Abstract: Juvenile mortality in cheetahs was found to be extremely high compared to other large mammals, with approximately 72.2% of litters dying before they emerged from the lair at eight weeks of age. An average of 83.3% of cubs alive at emergence died by adolescence at 14 months of age, thus cheetah cubs were estimated to have only a 4.8% chance of reaching independence at birth. The instantaneous rate of mortality was highest immediately after cubs emerged from the lair. Before emergence, lion predation was the major source of this mortality, although some cubs died from starvation after they were abandoned by their mothers, or as a result of grass fires and inclement weather. After emergence, predation again accounted for virtually all cub mortality, with lions and spotted hyenas taking approximately the same proportion of cubs. Overall predation accounted for 73.2% of cheetah cub deaths in this study, with 78.2% of these being killed by lions. The extent of maternal care, in the form of vigilance and antipredator behaviour, mirrored cub susceptibility to mortality and, in the case of vigilance, possibly also starvation. The probability of a cheetah mother responding aggressively to a predator was found to also depend on the species of predator. This study highlights the importance of the influence of juvenile mortality on patterns of parental care.

High juvenile mortality in cheetahs (*Acinonyx jubatus*) and its consequences for maternal care

M. Karen Laurenson

Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK and Serengeti Wildlife Research Institute, P.O. Box 661, Arusha, Tanzania

(With 5 figures in the text)

Juvenile mortality in cheetahs was found to be extremely high compared to other large mammals, with approximately 72·2% of litters dying before they emerged from the lair at eight weeks of age. An average of 83·3% of cubs alive at emergence died by adolescence at 14 months of age, thus cheetah cubs were estimated to have only a 4·8% chance of reaching independence at birth. The instantaneous rate of mortality was highest immediately after cubs emerged from the lair. Before emergence, lion predation was the major source of this mortality, although some cubs died from starvation after they were abandoned by their mothers, or as a result of grass fires and inclement weather. After emergence, predation again accounted for virtually all cub mortality, with lions and spotted hyaenas taking approximately the same proportion of cubs. Overall predation accounted for 73·2% of cheetah cub deaths in this study, with 78·2% of these being killed by lions. The extent of maternal care, in the form of vigilance and antipredator behaviour, mirrored cub susceptibility to mortality and, in the case of vigilance, possibly also starvation. The probability of a cheetah mother responding aggressively to a predator was found also to depend on the species of predator. This study highlights the importance of the influence of juvenile mortality on patterns of parental care.

Contents

Present address: Upland Research Group, The Game Conservancy, Crubenmore Lodge, Newtonmore, Inverness-shire PH20 1BE, Scotland

Introduction

Juvenile mortality is a critical selective force on most animal populations, with its extent, timing and causes influencing patterns of parental care, life-history strategies, population dynamics and conservation biology. Parental care, for example, can only enhance an individual's reproductive success if offspring mortality is caused by factors that can be alleviated, such as predation or starvation (Andersson, Wiklund & Rundgren, 1980). In contrast, there will be only weak, or no, selection pressures for care when mortality is caused by factors, such as disease, that are unpredictable or cannot be reduced. The extent of juvenile mortality is also a fundamental determinant of life-history strategies (Lack, 1968; Case, 1978; Harvey & Zammuto, 1985; Promislow & Harvey, 1990; Gittleman, 1993). Recent reanalyses of life-history strategies have emphasized the critical importance of separating the causes of juvenile mortality into those that are intrinsic (i.e. a consequence of a life-history trait such as fast metabolic or growth rates) or extrinsic (i.e. causes independent of life-history traits, such as predation, parasites, or adverse ecological conditions), because intrinsic sources of mortality may actually be a consequence rather than a determination of 'fast' life histories (Promislow & Harvey, 1990; Gittleman, 1993). Juvenile mortality is also important for understanding population dynamics and its causes are often the key factors limiting or regulating populations (Sinclair, 1989). Finally, in order to prevent population extinctions, knowledge of the principal causes of juvenile mortality is crucial for making sound management decisions (Gilpin & Soule, 1986; Lande, 1988).

Despite its role in understanding many aspects of biology, juvenile mortality is difficult to document (Gittleman, 1993). This is particularly true of carnivore species where offspring are often sequestered for the first few weeks or months of life and therefore cannot be monitored without sophisticated techniques. In the first part of this paper I partially redress this situation by documenting the extent, timing and causes of mortality in juvenile cheetahs, a species suspected to suffer high mortality rates in the wild (Schaller, 1972; Frame & Frame, 1981).

In the second part of the paper, the ramifications of high juvenile mortality are considered for just one facet of the species' biology, parental investment. Most studies examining the influence of offspring-related factors on parental investment have concentrated on the effects of offspring age (Andersson, Wiklund & Rundgren, 1980; Redondo & Carranza, 1989), offspring quality (Stamps et al., 1985; Curio & Regelmann, 1987) or brood size (Lazarus & Inglis, 1986; Caro, 1987; König, Riester & Markl, 1988), as these factors are theoretically important (Winkler, 1987; Clutton-Brock, 1991). It is nevertheless acknowledged that the causes and timing of juvenile mortality can modify theoretical predictions by altering the relationship between offspring age, value and vulnerability (Patterson, Petronovich & James, 1980; Montgomerie & Weatherhead, 1988), but few studies have looked for such effects in mammals (Hauser, 1988). Thus, in this paper I also consider how maternal care in cheetahs, in the form of vigilance and antipredator behaviour, are influenced by the timing and causes of juvenile mortality. Consequences of juvenile mortality for the population dynamics (Laurenson, In press a) and conservation biology (Caro & Laurenson, 1994) of cheetahs are discussed elsewhere.

Materials and methods

Study site and general methods

A long-term study of cheetahs on the central plains and woodland edge of the Serengeti National Park and Ngorongoro Conservation Area in Tanzania has been carried out since 1980 (see Caro & Collins, 1986 for a description of the 2500 km^2 study area). Approximately 250 lions (*Panthera leo*), 50 wild dogs (*Lycaon pictus*), and up to 5000 spotted hyaenas (*Crocuta crocuta*) and 300 cheetahs live within the study area, although considerable fluctuations occur as predators follow the seasonal migrations of the prey populations (Kruuk, 1972; Durant *et al.*, 1988; Hanby, Bygott & Packer, In press). In this area, most rainfall usually occurs between November and May, the wet season months, while rainfall is scarce in the dry season, June to October. Female cheetahs have annual home ranges averaging 800 km^2, as they follow the migration of their main prey, Thomson's gazelles (*Gazella thomsonii*) (Schaller, 1972).

As part of this long-term study, I collected data on cub mortality from October 1987 to September 1990 by relocating 20 radio-collared females (out of a population of approximately 200 females that use the plains area) on a monthly basis, by assessing visually their reproductive status and then by pinpointing the time that they gave birth. 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 considered pregnant, females were checked within 2 weeks to ascertain whether cubs had been born and, if lactating, females were followed until the lair site was found. Lairs were entered after the mother had left to go hunting in order to count cubs and estimate their age. Lairs were then checked weekly until they died or left the lair at approximately 8 weeks of age (Laurenson, 1993). Stringent checks compared the frequency at which litters that died of different causes were visited, entered or that cubs were handled, the distance to which these lair sites were approached and the severity of tracks around the lair. No effects of these activities could be found on either the overall likelihood of cubs dying or the chance of their being killed by predators or being abandoned (Laurenson & Caro, 1994).

Radiocollars were removed from females when cubs were approximately 10 weeks old. Families, or lone females who had lost cubs, were subsequently resighted and identified sporadically as part of the long-term demographic study of this population.

Determination of the causes of cub mortality

In some cases, mortality was observed directly, but in other cases it was not possible to be sure of the cause of mortality, as cubs and mothers disappeared between my visits to lairs. In many cases, however, field observations and a knowledge of maternal behaviour enabled me to estimate the cause of death, for example, when the remains of cubs were found in or near the lair and when mothers were showing great aversion to predators around a lair from which cubs had disappeared. If a mother of a previously healthy litter was found alone near the lair site within a week of the last visit, it was probable that the cubs had been killed by a predator (see also Table II).

