Laurenson MK. 1993. Early Maternal Behavior of Wild Cheetahs: Implications for Captive Husbandry. Zoo Biology 12(1):31-43.

Keywords: 1TZ/Acinonyx jubatus/behavior/captive breeding/cheetah/cub/denning behavior/home range/husbandry/maternal care

Abstract: Against a background of poor breeding success and cub survival in captive cheetahs, a knowledge of the early maternal behaviour 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 behaviour 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.

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Zoo Biology 12:31–43 (1993)

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,

Received for publication July 1, 1992; revision accepted September 21, 1992.

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1989]. Compounding the failure of individual cheetahs to breed, juvenile mortality of captive born cubs is high compared to other species of mammals, at an average of 36.4% [Bertschinger et al., 1984; O'Brien et al., 1985; Marker and O'Brien, 1989]. There is, however, considerable variation between establishments, and mortality is actually no higher than in other captive felid or carnivore species [Loudon, 1985]. Nonetheless, the combination of the failure of many cheetahs to breed, and the scale of juvenile mortality has meant that the captive cheetah population is not self-sustaining [Marker and O'Brien, 1989].

In the wild, juvenile mortality is even higher, with only 5% of cubs reaching independence [Laurenson et al., 1992]. During the first 2 months of cubs' lives, when they are hidden in a lair, mortality is high with 72.2% of entire litters dying. The instantaneous mortality rate is, however, highest in the first weeks after cubs emerge, although it decreased again later. Lion (*Panthera leo*) predation accounts for the vast majority of this mortality, although some cubs die from starvation when abandoned by their mothers in times of prey scarcity (Laurenson, 1992a). In contrast, although it has been suggested that the cheetah's genetic homozygosity may contribute significantly to this mortality [O'Brien et al., 1985], causes associated with poor mothering (neglect, cannibalism, and abandonment) actually account for the greatest proportion of cub deaths in captivity, more than premature, stillbirths, and congenital defects combined (calculated from Marker-Kraus [1990]). Mortality would be even higher if cubs were not hand reared after abandonment. Most of the captive mortality occurs within the first month of life, with the first week being a particularly vulnerable period [Degenaar, 1977; Marker and O'Brien, 1989].

A multidisciplinary research program run by the AAZPA (American Association for Zoological Parks and Aquaria) has concentrated on unravelling the reasons behind the failure of captive cheetahs to conceive [Wildt et al., 1983, 1987, 1993; O'Brien et al., 1985]. Evidence from the wild, where female fertility is high [Laurenson et al., 1992], and from captivity [Lindburg et al., 1993; Wildt et al., 1993] is accumulating that suggests that behavioral and husbandry factors may be at the root of these captive breeding problems. In contrast, little effort has gone into examining the key factors affecting cub survival in captivity [Loudon, 1985], or how rearing conditions can be improved. A few individual establishments, however, have improved cub survival by changing husbandry techniques [Brand, 1980; Cupps, 1985], and juvenile mortality rates have declined somewhat in recent years [Grisham, 1992]. Nonetheless, in order to ascertain whether husbandry techniques and maternal behavior in captivity are contributing to poor cub survival, a knowledge of maternal behavior during the crucial first weeks of cubs' lives in the natural situation is essential.

This paper documents the characteristics of the lair sites used by wild females in the Serengeti National Park, Tanzania, as well as aspects of the behavior of these females while their cubs are concealed in the lair. In addition, the relevance of these observations to captive breeding is discussed, with particular reference to possible improvements in husbandry techniques.

MATERIALS AND METHODS

This study was conducted in an approximately 2,500-km^2 area of the central plains of the Serengeti National Park and Ngorongoro Conservation Area in Tanzania.

