Laurenson MK, Caro TM, Borner M. 1992. Female cheetah reproduction. National Geographic Research & Exploration 8(1):64-75.

Keywords: 1TZ/Acinonyx jubatus/cheetah/conception/cub mortality/Gazella thomsoni/lion/litter/ National Park/predation/prey/reproduction/reproductive success/Serengeti/Thomson's gazelle

Abstract: To provide baseline information for the mounting effort to conserve cheetahs, female reproduction and offspring mortality were studied in a free-ranging population in the Serengeti National Park, Tanzania. Most adult females were capable of reproduction; conceptions were more frequent in wet season months, possibly as a result of increased food availability in the form of newborn Thomson's gazelles. Cub mortality was extremely high, and cheetahs had only a 6% chance of reaching independence at 18 months of age. Predation by lions was the principal source of mortality, although some litters were abandoned by their mothers when nearby prey was scarce. Mothers produced new litters rapidly following the loss of an unweaned litter. These findings suggest that cheetahs may not be able to maintain high densities in the presence of other large carnivores, and that many of the problems zoological institutions experience in breeding cheetahs are specific to the captive context.

Female Cheetah Reproduction

M. KAREN LAURENSON, TIM CARO, AND MARKUS BORNER

Patterns of Female Reproduction in Wild Cheetahs: Implications for Conservation

To provide baseline information for the mounting effort to conserve cheetahs, female reproduction and offspring mortality were studied in a free-ranging population in the Serengeti National Park, Tanzania. Most adult females were capable of reproduction; conceptions were more frequent in wet season months, possibly as a result of increased food availability in the form of newborn Thomson's gazelles. Cub mortality was extremely high, and cheetahs had only a 6% chance of reaching independence at ~18 months of age. Predation by lions was the principal source of mortality, although some litters were abandoned by their mothers when nearby prey was scarce. Mothers produced new litters rapidly following the loss of an unweaned litter. These findings suggest that cheetahs may not be able to maintain high densities in the presence of other large carnivores, and that many of the problems zoological institutions experience in breeding cheetahs are specific to the captive context.

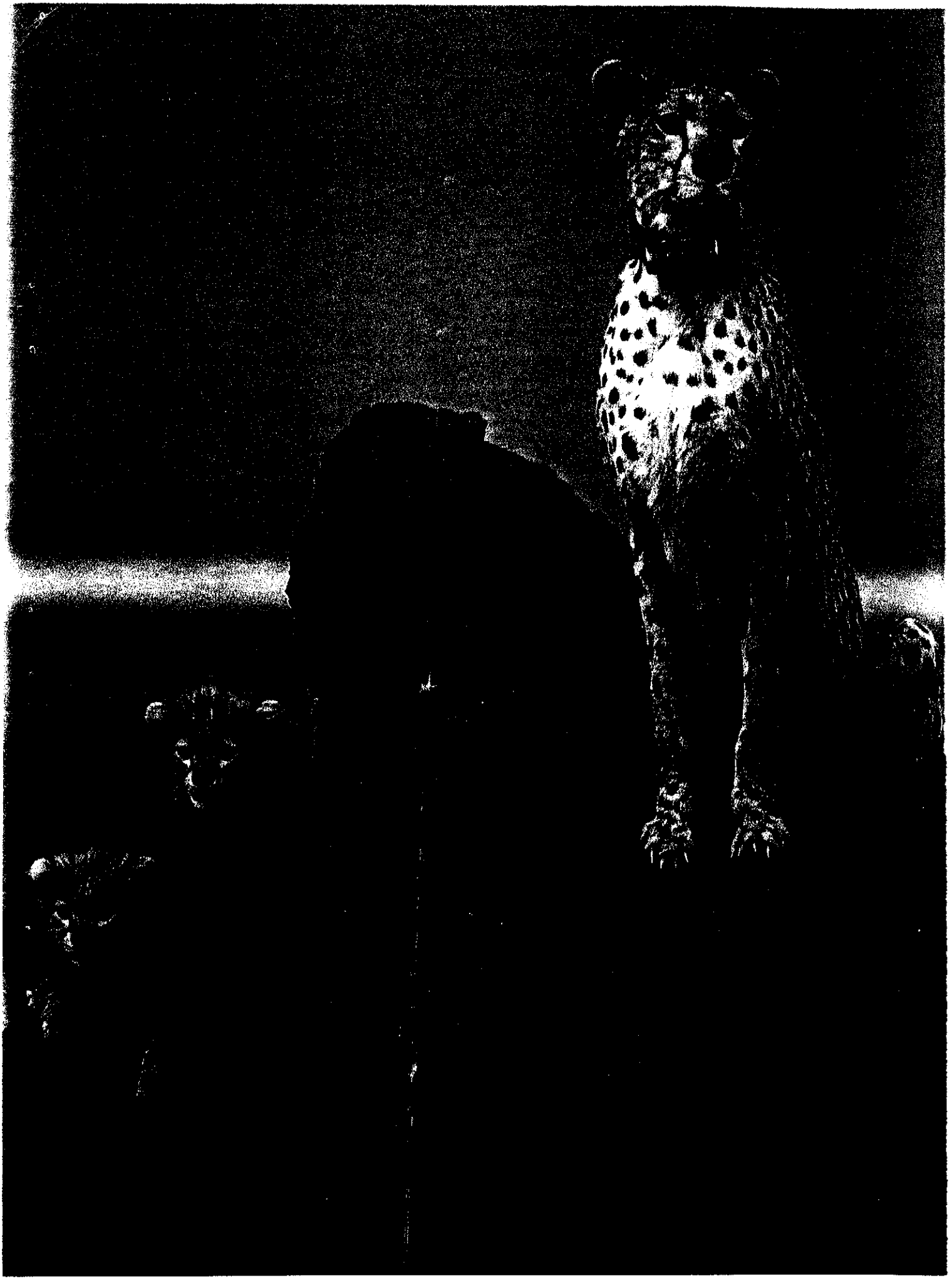
Figure 1.
Female cheetah with 2-month-old cubs (see cover). M. KAREN LAURENSON

AS A CHARISMATIC LARGE CARNIVORE, the cheetah (*Acinonyx jubatus*) (Figure 1) has occupied human attention for millennia.[2] Respected by sportsmen in central Asia who trained it to course for antelope and deer, it has now become a flagship species for dwindling savannah ecosystems. Unfortunately our reverence for this species is not yet matched by our knowledge of its breeding biology and behavior. Without such understanding, the ability of management to increase cheetah numbers in protected areas or to carry out successful captive breeding programs and reintroductions will almost certainly fail.

