

Laurenson MK. 1995. Behavioural costs and constraints of lactation in free-living cheetahs. *Animal Behaviour* 50:815-26.

Keywords: 1TZ/*Acinonyx jubatus*/cheetah/cub/hunting/lactation/prey/reproductive biology/Serengeti

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Behavioural costs and constraints of lactation in free-living cheetahs

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Abstract. Increased energetic expenditure during lactation must be met either from metabolic stores or by increasing food intake. Additional behavioural costs and constraints may be imposed on those species that conceal their young in a fixed place. This study examines how wild cheetahs, *Acinonyx jubatus*, alter their behaviour during lactation and whether denning involved extra costs or constraints. Females almost doubled their food intake when lactating, although only mothers with cubs in the lair increased the time they spent drinking. Higher levels of food intake were achieved by catching a greater proportion of larger prey items, hunting these at a higher rate and by increasing the success rate of hunts. Lactating females with emerged cubs increased the proportion of time they spent observing and hunting relative to time spent resting and moving. When lactating females had cubs in the lair they were on the move for longer each day, travelled further, had restricted ranging patterns and tended to make more kills in the heat of the day than when accompanied by their cubs. These latter results suggest that the need to find a safe place, near water, in which to conceal immobile and vulnerable cubs may impose additional behavioural constraints and costs on lactating females.

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Lactation is generally recognized to be the most energetically costly component of reproduction in mammals. Energy expenditure can increase two- to five-fold above basal metabolism and thus behavioural energetics may be important for measuring the actual cost of lactation and so also parental investment (Hanwell & Peaker 1977; Millar 1977; Oftedal 1985; Gittleman & Thompson 1988). Energy costs during lactation stem from several sources: from milk production, from changes in metabolic rate and from changes in activity level (Thompson & Nicoll 1986; Oftedal & Gittleman 1989). Activity levels rise if foraging behaviour increases to meet all or part of these new energetic demands (Altmann 1980; Gittleman & Thompson 1988), but may also increase in response to the need to care for young by defending, grooming or carrying them (Rood 1990; Altmann & Samuels 1992). In addition, activity levels may rise if lactating females are

forced to seek out water supplies on a regular basis to meet increased fluid requirements which can be twice those of basal needs (Pond 1977).

Many studies have examined the energetics of milk production (see Oftedal 1985; Gittleman & Oftedal 1987 for reviews) but fewer have examined the behavioural strategies that females adopt to meet these energetic demands in the wild (e.g. Altmann 1980; Clutton-Brock et al. 1982; Dunbar & Dunbar 1988; Higgins et al. 1988). These studies have found that the pressures to meet one requirement during lactation may be constrained by the need to meet a more critical one. For example, bighorn sheep, *Ovis montanus*, move to poorer quality pasture, compromising their energy intake, to reduce the predation risk to their neonates (Pesta-Bianchet 1988). Lactating Grevy's zebras, *Equus grevyi*, also use inferior pasture, but they do this in order to maintain access to water (Ginsberg 1989).

In general these studies have been conducted on species with relatively precocial offspring that accompany the mother. An additional constraint, or costs, may be imposed on the behaviour of species, such as carnivores, that conceal young in

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a fixed place such as a lair or den. For example, wild dogs, *Lycan pictus*, have a restricted ranging pattern at this time (Malcolm & Marten 1982), whereas recent work on spotted hyaenas, *Crocuta crocuta*, that rely on a migratory prey base (Hofer & East 1993) indicate that the commuting effort of denning females is 2.6–3.2 times greater than that of non-denning females. The constraints of denning have not, however, been considered in detail in these or other studies.

In this paper I ask two questions. First, what behavioural strategies does the cheetah, *Acinonyx jubatus*, a species that conceals its altricial young in a lair, adopt in order to meet the energetic demands of lactation? Specifically, changes in food and water intake, hunting behaviour, and activity budgets are investigated. Second, I ask whether the concealment of cubs in the lair imposes a constraint on maternal activity, or additional costs, by comparing these same behavioural measures before and after mothers lead their cubs from the lair.

METHODS

Study Area and Locating Study Animals

The study was carried out between October 1987 and August 1990 in a 2500-km² area of the central plains of the Serengeti National Park and Ngorongoro Conservation Area in Tanzania (see Sinclair 1979 for a general description). In most years rainfall increases between November and May, the wet season, and is scarce in the dry season, June–October. On the Serengeti plains, previous work has shown that cheetah females live alone or with their dependent cubs (Frame & Frame 1981; Caro 1991) and give birth for the first time at approximately 36 months of age (Laurenson et al. 1992). Males live either alone or in permanent coalitions of two or three individuals (Caro & Collins 1986). Some males exhibit territorial behaviour in small areas (40 km²) where female cheetahs congregate seasonally (Caro 1994). Females and non-territorial males have annual home ranges of 800 km² on average, with extensive range overlap. These cheetahs follow the Thomson's gazelle, *Gazella thomsoni*, migration, from the short grass plains in the wet season to the plains-woodland boundary in the dry season (Durant et al. 1988).