In this area, increased rainfall occurs in most years between November and May, designated the wet season, whereas rainfall is scarce in the dry season, June to October. Between October 1987 and September 1990, as part of a long-term study on this species [see Caro and Collins, 1986, for description of study area], cheetahs were located by searching a predetermined portion of the plains and scanning from hilltops using 10 × 50 binoculars. Cheetahs were identified by matching tail banding and the face, flank, and chest spot patterns to a photographic file index. Previous work has shown that females live alone or with their dependent cubs [Frame and Frame, 1981; Caro, 1991] and give birth for the first time at approximately 36 months of age [Laurenson et al., 1992]. Males either live alone or in a permanent coalition of two or three individuals [Caro and Collins, 1986]. Some males exhibit territorial behavior in small areas [30 km^2], where food and cover are abundantly available seasonally and where high concentrations of females are found [Caro, 1992]. Females and non-territorial males have annual home ranges of 800 km^2 on average, with extensive range overlap. During the dry season, these cheetahs follow the Thomson's gazelle migration to occupy the area on the boundary between the long grass plains and woodlands, whereas in the wet season, both Thomson's gazelles and cheetahs move to the short grass plains in the Ngorongoro Conservation area and the south and east of the Serengeti National Park [Durant et al., 1988].

Of a population of approximately 200 females inhabiting the central plains [Caro and Collins, 1986], 20 females, who were well habituated to the observer, were chosen for detailed study. Six of these females were less than 3 years old when collared and had not yet given birth to cubs and were classified as young females, while the other 14 were fully adult and had already raised litters to maturity. These animals were immobilized using a syringe dart containing 100 mg of ketamine (Vetalar, Parke Davis and Co., UK) and 125 mg of xylazine (Rompun, Bayer, UK), fired from a hand-held blowpipe or air powered dart gun. When recumbent, females were carefully examined, blood samples taken and radio-collars fitted. The effect of xylazine was then reversed using RX 821002A (Reckitt and Coleman, UK).

Radio-collared females were located at approximately monthly intervals, using aerial radiotelemetry, and then relocated from the ground vehicle as soon as possible afterwards. Females were observed for at least 10 min while their reproductive status was assessed. Well-developed mammary glands and a protruding stomach were indicative of advanced pregnancy, whereas brown rings around the nipples and full mammae indicated that females were lactating. If pregnant, females were checked within two weeks to ascertain whether cubs had been born and if lactating, females were followed until the area containing the lair site was found.

The lair site was located by radiotracking from the vehicle at daybreak, when mothers were almost always with their cubs. When the female left the lair to go hunting and could no longer see the lair site, the area was searched on foot, with the vehicle being left at least 30 m away, in order to avoid creating tracks and disturbing vegetation excessively. Cubs were counted, sexed, and weighed and their age estimated and then checked weekly, until they either emerged from the lair to follow their mother or died. Detailed observations and analysis showed that the mothers' behavior did not obviously change after lairs had been examined and that cub survival was not compromised [Laurenson and Caro, 1992].

Five out of six young females and 12 of the 14 older females gave birth during the study [Laurenson et al., 1992]. Data were collated from a larger study examining

maternal behavior throughout the period of lactation. Intensive 5- or 6-day observation periods were conducted when cubs were 3–5 weeks old, on 17 of the 36 litters born (three litters from one mother, two from three mothers, and one from eight mothers). In addition some observations were made on a further five litters when lairs were checked at weekly intervals. The data presented in this paper come from more than 1,600 observation hours divided over 131 days.

During observation periods, the time of day and the distance apart of lair sites were recorded if mothers moved cubs. The time of day that mothers left and entered the lair was noted and maternal belly size scored each morning on a scale of 1–14, as a measure of hunger [see Caro, 1987, for details and reliability of measures]. The influence of hunger on the time mothers left to go hunting each day was examined by entering each event separately and using analysis of variance techniques that treated belly size as a covariate. The amount of time that mothers spent away from their cubs each day was averaged for each female that was intensively observed.

RESULTS

Lair Types

Mothers were found to use a variety of lair types. These were classified according to their physical and geographical characteristics.

