly watched for 3 hour periods. Seventeen coalitions were observed for a total of 208.6 hours during which time physical contact and estimated distances between individuals were noted every 5 minutes. The percentage of 5-minute instantaneous samples, in which each individual was at a particular distance from others, was then calculated.

As in other fields [MacDonald et al., 1987], most affiliative behavior between adult males consisted of *grooming*, i.e., licking the fur of another animal and cap-

turing and eating hippoboscid flies and ticks. I recorded all bouts of grooming between cheetahs (which had to be separated by >10 sec) throughout the day, noting the actor, recipient, and whether *grooming was reciprocated*, defined as starting to groom one's partner while being groomed. Male-male aggression at kills was recorded by summing instances of slapping and biting another male or the carcass; growling was also noted. These measures were then divided by the total time any member of the group was feeding from the carcass, and by the number of cheetahs present, to obtain average rates per male per hour.

When independent male and female cheetahs were encountered together, the number of times the male walked toward the female (*approached*), *sniffed* her, or sniffed where she had been resting (*sniffed object*) were recorded. Instances of *slapping*, and of *growling* (here combined with *yowling*, a drawn out moan of variable pitch) at the female or toward other males were noted, as was *self-grooming*, *rolling over*, and *moving off* away from the female. *Yipping*, a bird-like call made by cheetahs in fearful situations, was also recorded. Cheetahs also *churred* or *stuttered* [Eaton and Craig, 1973], a vocalization indicative of estrus in females and of male interest in the opposite sex (D. Lindburg, personal communication). The number of times a female slapped a male, yipped, growled, rolled over, groomed herself, and moved off were also scored. Behavioral totals were divided by the number of hours that the observer stayed with the group to yield frequencies of behavior. Distances between participants in meters were estimated by eye, and noted each time a participant changed his or her position.

RESULTS

Behavior of Males in Coalitions

Affiliative behavior. In 181 sightings where coalitions were seen more than once, members were found together on 92.8% of occasions. Coalition partners were extremely tolerant of each other's close proximity. During the daytime rest period they spent an average of 53.1% (SE = 6.3, N = 17 coalitions) of the time less than 1 m apart. Indeed, they rested in contact for 12.0% (SE = 2.4, N = 17 coalitions) of the time. In many circumstances, where coalition members were only partially in shadow and had the opportunity to seek larger patches of shade behind trees or rocks some meters away, they still chose to stay next to their companions.

During the day, partners groomed each other an average of 0.19/hour (SE = 0.03, N = 12 coalitions) or once every 5 hours. They usually licked each other on the face, ears, and neck with bouts varying from a single lick to prolonged sessions lasting 3 minutes. Once a male had begun to lick another, grooming was reciprocated on 60.3% (SE = 7.8, N = 12 coalitions) of occasions. Very occasionally, purring was heard during these interactions.

Behavior toward non-littermate coalition members. One of the trios that I followed (JKL) was a group of adolescent males that had recently joined up sometime in the previous 55 days. Over a 4 day observation period, there were many instances of aggression by J and especially by K (the two littermates) toward L, who was not their sibling. For example, L was slapped by K on the only occasion L tried to groom him, and when L sniffed the same object as K. In addition to the behavioral discrimination shown by members of this trio, L spent a lower proportion of the daytime rest period in contact than did J and K, and was usually further away from them, though

TABLE 1. Percentages of 5-minute scans that members of 3 coalitions spent at different distances from each other and in contact during the daytime rest period*

	JKL		PQR		ABC	
	LM	Non-LM	LM	Non-LM	LM	Non-LM
0–1 m	87.2	35.9	49.8	55.6	54.0	55.5
2–5 m	7.4	60.0	35.3	26.4	29.3	34.7
>5 m	5.4	4.2	14.8	16.1	16.7	9.9
Contact	28.8	4.2	18.1	14.2	6.7	17.4

*J, K, and L had just joined up, P, Q, and R had been together for over a year, and A, B, and C for at least 4 years; they were watched for a total of 11.5, 21.0, and 16.5 hours, respectively, during daytime rest periods. LM denotes percentages of time that distances between littermates were maintained; non-LM, average percentages of time that distances between non-littermates were maintained.

rarely more than 5 m (Table 1). L would even rest entirely in the sun to be near J and K while they lay in the shade.

