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Abstract: Data are presented on the demography and reproductive success of cheetahs (*Acinonyx jubatus*) living on the Serengeti Plains, Tanzania over a 25-year period. Average age at independence was 17.1 months, females gave birth to their first litter at approximately 2.4 years old, inter-birth interval was 20.1 months, and average litter size at independence was 2.1 cubs. Females who survived to independence lived on average 6.2 years while minimum male average longevity was 2.8 years for those born in the study area and 5.3 years for immigrants, with a large proportion of males dispersing out of the Plains population. Females produced on average only 1.7 cubs to independence in their entire lifetime and their average reproductive rates were 0.36 cubs per year or 0.17 litters per year to independence. Variance in lifetime reproductive success in the cheetah is similar to that of other mammals. No significant negative correlations were found between adult cheetah population size and numbers of cubs reaching independence, implying that the Plains population had not reached carrying capacity. Annual numbers of adult female cheetahs only were correlated with rainfall. Adult female cheetah numbers were not correlated with adult female lion numbers on the Plains, however, reproductive rates of cheetahs were negatively correlated with the presence of lions while cheetahs had cubs. Moreover, cheetah reproductive success was lower during the period of high lion abundance (1980±1994) than during the earlier period of relatively few lions (1969±1979). Litter size at independence dropped from 2.5 to 2.0, lifetime reproductive success declined from 2.1 to 1.6 cubs reared to independence, and the reproductive rate (cubs/year) decreased from 0.42 to 0.36 from the earlier to the later period. Cheetah reproductive success showed little association with the presence of Thomson's gazelle at sightings except for a negative correlation between large numbers of gazelle (200±500) and reproductive success possibly because hunting success decreases with increasing prey herd size, or because cheetahs always lose in direct competition with other predators which are attracted to large congregations of prey. In addition, cheetah reproductive success was negatively correlated with the presence of Grant's gazelles (11 or more) perhaps because Grant's gazelles were more likely to occur consistently in dry areas.

Demography of the Serengeti cheetah (*Acinonyx jubatus*) population: the first 25 years

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Abstract

Data are presented on the demography and reproductive success of cheetahs (*Acinonyx jubatus*) living on the Serengeti Plains, Tanzania over a 25-year period. Average age at independence was 17.1 months, females gave birth to their first litter at approximately 2.4 years old, interbirth interval was 20.1 months, and average litter size at independence was 2.1 cubs. Females who survived to independence lived on average 6.2 years while minimum male average longevity was 2.8 years for those born in the study area and 5.3 years for immigrants, with a large proportion of males dispersing out of the Plains population. Females produced on average only 1.7 cubs to independence in their entire lifetime and their average reproductive rates were 0.36 cubs per year or 0.17 litters per year to independence. Variance in lifetime reproductive success in the cheetah is similar to that of other mammals.

No significant negative correlations were found between adult cheetah population size and numbers of cubs reaching independence, implying that the Plains population had not reached carrying capacity. Annual numbers of adult female cheetahs only were correlated with rainfall. Adult female cheetah numbers were not correlated with adult female lion numbers on the Plains, however, reproductive rates of cheetahs were negatively correlated with the presence of lions while cheetahs had cubs. Moreover, cheetah reproductive success was lower during the period of high lion abundance (1980–1994) than during the earlier period of relatively few lions (1969–1979). Litter size at independence dropped from 2.5 to 2.0, lifetime reproductive success declined from 2.1 to 1.6 cubs reared to independence, and the reproductive rate (cubs/year) decreased from 0.42 to 0.36 from the earlier to the later period.

Cheetah reproductive success showed little association with the presence of Thomson's gazelle at sightings except for a negative correlation between large numbers of gazelle (200–500) and reproductive success possibly because hunting success decreases with increasing prey herd size, or because cheetahs always lose in direct competition with other predators which are attracted to large congregations of prey. In addition, cheetah reproductive success was negatively correlated with the presence of Grant's gazelles (11 or more) perhaps because Grant's gazelles were more likely to occur consistently in dry areas.