On most mornings during the study, a predetermined area within the study site was searched for

cheetahs. The vehicle was driven to hill tops or other vantage points and the surrounding area, up to 2 km away, was scanned using 10 × 40 binoculars. When a cheetah was sighted, it was approached and identified by matching its unique pattern of spots or tail banding to a photographic file index. In some cases photos were taken for subsequent identification. Out of approximately 60 female cheetahs that use the central Serengeti plains, 20 well-habituated females were chosen for intensive study. Fourteen of these females were fully grown and had previously reared cubs to maturity. Six were young and had not reared cubs previously. Females were immobilized, fitted with a radio collar (see Laurenson & Caro 1994) and then relocated on a monthly basis by aerial radio telemetry and their reproductive status assessed by observing them on the ground as soon as possible after the flight. 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 the female was lactating, I located her den site by radiotracking from the vehicle at daybreak when mothers were almost always with their cubs (Laurenson 1993). When the female left to go hunting and was well away from the den, the cubs were counted, sexed, weighed and their age estimated. Neither cub survival nor mother's behaviour was overtly altered by these techniques (Laurenson & Caro 1994). Litters were then checked weekly until they either emerged from the lair at approximately 8 weeks of age, or died.

Observation Schedules

I conducted intensive 5-day observation periods at three stages when females were of different reproductive status: no cubs; females who had no dependent cubs; they could be pregnant; cubs in lair; lactating females who had 2.5–5-week-old cubs concealed in a lair; emerged cubs; lactating females who had cubs that had emerged from the lair within the previous 1–3 weeks.

Observations were made from a Land Rover during daylight hours, usually 0630–1900 hours. Cheetahs were watched from a distance of 0 m (when they sat on the vehicle) to 300 m using either 10 × 40 binoculars or the naked eye. It was not possible to collect full sets of data on all individuals, as cubs often died before emergence,

but 44 full follows were completed, over 2600 h of direct observations.

Behavioural measures

The activity of each cheetah, including cubs if present, was recorded using instantaneous sampling at 15-min intervals during daylight hours (Altmann 1974). Activities were defined as follows: Resting (lying with flank and hindquarters touching the ground), Observing (sitting up or standing still), Moving (walking or running), Hunting (crouching at, stalking, trotting towards, rushing at or chasing prey) and Eating (chewing meat). The number of scans in which females were recorded in each activity pattern was divided by the total number of scans per day, to give a measure of the proportion of time that females spent in each activity per day. A mean value for each female from each observation period, taken over all days, was used in the analysis. The proportion of time spent observing or resting was calculated as the sum of these activities inside and outside the lair. Time spent drinking was calculated as the time (s) that an individual spent lapping at water. Cheetahs stopped drinking to survey their surroundings frequently during bouts, but this was not included in drinking time.

Hunting behaviour

I recorded the time the hunt started and ended, the belly size of the cheetah, the type and height of vegetation, and the species, approximate number and age of animals in the group of prey. The age and sex of the particular quarry was recorded when the chase began, or when it was obvious which individual had been selected from the cheetah's orientation. Large prey were classified as half grown to adult gazelles and other adult antelope such as steenbok, *Raphicerus campestris*; small prey were hares and fawns of Thomson's or Grant's gazelles, *Gazella granti*. Time taken for stalking, trotting towards the prey and the final rush were also recorded. Hunts were deemed to have stopped when the cheetah caught its prey, failed to catch the quarry and stopped running, was seen and stopped stalking, or walked away from the prey. The outcome of the hunt and reasons for its failure were also noted. Hunting success was calculated as the proportion of hunts

that resulted in prey capture out of all hunts attempted.

Food intake

The amount (kg) of meat eaten per h of observation was determined by recording the age and sex class of the species of prey that was killed. Hares were classified as immature, small or large. Thomson's gazelles and Grant's gazelles were allocated to age classes according to Walther (1973) and Bradley (1977). I noted the sections of the carcass eaten and weighed the remains of large and partially eaten carcasses if possible. The amount of flesh and viscera eaten was then calculated from Blumenshine & Caro (1986) and from other data (T. Caro, personal communication). Females were sometimes found eating early in the morning on prey that had obviously been killed overnight and were included in analyses. On only 2 of 264 nights, cheetahs appeared to have eaten in the dark as their belly size was scored higher in the morning than the previous evening. No attempt was made to estimate their food intake overnight.

Emerged cubs of 9 weeks of age weighed approximately 9% of mother's weight (Laurenson, in press) and cubs of this age ate for only approximately half the time that their mothers did (unpublished data). Assuming their food intake was roughly proportional to their body size, each cub was estimated to eat 4.5% of what their mother ate at kills. The amount of food eaten by mothers of emerged cubs was therefore reduced in proportion to the number of cubs in the litter.