Marsh lairs. Marshes consisted mainly of aggregations of small sedges (*Juncus* spp.) approximately 1 m high. Areas ranged in size from 50 m × 20 to 300 m × 200 m. The marshes were uneven with lower wet areas and drier rises. Lairs were generally positioned in drier areas, and none of the 11 lairs found in marshes became waterlogged. Marsh lairs had little overhanging vegetation and so did not provide much shade or direct protection from rain. Cubs sometimes tunnelled into the mesh of reeds, however, affording themselves additional shelter.

Vegetation lairs. Patches of thick grass, tall herbs and bushy vegetation (e.g., *Solanum, Justicia, Hibiscus* spp.) were also used as lair sites. These types of vegetation were associated with wide and shallow drainage lines, or with the boundary between the plains and woodland areas where soil moisture was greater than on the open plains. The amount of shelter provided by vegetation type lairs was variable.

Gully lairs. Lairs were also found in more steeply sloping drainage lines or gullies and were often positioned under the bushes associated with these areas. These gullies often had steep banks and drops of up to 2 m, which would require athletic scrambling to negotiate. Lairs were never found in the bottom of these ditches where flooding might have occurred. These lairs usually provided good protection from the elements, as bushes and thick vegetation were abundant.

Kopje lairs. Kopjes in the Serengeti are granite outcrops and may consist of only bare rock or of an extensive network of large boulders, thick bushes, trees and other vegetation. Lairs on kopjes were situated in rocky crannies, amongst thick vegetation or under bushes which provided good cover from the weather. They often had a steep and tortuous access route.

Ideally, a lair site should provide shelter from the elements and protection from predators. Whereas shelter is provided by the local physical features of the lair, protection from predators may also depend on its location, for example, whether it was located in an area of high or low predator density or whether surrounding topography meant that mothers were visible when leaving or entering the lair.

TABLE 1. Summary of the cover and protection from predators provided by different lair types

		Visibility of cheetahs		Predator risk	
Lair type	Cover	Sitting up	Entering/ leaving lair	Use of area by predators[a]	Ease bound[b]
Marsh	Poor (variable)	High	Medium	Medium	Easy
Vegetation	Medium	Medium	Low	Medium/low	Difficult
Gully	Good	Low	Medium	Medium	Difficult
Kopje	Good	Low	Medium	High	Difficult

[a]Indicates the preference of large predators for using areas with that type of vegetation.
[b]Indicates how easy it was for the observer to find a lair in that type of vegetation.

The relative provision of cover and factors affecting the provision of protection from predators for each lair type is summarized in Table 1. Gully and vegetation lairs scored well on most of the measures of predation risk and provided adequate cover. Kopje lairs were similar, except that other predators frequently used them. As well as providing poor cover, marsh lairs were relatively easy to find, as females were quite visible, suggesting that they may not have been as safe as some of the other lair types.

Choice of Lair Types

The frequency with which each type of lair was chosen is summarized in Table 2 and separated according to the season. Although marsh and vegetation lairs were used more often than either gully or kopje lairs, it is difficult to know whether this was due to female preference or was a reflection of their absolute availability, as this was impossible to determine.

When the frequency that different lair types were chosen is examined according to season, little difference was found. If, however, the use of kopjes is examined by whether individual cheetahs were occupying their normal wet or dry season ranges rather than the actual season, there was a trend for kopjes to be avoided if possible, although the result did not reach significance at the 0.05 level (Fisher exact probability, $P = 0.07$, n = 18 lairs in dry season areas). Kopje lairs were never situated in dry season areas despite kopjes being widely available. They may have been avoided because kopjes are often used by lions as resting places and are also frequently the focus of male cheetah territories [Schaller, 1972; Caro and Collins, 1987].