The factors controlling carnivore numbers in the wild are not well understood, but low female fertility or high cub mortality, which would affect the numbers of juveniles recruited into the adult population, could limit population growth. Earlier fieldwork in the Serengeti National Park, Tanzania, has shown that almost half the males that leave their mothers disappear before reaching adulthood,[8] not through emigration but as a result of dying within the study area, almost certainly in fights with other male cheetahs.[6] Nevertheless, high male mortality is common to most carnivores and so could not explain why, in the Serengeti (~3000 km^2), for example, cheetahs live at much lower densities (500 to 900 individuals) than lions (*Panthera leo*) (~2500) or spotted hyaenas (*Crocuta crocuta*) (~5000).[4]

Cheetahs face additional problems in captivity. Since 1956 when the first litter was raised in a zoo, attempts have been numerous to increase captive stocks that would serve as a buffer against diminishing populations in the wild. However, despite a growing knowledge of baseline reproductive parameters,[28] these attempts have shown limited success. As of 1986, only 17 of 108 females and 12 of 85 males had ever bred in North American zoos.[18] These are far lower proportions than for other felids such as lions and tigers (*Panthera tigris*) where contraception has had to be employed to control reproduction. The captive population is not self-sustaining and falls well below the accepted definition of a viable population.[19] Cheetahs are now listed in Appendix 1 of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) and can be taken from the wild into captivity only in extraordinary circumstances.

In response to this, the American Association for Zoological Parks and Aquaria (AAZPA) launched a Species Survival Plan (SSP) under which a multidisciplinary research program, specifically directed at identifying the causes of poor reproduction in captivity, would be carried out. The purpose of our study was twofold: to provide baseline data on reproduction in



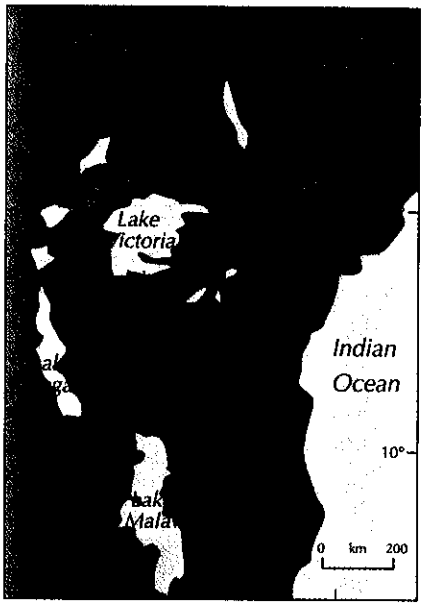


Figure 2.
Study area in eastern Africa, indicated by red square.

wild cheetahs to which captive breeding efforts could turn for comparison, and to determine which reproductive parameters could be responsible for cheetahs' low densities in the wild.

Methods

The study took place on the central plains in the southeast portion of the Serengeti National Park, Tanzania (~3000 km^2 in area, see Figures 2&4) from October 1987 to August 1990 as part of an ongoing long-term study (March 1980 to February 1991) of this carnivore (the park[27] and study area[7] have been described elsewhere). During the wet season (November through May) ~1.3 million wildebeests (*Connochaetes taurinus*), 0.2 million zebras (*Equus burchelli*), and 0.3 million Thomson's gazelles (*Gazella thomsoni*) graze and give birth on the short-grass plains.[27] During the dry season (June through October) these species move off the plains into the woodlands: wildebeests moving west then north, zebras mostly north, and Thomson's gazelles—the main prey of female cheetahs on the plains[24]—northwest, stopping at the plains–woodland border in the general vicinity of the park headquarters at Seronera.[12]

Cheetahs were located by searching a predetermined area of the plains and scanning from hilltops using 10 × 50 binoculars from the safety of a vehicle. Most cheetahs were identified directly or photographed using a 400-mm telephoto lens and subsequently matched to a photographic file index using the unique spot patterns on the flanks, face, and chest[7] or banding on the tail.[9] Previous work had shown that females live alone or with their dependent cubs (Figures 3,5,6) who, after independence, remain together as a sibling group before females leave to lead a solitary existence. Independent females younger than 22 months of age were classified as adolescents, those ~ 23 to 42 months old as young females, and those older than 3½ years as adult females. Males either lived alone or in small, permanent groups of two or three, usually brothers. Some of these males took up residence on a territory while others failed to do so.[8]

Of a population of ~200 females inhabiting the central plains,[7] 20 females were chosen for detailed study. These were animals that were well habituated to the vehicle, could be approached to within 15 m, and could therefore be immobilized using a syringe dart containing 100 mg of ketamine and 125 mg of xylazine fired from a hand-held blowpipe or dart-gun (Zoolu Arms of Omaha) (see Caro and coworkers[10] for details). Once individuals were recumbent, they were carefully examined, a blood sample was taken, and a radio-collar was fitted (Advanced Telemetry Systems, Minnesota). The effect of xylazine was then reversed using the alpha-2 adrenoreceptor antagonist RX 821002A.

Radio-collared females were relocated approximately monthly from a Cessna 182 aircraft with fixed antennae mounted to each wing strut, using a receiver that scanned all the frequency bands of the cheetahs that were collared that month. The pilot (MB) flew at ~610 m (~2000 ft) along a predetermined route until the first signal was picked up from as far away as 40 km but usually from 10 km. Using a switchbox that turned each antenna off alternately, the side of the aircraft from which the signal emanated could be determined. By positioning the aircraft for equal signal strength on both antennae and dropping to tree height, the exact location of the animal was pinpointed and marked on a map divided into 500- ×

M. KAREN LAURENSON, doctoral candidate, Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK.

TIM CARO, assistant professor, Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616.