Distance travelled

The odometer reading was recorded every 15 min and the distance travelled in that time was calculated. If the cheetah had moved less than 100 m, distance was estimated by eye. An effort was made to follow the path taken by the cheetah, but as it rarely travelled in straight lines and often wandered in tight circles, distances should be considered as minimums. Distance travelled at night was estimated by measuring from where the female was last seen at twilight to where she was found in the morning. These may have been slight underestimates, particularly for young females without cubs. This is unlikely to have biased results as only adult females, who rarely moved, were used in this analysis. The distance (km)

travelled each 24 h was averaged over all days of the follow.

Statistical Analysis

Raw data were tested for skewness and kurtosis and compared to a normally distributed data set using a Kolmogorov-Smirnov goodness-of-fit test. If logarithmic transformation did not normalize data, non-parametric tests were used. Two-tailed tests were used throughout. Previous studies (Clutton-Brock et al. 1982; Gittleman 1988) have shown that changes in behaviour across reproductive periods must be made after a baseline is established for individual females. Although data from 20 females without cubs (NC) were collected, data could be collected from only 14 of these females when they had cubs in the lair (LC) and seven when lactating with emerged cubs (EC). Thus I compared NC and LC females with a sample size of 14 using the appropriate parametric (paired *t*-test) or non-parametric matched-pairs test (Wilcoxon matched-pairs signed-ranks test) and NC and EC, or LC and EC females with a sample size of 7. I examined the baseline data from the 20 NC females for differences arising from female age or season. If age had an effect, then the comparison between reproductive statuses was also made using adult females only.

In the analysis of time budgets, the proportion of scans where an animal was observed in any category of behaviour was not independent from the proportion of scans where other categories of behaviour were observed, since proportions must sum to one. Thus the additive logistic transformation was performed (Aitchinson 1986). The time spent in each category of behaviour was divided initially by the proportion of time spent eating and so the five categories of behaviour were reduced to four new independent variables. I tested the hypothesis that the amount of time spent in any activity varied with reproductive status using analysis of variance techniques in the SYSTAT 5.0 package which took into account the pairing of sampling (Wilkinson 1990). Initial analysis revealed a significant difference in the activity budgets of females of different reproductive status ($F_{3,18}=2.67$, $P<0.05$). I examined changes in the time spent in each activity by considering all the potential log ratios and testing for significant differences using paired *t*-tests. When these were set into a matrix, it was obvious

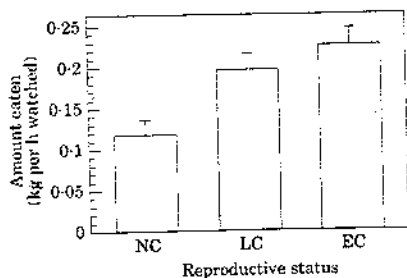


Figure 1. Means \pm SE of the amount (kg) of meat eaten per h watched by cheetah females according to reproductive status. NC: Females without cubs; LC: lactating females with cubs in the lair; EC: lactating females with emerged cubs (paired *t*-test: LC versus NC, $t = -2.68$, $df=13$, $P<0.01$; EC versus NC, $t = -5.23$, $df=6$, $P<0.01$; LC versus EC, $t = -1.69$, $df=6$, $P=0.14$).

that the proportion of time spent eating did not contribute to the variation and so further analysis concentrated on variation in the block of four remaining activities. Accordingly, I recalculated the proportion of time spent in the four remaining variables as a proportion of the time spent in only those four activities. The proportion of time spent resting was then used as the denominator, leaving three independent variables. Analyses revealed that significant differences were entirely attributable to EC females and there was no difference between NC and LC females. The log ratios for these statuses were duly combined and compared against EC females using the techniques described above, to examine where changes in activity were occurring. The signs of the differences of each log ratio difference for each pair were again set into a matrix from which rank preferences were read off.

RESULTS

Food and Water Intake

The rate of food consumption differed between females of different reproductive status (Fig. 1). Lactating females with cubs in the lair (LC) ate 65% more than solitary females, while lactating females whose cubs had emerged (EC) ate 97% more than solitary females but no more than females with cubs in the lair (15% increase). Lactating females with cubs in the lair drank for a significantly longer period each day than females

without cubs, but there was no difference between females with emerged cubs and other females (medians (IQR), NC, LC, EC, respectively: 8 (0-12), 59 (40-90), 16 (0-52) s; Wilcoxon matched-pairs signed-ranks tests: NC versus LC, $z = -2.80$, $N=11$, $P<0.01$; NC versus EC, $z=0.41$, $N=5$, ns; LC versus EC, $z = -1.46$, $N=6$, ns).