Observation schedules

Where possible, three 5-day periods of intensive observation were conducted on study females at different stages of reproduction. Each female's behaviour was sampled first when they did not have dependent cubs, second when they had 2·5 to 5-week-old cubs concealed in a lair and last, when they were accompanied by cubs that had emerged from the lair within the previous 2 weeks. During observation periods, cheetahs were watched, using either 10 × 40 binoculars or the naked eye, from a distance of 0 m (when they occasionally sat on the vehicle) but usually from about 50 m if the female was resting, or from 150 m to 400 m if she was moving or hunting. A total of 47 observation periods were completed, some 2940 hours of direct observations.

a. Activity patterns

During daylight hours (06:30–19:00 h) the activity of the females was noted every 15 min. The percentage of instantaneous samples that females were resting or observing (Table I) was calculated each day and an average taken for all the days in each observation period.

b. Vigilance during the day

During the middle of the day (09:30–17:30 h), or after the main hunting period, the vigilance and posture of female cheetahs was recorded in greater detail, according to the criteria in Table I. When the female had settled down to rest, often in shade, an observation period of 3 or occasionally 4 h was begun, in which the behaviour of the mother was recorded every 5 min. If the female started to hunt or was recorded as walking for more than 2 consecutive 5-min scans, the observation period was terminated and only data from previous complete half hour blocks were used in analysis. A new observation period was started once the female had settled down again. These criteria ensured that females were relatively relaxed when sampled (Caro, 1987). In many periods, in particular those sampling mothers who had cubs hidden in a lair, it was not possible to collect the target of 3 h of relaxed observations each day. Observations spanning less than 1·5 h and only 1 day were excluded. Thus data from only 6 mothers with cubs in the lair could be included.

c. Vigilance at kills

Mothers could have been vigilant for prey, because they were hungry, or for predators that might pose a threat to their cubs (Caro, 1987). After making a kill and while eating, cheetahs often scan the surroundings and this form of vigilance is primarily an anti-predator strategy rather than a way of locating further prey (Schaller, 1972; Caro, 1987). The interval between the death of the prey and the moment that the female cheetah started to eat was recorded, as was the number of times per minute that each female looked up and the length of each vigilance bout. The percentage of time spent looking up from the carcass while at the carcass was calculated. The depth of the vegetation was scored on a scale of 1–5 (1 =< 10 cm, 2 =< 20 cm, 3 =< 30 cm, 4 =< 40 cm, 5 => 50 cm) and the belly size, a measure of hunger, was recorded on a scale of 1–14 (see Caro, 1987). Prey size was classified as large or small (Table I) and included in analyses to take into account the greater proportion of large prey caught by lactating females (Laurenson, 1992).

TABLE I

List of terms and definitions used in vigilance analysis

Term	Definition
	Vigilance and posture
Resting	Lying with flank and hindquarters touching the ground
Observing, sitting up	Sitting on hindlegs with forelegs vertically supporting body
Lying flat out	Lying prone with head on ground
Lying out	Lying prone with head raised
Lying alert	Lying with flank and hindquarters flat on ground, forelegs tucked under body
Vigilant	Eyes open and looking around
Not vigilant	Eyes shut, or looking at ground, herself or cubs
	Prey size
Large	Half grown to adult Thomson's or Grant's gazelles and other adult antelope such as steinbok
Small	Hares and gazelle fawns

d. Vigilance and proximity to lairs

I examined the relationship between vigilance and distance from the lair by recording the number of seconds that females stopped to observe their surroundings, in two 10-min blocks. One block was recorded while females were walking directly back to the lair, but were more than 1 km from the lair and the other when females were within 1 km of the lair, usually within 500 m.

Antipredator behaviour

During observation periods, the species and number of predators (classified as those species which were a potential threat to cubs) within 1 km of the cheetah was recorded every 15 min. Cheetahs sometimes merely watched these predators if they saw them or reacted to them in a number of ways (Table II). Predators that were attracted to cheetah kills were excluded in the analysis, as cheetahs could have been defending food rather than themselves or cubs in those situations. Leaving, crouching and hissing were grouped together and defined as a defensive reaction, whilst the stalking, chasing and contacting were combined and termed an aggressive reaction. If a female reacted to a predator in more than one way, only the one which brought it into closest contact to the predator was used in the analysis as it was probably the most dangerous (see Caro, 1987).

Females were classified according to their reproductive status and, in addition, whether they were actually accompanied by cubs (Table II). The distance and the time of day when the interaction took place, as well as the vegetation height and maternal belly size scores were recorded. In addition, the degree of danger that the predator posed to the cheetah was scored (Table II).

Data analysis

Analyses of variance were used to examine the effect of reproductive status on vigilance; data obtained at kills were logarithmically transformed to achieve normality. Individual females were coded and included in

TABLE II

List of terms and definitions used in examination of antipredator behaviour

Terms	Definition
	Antipredator behaviour
Leaving	Slinking off, trying to be inconspicuous or trotting away
Crouching	Assuming a crouching position, usually if predator approached to within 40 m
Hissing	Standing up with back arched, pilo-erecting and hissing
Stalking	Approaching predator with head lowered, as when hunting prey
Chasing	Running after or rushing toward predator
Contacting	Slapping or attempting to bite predator
	Female groups
1	Female without cubs
2	Lactating female whose cubs were in a lair, but > 500 m from cubs lair at time of interaction
3	Lactating female resting with cubs in lair at time of interaction
4	Female accompanied by emerged cubs
	Danger score
0	Predator did not notice cheetah and not moving towards cheetah
1	Predator moving toward cheetah, but not directly at it. May or may not have noticed cheetah
2	Predator approaching or attacking cheetah

analysis of variance to test whether they had different levels of vigilance. If no significant effects due to individual mothers were found, this variable was dropped from the analysis. If a significant effect due to other variables was found, multiple comparisons between means analysis was performed using Duncan's multiple range test (Sokal & Rohlf, 1981).

Analysis of variance techniques were not suitable for examining maternal reaction to predators as the outcome was choice-based rather than continuous. Instead, a multinomial logit model was fitted to the data with the Limdep 5.1 program (Greene, 1990). This type of model, which examined the probability of a particular outcome occurring, was more accurate in predicting the outcomes than an ordered probit model. The final model included the set of causal variables that had a significant effect on the accuracy of predicting either a defensive or aggressive reaction.

Results

A. Juvenile mortality

Extent of juvenile mortality

Of the 36 litters that were born during the study to 17 mothers, a minimum of three and a maximum of four litters, from different mothers, survived to adolescence at 14 months of age (Table III), with every litter suffering some reduction in numbers. This represents 4·0–5·6% of the total number of 125 cubs estimated to have been born. At birth, therefore, a cub had approximately a 4·8% chance of reaching independence. It was most common for all cubs in a litter to die in the lair and so the extent of mortality in the litter was generally associated with litter size (see Tables IV, V). After cubs left the lair, however, only partial litter mortality occurred and cub losses were tied less closely to litter size (Table VI).

Timing of juvenile mortality

Cheetah cubs died throughout the period from birth to independence (Fig. 1). During the first eight weeks of life, when cubs were hidden in a lair, 72·3% ($n = 26$) of litters died, with mortality occurring at any time during this period (Mean number of days that litters lived, excluding survivors = 26·0, Range: 4–54, Table IV). There was no difference in the number of days that cubs in different sized litters survived (ANOVA; $F_{4,21} = 0·70$, NS).

Cubs were subject to the highest rate of mortality in the two weeks immediately following their emergence from the lair (Fig. 1). Only 51·4% of cubs that emerged from the lair were alive two weeks after emergence, whereas 27·8% were alive at four months of age. Between four and 14 months of age, however, the instantaneous mortality rate dropped.