MARKUS BORNER, East African representative, Frankfurt Zoological Society, c/o Tanzania National Parks, P.O. Box 3134, Arusha, Tanzania.

All three authors are also affiliated with the Serengeti Wildlife Research Institute, P.O. Box 661, Arusha, Tanzania.

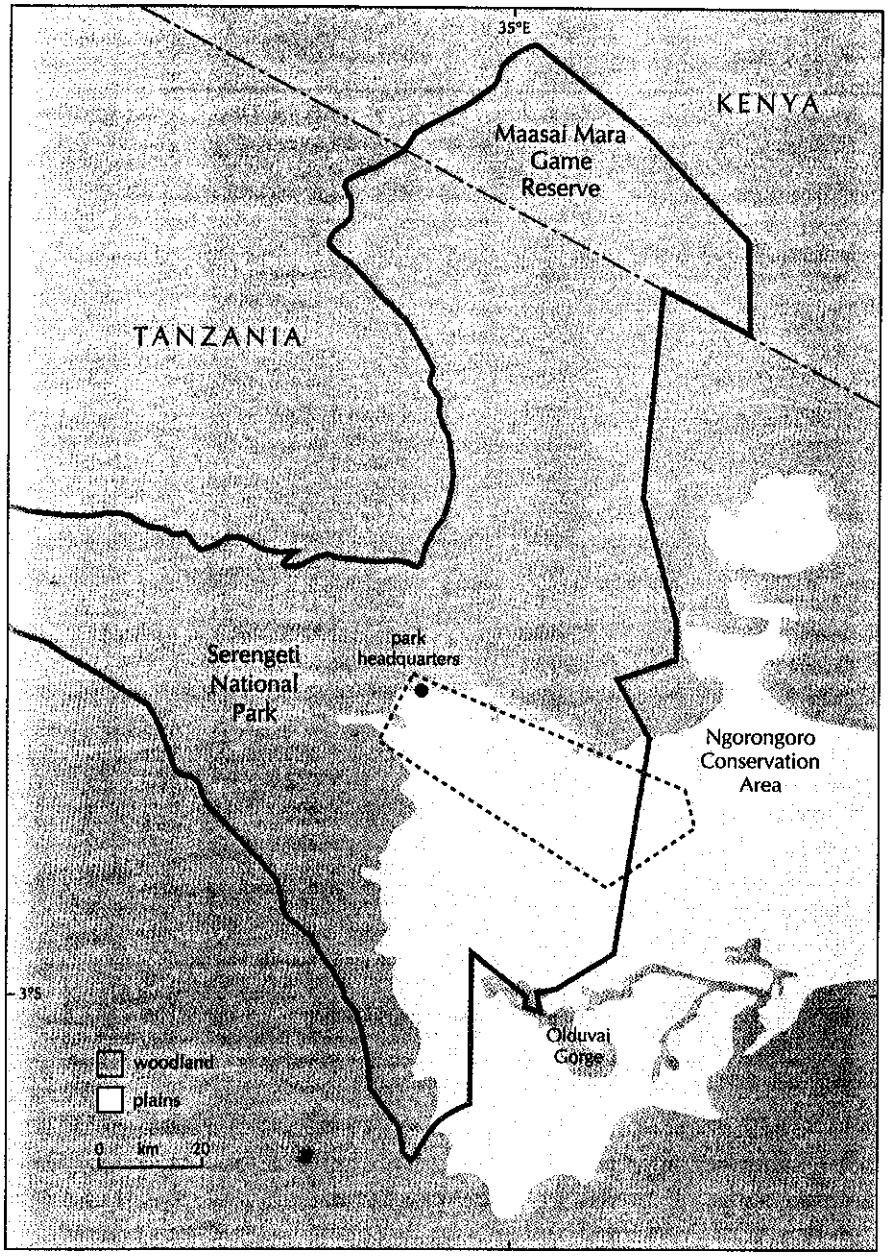


Figure 3.
Two cheetah cubs. Mortality among free-living cubs was high. Only 27.7% emerged from the lair.
M. KAREN LAURENSON

Figure 4.
Serengeti–Mara ecosystem: thick green line outlines the Serengeti National Park; the Masai Mara Game Reserve is in Kenya. The study was conducted on the Serengeti Plains in the southeast corner of the Ngorongoro Conservation Area. The approximate annual home range (800 km²) of a female cheetah is shown by the dashed line.

500-m grid squares. This frequency was then deleted from the receiver. The plane ascended again to 610 m and flew on until the next signal was picked up. The procedure was repeated until all females had been found.

After the flight most females were relocated from the ground vehicle and observed for at least 10 minutes while their reproductive status was assessed. If a female showed well-developed mammary glands and a protruding stomach, she was judged to be heavily pregnant, and was therefore checked again within two weeks to ascertain whether cubs had been born. If lactating, as determined by the presence of brown rings around her nipples and full mammae, she was followed until the lair site was found. When the female went hunting and could no longer see the lair site, MKL searched the marsh, rocky outcrop (locally called a kopje), or other dense vegetation for the cubs. The cubs were then counted, sexed, and weighed, and their age was estimated. Lairs were checked approximately weekly unless cubs died. Detailed observations showed that mothers' behavior did

Explanations that cheetahs exist at low density due to their preference for one type of prey, cannot be taken seriously since work elsewhere (unpublished) has shown that cheetahs have as catholic a diet as other carnivores and are not as specialist as commonly believed.