Key words: cheetah, demography, lifetime reproductive success

INTRODUCTION

Long-term studies of animal populations are rare. This is especially true for large carnivores whose long lifespan,

large home ranges, and elusive nature make them difficult to study. Yet long-term population studies yield the baseline demographic data necessary to understand the factors responsible for changes in population size over time and to construct population viability analyses or risk assessments for the conservation of a species (Soule, 1987; Burgman, Ferson & Akçakaya, 1993; Ruggiero, Hayward & Squires, 1994). Most demographic studies,

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however, rely on cross-sectional data collected at a particular point in time and have drawbacks. For example, it is difficult to estimate accurately demographic parameters such as survival at different ages, longevity, and, in particular, lifetime reproductive success and variation based on such data sets (Clutton-Brock, 1988a; Barrowclough & Rockwell, 1993; Rockwell & Barrowclough, 1995). In addition, cross-sectional data often fail to detect correlations between demographic parameters and environmental variables over time (Burgman *et al.*, 1993). Although recently some field studies have tracked reproductive success of individuals through multiple breeding attempts over most or all of their natural lifespans (see Clutton-Brock, 1988a; Newton, 1989), these longitudinal studies are still relatively unusual.

In this paper, we present demographic data from the first 25 years of study conducted on cheetahs (*Acinonyx jubatus*) of the Serengeti Plains, Tanzania. First, baseline demographic variables, including age at independence, age at first reproduction, interbirth interval, average litter size at independence, and longevity are documented. Differences in survival between males and females are illustrated using lifetime survivorship curves. Estimates of reproductive success for female cheetahs are given.

Second, we examine the factors that may affect the reproductive success of female cheetahs. Previous studies have indicated that predation on cheetah cubs, particularly by lions (*Panthera leo*), accounts for 73% of juvenile mortality (Laurenson, 1994) and may therefore be a critical selective force in limiting cheetah populations (Laurenson, 1994, 1995a). A subsequent study has also shown a positive correlation between reproductive success and behavioural avoidance of lions (SMD, unpublished data). Using our extended demographic data set, we test the hypothesis that predators, especially lions, may affect the lifetime reproductive success of cheetahs. In addition, Laurenson (1995a) has shown a positive correlation between cheetah biomass and prey biomass. To determine whether this relationship held true on a smaller scale, we test the hypothesis that reproductive success would increase with local prey availability.

Third, because it is likely that an increase in numbers of adult lions on the Plains would result in an increase in juvenile mortality in cheetahs, we compare annual cheetah numbers with annual lion numbers to examine the possibility that lions might limit the adult cheetah population size. Other mammal populations have been shown to be limited by density-dependent mechanisms (Clutton-Brock, Major & Guinness, 1985; Skogland, 1985). We therefore compare annual adult cheetah numbers to the number of cheetah cubs reared to independence per year in order to determine if density dependence is limiting cheetah population size. In addition, amount of yearly rainfall, an indirect indicator of prey availability, is compared to annual cheetah numbers.

Finally, we use our long-term records to examine reproductive success of females over time. Between the

mid 1970s and 1992, lion numbers on the Serengeti Plains increased (Hanby, Bygott, & Packer, 1995). We test the hypothesis that predators, especially lions, may affect the reproductive success of Plains cheetahs by comparing lifetime reproductive success of cheetahs during the period of high (1980–1994) versus low (1969–1979) numbers of lions.

MATERIALS AND METHODS

Study site and general methods

Cheetahs on the central plains of Serengeti National Park in Tanzania have been studied since the early 1960s, but systematic research did not begin until 1969 (Bertram, 1978). For a full description and map of the general area and the 2200-km² study area see Sinclair (1979) and Caro (1994). During most days of the study, a pre-determined area of the plains and woodland border was searched for cheetahs. Observations were made during daylight from a vehicle that was driven to locations providing a good view of the surroundings, such as rises, watersheds, and hilltops. Usually, the area was scanned slowly using 10 × 50 binoculars from the vehicle. Cheetahs habituated to vehicles and fearful cheetahs took the time to sit up and show themselves and could be seen from as far away as 2.5 km. They were then approached slowly, but not directly, until the vehicle was about 200 m away. Closer approach was made in a zig-zag fashion to decrease the chances of causing the animal to flee.