Causes of juvenile mortality

a. Mortality in the lair

Cubs died from predation, fire, exposure or because they were abandoned by their mother (Table IV). Of the 12 litters for which the cause of death was definitely or probably known, 58·3% were killed by predators (66·7% if the litter whose mother probably died due to predation is included). Abandonment accounted for 16·7% of litter deaths, and fire and exposure for 8·3% of litters each.

TABLE III

Extent and timing of cheetah cub mortality in the Serengeti National Park, Tanzania

	Birth	Emergence	Number at 2 weeks post emergence	4 months	14 months
Litters	36	10	5–7	5–6	3–4
Cubs	125*	36	19–20[@]	10–12[+]	5–7[@]

* Litters ($n = 6$) that died before being counted were estimated to be of average size (3·5)

[@] 2 of 3 cubs alive at 4 months and last seen when 7 months old

[+] 2 of 4 cubs alive when 9·5 weeks old but dead by 5 months

i. Predation. Table V outlines the circumstances surrounding predation on cheetah cubs in the lair, both in this study area and from other studies in the same ecosystem. In 82·4% of attacks ($n = 17$) by predators, all the cubs in the litter died. Where predator species was identified, lions were definitely or probably the culprits in 82·4% of cases ($n = 17$). Lions located mothers with cubs in the lair by seeing them sit up in the lair, or by noticing the mothers resting nearby. Lions then ran forward and searched for the cubs; mothers responded by rushing at the lion and threatening it. After biting through their skull or spine, lions rarely ate cubs and usually just left them in the lair. Cheetah mothers often ate their dead cubs once the lions had left.

One litter disappeared when the mother herself died. As both the mother and cubs were healthy when last observed, I suspect that predators may have been responsible for their demise. Her radiocollar was found within 400 m of the last known lair site in an area that was intensively used by a lion pride. Indeed, on the day that the collar was found, the pride was resting about 100 m from the lair site.
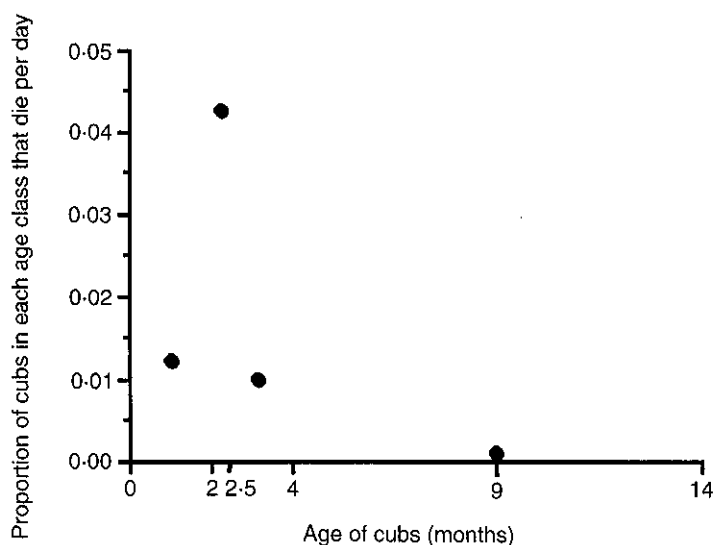
FIG. 1. The instantaneous mortality rate in different age classes of cheetah cubs in the Serengeti National Park, Tanzania. Cubs emerge from the lair at approximately 2 months of age. Ages were chosen on the basis of ontogenic stages through which cubs passed.

TABLE IV

Instances and circumstances surrounding cub mortality in the lair in this study

Litter identity	Litter size	Age at death	Mortality source	Certainty of cause of death
		Litters in which all cubs died		
MK 1	2	28	Predation	Definite
MQ 1	4	31	Predation	Definite
MSH 1	?	10	Predation	Probable
KC 3	3	31	Predation	Probable
TGG 3	5	16	Predation	Probable
MK 3	3	48	Predation	Probable
SGY 2	2	17	Predation	Probable
MTT 1	4	44	Predation	Possible*
MK 4	?	10	Predation	Possible@
SOF	5	34	Mother died	Probable predation
MTT 3	3	33	Abandoned (then predation)	Definite
MK 2	1	28	Abandoned	Definite
MV 2	5	32	Abandoned	Possible#
EMM 1	3	40	Abandoned	Possible#
EMM 2	2	30	Abandoned	Possible†
TGG 2	4	16	Fire	Definite
BHT 2	3	24	Exposure	1 Definite/ 2 Probable Possible
KC 1	?	10	Exposure	
MTT 2	3	54	Unknown	
SKU 2	4	28	Unknown	
KC 2	4	11	Unknown	
MV 1	3	15	Unknown	
DUT	3	45	Unknown	
BHT 1	?	13	Unknown	
SGY 1	?	5	Unknown	
AM 1	?	13	Unknown	
		Litters in which partial mortality occurred		
MTT 3	4	1 cub disappeared at 11–19 days		
MTT 4	5	1 cub disappeared at 28–42 days		

* Mother found only 2 km from the lair site, 10 days after previous visit. She did not return to lair. As this distance was too small to suggest abandonment, the interval between visits was great enough for the previously healthy cubs to have been lost early in that period and the mother was no longer returning to the lair each night, predation was the most likely cause of litter loss

@ Mother found to return each day and rest in the vicinity of a marsh (which was in area of very high hyaena density), that I suspected she had used as a lair site. However, as I had never seen the cubs, and they would have been less than a week old when I found the mother, I could not be as sure their demise was a result of predation

Abandonment likely as mother had experienced poor hunting success

† Mother could not be found near the lair site just two days after previous visit

Other large carnivores, such as spotted hyaenas and male cheetahs have also been reported as predators of cubs of this age in the same ecosystem (Table V; Burney, 1980). Raptors may also attempt to kill young cubs (Maugham, 1914) and I have a report of a secretary bird (*Sagittarius serpentarius*) that intentionally stamped on and killed one cub that the mother had dropped while moving the litter to a new lair site (D. Richards, pers. comm.). Other felids, viverrids, jackal species and snakes could conceivably kill cubs of this age when mothers were absent.

ii. Abandonment. Abandonment was the second most common cause of mortality, albeit of little importance compared to predation. Two litters of apparently healthy cubs were definitely abandoned by their mothers (16·7% of litters of known or probable causes ($n = 12$), although it was considered the most likely cause of mortality in another three cases, classified as 'possibly abandoned' in Table IV.

Abundance of prey and the difficulty in obtaining sufficient food played a primary role in the likelihood of cubs being abandoned. Fewer Thomson's gazelles were counted around the lairs of litters that were definitely abandoned ($n = 2$), than lairs from which litters emerged ($n = 10$, Fig. 2). Comparisons between one female who abandoned her litter with observations from mothers of other litters, revealed that she ate less meat per hour watched (mean (S.E.) for mother of abandoned litter ($n = 1$), other mothers ($n = 14$), respectively: 0·06, 0·2 (0·02)), travelled further per day (11·5, 6·6 (0·7)) and spent more minutes hunting per hour watched (1·21, 0·99 (0·23)). This female had given birth to her cubs in a marsh that was situated approximately 12 km from the main concentrations of gazelles.

iii. Other causes. Litters also died from environmental causes such as fire or bad weather. A fire killed one litter of four immobile 10-day-old cubs in the dry season of 1988. A litter of three relatively mobile six-week-old cubs survived nearby, but were singed and had burns on their extremities. A pneumonia infection, secondary to exposure, was the cause of death of at least one, and probably all three, cubs in one litter. This cub was moribund, hypothermic, dehydrated and wheezing when last seen alive and, on post-mortem, was very emaciated, had no gastro-intestinal tract contents and had congested lungs caused by a pneumonia infection (A. Cunningham, pers. comm.).

