Laurenson MK. Implications of high offspring mortality for cheetah population dynamics. In: Sinclas ARE, Arase P, editors. Research, Conservation and Management of an Ecosystem. Chicago: University of Chicago Press.

Keywords: 1TZ/Acinonyx jubatus/cheetah/conservation/cub mortality/ecosystem/intraguild predation/management/mortality/population dynamics/reproduction

Abstract: In this chapter recent findings on the causes of juvenile mortality in cheetahs are discussed and preliminary data presented suggesting that predation on cheetah cubs is an important factor affecting the Serengeti cheetah population. First, the relative importance of factors affecting cheetah fecundity and mortality is considered and second, the effect of variation in fecundity and mortality factors on female lifetime reproduction and cub recruitment rates is simulated. In addition, the implications for cheetahs of recent changes in carnivores numbers in the Serengeti-Mara ecosystem are discussed. Finally, the relevance of these findings for cheetah populations elsewhere in Africa and their application to future conservation is considered. Although there is little information on the factors affecting adult mortality in females, these findings provide tentative evidence that offspring mortality, in particular from lion predation, may have a critical effect on the size of the Serengeti cheetah population. Interaction between cheetahs and other predators are potentially important for the population dynamics of cheetahs in the Serengeti-Mara ecosystem and deserve further scrutiny. The suggestion that other large predators have a detrimental effect on cheetah population size, is important from conservation perspective. Some pastoralists and ranchers tolerate cheetahs to a greater extent than lions or hyenas and cheetahs seem to prosper in these areas. As cheetahs may have difficulty in reaching large numbers in isolated protected areas, it is perhaps in these multiple land use areas that conservation efforts should be concentrated to find ways in which continuing conflicts between cheetahs and man can be minimized.

In Press: Serengeti II: Research, Conservation & Management of an ecosystem. Eds: ARE Sinclair + P. Arcese. U of Chicago Press {17923}

IMPLICATIONS OF HIGH OFFSPRING MORTALITY FOR CHEETAH POPULATION DYNAMICS.

M. Karen Laurenson

Department of Zoology
University of Cambridge
Downing Street,
Cambridge, CB2 3EJ.

Serengeti Wildlife Research Institute
PO Box 661,
Arusha,
Tanzania

Contact address; Upland Research Project
Crubenmore Lodge
Newton More
Invernesshire PH20 1BE.
Scotland, UK

Tel: (0)540-673510
Fax: (0)540-673533

INTRODUCTION

The modern cheetah, *Acinonyx jubatus,* once roamed throughout Africa, the Middle East and India. A sharp decrease in both the range and density of this species over the last 100 years has left only a small relic population in Iran and the largest populations in east and southern Africa (Myers 1975). Although it is often assumed that large carnivores will continue to exist in Africa's network of protected areas, cheetahs may face additional problems because they live at low density compared to other large carnivores. Species living at low densities rarely exist locally in large numbers and, as a consequence, may have difficulty in maintaining a minimum viable population size and genetic diversity (Franklin, 1980; Gilpin & Soule, 1986). Small populations are also more vulnerable to demographic and environmental stochasticity (Simberloff, 1986).

The reasons that cheetahs live at low density are not, however, well understood. In general, carnivore numbers are thought to be limited by the size of the prey populations on which they depend (Bertram, 1975: Brand & Keith, 1979: Fuller, 1989). Previous reports, however, suggest that juvenile mortality may be high in cheetahs and that predation by other large carnivores may account for a substantial proportion of this mortality (Schaller 1972; Frame & Frame 1981). The concept that predators themselves may be limited by other predators is unusual although there are no theoretical reasons to oppose it.

In this chapter I discuss recent findings on the causes of juvenile mortality in cheetahs (Laurenson, in press a) and present preliminary data that suggest that predation on cheetah cubs is an important factor affecting the Serengeti cheetah population, with the hope that this will stimulate additional study. First, I consider the relative importance of factors affecting

cheetah fecundity and mortality and second, simulate the effect of variation in fecundity and mortality factors on female lifetime reproduction and cub recruitment rates. In addition, the implications for cheetahs of recent changes in carnivore numbers in the Serengeti-Mara ecosystem are discussed. Finally, I consider the relevance of these findings for cheetah populations elsewhere in Africa and their application to future conservation.

METHODS

A study of the cheetahs of the Serengeti plains and woodland edge has been carried out since 1980 (see Caro, in press). As part of this long term study, I collected data on cub mortality and reproduction from 1987 to 1990 by closely monitoring 20 radio collared females and pinpointing the time that they gave birth. After locating lairs, cubs were counted and their age estimated. They were then checked weekly until they died or left the lair. A five-day period of intensive observation was conducted when the cubs were approximately four weeks old, (detailed methods are described in Laurenson *et al.* 1992; Laurenson 1993). Extensive analyses could find no effect of observations or handling on cub mortality (Laurenson and Caro in press).

Determination of cause of cub mortality

In some cases I witnessed cub dying and in cases where cubs disappeared between my visits to the lair, circumstantial evidence, such as cub remains or maternal behaviour allowed causes of cub death to be inferred (see Laurenson in press a, for methods). Only cases where I knew or was almost certain of the reason that cubs died were included (Table 6.1). Data from parallel studies and other observers in the ecosystem were used to assess the relative importance of different species as predators of cheetah cubs.