Judging from data obtained on the ranging pattern of females, lairs were generally situated in the general area that females were using prior to parturition. This position was usually determined by the distribution of Thomson's gazelles [Durant et al., 1988]. Some cheetah mothers, however, moved several kilometers from their hunting grounds to find what they considered a suitable lair site. The proximity of water may have also been an important factor determining the suitability of sites, because lactating cheetahs significantly increase the time they spend drinking [Laurenson, 1992b]. Water was available within 500 m of 23 (67.6%) of the 34 known lair sites. Of the 11 (33.4%) sites where water was not so readily available, four (36.4%) of the females were seen to drink during the observation period, and another four were not followed. Therefore females at a minimum of 90% of the lair sites that were watched were known to have relatively easy access to water at this stage of lactation.

TABLE 2. The frequency with which different types of lair were used by females, compared to the frequency with which cubs survived to emergence, separated according to season

	Wet season		Dry season		Totals	
Lair type	Chosen	Emerged	Chosen	Emerged	Chosen	Emerged
Marsh	8	2	3	1	11	3
Vegetation	5	0	8	4	13	4
Gully	2	1	2	1	4	2
Kopje	1	0	2	1	3	1
Unknown	2	0	3	—	5	0
Total	18	3	18	7	36	10

Maternal Behavior Associated With the Lair

Periparturient behavior. One mother was intensively observed around the period she gave birth to a litter of four cubs in a marsh. She left the lair for less than 1 hr on the first 2 days after giving birth and for only 2 hr on the third day, when she drank for about 65 sec. While with her cubs, she sat up only once or twice each day. On the fourth and fifth days she attempted, unsuccessfully, to hunt before being accosted by two males, whom she did not escape until the sixth day. Thus she did not eat for at least 5 days after the cubs were born.

Duration of occupation. Cubs were concealed in the den for an average of 58.2 days (n = 9 litters from 8 different mothers) or 8.2 weeks (range 7.4–9.4 weeks). This is considerably longer than the 5–6 weeks estimated by previous workers [Schaller, 1972; Frame and Frame, 1981; Caro, 1987], but corresponds to the age at which captive cubs begin to explore away from the lair [Grisham, 1992]. When length of lair occupation was analyzed in relation to litter size and season (Fig. 1), there was a trend for larger litters to spend less time in the lair than small litters (ANOVA: litter size; $F_{2,4} = 4.60$, $P = 0.07$; Season; $F_{1,4} = 2.13$, NS). It is likely that the increased energetic requirements of felid mothers with larger litters [Deag et al., 1987; Laurenson, 1992c], which may have been more difficult to meet under the constraints acting when cubs are in a lair [Laurenson, 1992b], explains this result.

Patterns of lair site visitation. Females stayed in the vicinity of the lair on 29.0% of days watched (n = 93 days) during intensive observation periods and did not hunt. Although some females remained in the lair all day, others left their cubs for up to 4 hr to rest nearby. On the days that mothers went hunting, they left the lair between 0630 hours and 1430 hours, leaving most frequently between 0831 and 0930 (Fig. 2a). The time that mothers left was influenced by their belly size and their identity (2-way ANOVA: belly size: $F_{1,56} = 18.0$, $P < 0.001$: identity; $F_{13,56} = 2.2$, $P = 0.02$). Mothers with smaller belly sizes, who were probably hungrier, left the lair significantly earlier in the morning than those who were less hungry, and some females were habitual early or late risers (Table 3).

Mothers spent on average 9.6 (SE 0.67) hours (n = 14 mothers) away from their cubs on the days they went hunting although there was considerable variation within individuals from day to day (range 3.8–27.8 hr). They returned to the lair between 1015 hours and 2200 hours on these days, most frequently between 1900 and 2000 hours (Fig. 2b). Thus they returned after dark to the lair on more than half of occasions (54.7% of 53 returns observed), perhaps to avoid drawing the attention of