TABLE V

Circumstances surrounding predation on cheetah cubs in the lair in the Serengeti ecosystem. (Sources 1, 2, 6 from Serengeti National Park, Tanzania and 3–5 from Masai Mara Game Reserve, Kenya)

Number killed	Lair site	Predator	Certainty cubs killed by predator	Cubs eaten by predator?	Source
2/2	marsh	lion	definite	1 half eaten	1
4/4	marsh	lion	definite	no	1
3/4	kopje	lion	definite	no	1
4/4	marsh	lion	definite	no	2
3/3	marsh	lion	definite	no	2
all	marsh	lion	definite	?no	2
all	kopje	lion	definite	?no	2
all	kopje	lion	definite	?no	2
1 cub survived	kopje	lion	definite	?no	2
3/3	vegetation	? lion	definite	no, 2 cubs found	1
5/5		lion	definite	3 no, 2 yes	3
3/3		spotted hyaena	definite	?	3
1/4	vegetation	secretary bird	definite	?	4
all	marsh	?lion	probable	?	1
5/5	bush	lion	probable	no, 4 found	5
2/2	bush	?male cheetah	possible	?	3
2/2	?bush	?lion	possible	?	6

Sources: 1. This study; 2. G. Domb & M. Smits van Oyen, pers. comm.; 3. Burney, 1980; 4. D. Richards, pers. comm.; 5. Ammann & Ammann, 1984; 6. Frame & Frame, 1981.

Two cubs disappeared from otherwise healthy litters. One was very lethargic compared to its littermates and died when 10–17 days old. The other appeared to be normal at one month of age, but disappeared within the next two weeks. These cubs could have had congenital problems, or died through accidents. Mortality due to congenital problems in the early postnatal period could not be monitored, but may not be substantial because average litter sizes were similar to those in captivity (Laurenson, Caro & Borner, 1992).

b. Post-emergence mortality

Causes of mortality after cubs emerged from the lair were more difficult to decipher. Litters were frequently resighted with a diminished number of cubs but with no clue as to why they might have disappeared. Nevertheless, spotted hyaenas were observed carrying off and killing all four cubs from one litter, and a single cub from another litter of four cubs. Other observers have documented predators such as lions and Masai dogs killing newly emerged cubs in the same ecosystem (Table VI). Partial litter mortality occurred in six out of seven incidents and is consistent with predation being responsible for the majority of cub losses. Cubs scattered and hid when attacked, so only one or two cubs were usually killed, particularly if there was just a single predator.

Some cubs may die for other reasons, such as injury or illness, although there are few data available. Caro (1994), however, reports the death of a weak cub in an otherwise healthy litter. It is also possible that some cubs disappeared because they became separated, perhaps during hunts or in the panic of a predator attack. It is likely that they would be killed by predators or starve to death, as they were inept at hunting. Lone cubs, however, are sometimes adopted by other unrelated families (Caro, 1994, pers. obs.).
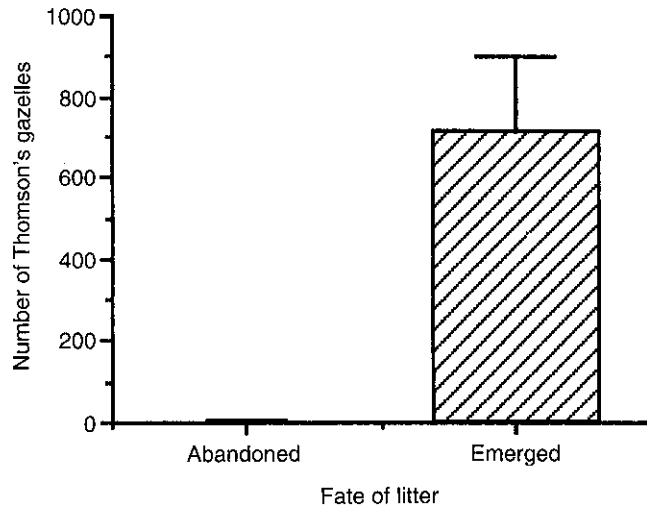
FIG. 2. The mean number of Thomson's gazelles that were counted around lair sites where cubs were abandoned ($n = 2$) and those where cubs survived to emergence ($n = 10$). Number of gazelles calculated as the sum of those counted within a radius of 1 km at nine points; at the lair site and 0, 2 and 4 kilometres from the site, on each compass point. Mann-Whitney U test, $U = 0$, $P < 0.05$.

Summary

Assuming that the causes of mortality for cubs that died of unknown causes occurred in the same proportion as known or probable causes, predation accounted for 73·2% of the 119 cub deaths between birth and independence in this study, environmental causes for 14·4%, abandonment and starvation for 8·2% and inviable cubs for 4·1%. Lions accounted for 78·2%, and spotted hyaenas for 12·5% of the predation of 64 cheetah cubs in the ecosystem. Lion predation is therefore by far the most important factor affecting cheetah cub survival.

B. Maternal responses to juvenile mortality

There are a number of antipredator strategies that cheetah mothers could adopt to improve the survival of their cubs in the face of high juvenile mortality due to predation. Encounters with predators could be minimized by mothers being more vigilant, detecting predators more often and taking evasive action (Caro, 1987; Endler, 1991). Alternatively, if encounters did take place, mothers could minimize the predator's effect by defending cubs vigorously.

Vigilance

a. Vigilance during the day

The proportion of time that females spent observing each day differed with reproductive status (ANOVA, $F_{2,41} = 4·75$, $P < 0·05$; Fig. 3). Mothers with emerged cubs spent more time observing than other types of females. Lactating females of both types spent less time resting than solitary females (ANOVA, $F_{2,41} = 4·08$, $P < 0·01$; Fig. 3).

Lactating females, whether or not the cubs were in the lair, were more vigilant (lair: $P < 0·05$; emerged: $P < 0·01$) during the daytime rest period than females without cubs (ANOVA, $F_{2,29} = 7·75$, $P < 0·01$; Fig. 4a). Females with emerged cubs also spent more time sitting up than females without cubs (ANOVA: Status; $F_{2,29} = 5·00$, $P < 0·01$: Fig. 4b). Increased vigilance levels of females with emerged cubs probably explains why they spotted predators more often than other females, perhaps as a consequence of their increased vigilance (Table VII; $\chi^2 = 16·7$, $d.f. = 2$, $P < 0·01$).

TABLE VI

Instances of cub mortality in litters that had emerged from the lair in the Serengeti ecosystem. (Sources 1, 2, 6 from Serengeti National Park, Tanzania and 3–5 from Masai Mara Game Reserve, Kenya)

Cub age	Number killed	Predator	Certainty	Cubs eaten	Area	Source
9 weeks	4/4	spotted hyaena	definite	yes	Serengeti	1
8 weeks	1/4	spotted hyaena	definite	yes	Serengeti	1
8 weeks	1/3	lion	definite	yes	Serengeti	2
8 weeks	2/4	lion	definite	yes	Serengeti	2
3 months	2/4	Masai dogs	possible	?	Masai Mara	3
6 months	1/2	lion	definite	no	Serengeti	4
9·5 months	1/4	leopard then hyaena	probable	no	Masai Mara	3

Sources: 1. This study; 2. Caro, 1987; 3. Burney, 1980; 4. M. Smits van Oyen, pers. comm.