Cheetah cub recruitment

A simple equation was used to estimate cub recruitment because it was more convenient to manipulate with the available reproductive and mortality parameter values than using Lotka's equation or a Leslie matrix formulation (Begon *et al.*, 1991). The number of female cubs that a female cheetah could raise in her lifetime was estimated using the following, taking into account the high litter mortality rate:

$$\text{Female cubs raised} = (1-m).n.e / (a + bc),$$

where

a= Number of months that each successful litter takes to reach independence (time taken to conceive after litter lost + gestation + months with mother).

b= Number of months spent on each litter that is lost (Conception time + gestation + life of litter).

c= Number of dead litters for every one which survives [(1-d)/d], where d is the proportion of litters born that survive.

e= Reproductive lifespan of females in months.

n= Average number of female cubs in litters that reach independence.

m= Proportion of adolescents that die.

Parameter estimates were obtained from this study or from the long term study of this cheetah population (Caro, in press).

RESULTS

FACTORS AFFECTING CHEETAH ABUNDANCE IN THE SERENGETI-MARA ECOSYSTEM

Juvenile mortality

Juvenile mortality was found to be extremely high for cheetahs on the Serengeti plains, 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. Predation was the major source of mortality accounting for 73.0% of cub deaths overall (Table 6.1). Lions (*Panthera leo*) were the primary predators of cubs in the lair, whereas spotted hyaenas (*Crocuta crocuta*) and lions took approximately the same proportion of emergent cubs (Table 6.2).

Other causes of mortality were of relatively little importance, but some cubs died of starvation when abandoned by their mothers (7.7%) and others died as a result of unpredictable events such as fire (7.7%) or exposure (5.7%). The availability of prey and the difficulty in obtaining sufficient food may play a role in the probability of abandonment. Fewer Thomson's gazelles were counted around the lairs of litters that were definitely abandoned than lairs from which litters emerged ($n=2,10$ respectively; Medians: 2, 555; Mann Whitney U test, $U=0$, $p<0.05$).

Adult mortality

The causes of adult mortality and their relative importance are difficult to discern. Nevertheless, approximately 50% of young males are known to die in intraspecific fights (Caro, in press). Predation by lions, spotted hyaenas and leopards undoubtedly occurs but may be secondary to other problems such as disease, starvation or injuries; two unsuccessful predation attempts on healthy individuals were observed in this study. Serengeti cheetahs have been exposed to a variety of feline diseases (Heeney *et al.* 1992; Evermann *et al.* 1993) and some adult deaths may be attributable to disease (S. Gascoyne, pers. comm., A.Cunningham, pers. comm.) although sarcoptic mange infection, the most common overt health problem (pers. obs.), is probably secondary to stress (Caro *et al.*, 1989) or other causes of ill health. Starvation is most likely to occur in adolescents, particularly if few gazelle fawns or hares are available, as they depend heavily on these prey items whilst perfecting their hunting techniques (Caro, in press). Death by snaring is rare, but has occurred in this ecosystem (K. Campbell, pers. comm.).

Adult mortality rates are also difficult to quantify for wild cheetahs but data from radiocollared females in this study was used to estimate mortality rates. Dividing the number of females in each of three age classes (Adolescent; <3 years old: prime, 3-9 years: old, >9 years)that died whilst radiocollared by the total number of years they were radiocollared gave the rate at which females died each year. Thus adolescent females (n=6) died at a rate of 0.153 per year, prime females (n=18) at 0.227 per year and old females (n=2) at a rate of 0.55 per year. The mean life expectancy of females reaching 3 years of age was therefore 3.9 years

<u>Female fecundity</u>

Female fecundity is affected by the age at first and last successful breeding attempt, litter size and the interval between births. In many species these are primarily influenced by nutrition and food availability (Sadleir, 1969; Mitchell, 1973; Rattray, 1977). In the wet season when Thomson's gazelles fawns are abundant, there was some evidence that female cheetahs were more fertile. More litters were conceived during the wet than the dry season and females that lost litters in the dry season took longer to conceive successfully again than those losing litters in a wet month (Laurenson *et al.*, 1992). In addition, there was a non-significant trend for litters conceived in the wet season to be larger than those conceived in the dry season (Laurenson *et al.*, 1992). Thus, although there is little information on the factors affecting the age of first and last breeding in female cheetahs, there is some evidence that nutritional factors and prey availability may affect reproductive rates in this species.

CUB RECRUITMENT RATES

The effect of variation in fecundity and mortality on the number of female cubs produced in the lifetime of an adult female was modelled (Table 6.3). Overall, factors affecting juvenile and adult survival had a greater effect on cub recruitment than those affecting fecundity. Variations in offspring survival, through its effect on both parameters d and n, were substantial, yielding ranges of 0.35-1.86 and 0.37-1.32 respectively in the number of female cubs raised. These parameters should not be treated independently, as they positively covary, but it was impossible to quantify this relationship. Thus offspring survival would cause a greater alteration in the number of cubs raised than simulated here, where only these parameters were varied independently.