Two other trios were also observed in which two members were littermates but the third was not. When behavioral observations began, P had been with littermates Q and R for a minimum of 12½ months but no longer than 20 months. In another trio, B, the non-littermate, had been together with littermates A and C for at least 4 years. This provided a limited opportunity to examine whether relationships between unrelated coalition members changed over time. Differences in daytime proximity shown by J and K to L were no longer evident in the more established trios (Table 1). For both J, K, and L and P, Q, and R, however, the distribution of grooming bouts was significantly different from expected with both L and P (the unrelated members) grooming other coalition members least in their respective trios, whereas B groomed as expected with his companions (JKL, $\chi^2 = 17.872$, df = 2, $P < .001$; PQR, $\chi^2 = 16.760$, df = 2, $P < .001$; ABC, $\chi^2 = 1.786$, df = 2, NS). Thus, discrimination on the apparent basis of kin continued for longer with regards to grooming than to resting proximity.

Aggressive behavior between coalition members. Some aggression was seen in 57.8% of the 45 situations where males in coalitions ate together, and growling was heard on 51.1% of these occasions. Aggression, where males lightly bit or slapped each other or hit the carcass itself, was highest at intermediate-sized kills (Kruskal-Wallis test, H = 6.870, df = 2, $P < .05$; Fig. 1). Toward the end of the meal, males entered into competition for remaining morsels that were still attached to the skeleton and could not be carried off. Nevertheless, escalated fighting between group members never occurred presumably because the pay-offs of winning scraps of meat were minor compared to risks of injury. Growling was highest at small kills but not significantly so (H = 3.658, df = 2, NS; Fig. 1). Here one male attempted to monopolize the prey by carrying it off every time his companion approached. Rather than approaching his partner head on, the other male waited until his companion moved, and then fed on any scraps that had fallen off the carcass.

Behavior of Males on Seeing a Female

It was difficult to discern pregnancy in the field, but demographic records showed that the majority of lone females and some mothers with old cubs were pregnant and were therefore not in estrus [Laurenson et al., 1992]. Nevertheless,

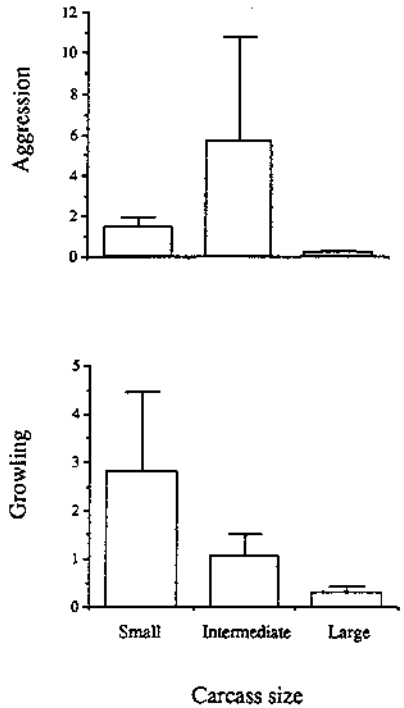

Fig. 1. Mean (and SE) rates of aggression (slapping and biting combined) and growling per male per hour shown by members of pairs and trios of males (combined) at small kills (hares and neonate Thomson's gazelles; N = 9 coalitions), intermediate kills (neonate Grant's gazelles, halfgrown, subadult, and adult Thomson's gazelles; N = 4 coalitions), and large kills (wildebeests; N = 9 coalitions). Average rates of behavior were derived for each coalition eating different-sized prey, and then a mean of these figures was calculated; thus, the same coalition might be represented at different-sized kills.

males cautiously approached 68.9% of single females that they saw (N = 45 occasions), sometimes stalking, but would chase after and slap them down if they fled. They also approached mothers with cubs (25.5%, N = 40) but to a lesser extent as might be predicted from the demographic data. Males may not have visited every female they saw because they already knew of her reproductive condition. For example, I noticed that males might visit a family but then not bother to approach on subsequent days presumably because they remembered the mother's identity and reproductive state. Additionally, they may have mistaken some females for males and kept their distance.