(a) Amount of time spent resting
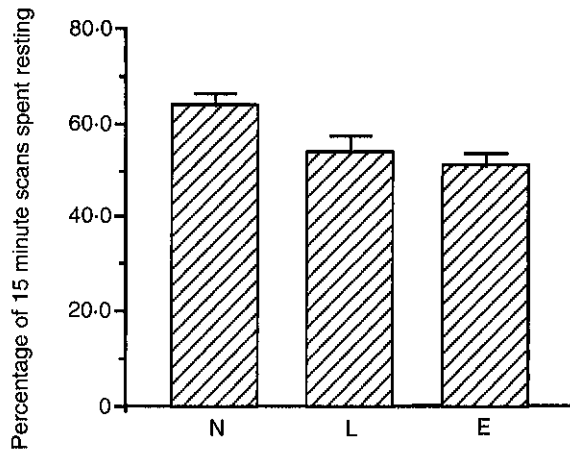
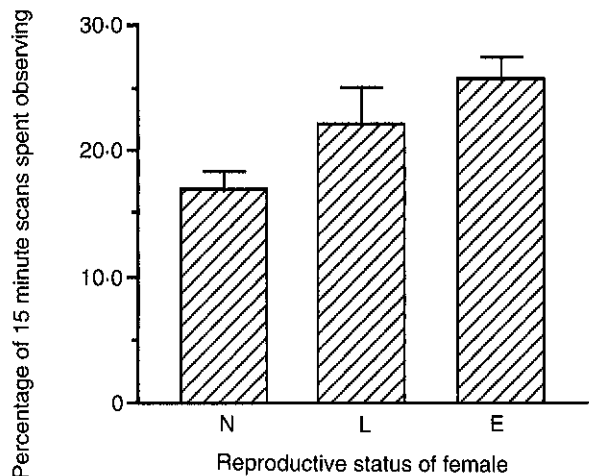(b) Amount of time spent observing

FIG. 3. Effect of reproductive status on the mean (S.E.) percentage of time spent in various activities by female cheetahs. N = females with no cubs ($n = 20$), L = lactating females with cubs in the lair ($n = 9$), E = lactating females with emerged cubs ($n = 7$).

b. Vigilance at kills

Reproductive status affected the length of time that mothers paused before eating at kills although this was also related to the size of prey they had caught and the female's identity, but not to their belly size or the height of the surrounding vegetation (Table VIII). Females accompanied by cubs spent significantly longer observing their surroundings at kills than either females with cubs in the lair or non-lactating females. The length of time that these mothers with cubs spent observing during a meal was also significantly greater than other females

TABLE VII

Frequency with which female cheetahs observed predators that were recorded within 1 km of their position. Predator sightings were treated as independent events

Reproductive status	n	No. of occasions that cheetah saw predator (%)
Solitary	277	26·7
Lactating, with cubs in lair	253	26·5
Lactating, with emerged cubs	72	50·0

(Table IX) and was due to longer bout lengths (Bout length, $F_{2,122} = 2·58$, $P < 0·01$; individuals: $F_{18,122} = 4·37$, $P < 0·001$).

c. Vigilance and proximity to the lair

When resting with their cubs in the lair, mothers did not notice or react to predators as often as when they were in the open ($\chi^2 = 9·06$, $d.f. = 1$, $P < 0·01$; In lair, predator recorded 109 times, cheetah noticed 16; In open: 160 recorded, 51 reacted). These females did not notice predators because they rarely sat up while resting in the lair with cubs. Lying low while in the lair was a good antipredator strategy, as passing predators would have less chance of finding a lair site by accident. In both cases of lion predation that I observed, lions were alerted to the presence of the lair only when the female sat up.

Females were extremely vigilant when returning to lair. They spent a greater proportion of time stopping to observe their surrounding when they were within 1 km of the lair than when they were further away (Fig. 5; Paired t-test, $t = 3·75$, $d.f. = 10$, $P < 0·01$).

Antipredator behaviour

The model that most accurately predicted the reaction of female cheetahs to predators ($\chi^2 = 117·2$, $d.f. = 22$, $P < 0·0001$) included the variables representing different predator species, the reproductive status of females, whether vegetation height was greater or less than 10 cm, whether the distance between the cheetah and predator was greater or less than 150 m and the danger that the predator posed (Table X). Jackals and females in Group 1 were included in the constant to which other predator species and female groups were compared. Although the interaction between females in Group 1 and predators at a distance greater than 300 m did not improve the significance of the model ($P = 0·14$), it did allow another nine cases where females were merely watching predators to be accurately predicted by the model. As watching the predator was the reaction which was most poorly predicted, this interaction was included. Thus 44·2% ($n = 52$ interactions), 88·6% ($n = 105$) and 55·6% ($n = 36$) of watching, defensive and aggressive reactions, respectively, were predicted by this model.

Females in close proximity to cubs that had either emerged from the lair or were still in it (i.e. Groups 1 and 2) were more likely ($P < 0·01$) to attack predators than those females who were not with their cubs, or that did not have cubs. Females at the lair site were less likely ($P < 0·05$) to act defensively to predators and this maternal reaction was never recorded in 16 interactions.

The species of predator involved in the interaction also affected the probability of a particular reaction occurring. If it was a lion, cheetah or hyaena, females were more likely ($P < 0·001$) to

(a) Amount of time females were vigilant
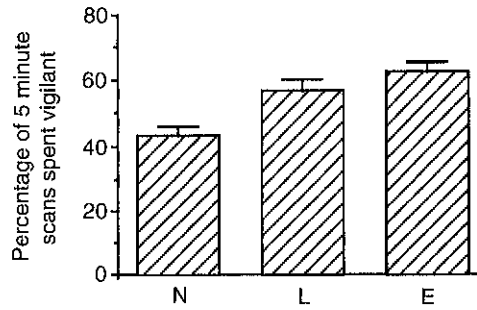
(b) Amount of time females spent sitting up
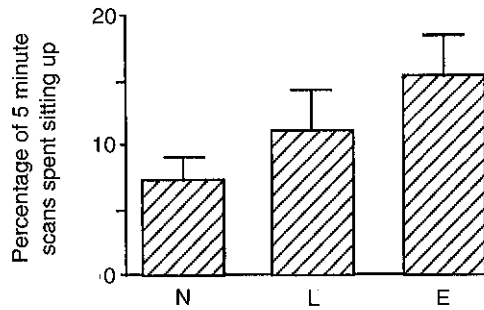
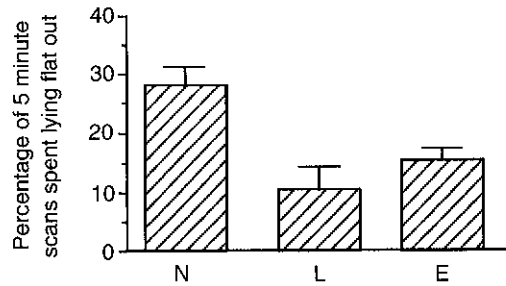(c) Amount of time females spent lying flat out

FIG. 4. The effect of reproductive status on the mean (S.E.) of the percentage of time spent being vigilant or in certain body positions in the daytime rest period. N = female with no cubs ($n = 18$), L = lactating females with cubs in the lair ($n = 6$), E = lactating females with emerged cubs ($n = 6$).

TABLE VIII

Result of the analysis of variance of the factors affecting the length of time that female cheetahs paused before eating. F values are adjusted for the influence of other variables

Source of variation	d.f.	F	Significance
Reproductive status	2,109	6·32	0·003
Prey size	1,109	15·24	0·000
Identity of cheetah	17,109	1·77	0·042
Vegetation height	4,109	0·44	NS
Belly size of cheetah	1,109	0·55	NS

TABLE IX

Results of the analysis of variance on the factors affecting the percentage of time that female cheetahs spent looking up while eating. F values take into account the effect of other variables

Source of variation	d.f.	F	Significance
Reproductive status	2,109	6·07	0·003
Prey size	1,109	8·92	0·003
Identity of cheetah	17,109	2·06	0·014
Vegetation height	4,109	0·90	NS
Belly size of cheetah	1,109	0·01	NS
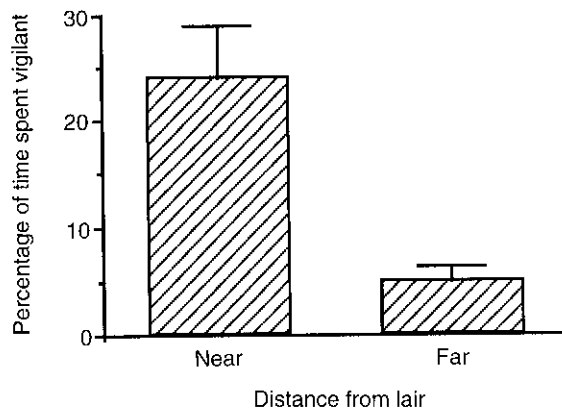
FIG. 5. Effect of proximity to lair on the percentage of time that mothers ($n = 11$) were vigilant while returning to the lair. Bars represent means with S.E. shown as vertical lines. Near = mother was within 1 km of lair, Far = mother further than 1 km from lair.

respond defensively than if the predator was a jackal. There was also a tendency ($P < 0·1$) for females to respond more defensively to servals (*Felis serval*). In addition, females were more likely ($P < 0·05$) to attack hyaenas than any other predator. The number of predators involved in the interaction did not have a significant effect in predicting females' reactions.