From 1969 until 1991, cheetahs at most sightings were not distinguished from each other individually when spotted in the field and were photographed for identification at a later date. By 1991, a backlog of over 10,000 photographs of unidentified cheetahs existed. MJK used a computer-aided matching program to assist in matching photographs of individual cheetahs. Since each cheetah has a unique spot pattern, and because this pattern does not change over the lifespan of a cheetah, individuals could be recognized from photographs and followed through time. (See Hiby & Lovell, 1990; Kelly *et al.*, In prep., for a complete description and evaluation of the computer-aided matching technique.) Relatedness of individuals could be traced only through the female line since very few matings have been observed in the wild. Maternity was established by seeing a mother with her cubs in photographs and later matching those cubs to photographs of adult animals. Although adoption of cubs does occur, its incidence is very low (1.9%, $n = 8$ cubs out of 426) and adoptees are usually easy to identify behaviourally (Caro, 1994).

Demographic and behavioural data were recorded at each sighting by 1 of the 7 different observers in the field from 1969 to 1994 (Table 1). Life histories of individual cheetahs were then reconstructed by compiling data accompanying each sighting. Cheetah matrilineages were closely monitored and mapped out in detail for as many as 7 generations. We used non-parametric statistics for

Table 1. History of Serengeti cheetah study. Names, months, and years of observers present and data recorded relevant to this paper. Craig Packer and Anne Pusey collected occasional data from 3/78 through 12/79 which George Frame compiled. Sarah Cleaveland collected data from 9/90 to 1/91 and Tim Caro periodically recorded data from 1/85–5/89 including the gap from 3/87–10/87

Researcher	Dates	Data recorded
Brian Bertram	8/69–12/73	1
George Frame	3/73–3/78	1
Tim Caro	3/80–12/83	2
Anthony Collins	11/83–10/84	2
Clare FitzGibbon	1/85–3/87	2
Karen Laurenson	9/87–9/90	2
Sarah Durant	3/91–12/94	1

1. Date, location, age, sex, reproductive condition, group size and composition.
2. Same data as in 1 plus cheetah belly size, amount and type of all predators and prey present.

most of the analyses owing to small sample sizes and/or non-normally distributed data.

Independence, first reproduction, interbirth interval and litter size at independence

Only cheetahs of known age (i.e. those born in the study area) were used to estimate the age at which cubs left their mothers and the age at first reproduction for females. Cubs seen without their mothers after the age of 12 months (the youngest age at independence) were considered independent. Only cubs seen consistently (at least 3 times) during the time they neared independence (from 12–24 months) were used in calculating average age at independence because large gaps could lead to an overestimate of this parameter.

Age at first reproduction for females is defined as the age a female gave birth to her first litter. Since gestation for cheetahs is 3 months, a cheetah not seen for 3 months or more may produce a litter which died and therefore birth of her first litter went unnoticed. For this reason, any female not seen for 3 or more months during the year and a half after independence was excluded. Age at first reproduction could not be determined for the males due to the rarity of observed matings.

Interbirth interval for mothers whose previous litter survived was estimated from those females who were seen frequently between the time of independence of the previous litter and birth of the next. Again cheetahs were excluded from this analysis if gaps of 3 months or more occurred during this critical time, since females could have produced a litter that subsequently died without being seen.

Cubs are completely hidden until 2 months old when they emerge from the lair (Laurenson, 1993) and it was not possible to estimate the number of cubs born per litter using this data set. Instead, the number of cubs reaching 4 months of age, and then reaching indepen-

dence, was calculated. Four months of age was chosen since previous data have shown that juvenile mortality declines after this age (Laurenson, 1994).

Longevity and survivorship

Longevity for cheetahs that reached independence was determined in 2 ways. Individuals born in the study area (i.e. first seen as cubs with their mothers) were analysed separately from cheetahs first seen as adolescents without their mothers or from those first seen as adults. Estimated ages of cubs with their mothers follows Caro (1994) and has proven highly reliable. Adolescents are recognized in the wild and in photographs by long, fluffy, white hairs on the scruff of the neck. These were assigned an age of 17 months (the average age of independence in this study). Animals first seen as adults were assigned an age of 3 years, since by this age they have definitely lost their fluffy hairs (Caro, 1994). These age assignments are probably minimum values; therefore longevity for estimated-age animals is likely to be a minimum. Cheetahs born in the study area are henceforth referred to as known age animals, while those cheetahs first seen as adolescents or adults are termed estimated-age animals. Death is rarely witnessed or confirmed in the wild and absence does not necessarily indicate death because animals may travel widely at intervals. Therefore, for this analysis, cheetahs were considered dead at the point of their last sighting if they had not been seen within 2 standard deviations (S.D.s) of their mean inter-sighting interval (ISI) (Caro, 1994). Although some animals re-appeared in the study area after an absence of more than 2 S.D.s of their ISI, these incidents were very rare (3.1%, $n = 96$ cheetahs). Longevity of territorial and floater males was also calculated. For this analysis, we included only resident males, those which were in the study area for at least a year as independents.