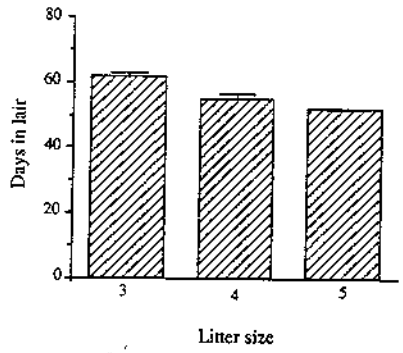

Fig. 1. The mean (SE) of the number of days that cubs in litters of 3 (n = 5), 4 (n = 3), or 5 (n = 1) are concealed in the lair in the Serengeti National Park, Tanzania.

other predators to the position of the lair site [Laurenson, 1992a]. Mothers returned to the lair the same day on 95% of days when they had not caught any prey (n = 21 days) and only stayed away overnight three times altogether, excluding cases when litters were abandoned. Females did abandon litters if they could not catch enough food (Laurenson, under review) and so hunting success was ultimately important in determining whether mothers stayed away overnight. However, the likelihood of mothers returning to the lair at night was probably also affected by the distance that mothers were from the lair at the end of the day, as two of the three females who did not return to the lair at nightfall had eaten, but were more than 8 km away.

Moving lairs. Cubs were moved on 18% of days that females with cubs in the lair were watched (n = 131 days), or every 5.6 days. All litters that reached four weeks of age (n = 22 litters) were moved at least once. It appeared that litters were often (67%, n = 9 litters where position of first site was definitely known) left in the first lair for about 10–14 days, but were moved more frequently thereafter. The maximum number of alternative sites found by the time cubs emerged was six, although it was impossible to be sure that all the sites that had been used were found.

Mothers moved young cubs by carrying them in their mouths, usually by the scruff of the neck, but occasionally somewhat inelegantly by a tail or leg. Cubs older than 4 weeks were relatively mobile, and mothers found these heavier cubs difficult to carry. As a result, they often gave up carrying the cubs and left them to scramble along behind when she called to them. Cubs never appeared to be damaged in any way by their mothers while being moved. Mothers usually judged their number of cubs accurately but checked the old lair for additional cubs on four (21%) of the 19 moves observed. They were never seen to leave a member of the litter by mistake, and this seemed unlikely to occur as lone cubs often "cheeped" repeatedly in distress.

Mothers reconnoitred the new lair site immediately before 37% of the moves actually observed (n = 19). It was probable, however, that females already knew the surrounding area well as they often spent time resting nearby. New lair sites were an average of 120 meters from the previous site (n = 42 pairs of sites). Although the range was large (5m-1km), the vast majority (78.6%) of lair sites were less than 100 m apart. Lair site moves of greater than 800 m (n = 2 moves) occurred at the end of the period in the lair, with the new site being closer to prey concentrations.

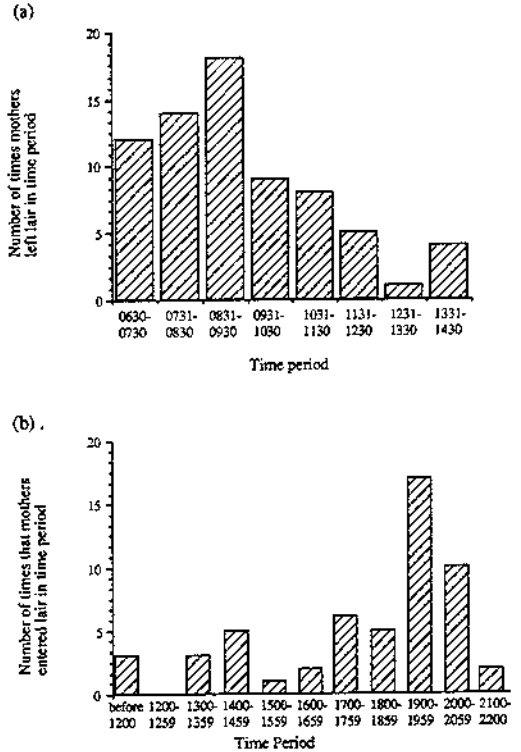

Fig. 2. The number of times that 14 different cheetah mothers left and entered the lair each hour. a: Time mothers left the lair. b: Time mothers entered the lair. Daylight hours were between 0630 and 1900 hours, approximately.