CORRESPONDENCE

Table 1. **Radiotelemetry of Female Cheetahs, October 1987 to August 1990**

Female Identity	Total Number of Days Female Was Collared	Number of Days from Collaring to Birth of Next Litter	Number of Litters Born
Immobilized as Adults			
MK	535	0*	4
Tigg	520	36	3
Emma	476	11	3
KC	330	52+	3
Siku	491	87	2
Siggy	274	27•	2
Moshi	249	39	2
Maeve	197	35•	2
MQ	181	0*	2
Dutwa	166	108	1
Ndoto	161	83	1
Sophie	158	103+	1
Kosa	161	—	0★
Sarah	280	—	0▲
Immobilized as Young			
Matti	592	2	4
Bellatrix	561	262	2
Bahati	768	327	2
Rigel	173	114	1
Anna-Mary	356	264	1
Malaika	226	—	0

*Collared while lactating; + decollaring date was taken as the date of mother's death; • day of collaring was taken as the date the previous grown cubs were estimated to have separated from their mother; ★ this female had raised a daughter to independence and was collared just after another 5-month-old cub had disappeared; ▲ this female was never seen heavily pregnant or lactating although resighted approximately once a month while collared.

Figure 5.
Cheetah cub. Between two and five litters were abandoned by mothers who had to move long distances to find herds of gazelles.
M. KAREN LAURENSON

not obviously change after dens had been examined, and such dens were no more subject to predation (Fisher exact probability test, $p>0.3$) or abandonment (Fisher test, $p>0.3$) than were those that had not been entered.

Results

PATTERNS OF REPRODUCTION

Cheetahs are polyestrus, cycling approximately every 12 days (range 10 to 21 days),[3] and are probably induced ovulators (correspondence 1990, D. Wildt, reproductive physiologist for felids). Since estrous behavior is difficult to identify both in captivity and in the wild[25] and we never witnessed a mating during 10 years' observations, the best method of determining estrous activity and fecundity is to monitor subjects' reproductive condition regularly and pinpoint the times that they give birth. Conception dates can then be estimated by subtracting 93 days, the length of the gestation period.

REPRODUCTIVE POTENTIAL

Most female cheetahs in our detailed study appeared capable of reproduction. Only two of 14 adult females failed to reproduce during the time

they were radio-collared (Table 1). One of these was known to have reproduced successfully just beforehand and was only followed for five months. The other had raised a cub two years before but was now an old female. One young female also failed to reproduce, but judging from the time it took others to give birth, she may not have been followed for long enough. Taking adult and young females together, 15% (n=20) failed to reproduce while collared but only 5% (one young female) had never had cubs. These figures contrast sharply with data from captive animals where 84.3% of females were barren.[18]

Females readily conceived again after losing a litter. Table 2 shows the estimated number of days from the death of a previous litter to the birth of the next. By subtracting gestation length, it can be seen that, on average, adult females mated within three weeks of losing the previous litter. Some individuals conceived at first resumption of estrus just two and five days later. A tame cheetah of Joy Adamson's[1] also conceived again three weeks and then again one week after losing two unweaned litters.

The interval between the death of the previous litter and next successful conception was longer for young (n=3 different mothers, $\bar{x}$=86.3 days) than for adult females (n=9, $\bar{x}$=17.8 days) (Mann-Whitney U test, U=1, p<0.02) (Table 2). At present we are unable to explain the difference, but younger females may have been less fecund than older females.

Mothers who successfully raised litters did not have to wait until their grown up cubs left them before reproducing again; they often conceived before the previous litter had left although none gave birth before the family split up (Table 3). Adamson[1] reported a female that gave birth to her second litter while accompanied by her first, although this female was additionally provisioned.

SEASONALITY OF CONCEPTIONS AND BIRTHS

Although litters were conceived throughout the year in Serengeti, fewer litters were conceived during dry season (n=7 litters) than wet season months (n=29 litters, χ^2=6.32, df=1, p<0.02, basing expected values on seven wet and five dry season months) (Figure 7).

The seasonality of conceptions was surprising since females readily conceived after losing a previous litter, although George Schaller also noted that, in a smaller sample of 14 litters, none were born between September

Table 2. **Interval between Reproductive Events**

Female Identity	Death Of Previous Litter To: (estimated in days)	
	Next Birth	Next Successful Conception
Adult Females		
Tigg	117	24
Tigg	131	38
MK	108	15
MK	115	22
MK	120	27
Emma	98	5
Emma	223	130*
Maeve	101	8
Siku	140	47
Moshi	105	12
KC	95	2
KC	110	17
MQ	106	13
Siggy	106	13
Mean	111.7	18.7
Young Females		
Matti	157	64
Matti	116	23
Matti	123	30
Btrx	161	68
Bhti	245	152
Mean	160.4	67.4

* A female with pyometra of the uterus was not included in calculation of the means.

Table 3. **Evidence of Conception before the Previous Family Separated**

Female Indentity	Date Previous Litter Left	Estimated Date of Conception of Next Litter	Estimated Birth Date of Next Litter	Conceived Before Previous Left?
MQ 1	6/02/88 (±58)	2/01/88	4/04/88	possibly
MQ 2	27/07/89 (±16)	30/05/89	1/09/89	yes
Emma	16/03/88 (±12)	25/01/88	27/04/88	yes
Ndoto	10/11/88 (±34)	6/12/88	8/03/89	possibly
Maeve	16/01/89 (±30)	19/11/88	20/02/89	yes
Siku*	28/02/89 (±59)	24/04/89	26/07/89	no
Siggy	13/04/90 (±29)	7/02/90	10/05/90	yes

* Cub may have died as it was only 12 to 13 months old at separation.
Brackets refer to the number of days either side of the given date that the previous litter could have left the mother