Survivorship curves for males and females were constructed separately using known age animals only that were believed to have died between 1969 and 1994. Animals of estimated age were excluded from this analysis since no data exist on survivorship before they were seen. Since the sex ratio of cubs at birth does not differ from unity (Laurenson, Caro & Borner, 1992), all cubs that died before being sexed were pooled and we considered that half were males and half females for estimates of survival to one year of age.

The current analysis relies on sightings and photographs of cubs only after emergence from the den (2–4 months). Cubs that died in the lair go unreported which leads to a considerable underestimate of mortality between 0–1 year. In light of Laurenson's (1994) data on survivorship of cubs in the den, we have reconstructed the survivorship curve for females using her data for survival to independence and combined it with the data from this study for survival at other ages. In addition, we present age-specific mortality rates for female cheetahs of one year or older.

Reproductive success

Reproductive success of females was measured in 3 ways: 1) the number of *litters* (i.e. any number of cubs per litter) that reached independence divided by the time the mother was seen in the study area as an independent; 2) the total number of *cubs* raised to independence divided by the time the mother was seen independent; and 3) the *total number of cubs* raised to independence throughout a female's adult lifespan (defined as time spent independent in the study area). Only cheetahs assumed to be dead were included and the fate of all their litters had to be known. The first two measures are reproductive rates – litters or cubs to independence per year. Although it has been argued that lion cubs of the same litter cannot be treated as statistically independent since they are born and often die together (Packer *et al.*, 1988), this may be less important in cheetahs. Although cheetah cubs of less than 2 months often die together in the lair from predation, partial litter mortality is common after this age as cubs are more mobile and able to scatter from danger (Caro, 1987; Laurenson, 1994). The number of cubs surviving to independence, therefore, may be a more sensitive measure of reproductive success than litter survival. Measures 1 and 2 were based on 103 females from 1969 to 1994, whereas measure 3 was based on the performance of 108 independent females. From the successful litters we calculated average number of cubs surviving to independence per litter, as well as average litter size at emergence from the lair (4 months old).

Using data from 1980–1994, we measured the survival of a mother's first litter versus subsequent litters, as defined by survival to independence of one or more cubs. Cheetahs were included in the analysis only when exact litter number was known and until we lost track of the number of litters she produced. Since gaps in sightings are quite common, sample sizes are greatly reduced in this analysis, especially with later litters. Thus, we combined litters 6 through 9. From the same data set, we calculated the survival of litters and cubs per litter based on the age of the mother when the litter was born. Again, for reasons of small sample size, we combined the mother's ages of 8 through 12 years.

Correlates of reproductive success

At each cheetah sighting, the presence of predators and prey within a 1 km radius of the cheetah's location was recorded. The cheetah's belly size was also recorded on a 14 point scale. These variables were compared to the lifetime reproductive success of females. We used data from 1980 through 1990 since data collection was standardized over this period. In order to be biologically meaningful, such analysis requires many sightings of cheetahs over several reproductive attempts. Cheetahs had to be seen at least 25 times while they had cubs under 4 months and the fate of all their litters had to be

known. Only 7 females met these criteria. These cheetahs were seen as independent for between 5.7 and 9.8 years on the Plains (\bar{x} = 8.1 years). For each female, MJK calculated the proportion of sightings in which predators and prey herds of various sizes were present and these measures were subsequently compared with cheetah reproductive success. For belly sizes, both mean and standard deviation were compared with reproductive success across females.

Presence of predators

Under 4 months, cubs are particularly susceptible to predation since they are not fast enough to outrun all predators. Lions are the primary predators of cubs in the lair, while spotted hyenas (*Crocuta crocuta*) and lions kill emergent cubs in equal proportions (Laurenson, 1994). Adult cheetahs, particularly males, have also been considered a threat to cheetah cubs (Burney, 1980). Presence of lions, spotted hyenas, and other cheetahs was recorded separately at each cheetah sighting, while all other predators were lumped together. These other predators included: leopards (*Panthera pardus*), black-backed jackals (*Canis mesomelas*), side-striped jackals (*Canis adustus*), golden jackals (*Canis aureus*), wild dogs (*Lycaon pictus*), bat-eared foxes (*Otocyon megalotis*), and baboons (*Papio anubis*). We analysed the relationship between presence of predators and reproductive success using first, cheetahs with cubs under 4 months, and second, cheetahs with cubs of any age. We could not run this analysis on cheetah mothers with cubs only over 4 months of age owing to infrequent sightings.