When a male encountered a female, he set about smelling the vegetation close to where she lay and, less often, sniffed her vulva in an attempt to determine whether she was in estrus. Males in coalitions sometimes threatened each other by growling or hissing, but overt aggression between them occurred in only 1 out of 7 coalitions, the only one that contained a non-littermate. Here, brothers A and C were aggressive

only to their unrelated companion (A and C directed no slaps or bites to each other, but 6 and 2, respectively, to B). Though suggestive, the sample size is clearly much too small to claim that relatedness is an important factor in determining intermale aggression. Data from free-living lions show that male aggression over females depended on whether ownership was undecided, rather than on kinship [Packer and Pusey, 1982].

I had no information on whether aggression between males was more pronounced when females were ready to mate, since neither my colleagues (A. Collins, C. FitzGibbon, and K. Laurenson) nor I saw cheetahs mating in 10 years of continuous fieldwork. Mating may occur in less than a minute in captivity [Tong, 1974]. Occasional reports of wild cheetahs mating indicate variability in the extent of male-male competition. In one instance, males competed to mount the female by pushing each other off her with their heads [reported in Caro and Collins, 1987]. M. Deeble (personal communication to K. Laurenson) noted that the male that arrived first would not let his partner come close to the female, whereas McLaughlin [1970] described one free-living male mounting a female, while his partner slept or watched for prey.

Behavior of Males in the Presence of a Female

Once males had surrounded a female, she tried to break away from them whenever possible. After carefully smelling where she had sat or lain, males walked or trotted after her. These behavior patterns were therefore correlated with the female attempting to leave (N = 26 female-male encounters, male sniffing, $r_s = 0.827$, $P < .01$; male approaching $r_s = 0.648$, $P < .01$). On average, males sat an estimated 6 m from the female, but sometimes less than 1 m away, especially when they first encountered her.

In general, the behavior of individual males in the presence of females was little affected by male group size (Table 2). Females, however, could move away from singletons and pairs more easily than from trios. Consequently, there was a tendency for males in smaller group sizes to approach the female and sniff the vegetation in which she had sat more frequently than those in larger coalitions (Table 2). Also, males in smaller groups groomed themselves more often in the presence of females (Table 2); indeed, singletons' rates were, on average, ten times higher than grooming between males in the absence of females (I did not record rates of self-grooming in situations where females were absent). High grooming rates in this context may have been a displacement activity associated with fear of being close to a strange cheetah. Males were heard to stutter in only 4 out of 27 lengthy encounters with females ($\bar{X} = 12.1$, SE = 10.2 times per hour in the 3 encounters where it could be scored), and urine spraying in the presence of a female was witnessed rarely.

Behavior of Females in the Presence of Males

Females usually trotted away from males if they saw them, but were pursued, invariably caught, and knocked to the ground where, yipping loudly, they lay dorsally in a defensive threat and struck out if the male(s) came too close. Once pinned by males, females' behavior differed little in the presence of different numbers of males, except that they growled more at large groups, perhaps because they were more fearful of them (Table 3).

Rates of rolling and self-grooming (all parts of the body including the genitals)

TABLE 2. Mean rates of behavior per hour shown by individual males toward females, and the average distance spent from the female in meters*

	Male group size				
	1 (N = 4)	2 (N = 6)	3 (N = 2)	H value	*P* value
Approach	4.5	4.3	0.8	4.673	<0.1
Sniff object	8.0	6.2	1.2	5.417	<0.1
Sniff female	0	0.3	0.1	1.848	NS
Slap female	0	1.4	0.1	3.776	NS
Yip	0.4	0.5	0.1	0.184	NS
Growl	0	0	0.1	2.341	NS
Roll over	0.7	0.6	0.9	0.159	NS
Groom self	2.2	0.5	0.1	5.273	<0.1
Move off	1.9	3.0	0.7	4.154	NS
Average distance	3.2	6.6	11.9	2.099	NS

*Individual male rates of behavior at each encounter with a female were averaged across coalition members, then across encounters, and finally across different coalitions. H values on Kruskal-Wallis tests (df = 2) and significance levels are on the right; NS refer to number of coalitions.

were significantly correlated in females during encounters with males ($N = 26$, $r_s = 0.517$, $P < .01$), and are sometimes used to identify estrus in captivity [Florio and Spinelli, 1967; Foster, 1977; Grisham, in prep]. Rates of these behaviors, however, did not differ in the presence of different numbers of males (Table 3). Females stuttered infrequently in only 2 out of 27 lengthy encounters with males.