There was a significant positive relationship between the scale of threat posed by a predator

TABLE X

The causal variables influencing the probability of defensive or aggressive behaviour occurring when female cheetahs interact with predators. The constant represents the response by solitary females (Group 1) in interactions with jackals. Levels of significance; †= $P < 0.1$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$

Variable	Cheetah reacts by leaving, crouching, hissing		Cheetah reacts by stalking, chasing, slapping	
	Coefficient	t	Coefficient	t
Lactating female with emerged cubs (Group 4)	−0·87	−1·14	2·85	3·12**
Lactating female resting in lair (Group 3)	−2·26	−2·04*	3·29	3·08**
Lactating female out of lair (Group 2)	−0·01	−0·11	0·74	0·90
Lion	4·02	3·31***	−0·15	−0·14
Hyaena	3·48	4·03***	1·54	2·10*
Cheetah	3·52	3·82***	0·38	0·41
Serval	1·97	1·76†	−0·20	−0·19
Vegetation < 10 cm	−0·01	0·42	1·20	1·87†
Distance > 150 m	−0·29	−0·46	−2·15	−2·68**
Degree of danger	0·63	1·77†	0·84	2·08*
Solitary female × distance > 300 m	−1·21	−1·46	−14·14	−0·01
Constant	−1·99	−2·20*	−2·94	−2·97**

and the scale of the female cheetah's reaction ($P < 0.05$, Table X). If a predator did not see, or ignored the cheetah, the cheetah was likely just to watch it. If, however, the predator approached the cheetah directly, the cheetah was more likely to retaliate by attacking it. The relationship between the proximity of the predator and likelihood of a cheetah attacking ($P < 0.01$) may be influenced by these interactions where the cheetah came close to slap the predator. If vegetation height was very low, there was a trend ($P < 0.1$) for female cheetahs to attack the predator, perhaps because there was little cover in which to hide. Cheetahs may have been likely just to observe predators ($P = 0.14$) if females did not have cubs and if the predator was more than 300 m away. In this situation, where the threat posed by the predator was particularly low, there was no need for cheetahs to react.

Discussion

Extent of mortality

When compared to demographic patterns of other large mammals (Caughley, 1966; Loudon, 1985), cheetah cub mortality was found to be extremely high in this study, with approximately 95·2% of cubs dying before reaching independence. There are few comparable data available from other felid species, but the estimated mortality rates for lion cubs between emergence from the lair and one year of age are 67% in the Serengeti and 33·3% in the Ngorongoro Crater (Packer *et al.*, 1988). Between 81–86% of cheetah cubs in the Serengeti are estimated to die over the same time span. In a long-term study of tigers in Nepal, Smith & McDougal (1991) found that mortality in the first year of life was 34% and 17% in the second year. Cheetah cub mortality is also high compared to former estimates (30–60%) in East Africa (McLaughlin, 1970; Schaller, 1972; Burney, 1980; Frame & Frame, 1981), but many of these estimates failed to take into account, or knew, the scale of mortality in the lair.

Timing of mortality

Cub survival did not increase linearly with cub age as the instantaneous juvenile mortality rate peaked at 2–2·5 months of age, just after cubs left the lair. Mortality rates of cubs in the lair were similar to those of 2·5–4 months of age cubs, suggesting that hiding cubs in long vegetation or in an inaccessible area is an effective strategy for reducing offspring mortality. Newly emerged cubs, in contrast to those in the lair, are more visible and are also relatively slow at running away from predators. Indeed, these cubs may not even recognize that other large carnivores are dangerous (Caro, 1987, pers. obs.).

The ability to escape from predators is probably responsible for the observed decline in mortality rates after four months of age. Once cubs become more mobile, they are relatively swift on their feet and are usually able to outrun predators, at least over short distances (McLaughlin, 1970; Caro, 1987; Laurenson *et al.*, 1992). Correspondingly, predators were less persistent in attacks (Laurenson, pers. obs.), although predators do sometimes succeed in killing older cubs (Table V).

Causes of mortality

Predation by other carnivores has been commonly cited as the most important cause of cub mortality in cheetahs, but there has been little evidence to substantiate these claims (Schaller, 1972; Eaton, 1974; Myers, 1975). Results presented here indicate that predation, mainly by lions, is indeed the major cause of cub mortality, accounting for some 78% of mortality between birth and independence. Abandonment, which has not been previously reported as a cause of mortality in this species, fire and bad weather each accounted for a smaller proportion of mortality.

Predation is more commonly regarded as an important cause of juvenile mortality in non-predatory mammalian species such as ungulates or primates (Caughley, 1966; Lent, 1974; Cheney & Wrangham, 1987). Infanticide, by male conspecifics, is, however, the major cause of cub mortality in lions and tigers, *Panthera tigris* (Packer *et al.*, 1988; Smith & McDougal, 1991). Cheetahs may be the only mammalian terrestrial predator species where the majority of young die as a result of interspecific predation. Even in marine species such as seals, where predation by bears, other seals or whales is the major cause of pup mortality, its frequency is much lower and it is probably not the limiting factor on population size. For example, sea lions kill a maximum of only 20% of South American fur seal pups, *Arctocephalus australis* (Harcourt, 1992). In contrast, it is possible that lion predation on cheetah cubs is the factor limiting the size of the Serengeti cheetah population (Laurenson, In press *a*).

Cheetahs will kill, and normally eat, almost any species that they can easily catch, even conspecifics in some cases (Kruuk, 1972; Schaller, 1972; Packer & Pusey, 1984). It is relatively difficult, however, to determine whether the killing of cheetah cubs by other carnivores represents predation (for food) or interspecific competition. In the case of lions, predation for food does not explain this behaviour, as they rarely eat the cheetah cubs. The degree of interspecific competition from cheetahs is slight for lions because the main prey of cheetahs are Thomson's gazelles and those of lions, zebras and wildebeest (Schaller, 1972; Frame, 1986). The degree of competition may, however, increase in the dry season (Schaller, 1972). In addition, lions and hyaenas often scavenge from cheetahs, thereby further decreasing the degree of competition. None the less, the costs of killing cheetahs cubs are probably small, so any marginal benefits might select for this behaviour. Whatever the adaptive explanation, this is an important example of intraguild predation, where the cheetah, as an intermediate predator, faces both competition and predation from top predators (Polis, Myers & Holt, 1989).

Juvenile mortality and the evolution of life-history strategies

Both theoretical considerations and empirical cross-species analyses indicate that juvenile mortality may be a fundamental determinant of life-history traits; juvenile mortality is highly correlated with life-history parameters, such that species with high mortality reproduce and develop rapidly (Stearns, 1976; Promislow & Harvey, 1990; Lessells, 1991; Gittleman, 1993). Mortality must, however, be caused by extrinsic factors and survival be unpredictable or unlikely for a large litter of small neonates to maximize fitness in good years, but minimize maternal losses in bad years (Promislow & Harvey, 1990).

The high mortality rates of cheetah cubs may, therefore, explain the evolution of the life-history strategy of this species. Cheetahs have large litter sizes compared to other felids (Caro, 1994), low neonate and litter birth weights for their bodyweight (Oftedal & Gittleman, 1989) and high growth rates (Laurenson, In press *b*). In addition, they return rapidly to oestrus after the loss of an unweaned litter (Laurenson *et al.*, 1992). Thus cheetahs appear to have a fast reproductive rate, putting little effort, which might be wasted, into each reproductive iteration and investing rapidly in their young after birth, perhaps to minimize the period of vulnerability (Laurenson, In press *b*), but having large litters to increase the chance that some individuals might survive.