The number of cubs raised also varied considerably in response to changes in reproductive lifespan, although the magnitude of this variation was due to the wide range of the age at death (42-144 months), rather than range in the age at first reproduction (range; 24-38 months). Variations in *a* and *b* (the time taken to return to oestrus and the length of time that mothers provided care for their offspring) had relatively little effect on lifetime reproductive success.

The effect of demographic conditions on cheetah population dynamics was also examined. The combination of parameter values yielding net recruitment rates of 1 were calculated and a three dimensional surface drawn (Fig.6.1), allowing values of *d*, *n* and *e* to vary between 0-1, 0-144 and 0-2 respectively. The parameters *a*, *b* and *m* were treated as constants (with values 21.7, 4.9 and 0.15 respectively) as they had relatively little effect on reproductive rates. Points lying in the region above the surface represent demographic conditions resulting in an expansion of the cheetah population whereas points lying below the surface represent conditions where the population will decline.

Using mean values for these demographic parameters calculated from individuals in this study (from Laurenson *et al* 1992) only 0.66 female cubs will be raised by each adult female. This suggests that cub recruitment is not presently sufficient to maintain the cheetah population on the Serengeti plains.

THE INFLUENCE OF CHANGES IN CARNIVORE NUMBERS ON THE CHEETAH POPULATION

Natural changes in predator numbers have recently occurred in the Serengeti-Mara ecosystem due to changes in prey numbers. An increase in the population of wildebeest during the

1960s and 1970s due to the control of rinderpest (Sinclair, 1979) to its present level of approximately 1.4 million (Campbell, 1989), combined with a series of years of favorable rainfall, has led to an increase in the lion population (Hanby & Bygott, 1979). In particular, lion numbers on the plains have increased from approximately 25 in the 1960s (Schaller, 1972) to about 80 in the 1970s, and possibly 250 recently (Hanby *et al.*, this volume). The total number of spotted hyaenas have probably also increased since the mid 1960s to current estimates of 7200-7700 in the ecosystem, with a core population on the plains of some 5200 (Hofer & East, this volume). If predation by these carnivores is important in limiting the cheetah population, then they may have had an increasing effect recently.

Although there are no long-term census data for cheetahs between the 1960s and 1990s, some demographic parameters are available from George Frame's study in the period 1974-1976 (Frame 1976). The average litter size of cubs aged 8-18 months in the study area decreased significantly between the mid 1970s and late 1980s (Fig. 6.2). If adolescent mortality did not change over the same period, recruitment of cheetahs into the adult population probably declined.

Decreased litter size at independence could be explained by a reduction in the number of cubs born or by an increase in partial litter mortality after birth. Reduced litter size at birth is less likely because the average litter size of cubs less than 4 weeks old did not change significantly between 1969-76 and 1987-90 (Fig.6.2) and because both figures are comparable to captive litter sizes (Marker & O'Brien, 1989). In consequence, the observed decline in the litter size of grown cubs is probably due to increased mortality rates after birth. Partial litter mortality before emergence from the lair was rare in this study (2 out of 28 mortality events) whereas post-emergent mortality occurred in 10 out of 10 litters, caused almost exclusively by predation (Laurenson, in press a).

Litter size at independence may be a useful indicator of the level of predation pressure on cheetah cubs. Support for this relationship comes from Namibia where the average size of nine litters of ten-month old cubs was 4.0 on ranchland where lions and hyaenas had been eliminated (McVittie 1979). This discrepancy is highly unlikely to be due to latitude or ecological conditions because litter sizes in the nearby Etosha National Park are no greater than on the Serengeti plains (P. Stander, pers. comm). Thus an increase in the rate of predation of cubs between 2 and 18 months is the most likely explanation of a decrease in observed litter size at independence over the last 15 years on the Serengeti plains.

DO LARGE CARNIVORES INFLUENCE CHEETAH POPULATIONS ELSEWHERE?

Cheetahs live at low densities throughout their range in a wide variety of habitats and ecological conditions (Myers 1975; Stander 1991). To assess whether other carnivores have an impact on cheetahs elsewhere in Africa, the relationship between cheetah, prey and predator biomass was examined using data collated by Stander (1991) from nine protected areas in east and southern Africa, but including updated data from the Ngorongoro Conservation Area and Serengeti National Park (Hanby *et al.*, this volume, Hofer & East, this volume). The model that best explained cheetah biomass included the variables medium-sized prey biomass (*i.e.* prey that were in the size range 15-60 kg *e.g.* Thomson's gazelles, Grant's gazelles, impala) and lion biomass ($r^2=0.82$, df=6, $p<0.01$). Prey biomass had a positive relationship with cheetah biomass ($t=5.23$, $p<0.01$; Fig. 6.3a), whereas lion biomass had a negative effect on cheetah biomass ($t=-2.69$, $p<0.04$; Fig. 6.3b). The combined biomass of lions and spotted hyaenas also had a significant negative effect on

cheetah biomass, taking into account the effects of prey biomass ($r^2=0.79$, df=6, $p<0.01$).

These results suggest evidence of a negative effect of large predators on the size of cheetah populations. Nevertheless, it should be noticed first, that population estimates of carnivores are often unreliable and that the total number of areas is few. Second, the result was primarily driven by the inclusion of the Ngorongoro Crater and Serengeti data points. (Regression statistics for variables in model excluding Ngorongoro; Prey biomass, $t=4.55$, $p=0.04$; Predator biomass, $t=-1.37$, NS; Lion, $t=-1.07$, NS; spotted hyaena, $t=-1.04$, NS). As few data are available, the analysis does not take into account possible effects of differences in ecological conditions such as prey distribution, migration or habitat type, which might explain much of the variance in cheetah biomass.