Most (63%) of the 19 moves observed took place in the morning by 1100 hours before mothers left to go hunting. Of the seven moves made later in the day, four were by mothers who did not leave to hunt that day, and two were made by mothers who had stayed away overnight and had only just returned to their cubs.

After litter loss. After litters were killed by predators, fire, or disease, cheetah mothers returned to the lair to search and call for their cubs. One mother who was closely observed, remained near the lair site for at least four days after her cubs perished in a fire, although she left for brief hunting trips when hungry. Other females were less systematically observed, but in eight cases mothers were known to return to the lair site after their cubs were killed or disappeared. Frame and Frame [1981] reported similar behavior in one female whose litter disappeared while she was out hunting.

Survival of Litters to Emergence

Seasonal effects. Only 10 (27.8%) litters, from 9 different females, out of the 36 litters that were born, survived to emerge from the lair (Table 2). There was a

TABLE 3. Variation between individual female cheetahs in the time they left the lair on days they went hunting

Female	No. of days	Time	SE
TGG	8	1118	40
NDO	2	1055	105
BHT	5	1055	33
MK	4	1028	87
BTX	6	1005	49
MV	7	0934	42
MTT	12	0908	29
EMM	7	0902	32
MSH	3	0857	95
DUT	3	0830	42
MQ	4	0825	17
SOF	4	0810	52
RGL	2	0730	10
SKU	4	0709	16
Mean of cases	71	0929	15

tendency for fewer litters to emerge from wet rather than from dry season lairs, although this result did not reach significance (Fisher exact probability, $P = 0.09$). Any seasonal effect on cub survival may result from greater exposure to other predators in the wet season, or possibly from climatic factors.

Effect of lair type. There seemed to be no obvious influence of lair type on the likelihood of cubs surviving to emergence if both seasons are combined, although cell sizes are too small to test (Table 2). However, when the success rate of each lair type was examined by season there was a tendency for vegetation lairs to be less successful than other types of lair in the wet season (Fisher exact probability, $P = 0.07$). Differences in lair type quality may, however, have been obscured by the high mortality rate and the essentially stochastic nature of attacks by predators [Laurenson 1992a].

Effect of mother's age and experience. There was no indication that mother's age or experience had a significant effect on litters' survival. Firstly, the first litter from a young mother was as likely to survive to emergence, and to five months of age, as any other litter (survival to emergence; Fisher exact probability, $P = 0.7$, NS; survival to 5 months: $P = 0.6$, NS). Similarly, the survival rate of all litters from young mothers was comparable to that of all litters from older mothers (emergence, $P = 0.6$, NS: 5 months, $P = 0.6$, NS). Again, the high rate and stochastic nature of mortality in the lair, in combination with a small sample size, may have obscured any differences between young and older mothers.

DISCUSSION

Several strands of evidence suggest that wild cheetah females in the Serengeti National Park, Tanzania, appear to be good mothers and rarely neglect their cubs. Firstly, primiparous females were as successful as more experienced females in raising their cubs. In addition, mothers who had failed to catch prey by nightfall nearly always returned to their cubs at dusk. Lastly, mothers returned to the lair to

search and call for their offspring for several days following the death or disappearance of their litter. Cub abandonment, a major cause of neonatal mortality in captivity, does not often occur in the wild, except under conditions of severe prey scarcity [Laurenson, 1992a]. Although there is little comparative data available from cheetahs under different ecological conditions elsewhere in Africa, this behavior is probably abnormal and specific to the captive situation.