Presence of prey

In many species reproductive success is influenced primarily by nutrition and food availability (Sadler, 1969; Rattray, 1977). There is evidence that food availability and nutritional factors may affect reproductive rates in cheetahs (Laurenson, 1992, 1995b). Laurenson (1995a) has shown that starvation, due to abandonment by mothers, accounts for 7.7% of total cub mortality, and that the availability of prey and difficulty in obtaining food may play a role in the probability of abandonment. The favoured prey of female cheetahs on the Serengeti Plains are Thomson's gazelles (*Gazella thomsoni*) (Fitz-Gibbon, 1990) and female cheetahs follow their movements (Durant *et al.*, 1988). Grant's gazelles (*Gazella granti*), however, are also killed and wildebeest (*Connochaetes taurinus*) are taken by males (Caro, 1994). Since young cubs are less able to accompany their mothers on long feeding forays, gazelle presence while cheetahs have cubs under 4 months was analysed as this may be the period when cubs are most sensitive to the vagaries of prey abundance. All other prey species, i.e. eland (*Taurotragus oryx*), hartebeest (*Alcelaphus buselaphus*), warthog (*Phacochoerus aethiopicus*),

topi (*Damaliscus korrigum*), impala (*Aepyceros melampus*), reedbuck (*Redunca redunca*), steinbok (*Raphicerus campestris*), giraffe (*Giraffa camelopardalis*), zebra (*Equus burchelli*) and ostrich (*Struthio camelus*), were combined.

Prey species present were divided into abundance categories as follows: 0 prey, 1–10 prey, 11–50 prey, 51–200 prey, 200–500 prey, and >500 prey. We then tested whether no prey or different herd sizes had an effect on cheetah reproductive success.

Belly size

Belly size was scored on a 14 point scale. Such scales have been shown to be a reliable measure of food intake for cheetahs (Frame & Frame, 1981; Caro, 1994) and lions (Bertram, 1978; Packer, 1986). Belly sizes of females were then compared to their reproductive success.

Annual cheetah population size, rainfall and lion numbers

All independent cheetahs were included in the adult cheetah population size estimates unless they were deemed transient and hence just passing through the study area. Transient cheetahs were those seen no more than three times within a single year and who were never seen again. Cheetahs with gaps in sightings of a year or more were assumed to be in the study area but missed by observers and were included in population estimates in those missing years. Total numbers of cubs reaching independence (i.e. first seen alone without their mothers) were counted for each calendar year. Annual numbers of adult cheetahs were compared to annual numbers of cubs reaching independence in order to examine if density dependence was operating on the cheetah population

Prey availability on the Plains is positively linked to rainfall. In particular, Thomson's gazelle, wildebeeste, and zebra occur on the Plains in response to the onset and amount of rainfall (Durant *et al.*, 1988; McNaughton, 1990). Annual cheetah population size was therefore compared to average rainfall per year, an indirect measure of prey availability. Monthly rainfall totals from Seronera were available from the Serengeti Ecological Monitoring Programme. We chose Seronera as many cheetahs using different parts of the Plains aggregate here in the dry season.

Since lions have been shown to be the primary predators on cheetah cubs (Laurenson, 1994), it is possible that higher numbers of lions could lead to higher amounts of predation and hence lower adult cheetah numbers. We therefore compared the number of adult female cheetahs to the number of adult female lions occurring on the Plains each year. C. Packer provided yearly female lion totals.

Comparison of reproductive success over different time periods

Cheetahs suffer high juvenile mortality due to predation by lions (Laurenson, 1994) and Hanby *et al.* (1995) have shown a dramatic increase in lion numbers on the Plains beginning in the late 1970s. The average number of adult female lions from 1969–1979 was 26.5 (S.D. = 6.7), while from 1980–1990 the average was 42.5 (S.D. = 3.4) (C. Packer, pers. comm.). Therefore, the reproductive success of all female cheetahs and of breeding females only (see Clutton-Brock, 1988a) from 1969 to 1979 was compared to the success of those between 1980 and 1994. Owing to our two year gap in data collection, from 1978 until 1980, there were sufficient data to calculate lifetime reproductive success for only three cheetahs alive through both time periods. These cheetahs were excluded from this analysis.