DISCUSSION

MORTALITY, FECUNDITY AND THE POPULATION DYNAMICS OF SERENGETI CHEETAHS

It seems likely that cub mortality is a major factor affecting the size of the cheetah population on the Serengeti plains. When compared to demographic patterns of other large mammals (Caughley 1969, Loudon 1985), cheetah cub mortality was extremely high in this study, with 95.2% of cubs dying before reaching independence. Cheetah cub mortality is also high compared to former estimates (30-60%) in East Africa (McLaughlin 1970; Schaller 1972; Frame & Frame 1981; Burney 1980) but many of these estimates did not know of the scale of mortality in the lair. Predation by other carnivores has been commonly cited as the most important source of cub mortality in cheetahs, but there has been little evidence to substantiate these claims (Schaller 1972; Eaton 1974; Myers 1975). Results of this study indicate that predation, mainly by lions, is indeed the major cause of cub mortality, accounting for approximately 73% of mortality between birth and independence. Abandonment, which has not previously been reported as a cause of mortality in this species, fire and bad weather each accounted for a smaller proportion of mortality.

That predation is a factor affecting cheetah population dynamics in the Serengeti is supported by the decline in cheetah litter size at independence since the 1970s, which has coincided with a rise in lion and spotted hyaena numbers on the Serengeti plains. Assuming that mortality from other sources has continued at a constant rate, the decrease in litter size at independence could be explained by additional mortality from predation on cheetah cubs after emergence.

The increase in lion numbers may have had a disproportionate effect on cheetahs above that of a simple increase in pride size, because it has led to an expansion of the lions' range. Lion prides now inhabit a large area of the plains rather than just the woodland edge year round (Hanby *et al.*, this volume). Lair sites used by female cheetahs on the short and medium grass plains (Laurenson 1993), probably relatively free of predation previously, may now be suffering substantially higher mortality rates.

The magnitude of juvenile mortality resulting from predation (Table 6.1) suggest that this factor may be particularly important in affecting cheetah population density. Nonetheless, other factors such as food availability, disease, parasites and social structure are know to be important in limiting the size of other vertebrate populations (Sinclair 1989), with the

availability of prey being the major factor limiting many predator populations (lions; Bertram, 1975: lynx, *Lynx canadensis*; Brand & Keith, 1979: wolves, *Canis lupus*; Fuller, 1989). Food limitation could act through decreasing reproductive rates such as lowered conception rates or litter size or, alternatively, by increasing mortality from starvation. There is, however, little evidence that cheetah numbers in the Serengeti-Mara ecosystem are currently determined by prey abundance. Conception rates and litter size, are similar to those in captivity and cub growth rates are also equivalent (Laurenson, in press b). Wild cheetahs were also in comparable physical condition to captive cheetahs using physical, haematological, biochemical and hormonal measures (Caro *et al.*, 1987; Laurenson, 1992). Furthermore the biomass of prey weighing 15-60 kg in Serengeti is greater than that required to support an equivalent biomass of cheetahs elsewhere in Africa (Fig. 6.3) and the availability of prey, such as hares, weighing less than 15kg is not even included in this calculation. These prey species can be an important component of cheetah's diet, particularly for adolescents or when other prey are scarce (Caro in press). Finally, cub abandonment only accounted for 9.5% of juvenile mortality in this study and was related to local scarcity of migrating Thomson's gazelles. In summary, although nutritional status may cause some variations in fertility, such as lowered conception rates in the dry season (Laurenson *et al.* 1992), food availability probably has little impact on cheetah numbers in this ecosystem at present.

Simulation of the effect of variations in fecundity and mortality rates also suggest offspring survival has a powerful influence on cub recruitment, primarily by altering the number of litters that did not survive. Although partial litter mortality also affected recruitment, there was less variation in total cub production, particularly because initial litter size was determined by female fecundity. Differences in fecundity, such as the time taken to return to oestrus or the length of the reproductive lifespan may also alter the potential number of cubs produced but, for example, beginning to breed at two years of age rather than three has little effect on reproductive success compared to increasing cub survival by avoiding predators.

In summary, although there is little information on the factors affecting adult mortality in females, these findings provide tentative evidence that offspring mortality, in particular from lion predation, may have a critical effect on the size of the Serengeti cheetah population. Interactions between cheetahs and other predators are potentially important for the population dynamics of cheetahs in the Serengeti-Mara ecosystem and deserve further scrutiny.

INFLUENCE OF MAJOR CARNIVORES ON CHEETAH POPULATIONS IN AFRICA.