High juvenile mortality of cheetahs is not intrinsically related to traits such as rapid growth rate or short gestation period, but has an extrinsic source, predation, which is essentially stochastic. High juvenile mortality in cheetahs is unlikely to be a consequence of the species-characteristic life-history traits. It is more likely that these traits have evolved as a response to such high mortality. These results emphasize the importance of determining the causes of juvenile mortality when explaining the evolutionary relationship between life-history strategies and mortality (Case, 1978; Promislow & Harvey, 1990; Gittleman, 1993).

The impact of juvenile mortality on patterns of maternal care

The results of this study indicate that female cheetahs alter their behaviour after cubs are born in an attempt to ameliorate high mortality. The causes and timing of mortality appear to be critical, however, in determining the extent, type and timing of maternal strategies that are adopted.

a. Determination of antipredator strategies

Due to developmental constraints on mobility, cheetahs are forced initially to conceal their altricial offspring in a fixed place. Nevertheless, cubs are also safer in these lairs, with mothers relying primarily on crypsis to combat predation of the relatively immobile and defenceless cubs. Cheetah mothers avoided revealing the family's hiding place by only rarely sitting up and consequently did not notice passing predators frequently. Furthermore, they were extremely vigilant when returning to the lair and also returned after dark on more than half the days they were observed (Laurenson, 1993). The lower mortality rate in the lair than that immediately after emergence suggests that these may be relatively successful antipredator strategies. In addition, observations of instances of predation in this study indicate that it was the mothers themselves that revealed the position of their lairs, as lions attacked litters when mothers sat up, or when they saw mothers entering or leaving lair sites. This parallels nest predation in birds where some nest sites are detected by predators observing parents provisioning their broods (Ricklefs, 1969; Montgomerie & Weatherhead, 1988).

When confronted by predators, the presence or absence of cubs was a major determinant of the mothers' antipredator strategy. Unaccompanied females were less likely to attack predators, and females with their cubs in the lair were as likely to attack predators, as females accompanied by their emerged cubs. Females with cubs in the lair never reacted defensively by abandoning their immobile cubs to their fate, but chose always to try and drive predators away.

Mothers with emerged cubs may, however, still have relied on crypsis for cub defence in certain circumstances. For example, they very rarely moved more than a few metres overnight and often left cubs in longer vegetation during hunts. Once cubs left the lair and became more mobile, predator avoidance and defence of cubs were, however, more important antipredator strategies.

b. Influence of mortality timing

The extent of maternal aggressiveness and maternal vigilance were also determined by the timing of mortality after emergence. Caro (1987) showed that mothers were more aggressive to predators and more vigilant when accompanied by young cubs (2–4 months of age) than by older cubs. Thus, the overall pattern of maternal antipredator behaviour mirrors the susceptibility of cubs to predation, with these behaviours peaking when cubs are between two and four months of age, the time of peak mortality. These results highlight the critical importance that offspring vulnerability can have in determining patterns of parental care. A similar result has been found in vervet monkeys where juvenile mortality occurs in two peaks at four and 8–9 months of age (Hauser, 1988). By using playback experiments, maternal responsiveness was shown to be greater when predator alarm calls were played just before these mortality peaks than at other times.

c. Influence of predator species

The cause of the predation mortality also affected the pattern of maternal care. Cheetah mothers were more likely to run away or react defensively when confronted by lions, spotted hyaenas or conspecifics than by jackals or small felids. This almost certainly reflects the risk that these predators posed to cubs. Lions and spotted hyaenas are major predators of cheetah cubs and it is possible that conspecifics, particularly males, are also a threat (Burney, 1980).

Personal risk of injury also played some role in determining maternal antipredator behaviour. Mothers were less likely to stalk, chase or slap the assailant if it was a lion rather than another predator species. Lions are considerably larger than adult cheetahs and a single cheetah is little deterrent to a lion. The best antipredator strategy is to detect lions as early as possible and then avoid them. In contrast, cheetahs can harass and drive off a hyaena or other predators and so aggressive behaviour to these other species may have been effective and therefore worth the risk involved.

d. Effect of interactions between mortality components

Mortality rates in the lair are lower and also due to a wider variety of causes than after emergence. In particular, cubs in the lair are at risk of abandonment and starvation if their mothers are unable to catch enough food to meet energetic requirements while also maintaining regular visits to the lair for suckling cubs. Thus, capturing food efficiently may be particularly important for mothers when cubs are in the lair than when cubs are older.

Lactating females with cubs in the lair, when compared to females without cubs, were more vigilant, sat up and observed their surroundings in the middle of the day more often and rested

less. These lactating females did not, however, show increased vigilance at kills. Vigilance during the day is statistically associated with hunting behaviour, but at kills is related to antipredator behaviour (Caro, 1987). Thus females with cubs in the lair may have increased their vigilance when out in the open away from their cubs, in order to acquire food as well as to detect predators. The increases in food intake at this time (Laurenson, 1992) suggest that vigilance may be primarily related to the increased energetic needs and the cubs' susceptibility to abandonment or starvation, rather than an antipredator strategy. Mothers' vigilance during the day after cubs left the lair may, in contrast, be concerned with detecting predators as well as capturing more food. Lactating females with newly emerged cubs were also more vigilant at kills than females without cubs and were particularly aggressive to predators. As cubs grow older, however, measures of vigilance during the day declined and showed little association with antipredator behaviour, but did with hunting activity (Caro, 1987). This suggests that mothers' vigilance levels during the day when cubs are older may be primarily related to provisioning offspring with food, a similar situation to when cubs are in the lair.

In sum, maternal vigilance for prey is high when offspring are susceptible to starvation but declines as the probability of starvation decreases and cubs are more able to fend for themselves. However, the overall level of maternal vigilance is highest when cubs emerge from the lair and is then associated with antipredator behaviour, reflecting the cubs' vulnerability to predation and the importance of antipredator strategies at that time.

Interactions between the timing and causes of juvenile mortality may explain observed patterns of maternal care in other species. For example, the degree of responsiveness by vervet monkey mothers was greater before the first than the second peak of juvenile mortality in Hauser's (1988) study. Recent results suggest that the first mortality peak stems primarily from predation, and the second peak from starvation (Cheney & Seyfarth, 1990). The interaction between the timing and cause of mortality could potentially explain the differential maternal responsiveness before the two mortality peaks; responding to predator alarm calls by gathering up offspring would have little effect on decreasing mortality from starvation. Future studies examining the influence of juvenile mortality on the evolution of patterns of parental care should therefore consider the impact of interactions between its components.

REFERENCES

Ammann, K. & Ammann, K. (1984). *Cheetah*. Camerapix Pub. Int. Nairobi.
Andersson, M., Wiklund, C. G. & Rundgren, H. (1980). Parental defence of offspring: a model and an example. *Anim. Behav.* **28**: 536–542.

Burney, D. (1980). *The effects of human activities on cheetahs (Acinonyx jubatus Schr.) in the Mara Region of Kenya*. MSc thesis, University of Nairobi.

Caro, T. M. (1987). Cheetah mothers' vigilance: looking out for prey or for predators? *Behav. Ecol. Sociobiol.* **20**: 351–361.

Caro, T. M. (1994). *Cheetahs of the Serengeti Plains: patterns of grouping in an asocial species*. Chicago: University of Chicago Press.

Caro, T. M. & Collins, D. A. (1986). Male cheetahs of the Serengeti. *Natn. geogr. Res.* **2**: 75–86.

Caro, T. M. & Laurenson, M. K. (1994). Ecological and genetic factors in conservation: A cautionary tale. *Science, Wash.* **263**: 485–486.

Case, T. J. (1978). On the evolution and adaptive significance of post-natal growth rates in terrestrial vertebrates. *Q. Rev. Biol.* **53**: 243–281.

Caughley, G. (1966). Mortality patterns in mammals. *Ecology* **47**: 906–918.

Cheney, D. L. & Seyfarth, R. M. (1990). *How monkeys see the world*. Chicago: University of Chicago Press.