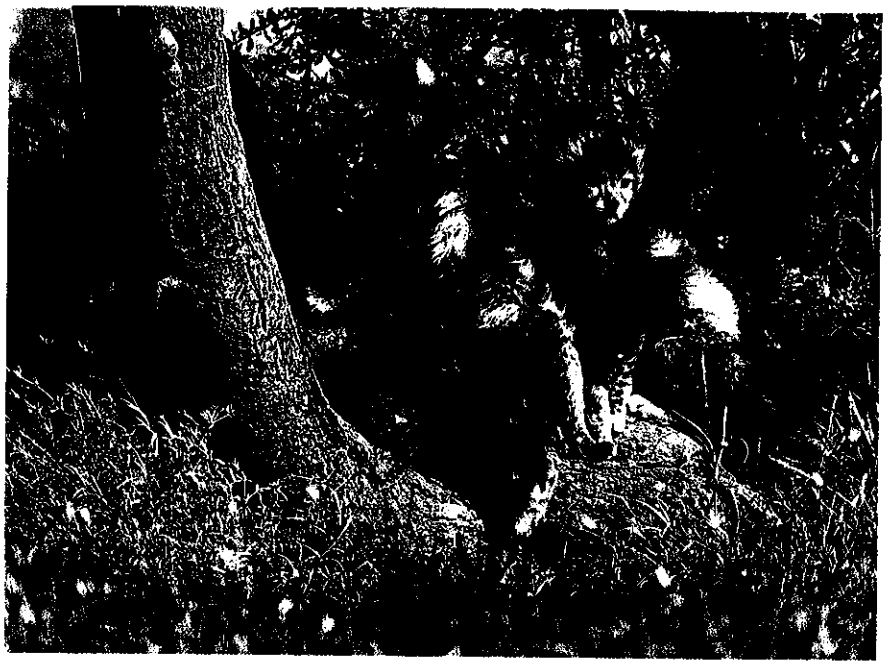


Figure 6.
Two 8-week-old cubs.
M. KAREN LAURENSON

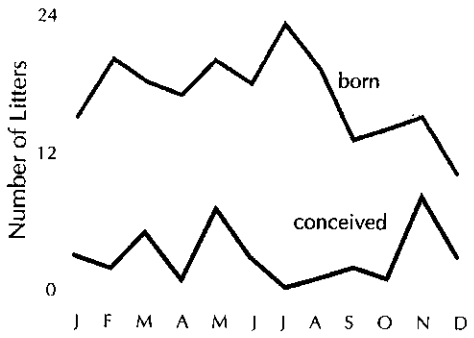


Figure 7.
Reproductive events during each month of the year.

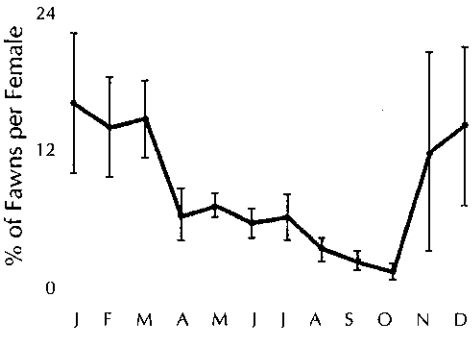


Figure 8.
Mean and SE percent of Thomson's gazelles neonates and fawns per reproductive female each month of the year.

and December,[24] also corresponding to fewer conceptions in the dry season. Timing of offspring mortality could not account for this since there was no difference in the number of litters dying in the wet (n=16 litters) and dry (n=10 litters) seasons (χ^2=0.110, df=1, NS). However the next conception was more probable in a wet season month (n=15 conceptions) than in a dry season month (n=4 conceptions) following the loss of an unweaned litter (χ^2=3.322, df=1, p<0.1). Also, females that lost a litter in the dry season took somewhat longer to conceive successfully again than those that lost theirs in a wet month (n=5 losses, $\bar{x}$=49.4 days; n=9, $\bar{x}$=15.0 days, respectively, Mann-Whitney U test, U=8, p<0.1).

Furthermore, litters conceived in the wet season may be larger than those conceived in the dry season, although the difference was not significant (mean litter sizes: wet=3.6 [n=23], dry=3.0 [n=7], Mann-Whitney U test, U=51.5, p=0.13, NS).

Day length varies little on the equator so was unlikely to be responsible for the observed seasonality. Shortage of males could not account for it either, as females encountered them on their territories or were sought out by roving males year round. Radio-collared female lions in the Serengeti came into estrus more often during the time of prey abundance than when prey was scarce.[22] In domestic mammals, a decrease in nutrition can lengthen the interval between estrous periods and cause the suppression of behavioral estrus.[23] In agricultural practice, it is common to increase the plane of nutrition (known as "flushing") to enhance both the number of livestock coming into estrus and litter size. A difference in nutrition between wet and dry seasons might therefore account for the observed seasonality of conceptions. Female cheetahs closely follow the movements of Thomson's gazelles throughout the year so adult gazelles are available in all seasons. Nonetheless, more Thomson's gazelle fawns are born in the wet than in the dry season (Figure 8), and these young gazelles are the preferred prey of adult females[15] because they are easy to catch.[14] We suspect that availability of gazelle fawns, rather than the distribution of adult gazelles, could be an important factor in promoting conception.

Despite more litters being conceived in the wet season, no more litters were born then (n=20 litters) than in the dry season (n=16 litters, χ^2=0.114, df=1, NS). This is not surprising given that the length of the