Initial analysis of the relationship between the biomass of cheetahs, their prey and their predators, suggested that cheetah biomass across nine protected areas in Africa was primarily determined by the biomass of prey available to cheetahs. In most protected areas therefore, their low density can be explained primarily by the low density of the prey species on which they depend. Nevertheless, the biomass of lions and spotted hyaenas combined, or lions alone, also had a significant negative effect on cheetah biomass in this analysis. This result, however needs further validation and furthermore, makes no distinction between the effect of predators on cheetah numbers through competition for resources and the more direct effect of cub mortality observed in the Serengeti. Also the relationship between lions and cheetah density was driven by the high density of lions and hyaenas in the Ngorongoro Crater and a scarcity of cheetahs in the Serengeti ecosystem, suggesting that the effect of other predators

may not be as strong in other protected areas. The migratory system in the Serengeti may depress the biomass of cheetahs that can be supported, whereas the exceptional productivity of the Ngorongoro Crater may gives rise to extremely high lion and spotted hyaena densities. Thus differences may exist in the cheetah-predator relationship in these areas and elsewhere. Nevertheless, the density of other predator may depress cheetah density even when predator density is not exceptionally high. On ranchland in Namibia where ecological conditions are similar to Etosha National Park, other predators have been largely eliminated. Under these conditions of release from predation pressure, cheetahs appear to flourish and the litter size at independence is extremely high at 4.0 (McVittie 1979). Thus large predators can potentially have an effect on cheetah populations in a variety of ecological conditions. The prospective analyses presented here and the questions they raise clearly point that closer scrutiny of the cheetah-predator relationship is warranted.

IMPLICATIONS FOR CONSERVATION

The suggestion that other large predators have a detrimental effect on cheetah population size, is important from a conservation perspective. Although protected areas such as national parks are often considered to be a universal panacea for species survival, this may not be the case for cheetahs because of the protection afforded to other large predators. The elimination of these large predators in these areas is not, however, a desirable or realistic management option. Nevertheless there are areas where these predators exist at very low numbers or have been eliminated by humans. Some pastoralists and ranchers tolerate cheetahs to a greater extent than lions or hyaenas and cheetahs seem to prosper in these areas (McVittie, 1979; Burney, 1980). As cheetahs may have difficulty in reaching large numbers in isolated protected areas, it is perhaps in these multiple land use areas that conservation efforts should be concentrated to find ways in which continuing conflict between cheetahs and man can be minimised (Laurenson *et al.*, 1992).

ACKNOWLEDGEMENTS

I am grateful to the Government of Tanzania, Tanzania National Parks and the Serengeti Wildlife Research Institute for permission to conduct this research and in particular, David Babu, Karim Hirji, Hassan Nkya and Asukile Kajuni for their assistance. My thanks also to Barbie Allen, Markus Borner, Peter Hetz, Marianne Kuitert and Charlie and Lyn Trout who helped me enormously while I was in Serengeti and Tim Caro for his support at all stages of this project. Steve Albon, Peter Arcese, Tim Caro, Bryan Grenfell, Philip Stander and an anonymous reviewer provided constructive comments on the manuscript. This work was supported by the Frankfurt Zoological Society, the Leverhulme Trust, The Messerli Foundation, the National Geographic Society and Cambridge Philosophical Society.

LITERATURE CITED

Ammann K., and Ammann, K. 1984. *Cheetah.* Nairobi: Camerapix Pub. Int.

Bertram, D. 1975. Social factors influencing reproduction in wild lions. *J. Zool.* 177:463-482.

Begon, M.; Harper, J.L.; and Townsend, C.R. 1989. *Ecology; individuals, populations and communities*. 2nd Edition. Oxford: Blackwell Scientific Publications.

Berry, H.H. 1981. Abnormal levels of disease and predation as limiting factors for wildebeest in the Etosha National Park. *Madoqua*. 11:242-253.

Bothma, J. du P. and Le Riche, E.A.N. 1986. The influence of increasing hunger on the hunting behaviour of southern Kalahari leopards. *J. Arid. Environ.* 18:79-84.

Brand, C.J.; and Keith, L.B. 1979. Lynx demography during a snowshoe hare decline in Alberta. *J. Wild. Manag.* 43 (4); 827-849.

Burney, D.A. 1980. The effects of human activities on cheetahs (*Acinonyx jubatus schr.*) in the Mara region of Kenya. MSc Thesis, University of Nairobi.

Campbell, K. 1987. Serengeti Ecological Monitoring Programme. In *S.W.R.C. Biennial Report,*

1986-87, pp4-14.

Campbell, K. 1989. Serengeti Ecological Monitoring Programme. In; *S.W.R.C. Biennial Report, 1988-89,* pp 5-13.

Caro, T.M. 1994. *Serengeti cheetahs; studies of grouping in an asocial species.* Chicago: U. of Chicago Press.

Caro, T.M.; Holt, M.E.; FitzGibbon, C.D.; Bush, M.; Hawkey, C.M. and Kock, R.A. 1987. Health of adult free-living cheetahs. *J. Zool.* 212;573-584.

Caro, T.M.; FitzGibbon, C.M. and Holt, M.E. 1989. Physiological costs of behavioural strategies of male cheetahs. *Anim. Behav.* 38:309-317.

Caughley, G. 1966. Mortality patterns in maamals. *Ecology*. 47:906-918.

Dublin H.T.; Sinclair, A.R.E.; Boutin, S.; Anderson, E.; Jago, M.; and Arcese, P. 1990. *Oecologia* 82:283-288.

East, R. 1984. Rainfall, soil nutrient status and biomass of large African savanna mammals. *Afr. J. Ecol.* 22:245-270.