Females growled if males sniffed vegetation close by ($N = 26$ encounters, $r_s = 0.351$, $P < .1$). If a male sniffed the female herself, she usually slapped him ($N = 26$, $r_s = 0.927$, $P < .01$) and showed fear by yipping ($N = 26$, $r_s = 0.856$, $P < .01$). Similarly, if she was slapped down by a male, she often slapped him back ($N = 26$, $r_s = 0.887$, $P < .01$) and reciprocal bouts could last up to 5 seconds; however, I never saw free-living males biting females as reported by H. van Lawick (personal communication). If slapped, females usually backed off a meter or two ($N = 26$, $r_s = 0.629$, $P < 0.01$). Finally, the rate at which males rolled over was correlated with both the rate at which females rolled over ($N = 26$, $r_s = 0.419$, $P < .05$) and the rate at which females groomed themselves ($N = 26$, $r_s = 0.425$, $P < .05$). I have no satisfactory explanation for the function of these activities, but self-grooming may reflect levels of tension among the participants, as suggested earlier.

Males stayed with a female for as little as 3 minutes to over 2 days. While short stays could have been attempts to determine whether she was in estrus, longer stays may have been guarding her in anticipation of estrus or after mating. The majority of associations dissolved because males left, but if a male fell asleep, a female could slink away. Cubs normally stayed within 50 m of their mother during the course of an interaction, with males occasionally growling at them.

DISCUSSION

Behavior of Males in Coalitions

Certain zoos have long recognized the importance of social factors in promoting captive breeding of felids [Mellen, 1991], and have kept male cheetahs together for the purposes of breeding, education, and saving space. Others have been more uncertain of this practice. Although the confines of the captive environment alter the behavior of cheetahs, findings presented here should allay fears of keeping males together. Free-living male coalitions were characterized by amicable relations, even amongst unrelated males once a period of months had elapsed. Males fought rarely and only over the remains of small or intermediate-sized carcasses, or sometimes over females. In both circumstances levels of aggression were low with males receiving only a scratch at most.

Captive experience has found that affiliative behavior is normally shown by sibling males cohabiting since cubhood or by unrelated males, provided they were introduced when one was less than 20 months old. However, encounters between males first introduced to each other as adults are unpredictable. As wild unrelated males normally join up in the first 3 years of life, they reinforce these observations and indicate it is preferable to introduce unrelated males together before 2 years of age. As the majority of males in Serengeti lived in coalitions, it may be important to allow them to be social in captivity for reasons not yet understood. At the very least, such housing arrangements can enlighten the public about the habits of this species in the wild, if educational information is provided.

TABLE 3. Mean rates of behavior per hour shown by females toward single males, two males, or three males*

	Number of males				
	1 (N = 7)	2 (N = 10)	3 (N = 9)	H value	*P* value
Slap male	0.3	2.6	0.3	1.058	NS
Yip	6.9	20.1	2.3	1.613	NS
Growl	0	1.2	3.0	8.379	<.02
Roll over	2.0	0.9	0.8	1.700	NS
Groom self	2.3	0.2	0.3	3.810	NS
Move off	1.6	2.4	0.8	2.200	NS

*Individual female rates of behavior at each encounter with males were averaged across coalitions of each group size. Also shown are H values on Kruskal-Wallis tests (df = 2) and significance levels; NS refer to number of occasions a female was seen with males from each group size.

Behavior of Males and Females in Each Other's Presence

Opinion is divided as to whether competition between males in captivity increases female libido [Benzon and Smith, 1974, 1975] or interferes with breeding [Skeldon, 1973; Tennant and Craig, 1977]. Though females can produce litters as a result of a single mating with a single male [Thompson and Landreth, 1973; Lindburg et al., 1993] or when introduced to several males [Tennant and Craig, 1977], the probability that a captive female will mate, or produce a litter, depending on male group size, requires systematic investigation. When cohabiting males are introduced to an estrus female in captivity, fighting between males is common, although serious injuries do not usually occur [e.g., Degenaar, 1977]. In certain situations, however, such introductions have resulted in death, as for example, when two males killed two females at Phoenix Zoo [N. Wielebnowski, personal communication]. In the absence

of information summarizing the probability of injury or mortality associated with various introduction protocols, observations from the wild can be informative.