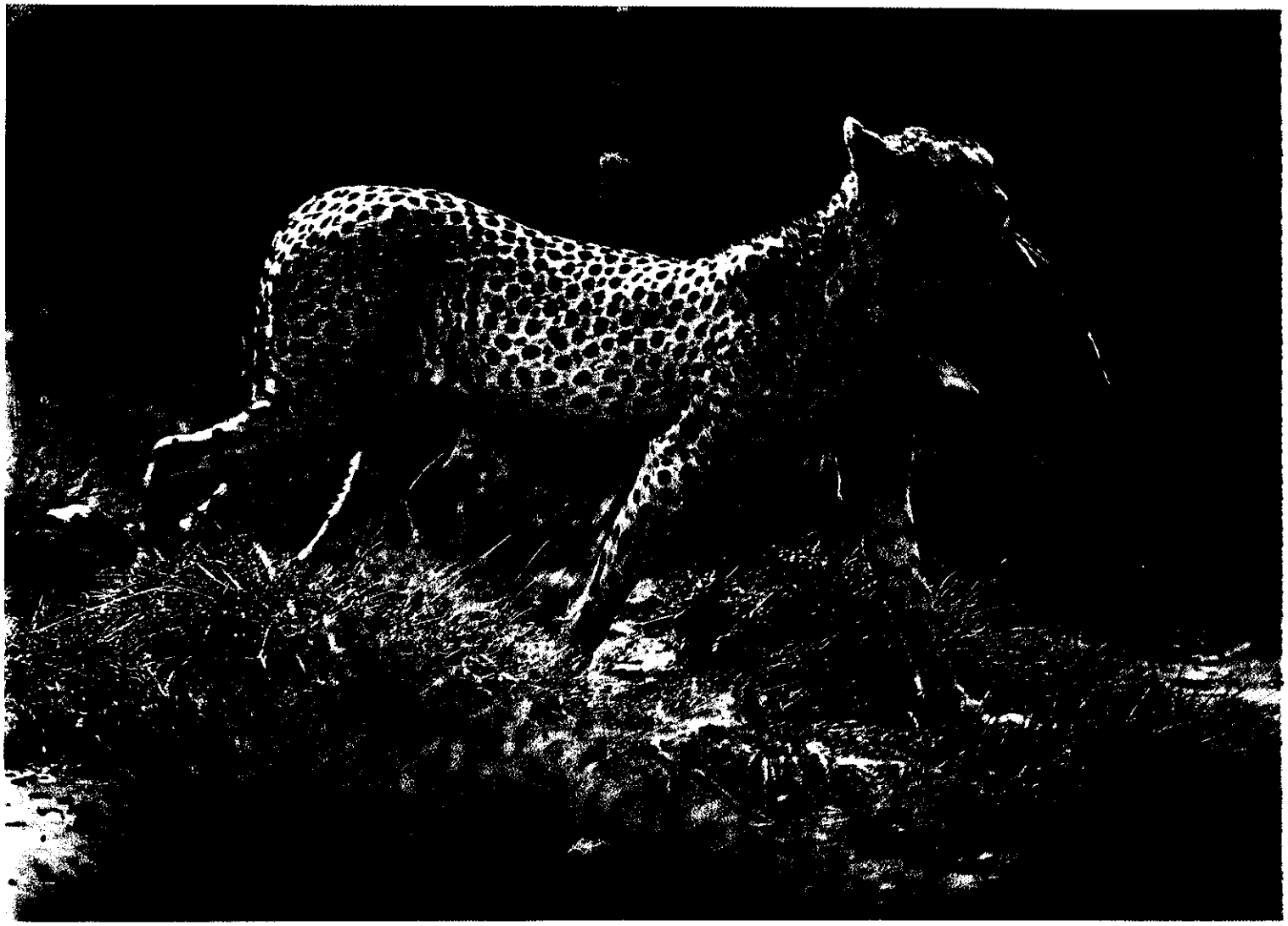


Figure 9 (above).
Female cheetah with cub killed by a lion. Mothers are unable to defend their cubs against the much larger lion.
M. KAREN LAURENSON

Figure 10 (left).
One-week-old cubs in a long grass lair.
M. KAREN LAURENSON

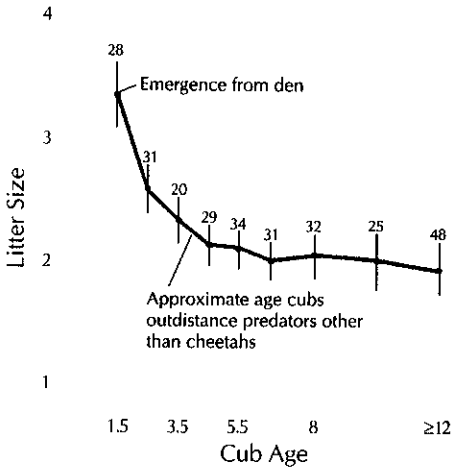


Figure 11.
Mean number and SE of cubs seen in different-sized litters plotted against cub age over the 10-year study.

gestation period may often take the birth date into a different season. Using a larger sample of litters from our 10-year study period that were first observed only after emerging from the lair, 115 and 87 litters were born in the wet and dry seasons, respectively (χ^2=0.017, *df*=1, NS), confirming the earlier result (Figure 7).

TIMING OF FIRST BREEDING

Cubs that survived and retained contact with their families stayed with their mothers for an average of 509.4 days (*n*=17, SE=10.5 days, range 433 to 577 days), or 18.2 months. After offspring had left their mothers, they remained together as a sibling group for an average of 186.7 days (6.7 months, *n*=8 litters). Females thus separated from their littermates between 647 and 760 days of age (23.1 to 27.1 months, *n*=8 litters) and first gave birth at an average of 36 months (*n* = 4 females). This is a year later than the two individuals Schaller[24] recorded in the same study area (24 months) and Adamson[1] recorded for a tame but free-living female (25 months). Individual differences might possibly account for this discrepancy. Our figures are within the range observed in captive females.[17]

Cub Mortality

The mean number of cubs at birth was 3.5 with the modal litter size being 3 (Figure 11). The mean was probably an underestimate, since litters were not examined at birth but, on average, 14.8 days after parturition (range 6 to 35 days), and some cubs may have died before counting. For comparison, 3.7 was the average litter size in captivity in North America from 1956 to 1985,[18] and 3.9 was the average for litters in South Africa from 1973 to 1977.[11] Sex of cubs in the lair did not differ from unity (51 males and 39 females, binomial test, z=−1.160, NS).

Mortality among free-living cheetah cubs in the lair was high. Of the 36

Figure 12.
Cubs killed by a lion. Lions sometimes located lairs by observing cheetah mothers sit up in the marsh or bush where cubs were hidden.
M. KAREN LAURENSON

litters born, only 10 (27.7%) emerged from the lair, or 34.6% of the 104 cubs counted while still in the lair (Figures 10&13). The principal cause of cub mortality in the lair was predation. In our study, lions were seen killing two litters, and predation was suspected in another nine cases because, for example, the mother was found near the lair site although her previously healthy cubs had suddenly disappeared. Lions sometimes located lairs by observing cheetah mothers sit up in the marsh or bush in which cubs were hidden. They would then rush at the cheetah family and kill the relatively immobile cubs with a bite through the head or spine, but did not always eat them. Mothers were unable to defend their cubs against these much larger predators (Figures 9&12). Between two and five litters were abandoned by cheetah mothers when females had to move long distances (18-km round-trips) from the lair to locate herds of Thomson's gazelles. In addition, two litters probably perished as a result of exposure and one died in a grass fire; causes of death of the other seven litters were unknown.