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

Evermann, J.; Laurenson, M.K.; Caro, T.M; and Mc Kiernan, A. 1993. *Zoo Biol.* 12:125-133.

Frame, G.W. 1976. Cheetah ecology and behaviour. *S.R.I Annual report, 1975-76*, pp.74-87.

Frame, G.W. and Frame, L.H. 1981. *Swift and Enduring: cheetahs and wild dogs of the Serengeti.* E.P. Ditton, New York.

Franklin, I.A. 1980. Evolutionary change in small populations. In *Conservation Biology; An evolutionary-ecological perspective* , eds. M.E. Soule and B.A. Wilcox, pp 135-149. Sinauer Assoc., Sunderland, Mass.

Fuller, T.K. 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs* No.105.

Gasaway, W.C., Mossestad, K.T. and Stander, P.E. 1989. Demography of spotted hyaenas in Etosha National Park, Namibia: predation versus scavenging. *Afr. J. Ecol.* 29:64-75

Gilpin, M.E. and Soulé, M.E. 1986. Minimum viable populations:processes of species extinction. In *Conservation Biology* , ed. M.E. Soulé, pp. 19-34. Sinauer Assoc.

Serengeti; Dynamics of and Ecosystem. Eds. A.R.E. Sinclair and M. Norto Griffiths, pp. 249-262. Chicago: U. of Chicago Press.

Hanby, J.P.; Bygott, J.D.; and Packer, C. (this volume) Comparative ecology, demograph and behaviour of lions in two contrasting habitats: Ngorongoro Crater and th Serengeti Plains.

Heeney, J.L., Evermann, J.F., McKeiran, A.J., Marker-Kraus, L., Bush, M., Wildt, D.E. Meltzer, D.G., Colly, L., Lukas, J., Mantan, J., Caro, T. and O'Brien, S.J. 1990. Prevalence and implications of feline coronavirus infections of captive and free-ranging cheetahs (*Acinonyx jubatus*). *J. Virology*, 64:1964-1972.

Hofer, H. and East, M. (this volume). Population dynamics, population size and the commuting system of spotted hyaenas in the Serengeti.

Kruuk, H. 1972. *The spotted hyaena.* Chicago; U. of Chicago Press.

Laurenson, M.K. 1992. Reproductive strategies in wild female cheetahs. Ph.D. thesis, U. of Cambridge.

Laurenson, M.K. 1993. Early maternal behavior of cheetahs in the wild: implications for captive husbandry. *Zoo Biol.* 12:31-45.

Laurenson, M.K. In press a. High juvenile mortality in cheetahs and its consequences for

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

Laurenson, M.K. In press. High juvenile mortality in cheetahs and its consequences for maternal care. *J. Zoology.*

Laurenson, M.K.; Caro, T.M. and Borner, M. (1992). Patterns of females reproduction in wild cheetahs. *Research and Exploration.* 8(1):64-75.

Laurenson, M.K and Caro, T.M. (In press). Monitoring the effects of non-trivial handling in free-living cheetahs. *Anim Behav.*

Lindeque, M and Lindeque, P.M. 1987. September 1987 aerial census of Etosha National Park. Unpub. report, Directorate of Wildlife and Conservation, Namibia.

Loudon, A.S.I. 1985. Lactation and neonatal survival in mammals. *Symp. Zool Soc Lond.* 54:183-207.

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

McVitie, R. 1979. Changes in the social behaviour of South West African cheetah. *Madoqua,* 2(3), 171-89.

Marker, L. and O'Brien, S.J. 1989. Captive breeding of the cheetah (Acinonyx jubatus) North American zoos (1871-1986). *Zoo Biology* 8:3-16.

Mentis, M.T. 1980. Towards a scientific management of terrestrial ecosystems. *S. Afr. J. S* 76:536-540.

Mills, M.G.L. 1990. *Kalahari hyaenas.* London: Unwin Hyman.

Mitchell, B. 1973. The reproductive performance of wild Scottish red deer *Cervus elaphus. Reprod. Fertility* 19:271-285.

Myers, N. 1975. *The status of the cheetah in Africa south of the Sahara.* I.U.C.N. Morges

Pienaar, U de V. 1969. Predator-prey relationships amongst the larger mammals of Kru National Park. *Koedoe* 12:160-176.

Rattray, P.V. 1977. Nutrition and reproductive efficiency. In *Reproduction in Dome. Mammals.* Eds. H.H.Cole and P.T. Cupps. pp.553-575 London: Academic Press.

Rudnai, J.A. 1974. The pattern of lion predation in Nairobi Park. *E. Afr. Wild. J.* 12:213-2

Sadleir, R.M.F.S. 1969. *The ecology of reproduction in wild and domestic animals.* Lond

Metheun.

haller, G.B. 1972. *The Serengeti Lion.* Chicago: U. of Chicago Press.

mberloff, D.S. 1986. The proximate causes of extinction. In *Patterns and processes in the history of life.* Eds. D.M. Raup & D. Jablonski, pp.259-276. Berlin: Springer-Verlab.

nclair, A.R.E. 1989. Population regulation in animals. In *Ecological concepts,* Ed.J.M. Cherret, pp 197-241. Oxford: Blackwell.

nclair, A.R.E, 1979. The Serengeti envirnonment. In *Serengeti, Dynamics of an Ecosystem,* eds, A.R.E. Sinclair and M. Norton-Griffiths, pp. 31-45. Chicago: U.of Chicago Press.