Hunting Behaviour

Killing rates

Lactating females must have captured a greater weight of prey items in order to ingest more meat per unit time. This could be achieved by increasing their killing rate of the same sized prey and/or by catching larger prey, but at the same overall rate. There was no effect of reproductive status on the overall number of kills made per h by females (NC, LC, EC, respectively: $X = \text{SE} = 0.053 \pm 0.01$, 0.054 ± 0.01 , 0.052 ± 0.01 ; paired *t*-test: NC versus LC, $t = -0.02$, $df=13$; NC versus EC, $t=1.29$, $df=6$; LC versus EC, $t=1.15$, $df=6$, all ns). Several results support the second hypothesis. First, the proportion of kills that were large prey items was greater when females were lactating with emerged cubs than when females were not lactating and tended to be greater when females had cubs in the lair (medians (IQR) NC, LC, EC, respectively: 0.22 (0-0.65), 0.48 (0.28-0.71), 0.58 (0.45-0.75); Wilcoxon test: NC versus LC, $z = -1.84$, $N=14$, $P<0.07$; NC versus EC, $z = -2.20$, $N=7$, $P<0.02$; LC versus EC, $z = -0.21$, $N=7$, ns). Second, the number of large prey items killed per h by lactating females when cubs were in the lair or had emerged was greater than when females were solitary (medians (IQR) NC, LC, EC, respectively: 0.01 (0-0.02), 0.02 (0.02-0.04), 0.02 (0.02-0.03); NC versus LC, $z = -2.43$, $N=14$, $P<0.02$; NC versus EC, $z = -2.20$, $N=7$, $P<0.03$; LC versus EC, $z = -0.32$, $N=7$, ns). There was no significant difference in the number of small prey items killed per h (medians (IQR) NC, LC, EC, respectively: 0.04 (0.02-0.07), 0.02 (0.01-0.06), 0.02 (0.02-0.05); NC versus LC, $z=1.36$, $N=14$; NC versus EC, $z=1.52$, $N=7$; LC versus EC, $z=0.0$, $N=7$, all ns).

Hunting rates

Lactating cheetahs could have made more kills of large prey by either hunting large prey at a

greater rate but with the same success, by being more successful when hunting, or through a combination of these two strategies. The number of hunts of large prey per h was dependent on the age of the female as young females hunted more often than older females (medians (IQR): young: 0.14 (0.12-0.16); adult: 0.10 (0.06-0.20); Mann-Whitney *U*-test: $U=4.0$, $N_1=6$, $N_2=14$ females, $P=0.02$). Only adult females were therefore used in the following analyses. Results suggest that females with cubs in the lair attempted a greater number of hunts of large prey per h than females without cubs and that females with emerged cubs had a tendency to do the same (medians (IQR): NC, LC, EC, respectively: 0.09 (0.05-0.13), 0.11 (0.04-0.16), 0.13 (0.11-0.14); Wilcoxon tests: NC versus LC, $z = -2.31$, $N=10$, $P<0.02$; NC versus EC, $z = -1.75$, $N=5$, $P<0.07$; LC versus EC, $z=0.67$, $N=5$, ns).

In addition, when lactating females had cubs in the lair and possibly also when they had emerged cubs, they had a significantly higher success rate for hunts of large prey than when they were without cubs (medians (IQR) NC, LC, EC, respectively: 3% (0-22), 13% (8-57%), 20% (13-27%); Wilcoxon tests: NC versus LC, $z = -2.49$, $N=14$, $P<0.01$; NC versus EC, $z = -1.86$, $N=7$, $P<0.06$; LC versus EC, $z = -0.13$, $N=7$, ns). Thus it would appear that females may both increase the rate that they hunt large prey and also improve their hunting success, thereby increasing their food intake during lactation, although some results are just non-significant with the small sample size.

Hunting technique

Cheetahs usually hunt large prey by stalking to within 20-50 m of it at which point they make a fast, short chase, generally less than 300 m in length (Schaller 1972). The stalk is an important factor governing the outcome of a hunt and if cheetahs are detected whilst stalking, they abandon the hunt in 74% of cases (FitzGibbon 1989). If they continue to hunt, they have only a 6% chance of success. In addition, chases that start closer to the prey are more likely to be successful (Caro 1986). Hunting success might therefore be improved in a number of ways. One is that cheetahs could stalk more carefully, resulting in a greater proportion of hunts ending in a chase and also increasing the success rate of chases as chases

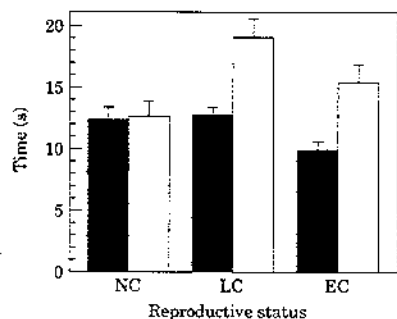


Figure 2. Means \pm SE of the time (s) that females spent chasing large prey in successful (■) and unsuccessful (□) chases. NC: Females without cubs ($N_1, N_2=8, 23$ successful and unsuccessful chases, respectively); LC: lactating females with cubs in the lair ($N_1, N_2=14, 29$); EC: lactating females with emerged cubs ($N_1, N_2=8, 18$).

might start nearer to the prey. Alternatively, or additionally, cheetahs could try harder in chases thus improving their success rate.