Once cubs had emerged from the lair and accompanied their mother, they were still subject to high mortality. Of the 10 litters that left the lair, three were lost entirely, and all suffered some reduction in number. Cub numbers were reduced by 52.8% from when they were first seen outside the lair until approximately 3 months of age. Causes of cub mortality were less easy to decipher at this stage because the family was simply relocated with a diminished number of cubs. However, we and other observers in East Africa have witnessed a variety of predators, especially lions and spotted hyaenas, taking cheetah cubs. Some cubs managed to escape predation because they scattered and hid when the predator rushed at them and subsequently were able to rejoin their mother.

Cub mortality declined somewhat in the fourth month, although it was still high in our detailed study. At least seven cubs (41.2% of cubs alive at 3 months) were known to have died, although this figure could be higher as only one litter has reached independence, and not all litters have been resighted. Nevertheless we suspect that predation had a lower impact at this time, since after 14 to 16 weeks cubs were usually swift enough on their feet to outdistance predators. Moreover, few observations have been recorded of cubs dying during this period; MKL had reports of one cub being killed by a lion, and David Burney[5] noted a 9 ½-month-old cheetah cub that was wounded by a leopard (*Panthera pardus*) and finished off by spotted hyaenas.

By the time cubs reach independence, 1.9 to 9.6% of the total number of cubs initially counted had managed to survive (Table 4). Thus at birth, cubs had approximately only a 6% chance of reaching independence.

We consider the section on the importance of these results for captive breeding to be vital to bridge the gap between the husbandry of cheetahs in zoos and their behavior in the wild. Given that cheetahs do not breed well in captivity, and that much time and effort is being invested to discover why this is the case, we feel that this information is particularly valuable.

CORRESPONDENCE

Table 4. **Survival of Cheetah Cubs**

	Litters	Cubs
Number Counted in the Den	36	104
Number Emerging from the Den	10	36
Number Alive at 3 Months	7	17
Number Alive at Independence	1–5	2–10

Discussion

PROTECTION IN THE WILD

Results presented here have implications for conservation of cheetahs both in the wild and in captivity. In the Serengeti, cheetah cub mortality is high compared with that of lions in the same area where two thirds of cubs die between emerging from the den and 1 year of age, and extremely high compared with the Ngorongoro Crater lion population where only one third die over the same age span.[21] Cheetah cub mortality over the same period is between 72 and 94% and from birth to independence is between 90 and 98%. Low cub survivorship may be a critical factor in

Figure 13.
Ten-day-old cubs in lair. Females readily conceived new litters after losing a litter. On average, adult females mated within three weeks of losing the previous litter.
M. KAREN LAURENSON

explaining low population density of cheetahs in the Serengeti. Although adult cheetahs can probably replace themselves during their lifetime because, on average, two of their cubs will eventually reach reproductive age, cub losses mean they cannot produce many more than this. After independence, a further 50% of males are lost from the population primarily due to competition over access to territories.[7] However, without data on adult female mortality we cannot assess whether cub or adult mortality is numerically more important in limiting cheetah numbers in the wild.

The principal source of mortality is predation in our study, especially from lions. Lion and spotted hyaena populations have risen sharply in the park over the last 20 years,[4] so their impact may also have increased. We cannot assess this directly, but the average cheetah litter size at independence was ~2.6 in the mid 1970s[16] compared with 1.9 in this study, although the litter sizes at emergence were similar (3.1 in the 1970s, 3.3 in the 1980s) (Figure 13).

Low densities of cheetahs in other protected areas and throughout their range[19] do not rule out the importance of predation on cubs elsewhere. Increasing human population pressure and agricultural practice outside park boundaries are already restricting large predators to protected areas. Paradoxically, cheetahs may fare better in areas that are not protected, provided the areas are not given over to agriculture and that cheetahs are tolerated by pastoralists. Burney[5] has already suggested that cheetahs do well outside the Masai Mara Game Reserve in Kenya for these very reasons.

BREEDING IN CAPTIVITY

Very few captive females have ever reproduced. Our limited data indicate that female cheetahs' fecundity is not physiologically or behaviorally compromised in the wild and that their inability to conceive is specific to the captive situation.

From our Serengeti findings estrus appears to be facilitated by enhanced access to food. However, captive females may already be receiving a high level of nutrition,[10] and obesity can contribute to estrus failure. Clearly, the possibility of promoting estrus by manipulating food supply—for example, by reducing food to then provide a rising plane of nutrition — demands attention.

In captivity, cub mortality remains high despite intensive management practice, but it is not appreciably greater than that of many other exotic species.[20] An average of 36.4% of cubs died before reaching 6 months of age at the De Wildt, Whipsnade, and North American breeding facilities. There were a variety of reasons,[18] but maternal neglect was important.[11] The variation in mortality rates among establishments suggests that husbandry conditions may be an important influence. In the wild, mortality stems primarily from predation, secondarily from environmental factors, and thirdly from abandonment. In neither situation is there strong evidence for mortality as a result of disease complications stemming from a compromised immune system or of poor offspring viability which could result from the cheetah's genetic monomorphism. The only common factor in the two situations is poor mothering, but in captivity it is often related to excessive human interference or loud noise[11] while in the wild, to circumstances related to lowered food intake. Thus the solutions to cub mortality in captivity must be sought within the husbandry system for captive cheetahs, not from the natural situation.