ınder, P.E. 1991. Aspects of the ecology and scientific management of large carnivores in sub-Saharan Africa. MPhil. Thesis. University of Cambridge.

ilson, E.O. 1975. *Sociobiology: the new synthesis.* Harvard University Press, Cambridge Mass.

Table 6.1. Summary of the numbers of cheetah cubs that probably died due to each cause of mortality between birth and independence. Only cases where the cause of death was definitely or almost certainly known (n=40.5) were used in estimating the proportion of mortality attributable to each cause in the lair. A litter whose size was unknown was assigned the average litter size of 3.5 cubs. 77.4% (n=115) of mortality occurred before cubs emerged from the lair, whereas 22.6% occurred after emergence. Ten percent of cubs dying after emergence were assigned to 'other' causes of mortality.

Cause	Percent of cub mortality		
	In lair	After emergence	Total (birth to independence)
Predation	67.8	90	73.0
Abandonment	9.9		7.7
Fire	9.9		7.7
Exposure	7.4		5.7
Possibly inviable cubs	4.9		3.8
Other		10	2.2

ble 6.2 Summary of the percentage of cheetah cubs in studies in the Serengeti-Mara system that were killed by six types of predators (see Table 5 of Laurenson, under review). ters of unknown size was unknown were assigned the average litter size of 3.5 cubs. Data m this study, Burney, 1980; Frame & Frame, 1981; Ammann & Ammann, 1984; Caro, 1987; Domb and M. Smits van Oyen, pers. comm.; D. Richards, pers. comm.

Predator	Percent of cubs killed		
	In lair n=53.5	After emergence n=12	Birth to independence n=65.5
Lion	88.8	33.3	78.6
Spotted hyaenas	5.6	41.7	12.2
leopard		8.3	1.5
cheetah	3.7		3.1
Maasai dogs		16.7	3.1
Raptors	1.9		1.5

Table 6.3 The range of the number of females cubs that could be produced by a female cheetah during her lifespan (r), depending on the upper and lower limits of the variables affecting fecundity and offspring survival. When one parameter is varied, other values were held at their mean value. Minimum and maximum values of a and b could only be varied together. If all the mean parameter values were used, 0.66 female cubs were raised in the lifetime of a female cheetah.

Parameter	Range of parameter values			No. female cubs raised in lifetime		% variation from mean
	min	max	mean	max	min	
a	17.3	24.65	21.7	0.76	0.56	+/- 15.2
b	4.4	5.8	4.9			
d	0.05	1	0.24	1.86	0.35	+181.8, -47
n	0.5	1.8	0.9	1.32	0.37	+100, -43.9
e	120	120	52.8	1.50	0.15	+127.3, -77.2
m	0	0.35	0.15	0.77	0.54	+16.7, -18.2