The hunts of large prey by females with denuded cubs tended to be more likely to end in a chase than those when the females were solitary, suggesting that they could have been stalking more effectively (medians (IQR) NC, LC, EC, respectively: 0.29 (0.19–0.43), 0.50 (0.36–0.74), 0.40 (0.31–0.75); Wilcoxon test: NC versus LC, $z = -1.88$, $N=14$, $P < 0.06$; NC versus EC, $z = -0.85$, $N=7$, ns; LC versus EC, $z = -0.68$, $N=7$, ns). Chases of large prey by females with cubs in the lair and emerged cubs were more likely to be successful than those when females were solitary (medians (IQR) NC, LC, EC, respectively: 0.12 (1–0.30), 0.42 (0.16–0.73), 0.63 (0.53–0.82); NC versus LC, $z = -2.85$, $N=14$, $P < 0.01$; NC versus EC, $z = -2.02$, $N=7$, $P < 0.05$; LC versus EC, $z = -0.42$, $N=7$, ns).

Both reproductive status and the successful or unsuccessful outcome of the chase had a significant effect on the duration of the chase (two-way ANOVA: reproductive status, $F_{2, 58} = 5.88$, $P < 0.02$; hunt outcome, $F_{1, 58} = 1.04$, $P < 0.05$; Fig. 2). Each hunt was entered separately in this analysis because there were insufficient data from each female to compare meaningfully these chase parameters by female. Successful chases were shorter ($X \pm s = 12 \pm 1$ s) than unsuccessful chases (16 ± 1.3 s) and females with cubs in the

lair were significantly more persistent (18 ± 2 s) in chases than solitary females (13 ± 1 s), owing primarily to differences in the length of unsuccessful, rather than successful chases between these females (Fig. 2).

The increase in lactating females' success rate when hunting large prey was therefore probably due primarily to a change in effectiveness of the stalk as there was no change in the value of the parameters of a successful chase. Lactating females may have ensured that they were always close enough to the prey before beginning a chase to increase their chance of success, but the data are inadequate to test this hypothesis.

Seasonality effects

Changes in prey availability between wet and dry seasons and a seasonal bias in sampling could drive the observed effects on food intake and hunting behaviour, rather than changes in female behaviour. Thomson's gazelles in the Serengeti migrate seasonally but since female cheetahs follow them, large prey are equally abundant all year (Durant et al. 1988). Although some Thomson's gazelle fawns are available all year, more are born in the wet than the dry season (percentage of females with fawns: wet 16%, dry 2%; Figure 8 in Laurenson et al. 1992). There was no difference in the abundance of hares, which constituted 36% ($N=118$) of small prey items, between wet and dry seasons (unpublished data). Thus, although the number of large prey is approximately constant, there are twice as many small prey in the wet than the dry season.

In this study, 43% ($N=14$) of the observations of the same females when without cubs and when lactating were conducted in the same season. All lactating females were sampled in the same season when cubs were in the lair and had left the lair. However, more females (75%) were first sampled without cubs during the wet season and then sampled in the dry season when lactating, than vice versa (25%), although this difference was not significant (binomial test: $P=0.3$). Thus, although seasonal bias was unlikely to account for the results, I also examined whether there were seasonal differences in the parameters tested. There was no difference in the amount of food eaten by solitary females between the wet and dry seasons (Mann-Whitney U -test: $U=37.1$, $N_1=8$, $N_2=12$, ns), nor in the number of large hunts per h

($U=35.5$, ns), the number of large kills per h ($U=34.5$, ns), the percentage of kills that were large prey ($U=26$, ns), the success rate of large hunts ($U=1.11$, ns), the percentage of hunts of large prey that ended in a chase ($U=45.5$, ns), or the percentage of chases of large prey that were successful ($U=38.0$, ns). However, more hunts and kills of small prey were made in the wet season (hunt: $U=19.0$, $P < 0.05$; kills: $U=21.9$, $P < 0.05$). There was, however, no statistical difference in the number of small prey killed according to lactational status, although seasonal differences might account for the apparently greater median number of small prey killed per h by non-lactating females as more (71.4%) of these females were sampled in the wet season. Overall, there is little reason to suppose that changing prey availability, rather than lactational status, drove the observed differences in food intake and hunting behaviour, although interaction effects between season and status could not be tested.