Evidence from both the wild and captivity suggests that excessive human disturbance may contribute to the expression of abnormal behavior. In captivity, human interference and excessive noise were cited as the principal cause of cub mortality at the De Wildt Breeding Center in South Africa [Degenaar, 1977; Brand, 1970]. These made mothers nervous and caused them to repeatedly move their cubs. Cubs were then often abandoned or they died from exposure and consequent pneumonia in adverse weather conditions. This type of abnormal behavior may, however, be more common in wild-caught females which are not used to human activities [D. Lindburg, personal communication]. For example, female cheetahs in San Diego Zoo which are deliberately habituated when young in order to reduce the stress of subsequent handling, have never abandoned any of the 24 litters born there [D. Lindburg, personal communication]. Similarly, increased keeper–animal interaction improved the reproductive success of captive small felids [Mellen, 1991].

Nonetheless, human interference may also contribute to cub mortality in the wild. In the Masai Mara Game Reserve in Kenya, one mother moved her cubs from their hiding place when several tourist vehicles approached extremely close to the lair. During the move, the mother was severely agitated and left one cub temporarily out in the open where it was killed by a secretary bird (*Sagittarius serpentarius*) [D. Richards, personal communication]. Moving cubs may also expose them to the risk of predation by other larger predators such as lions or spotted hyenas (*Crocuta crocuta*). Human interference in other studies may account for the higher rates of lair site moves recorded previously. Cubs were moved every 5.6 days on average in this study, whereas other studies reported moves every 1.5 days over 15 days [Frame and Frame, 1981], every 2 to 3 days [Adamson 1969, 1972] or every 4 days [Ammann and Ammann, 1984]. In the present study, no more than six lair sites were found for any litter, although this is a miminum figure, whereas Adamson's tame but free-living cheetah used 15 and 21 sites over two 6-week periods [Adamson, 1969, 1972]. The discrepancy in these measures may be explained by individual variation or by the continual human interference with the mother and her cubs in the other studies, particularly in Adamson's. Lower levels of interference in this study did not, however, appear to have any significant effect on either the frequency with which litters were moved or cub survival [Laurenson and Caro, 1992].

Taking into account these findings, the importance of providing secluded nest boxes for captive cheetahs is self evident as the lack of suitable denning conditions is a factor that has contributed to cub losses in captivity [Brand, 1980]. Nest boxes were found to improve breeding success in the De Wildt Breeding Center and Columbus Zoo, first because cubs could then be monitored and hand reared if their mothers abandoned them, and second because mothers did not move their cubs around as frequently [Degenaar, 1977; Brand, 1970; Cupps, 1985]. In addition, if video cameras or one-way glass in nest boxes are installed, this reduces human interference, facilitates monitoring, and so may also promote successful breeding [Bertschinger et al., 1984; Cupps, 1985].

In the wild, lairs are simple, consisting of flattened vegetation within an area of thicker cover. However, lair sites varied considerably in their physical features and the amount of protection they provided from the elements (Table I). Although litter survival primarily depended on the chance of avoiding a predator attack, protection from the elements was important in some instances. For example, when weather conditions were cold or wet, the ability of the lair to provide shelter may have been crucial. Young cubs have little thermoregulatory ability and have died from exposure and pneumonia both in the wild and in captivity [Degenaar, 1977; Laurenson, 1992a]. Thus captive nest boxes should be warm and dry, particularly in cold climates and when litters are small. In hot climates, boxes should be well ventilated to prevent susceptibility to disease. Considering the simplicity and variation in wild lair characteristics, it is probably unnecessary to provide elaborate furnishings in captive nest boxes.

Another common feature of lairs in the wild is that they were all in relatively secluded areas, where vegetation was dense or high. Some, particularly those in kopjes or gullies, had difficult access routes. This is probably primarily an antipredator strategy, but suggests that privacy is an essential feature of lair sites [Bertschinger et al., 1984]. Although such antipredator strategies are irrelevant to the captive situation, consideration of the importance that captive females might place on this factor should not be neglected.