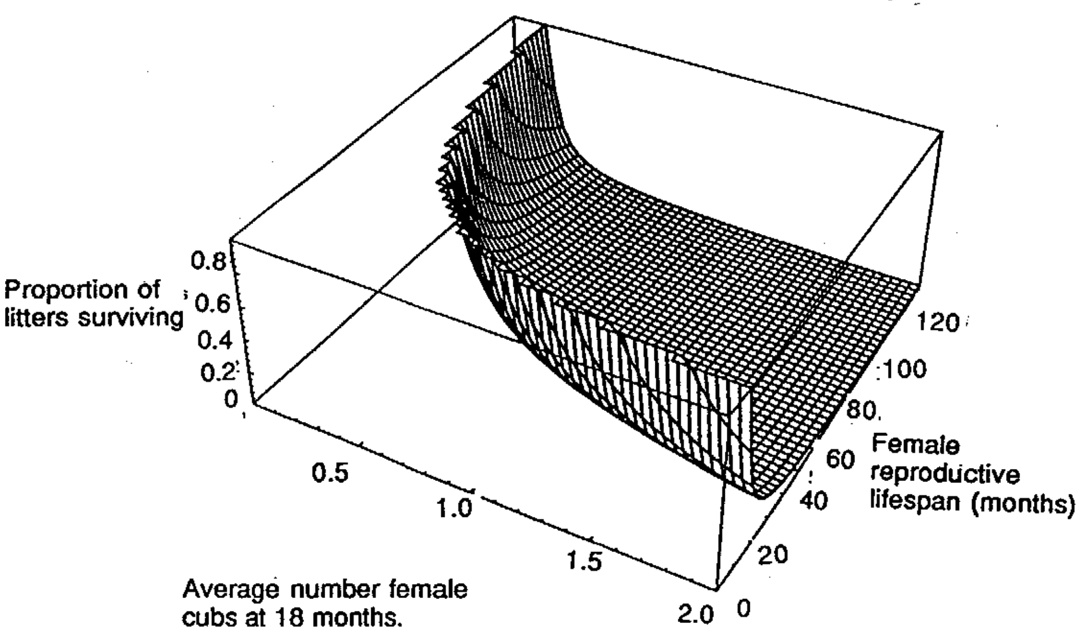
FIGURE LEGENDS

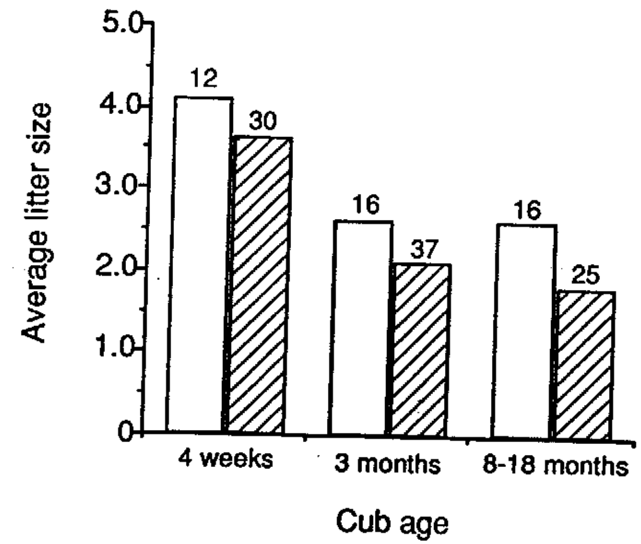
Figure 6.1. The relationship between the average number of female cubs per litter at independence, female reproductive lifespan and the proportion of litters born that survive, giving a stable cheetah population. Points lying above the surface represent combinations of values resulting in an expanding population, points below represent values associated with population decline.

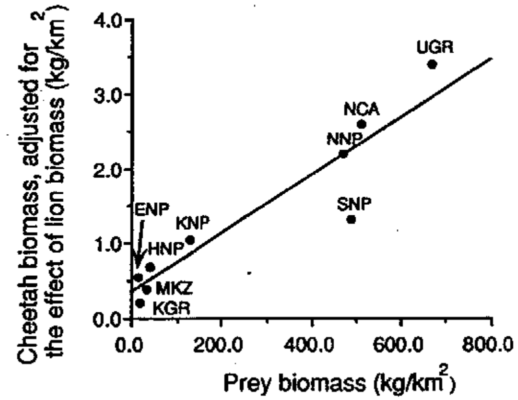
Figure 6.2. The average size of cheetah litters on the Serengeti Plains at different cub ages, during the mid 1970s (Frame 1976) and late 1980s (this study). Significant differences in litter size occur only between the oldest age class of cubs (Mann Whitney U test, $U=581$, $p<0.001$). Plain bars represent data from Frame's study, with sample sizes of 12,16 and 16 litters for 4 week, 3 month and 8-18 month old cubs. Hatched bars represent data from this study, with sample sizes of 30, 37 and 25 litters respectively.

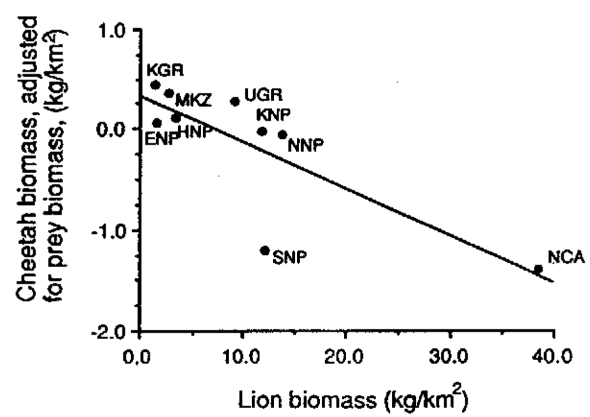
Figure 6.3a. The relationship between cheetah biomass and prey biomass across nine African protected areas, taking into account the effect of lion biomass, such that $y=0.34 + 0.0039x$. ENP= Etosha National Park, Namibia; HNP Hwange National Park, Zimbabwe; KGR=Kalahari Gemsbok National Park, S. Africa; KNP Kruger National Park, S.A; MKZ= Mkomazi Game Reserve, Tanzania; NCA=Ngorongoro Conservation Area, Tanzania; NNP= Nairobi National Park, Kenya; SNP= Serengeti National Park, Tanzania; UGR=Umfolozi Game Reserve, S.A.

Figure 6.3b. The relationship between cheetah biomass and lion biomass across nine African protected areas, taking into account the effect of prey biomass, such that $y=0.338- 0.046x$. Abbreviations for protected areas as in Figure 3.


Proportion of litters surviving
0.8
0.6
0.4
0.2
0
0.5
1.0
1.5
2.0
Average number female cubs at 18 months.
0
20
40
60
80
100
120
Female reproductive lifespan (months)


Average litter size
5.0
4.0
3.0
2.0
1.0
0
12
30
16
37
16
25
4 weeks
3 months
8-18 months
Cub age


Cheetah biomass, adjusted for the effect of lion biomass (kg/km2)
Prey biomass (kg/km2)
4.0
3.0
2.0
1.0
0.0
0.0
200.0
400.0
600.0
800.0
UGR
NCA
NNP
SNP
ENP
KNP
HNP
MKZ
KGR


Cheetah biomass, adjusted for prey biomass, (kg/km2)
Lion biomass (kg/km2)
1.0
0.0
-1.0
-2.0
0.0
10.0
20.0
30.0
40.0
KGR
MKZ
UGR
KNP
ENP
HNP
NNP
SNP
NCA