Timing of kills

Cheetahs were generally active in the morning and late evening and the majority of hunts and kills were made at these times (Schaller 1972). To test whether this pattern was altered during lactation, the time that a kill occurred was assigned to one of five periods (0631–0930, 0931–1230, 1231–1530, 1531–1830, 1831–0630 hours) and the number of kills in each period was summed according to reproductive status. Each period was sampled equally. The frequency of kills in each time block differed significantly with reproductive status (Fig. 3; G -test: $G=24.7$, $df=8$, $P=0.002$). Females without cubs killed less frequently than expected from the overall frequency distribution between 1531 and 1830 hours (binomial test: $P < 0.04$) and had a tendency to kill more frequently than expected early in the day between 0631 and 0930 hours (binomial test: $P < 0.08$). Females with cubs in the lair killed less frequently between 0631 and 0930 hours ($P < 0.02$) and had a tendency to kill more frequently than expected between 1531 and 1830 hours ($P < 0.1$). Females with emerged cubs did not kill more or less frequently than expected at any time.

Activity Budgets

There was an overall significant difference in the activity of females according to reproductive

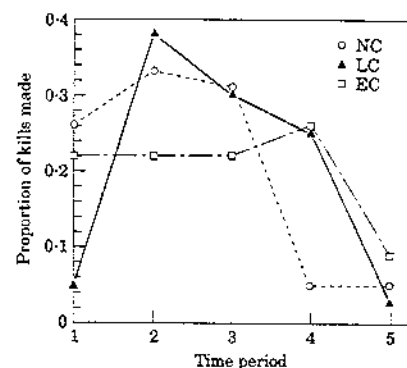


Figure 3. The proportion of kills made at different times during the day by females of different reproductive status. NC: Females without cubs ($N=61$ kills); LC: females with cubs in the lair ($N=66$ kills); EC: lactating females with emerged cubs ($N=23$ kills). Time period 1 (0631–0930 hours), period 2 (0931–1230 hours), period 3 (1231–1530 hours), period 4 (1531–1830 hours), period 5 (1831–0630 hours).

status (Fig. 4, Table 1; $F_{3, 118} = 2.67$, $P < 0.04$). More detailed analysis revealed that there was no significant difference between the activity of solitary females and those with cubs in the lair ($F_{3, 111} = 2.72$, $P = 0.09$), but that their combined activity budgets differed from those of females with emerged cubs ($F_{3, 10} = 7.42$, $P < 0.01$). Females with emerged cubs spent a greater proportion of time observing and hunting, but a smaller proportion resting and moving than other females.

Resting

When females had cubs in the lair they travelled further each 24 h than when they did not have cubs (medians (IQR) NC, LC, EC, respectively: 4.7 (4.3–5.7), 6.0 (4.4–7.7), 5.4 (5.0–5.6) km; Wilcoxon tests: NC versus LC, $z = -4.21$, $N=11$, $P < 0.01$; NC versus EC, $z = -1.40$, $N=5$, ns; LC versus EC, $z = 0.62$, $N=6$, ns). Only adult females were used in this comparison because young females ($N=6$) travelled further each day than adult females ($N=14$) when they were solitary (Mann-Whitney U -test: $U=15$, $P < 0.05$). These findings were surprising given that females would rest in or near the lair for 2–3 days after they had killed and eaten an adult Thomson's gazelle.

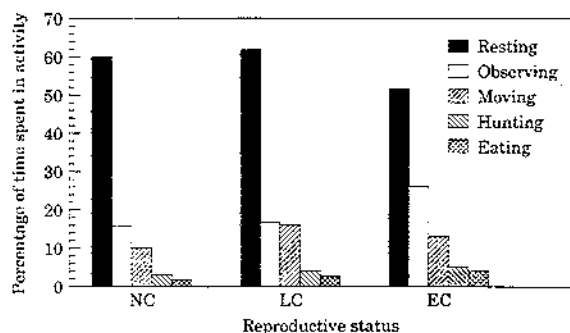


Figure 4. The proportion of 15-min scans that females were recorded in five activities, depending on their reproductive status. NC: Females without cubs ($N=14$ females); LC: lactating females with cubs in the lair ($N=14$); EC: lactating females with emerged cubs ($N=7$).

Table 1. Ranking matrix of log ratio differences of the activity of female cheetahs that either had no cubs or had cubs in the lair and those with emerged cubs

	Resting	Moving	Observing	Hunting	Rank
Resting	-	-	-	-	0
Moving	+	-	-	-	1
Observing	+++	+++	-	-	2
Hunting	+++	+++	+	-	3

+: Activity in row increased relative to that of column; -: activity in row decreased in relation to that of column; a triple sign represents a significant deviation from random at $P<0.05$. The row with the most plus values corresponds to the activity that increased the most overall when females had emerged cubs, whereas that with the most negatives decreased the most.