The provision of more than one nest box in captivity could also potentially improve breeding success. Both in the wild and in captivity, cheetah mothers frequently move their litters to new lair sites. While noise, disturbance and nervousness may precipitate mothers to move their cubs in captivity, the factors that prompted natural moves in the wild situation are less clear. However, the build-up of parasites or potentially predator-attracting odor may conceivably have been involved, as old lair sites were found to be hopping with hungry fleas 1 or 2 weeks later. It is also possible that disturbance by predators could precipitate moves as on one occasion a female moved her lair site 30 minutes after chasing away a hyena who had approached the lair site inadvertently. On other occasions, females did not, however, move the lair just after seeing a predator nearby. Whatever the proximate factors involved in the decision made by mothers to move their litters, the provision of more than one nest box will enable this natural behavior to be expressed in captivity [Grisham, 1992]. In addition, if captive mothers are accidentally disturbed, provision of more than one suitable lair site may prevent cub losses.

Examination of the patterns of lair site visitation by wild cheetahs also provides useful information to zoo managers. The observation that periparturient females may not eat for several days, noted also by Frame and Frame [1981], and may spend virtually all that time with their newborn cubs, indicates that managers should not be unduly worried if their charges exhibit similar behavior. Captive females should have access to water at all times as this is an important requirement during lactation [Laurenson, 1992b]. Cheetah mothers in captivity exhibiting normal maternal behavior must also be able to rest away from their offspring for at least part of the day and should not be shut into nest boxes. If, however, captive mothers are behaving abnormally by repeatedly moving their cubs, it may be advantageous to restrict their movements [N. Wielebnowski, personal communication].

Wild cheetah cubs can survive for many hours without suckling, as they are routinely left for over nine hours per day in the wild. A litter of three 4-week old cubs,

abandoned by their mother, survived more than 3 days without sustenance [Laurenson, 1992]. Hand-reared cheetah cubs, at least after the neonatal period, may not need to be fed every three hours day and night [Cupps, 1985], although the differential quality of maternal and commercial milk compounds may influence this feeding schedule. Regular feeding schedules that mimic natural conditions should suffice.

CONCLUSIONS

1. Wild female cheetahs used a variety of different lair types, which provided shelter from the elements, protection from predators and access to food and water for the mothers. Lairs in marshes and long vegetation were used more frequently than those in gullies or kopjes, but the relative availability of each lair type was unknown.

2. Primiparous females were as successful at raising cubs as were more experienced females, although differences may have been obscured by high mortality rates.

3. Mothers concealed their cubs in lairs for an average of 8.2 weeks, with larger litters tending to leave the lair at an earlier age than smaller litters. Cubs were moved to new lair sites approximately every 5.6 days.

4. There was considerable variation between individual mothers in the time they left their cubs to go hunting each morning, although the degree of hunger also had an effect. Mothers almost always returned to their cubs at the end of the day, whether they had eaten or not.

5. In captivity, the provision of several secluded nest boxes per enclosure and remote monitoring systems should promote breeding success. Noise and human disturbance should be kept to a minimum.

6. In the wild and in captivity, mothers may not eat for several days around the time of birth. It is normal for cubs to be left alone for many hours at a stretch. Hand-reared cheetah cubs need not be fed at regular intervals day and night.

ACKNOWLEDGMENTS

I would like to thank the Government of Tanzania, Tanzania National Parks, and the Serengeti Wildlife Research Institute for their permission and assitance in carrying out this project. Thanks are also due to Markus Borner who provided invaluable logistical assistance. The manuscript benefitted from comments by Keith Eltringham, Karen McComb, Philip Stander and, in particular, Tim Caro, as well as from discussion with Nadja Wielebnowski. Fieldwork was supported by the Frankfurt Zoological Society, the Leverhulme Trust, the Messerli Foundation and the National Geographic Society. whereas financial support for manuscript preparation came from Hatch funds to Tim Caro at the University of California, Davis.

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