Escalated aggression among coalition members or directed at the female was never witnessed during male-female liaisons, although yipping, growling, hissing, and yowling were heard. It might be argued that if females were not in estrus, levels of aggression between coalition members would be low. Females rolled and groomed themselves relatively often at least in the presence of single males as described in captivity [Foster, 1977; Brand, 1980], but other behaviors such as head rubbing, tail twitching, frisky behavior, treading, and urine spraying [Fitch et al., 1985; King, 1986; Sarri, 1991; Grisham, in prep] occurred infrequently or not at all, and mating was never seen. Nevertheless, coalition members were seen together repeatedly without new injuries, suggesting that they fought little when estrus females were encountered in my absence. Rates of scent marking and stuttering by males appeared lower than in captivity, possibly because of the absence of estrus [Degenaar, 1977; Sarri, 1991].

Females' behavior showed little change in the presence of different numbers of males, except that females may have been more fearful of several males. If females were not in estrus, however, this might account for lack of differential response to male groups of varying size. There are some reports of females preferring to mate with one of several males introduced at once [Degenaar, 1977], and this is the subject of a study in progress (N. Wielebnowski).

Neither males nor females were injured when male groups encountered females in the wild, but it is difficult to exclude this possibility in captivity where opportunities for escape are limited. Nevertheless, there are good reasons for pressing ahead with multimale introductions because in the wild most matings occur between females and coalition members and male-male competition may stimulate female excitement and interest. Though a number of zoos have already devised strategies to separate participants and provide refuges during multimale introductions, the practice is not yet widespread, and needs to be implemented particularly in zoos with weak breeding programs.

CONCLUSIONS

1. Free-living littermate and non-littermate males live in long-term stable associations. Zoos should, therefore, house males together to increase the probability of breeding success and enhance public understanding of the species. Captive males have been kept together for years, provided they are littermates or are introduced to each other before 20 months of age.

2. If zoos systematically documented the behavior of cheetahs during introductions using simple measures, it would be relatively easy to determine which breeding protocols are safe and successful. Instead, we have to turn to parallel situations in the wild. There, successful matings usually occur in the presence of several males. Thus, it is recommended that more institutions introduce a group of cohabiting males to a female, providing precautions to separate participants quickly are made in advance.

3. Free-living females are not adversely affected by the presence of a group of males. Anecdotal evidence suggests they may stimulate her to mate, and they potentially provide her with a choice of mating partner.

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Early Maternal Behavior of Wild Cheetahs: Implications for Captive Husbandry

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Against a background of poor breeding success and cub survival in captive cheetahs, a knowledge of the early maternal behavior in the wild may yield useful information for comparison with the captive situation. This paper documents the types of lair sites used by mothers to conceal their newborn cubs in the wild situation, and details patterns of maternal behavior observed during this period. Four kinds of lairs were used by cheetah mothers, and the amount of protection from the elements and predators was assessed for each. Lair type appeared to have little effect on cub survival. Cubs were concealed in lairs for 8.2 weeks on average, although larger litters tended to leave lairs earlier. During this period, cubs were moved to new lairs approximately every 5.6 days. Cubs were left for an average of 9.6 hours while their mothers went hunting, but mothers virtually always returned to them around nightfall, even if they failed to catch any prey. Maternal neglect and cub abandonment, which account for many cub deaths in captivity, are abnormal in the wild, except when prey is very scarce. Improved husbandry techniques, such as the provision of multiple, secluded nest boxes, and remote monitoring conditions should promote breeding success in captivity. In addition, noise and human disturbance should be minimized.

Key words: *Acinonyx jubatus*, **free-ranging, den, mothering, captive breeding**

INTRODUCTION

Zoo managers face a number of problems when attempting to breed cheetahs (*Acinonyx jubatus*) in captivity. Only a few establishments in Europe, North America, and South Africa have regularly bred cheetahs [Manton, 1969; Degenaar, 1977; Marker and O'Brien, 1989]. Furthermore, a limited number of founder animals are responsible for the majority of captive births [Manton, 1969; Marker and O'Brien,

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