When females were solitary they moved less than 500 m on only 3% of days ($N=99$) during follows compared to 21% ($N=86$ days) when they had cubs in the lair. Apparently the savings in distance travelled for these females were not sufficient to outweigh the greatly increased distance travelled on hunting days, when the media (IQR) distance travelled was 9.0 km (6.4–10.3).

The ranging pattern of females when their cubs were in the lair was restricted. The night resting spot of these females (effectively their lair site) did not vary by more than 100 m over the 5 days of observations, whereas those of females with emerged cubs were a median 5.3 km (4.3–5.9) apart.

DISCUSSION

Behavioural Changes during Lactation

Food intake

Increased energetic demands during lactation can be met by increasing food intake, by using metabolic stores, or through a combination of these strategies. In this study, female cheetahs whose cubs were either in the lair or had emerged ate significantly more than when they did not have cubs. It is not, perhaps, surprising that females increase their energy intake at this time, since it is unlikely that a species that relies on high-speed chases to catch prey would have evolved large fat storage capabilities, as there is an energetic cost to maintaining fat stores (Pond 1977). Nevertheless, small fat reserves may be of little consequence as, even with an increased food intake, lactating female cheetahs appear to operate at an energetic deficit: measurements of skin fat folds and biochemical parameters suggest that both subcutaneous fat and muscle mass may be metabolized during lactation (Laurenson 1992).

Few studies have been conducted in terrestrial carnivores examining the strategy females use to meet the energetic demands of lactation. Anecdotal reports from felids suggest that food intake may rise (serval, *Felis serval*; Goertsema 1985) or that meat may be carried back to the lair and augment the supply of milk at an early stage (leopard, *Panthera pardus*; Cavallo 1990). Social canids often regurgitate meat to the offspring at

the den (golden and black-backed jackals, *Canis aureus*, *C. melomensis*; Moehlman 1979; wild dogs; Malcolm & Marten 1982). Laboratory domestic cats, *Felis catus*, increase their food intake during lactation but also lose body condition and become nutritionally stressed when feeding large litters (Loveridge 1986; Deag et al. 1987).

The energetic requirements over the lactational period vary, increasing as the young grow, but then decreasing towards weaning as the young meet a greater proportion of their own energy requirements directly (Ofstedal 1984). It is probable that the energetic requirement of female cheetahs during lactation peaks immediately before the cubs emerge, because, although cubs' requirements continue to increase after emergence, they are then able to feed for themselves at kills. In this study, however, there was little difference in the amount eaten by females with cubs in the lair and those with emerged cubs. Although mothers with cubs in the lair may have had greater requirements than those with emerged cubs, they may not have been able to increase their food intake sufficiently under the constraints of denning. Two strands of evidence support this possibility. First, these females were particularly efficient at hunting but had physical and time limitations on their ability to catch prey as they spent the early part of each day in the lair and had to travel to hunting grounds (see below). Second, females lost body fat and possibly muscle mass during the period cubs were in the lair, suggesting that energy intake during this period did not meet their requirements (Laurenson 1992). Once cubs had emerged, females were relieved of constraints on the time they spent hunting and did not have to travel so far to make a kill. They may then have been able to increase their food intake and recoup some of their energy deficit. An alternative explanation for the similarity in maternal food intake was that the larger body size of 9-week-old cheetah cubs, even though they were only partially reliant on maternal milk, outweighed the lower expenditure on travel.

Hunting behaviour

Female cheetahs altered their hunting behaviour in order to increase their food intake during lactation. In principle, cheetahs might be able to achieve a higher rate of food intake by making

kills more often or by killing larger prey at the same overall rate. Although large prey offer a larger reward than small prey, hunts on large prey take longer, may involve greater risk of injury and have a lower success rate than those on small prey (Caro 1989, 1994). Larger kills are also more likely to be stolen (Caro 1994). Against this, large prey are relatively abundant compared to small prey (see Figure 8 in Laurenson et al. 1992). In a previous study Caro (1989) suggested that cheetahs can increase their food intake only by focusing on very small prey as the costs associated with hunting large prey are too high. My results, however, demonstrate that the principal strategy adopted by lactating cheetahs when increasing their food intake was to switch to larger prey. Lactating females were also able to increase their hunting success by improving their hunting technique on large prey. More stalks by these females ended in a chase and chases were more likely to be successful.

Female cheetahs that switch to large prey during lactation might also reduce their energetic expenditure on travel. Cheetah mothers with cubs in the lair travelled further than females without cubs, reflecting the necessity for denning mothers to return regularly to the lair to suckle their cubs. Thus they cannot remain near the concentrations of gazelles after feeding. These costs may be ameliorated to some extent by females who predominantly caught large prey, as these females would rest in or near the lair on the 2 or 3 following days. In contrast, females that caught small prey had to travel to and from prey concentrations and the lair each day.