Cheney, D. L. & Wrangham, R. W. (1987). Predation. In *Primate societies*: 227–239. Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (Eds). Chicago: University of Chicago Press.

Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton: Princeton University Press.

Curio, E. & Regelmann, K. (1987). Do great tit (*Parus major*) parents gear their brood defence to the quality of their young? *Ibis* **129**: 344–352.

Durant, S. M., Caro, T. M., Collins, D. A., Alawi, R. M. & FitzGibbon, C. D. (1988). Migration patterns of Thomson's gazelles and cheetahs on the Serengeti plains. *Afr. J. Ecol.* **26**: 257–268.

Eaton, R. L. (1974). *The cheetah: the biology, ecology and behaviour of an endangered species*. New York: Van Nostrand Reinhold.

Endler, J. A. (1991). Interactions between predators and prey. In *Behavioural ecology. An evolutionary approach*: 169–196. (3rd edn). Krebs, J. R. & Davies, N. B. (Eds). Oxford: Blackwell Scientific Publications.

Frame, G. W. (1986). *Carnivore competition and resource use in the Serengeti Ecosystem of Tanzania*. PhD thesis, Utah State University.

Frame, G. W. & Frame, L. H. (1981). *Swift and enduring: cheetahs and wild dogs of the Serengeti*. New York: Ditton.

Gilpin, M. E. & Soule, M. E. (1986). Minimum viable populations: processes of species extinctions. In *Conservation biology: the science of scarcity and diversity*: 10–34. Soule, M. E. (Ed.). Sunderland, Mass.: Sinauer Associates.

Gittleman, J. L. (1993). Carnivore life histories: a re-analysis in the light of new models. *Symp. zool. Soc. Lond.* No. 65: 65–86.

Greene, W. H. (1990). *The Limdep users manual and reference guide, version 6.0*. New York, Belport: Econometric Software Inc.

Hanby, J. P., Bygott, J. D. & Packer, C. (In press). Comparative ecology, demography and behaviour of lions in two contrasting habitats: Ngorongoro Crater and the Serengeti Plains. In *Serengeti II; Research, conservation and management of an ecosystem*. Sinclair, A. R. E. & Arcese, P. (Eds). Chicago: University of Chicago Press.

Harcourt, R. (1992). Factors affecting early mortality in the South American fur seal (*Arctocephalus australis*) in Peru: density-related effects and predation. *J. Zool., Lond.* **226**: 259–270.

Harvey, P. H. & Zammuto, R. M. (1985). Patterns of mortality and age at first reproduction in natural populations of mammals. *Nature, Lond.* **315**: 319–320.

Hauser, M. D. (1988). Variation in maternal responsiveness in free-ranging vervet monkeys: a response to infant mortality risk? *Am. Nat.* **131**: 573–587.

König, B., Riester, J. & Markl, H. (1988). Maternal care in house mice (*Mus musculus*): II. The energy costs of lactation as a function of litter size. *J. Zool., Lond.* **216**: 195–210.

Kruuk, H. (1972). *The spotted hyaena*. Chicago: University of Chicago Press.

Lack, D. (1968). *Ecological adaptations for breeding in birds*. London: Methuen & Co.

Lande, R. (1988). Genetics and demography in biological conservation. *Science, Wash.* **241**: 1455–1459.

Laurenson, M. K. (1992). *Reproductive strategies of wild female cheetahs*. PhD thesis, University of Cambridge.

Laurenson, M. K. (1993). Early maternal behaviour in cheetahs; Implications for captive husbandy. *Zoo Biol.* **12**: 31–43.

Laurenson, M. K. (In press *a*). Interspecific predation and cheetah population dynamics. In *Serengeti II; Research, conservation and management of an ecosystem*. Sinclair, A. R. E. & Arcese, P. (Eds). Chicago: University of Chicago Press.

Laurenson, M. K. (In press *b*). Cub growth and maternal care in cheetahs. *Behav. Ecol.*

Laurenson, M. K. & Caro, T. M. (1994). Monitoring the effects of non-trivial handling in cheetahs. *Anim. Behav.* **47** (3): 547–557.

Laurenson, M. K., Caro, T. M. & Borner, M. (1992). Female cheetah reproduction. *Natn. Geogr. Res. Explor.* **8**: 64–75.

Lazarus, J. & Inglis, I. R. (1986). Shared and unshared parental investment, parent-offspring conflict and brood size. *Anim. Behav.* **34:** 1791–1804.

Lent, P. C. (1974). Mother-infant relationships in ungulates. *IUCN Publs* (N. S.) No. 24: 14–55.

Lessells, C. M. (1991). The evolution of life-histories. In *Behavioural ecology. An evolutionary approach:* 32–68. 3rd edn. Krebs, J. R. & Davies, N. B. (Eds). Oxford: Blackwell Scientific Publications.

Loudon, A. S. I. (1985). Lactation and neonatal survival in mammals. *Symp. zool. Soc. Lond.* No. 54: 183–207.

McLaughlin, R. T. (1970). Aspects of the biology of cheetahs *Acinonyx jubatus* (Schreber) in Nairobi National Park. MSc thesis, University of Nairobi.

Maugham, R. C. F. (1914). *Wild game in Zambezia.* New York: Charles Scribner's Sons.

Montgomerie, R. D. & Weatherhead, P. J. (1988). Risks and rewards of nest defence by parent birds. *Q. Rev. Biol.* **63:** 167–187.

Myers, N. (1975). *The cheetah (Acinonyx jubatus) in Africa.* Morge, Switzerland: IUCN Monograph No. 4.

Oftedal, O. T. & Gittleman, J. L. (1989). Energy output during reproduction in carnivores. In *Carnivore behaviour, ecology and evolution.* Gittleman, J. L. (Ed.). Ithaca: Cornell University Press.

Packer, C. & Pusey, A. E. (1984). Infanticide in carnivores. In *Infanticide: comparative and evolutionary perspectives:* 31–42. Hausfater, G. & Hrdy, S. (Eds). New York: Aldine.

Packer, C., Herbst, L., Pusey, A. E., Bygott, J. D., Hanby, J. P., Cairns, S. J. & Borgerhoff Mulder, M. (1988). Reproductive success of lions. In *Reproductive success:* 363–383. Clutton-Brock, T. H. (Ed.). Princeton: Princeton University Press.

Patterson, T. L., Petronovich, L. & James, D. K. (1980). Reproductive value and appropriateness of response to predators by white-crowned sparrows. *Behav. Ecol. Sociobiol.* **7:** 227–231.

Polis, G. A., Myers, C. & Holt, R. D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *A. Rev. Ecol. Syst.* **20:** 297–330.

Promislow, D. E. L. & Harvey, P. H. (1990). Living fast and dying young: A comparative analysis of life-history variation among mammals. *J. Zool., Lond.* **220:** 417–437.

Redondo, T. & Carranza, J. (1989). Offspring reproductive value and nest defense in the magpie (*Pica pica*). *Behav. Ecol Sociobiol.* **25:** 369–378.

Ricklefs, R. E. (1969). An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* **9:** 1–48.

Schaller, G. B. (1972). *The Serengeti lion.* Chicago: University of Chicago Press, Chicago.

Sinclair, A. R. E. (1989). Population regulation in animals. In *Ecological concepts:* 197–241. Cherret, J. M. (Ed.). Oxford: Blackwell.

Smith, J. L. D. & McDougal, C. (1991). The contribution of variance in lifetime reproduction to effective population size in tigers. *Cons. Biol.* **5**(4): 484–490.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry: the principles and practice of statistics in biological research.* 2nd edn. New York: W. H. Freeman & Co.

Stamps, J., Clark, A., Arrowood, P. & Kus, B. (1985). Parent-offspring conflict in budgerigars. *Behaviour* **94:** 1–39.

Stearns, S. C. (1976). Life-history tactics: a review of the ideas. *Q. Rev. Biol.* **51:** 3–47.

Winkler, D. W. (1987). A general model for parental care. *Am. Nat.* **130:** 708–720.