Data showing that mothers can become pregnant before the previous

litter has departed are pertinent to captive management. Numerous studies, of primates in particular, indicate that early separation of offspring from mothers leads to behavioral disorders such as abnormal sexual behavior or inability to form social relationships.[26] Keeping mammalian offspring with mothers for as long as occurs in the wild is desirable but conflicts with zoos' other goal of maintaining a high reproductive turnover of animals. In cheetahs, these conflicting goals can be partially reconciled by introducing males to mothers before their large cubs are removed.

REFERENCES

1. **Adamson, J.**: *The Spotted Sphinx.* Collins, London; 1969.

2. **Ammann, K.; & Ammann, K.**: *Cheetah.* Camerapix Publishers International, Nairobi; 1984.

3. **Bertschinger, H.J.; Meltzer, D.G.A.; van Dijk, A; et al.**: Cheetah lifeline. *Nuclear Active* 30:2–7; 1974.

4. **Borner, M.; FitzGibbon, C.D.; Borner, M.; et al.**: The decline in the Serengeti Thomson's gazelle population. *Oecologia* 73:32–40; 1987.

5. **Burney, D.A.**: The effects of human activities on cheetah (*Acinonyx jubatus*) in the Mara region of Kenya. MSc thesis, University of Nairobi; 1980.

6. **Caro, T.M.**: *Cheetahs of the Serengeti Plains: Group Living in an Asocial Species.* University of Chicago Press, Chicago; in press.

7. **Caro, T.M.; & Collins, D.A.**: Male cheetahs of the Serengeti. *National Geographic Research* 2:75–86; 1986.

8. **Caro, T.M.; & Collins, D.A.**: Male cheetah social organization and territoriality. *Ethology* 72:52–64; 1987.

9. **Caro, T.M.; & Durant, S.M.**: Use of quantitative analyses of pelage characteristics to reveal family resemblances in genetically monomorphic cheetahs. *Journal of Heredity* 82:8–14; 1991.

10. **Caro, T.M.; Holt, M.E.; FitzGibbon, C.D.; et al.**: Health of adult free-living cheetahs. *Journal of Zoology* 212:573–584; 1987.

11. **Degenaar, J.P.**: Aspects of reproduction in captive cheetah (*Acinonyx jubatus*). MSc thesis, University of Pretoria; 1977.

12. **Durant, S.M.; Caro, T.M.; Collins, D.A.; et al.**: Thomson's gazelles and cheetahs on the Serengeti Plains. *African Journal of Ecology* 26:257–268; 1988.

13. **FitzGibbon, C.D.**: The antipredator behaviour of Thomson's gazelles. PhD thesis, University of Cambridge; 1988.

14. **FitzGibbon, C.D.**: Anti-predator strategies of immature Thomson's gazelles: Hiding and the prone response. *Animal Behaviour* 40:846–855; 1990.

15. **FitzGibbon, C.D.; & Fanshawe, J.H.**: The condition and age of Thomson's gazelles killed by cheetahs and wild dogs. *Journal of Zoology* 218:99–107; 1989.

16. **Frame, G.W.**: Cheetah ecology and behaviour. *Serengeti Research Institute Annual Report 1975–1976*, 74–87;1976.

17. **Marker, L.**: *North American Regional Cheetah Study Book.* Wildlife Safari Publications, Winston, OR; 1986.

18. **Marker, L.; & O'Brien, S.J.**: Captive breeding of the cheetah (*Acinonyx jubatus*) in North American zoos (1871–1986). *Zoo Biology* 8:1–20; 1989.

19. **Myers, N.**: *The Cheetah* (Acinonyx jubatus) *in Africa.* IUCN monograph, Morges, Switzerland; 1975.

20. **O'Brien, S.J.; Roelke, M.E.; Marker, L.; et al.**: Genetic basis for species vulnerability in the cheetah. *Science* 227:1428–1434; 1985.

21. **Packer, C.; Herbst, L.; Pusey, A.E.; et al.**: Reproductive success in lions. Clutton-Brock, T.H., editor: *Reproductive Success.* Chicago University Press, Chicago; 1988.

22. **Packer, C.; Scheel, D.; & Pusey, A.E.**: Why lions form groups: Food is not enough. *American Naturalist* 136:1–19; 1990.

23. **Rattray, P.V.**: Nutrition and reproductive efficiency. Cole, H.H. & Cupps, P.T., editors: *Reproduction in Domestic Animals.* Academic Press, New York; 1977.

24. **Schaller, G.B.**: *The Serengeti Lion: A Study of Predator–Prey Relations.* Chicago University Press, Chicago; 1972.

25. **Seager, S.W.J.; & Demorest, C.N.**: Reproduction of captive wild carnivores. Fowler, M.E., editor: *Zoo and Wild Animal Medicine.* W. B. Saunders, Philadelphia; 1978.

26. **Simpson, M.J.A.**: Tactile and sexual behaviour: Aspects of development with special reference to primates. Hutchison, J.B., editor: *Biological Determinants of Sexual Behaviour.* John Wiley and Sons, Chichester, 785–807; 1978.

27. **Sinclair, A.R.E.**: The Serengeti Environment. Sinclair, A.R.E. & Norton-Griffiths, M., editors: *Serengeti: Dynamics of an Ecosystem.* Chicago University Press, Chicago, 31–45; 1979.

28. **Wildt, D.E.; Platz, C.C.; Seager, S.W.J.; & Bush, M.**: Induction of ovarian activity in the cheetah (*Acinonyx jubatus*). *Biology of Reproduction* 24:217–222; 1981.

ACKNOWLEDGMENTS

We thank the government of Tanzania for permission to conduct research; the Serengeti Wildlife Research Institute and Tanzania National Parks for facilities and help; and the National Geographic Society, the Frankfurt Zoological Society, the Leverhulme Trust, and the Messerli Foundation for financing the project. We also thank Barbie Allen, Sarah Gascoyne, Peter and Marianne Hetz, Karim Hirji, Richard Kock, Hassan Nkya, and Charlie Trout for invaluable help in the field and for logistical support, Marcella Kelly for collation of data, and Clare FitzGibbon for allowing her gazelle-count data to be added to our own. She, Sarah Durant, and David Wildt made helpful comments on the manuscript.