As females with cubs were able to increase their food intake using this strategy, why did solitary cheetahs fail to adopt it in order to maximize food intake? By hunting small prey, were they foraging sub-optimally? I suggest that while solitary females could build up body reserves by exploiting large prey and hunting more efficiently, there may have been no fitness benefit in doing so. Larger reserves could restrict a cheetah's speed, thereby decreasing its hunting success or possibly increasing its vulnerability to predation. Reserves would also require more energy to maintain. Maximizing food intake is only one concern for a single foraging cheetah and may not be the correct currency against which to model optimality. For example, avoiding predators or conserving energy might be important concerns. Small prey may be

encountered sufficiently often by solitary females for them to adopt the 'safe bet' tactic of hunting small prey with a high success rate but a small reward. However, when extra food can be allocated to reproduction, females may benefit by maximizing their food intake. At such times they may hunt more large prey, but still take small prey when encountered.

Constraints and Behavioural Costs of Denning

Several strands of evidence emerging from the comparison of female cheetahs' behaviour during the two stages of lactation suggest that denning may impose additional behavioural costs above those associated with lactation and also constrain some aspects of behaviour.

Denning may increase the energetic costs associated with travelling and hunting because moving in a hotter ambient temperature requires greater energetic expenditure (Peters 1983). Most females did not leave their lairs until after 0830 hours because they were nursing their cubs (Laurenson 1993) and therefore travelled further and may have made more kills during the middle of the day. Cheetahs do not dissipate heat whilst sprinting and are thought to overheat rapidly during chases, thus limiting the distance that they can cover (Taylor & Rowntree 1973). Thus cheetahs hunting in the heat of the day may overheat particularly rapidly when chasing prey and be forced to give up or increase the time they need to cool down afterwards. There may, therefore, be a number of repercussions from travelling and hunting during the heat, including an increase in the energetic requirements.

Denning may also constrain lactating females' behaviour. Females with cubs concealed in the lair had restricted ranging patterns as females usually returned to the lair each night, whereas those with emerged cubs could move from area to area. Females could therefore hunt only within travelling distance of the lair and were no longer free to follow the vagaries of the Thomson's gazelle migration (Durant et al. 1988) during the 8-week denning period. This constraint is also illustrated by observations on mothers of two litters who covered between 25 and 30 km to areas of high prey concentrations within a few days of leading their cubs from the lair. Some females may therefore be forced to hunt in poor prey areas during the denning period. This restriction could limit

their ability to find sufficient prey and contribute to the abandonment of litters, as happened at least twice in this study (Laurenson 1994). Anecdotal reports suggest that other species of felids also have restricted ranging patterns at this time (Hornocker 1969; Sunquist & Sunquist 1991; Bailey 1993) and can also suffer detrimental consequences such as loss of home range (tiger, *Panthera tigris*) or increased susceptibility to human hunters (mountain lion, *Felis concolor*). Thus this constraint on ranging pattern may have a number of serious consequences.

Ranging patterns may also have been influenced during the denning period because lactating females increased their water intake. Although cheetahs are adapted to living in a semi-arid environment and their movements are normally little influenced by water requirements (Labuschagne 1974), I often observed lactating females with cubs in the lair making special journeys to get to water. Increased water requirements may also impose restrictions on the choice of lair site; nearly 70% of lairs ($N=34$) were within 500 m of water (Laurenson 1993).

In summary, female cheetahs may have both increased energetic expenditure and increased constraints on their behaviour during the time their cubs are in the lair. Although cheetah mothers must use lair sites because their neonate young are developmentally constrained, there are also clear advantages to sequestering cubs in the lair. Most importantly, mothers can benefit from lowered predation risks both to themselves and to their cubs (Laurenson 1994), but can also spend more time resting and less time observing. The extent of the behavioural costs and constraints acting on each mother may be an important factor determining the timing of cub emergence.

ACKNOWLEDGMENTS

I thank the Government of Tanzania for permission to conduct research, and Professor Karim Hirji and Hassan Nkya of the Serengeti Wildlife Research Institute, as well as David Babu and Bernard Maragesi of Tanzania National Parks for their help and support during the project. Tim Caro supervised this project both in the field and while writing up and deserves special thanks. In addition I am grateful to Barbie Allen, Markus Borner, Aadje Geertsema, Charlie Trout, Peter

Hetz and Marianne Kuitert for logistical support in the field and to my colleagues at SWRC for their friendship and discussions. Steve Albon and Nicholas Aebischer kindly provided statistical advice and Phyllis Lee, Karen McComb, Philip Stander gave encouragement and helpful comments on this work. Sarah Durant, Joshua Ginsberg and Simon Thirgood also constructively commented on the manuscript. Fieldwork was financed by the Frankfurt Zoological Society, the Leverhulme Trust, the Messerli Foundation and the National Geographic Society.

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