RESULTS

Baseline demographic data

Independence, first reproduction, interbirth interval, and litter size at independence

The mean age at independence for cheetahs from 1980–1994 was 17.1 months ($n = 70$ cheetahs, S.D. = 1.9) (see Table 2). Small litters of 1–2 cubs stayed no longer with their mothers than large litters of 3–4 cubs ($n = 55$ small, 15 large litters; $U = 393$; $P = 0.779$). Four was the largest litter raised to independence after 1980, whereas six was the largest from 1969 to 1980. Single sex male litters did not stay with their mothers longer on average than single sex female litters ($n = 15$, 25 litters; $U = 177.5$; $P = 0.778$), nor were there differences in this measure between single sex versus mixed sex litters ($n = 40$, 30 litters; $U = 505$; $P = 0.258$).

The average age that females first gave birth was 2.4 years (S.D. = 3.1 months) or 11.7 months after leaving

Table 2. Baseline demographic variables for Serengeti cheetahs

Variable estimated	Average value
Age at independence	17.1 months ($n = 70$ litters)
Age at first reproduction (birth of first litter)	2.4 years ($n = 22$ females)
Interbirth interval	20.1 months ($n = 36$ females)
Litter size at independence	2.1 cubs ($n = 105$ litters)
Female lifespan for those reaching independence	6.2 years ($n = 160$ females)
Male lifespan for those reaching independence	2.8–5.3 years* ($n = 124$ males)

* Values presented are for known age and estimated age males, respectively. Both are underestimates owing to difficulty in determining time of death and/or dispersal.

their mothers ($n=22$ females). Thus, on average, females first mated successfully at 2.16 years old.

Females whose previous litter survived gave birth again 20.1 months (S.D. = 3.0) after the birth of the previous litter which was 3 months after the previous litter left. Of the 36 females used in this analysis, 44% were already pregnant before the previous litter left, 26% were very likely to have been pregnant, although complete confirmation could not be made, and 30% were definitely not pregnant. The majority of females therefore came into oestrus and mated while still accompanied by old cubs.

Of litters surviving to independence, average litter size at independence was 2.1 cubs ($n=105$ litters, S.D. = 1.0). From Laurenson *et al.*'s (1992) previous study, average litter size at birth was 3.5. This mean may have been a slight underestimate, since litters were not examined at birth but, on average, 14.8 days after parturition (Laurenson *et al.*, 1992).

Longevity and survivorship

Since there was no difference in longevity between known age and estimated age females ($n=79$, 79 females, $\bar{x}s=6.2$, 6.2 years; $U=2893$, $P=0.43$), all females were combined for longevity estimates. Female cheetahs who survived to independence lived an average of 6.2 years ($n=158$ females; S.D. = 3.0) on the Serengeti Plains with the oldest female surviving to 13.5 years.

For male cheetahs, however, there was a marked difference in longevity between known age and estimated age cheetahs ($n=49$, 75 males, $\bar{x}s=2.8$, 5.3 years; $U=414.5$, $P=0.0001$) most likely because males born in the study area disperse out of it. Longevity for these known age males therefore, is probably an underestimate. For those surviving to independence, average lifespan on the Plains for males of known age was 2.8 years, with the oldest male surviving to 6.1 years, while estimated age males averaged 5.3 years and lived as long as 9.3 years on the Plains.

Territorial males did not live significantly longer than floater males using either known age males ($n=11$, 4 males; $\bar{x}s=3.83$, 2.5 years; $U=12$; $P=0.19$) or estimated age males ($n=29$, 20 males; $\bar{x}s=5.53$, 5.83 years; $U=252$; $P=0.438$), although sample sizes are small.

Survivorship curves clearly show the different pattern of survival between the sexes (Fig. 1a). All males born on the Plains disappear through death or dispersal before the age of 7 years old, while females can survive until 13 years or longer. These curves also show a higher mortality for males than females between 1 and 2 years, the age at which cubs leave their mothers. This difference is reflected in the skewed sex ratio at independence, 0.8:1.

In our analysis, survivorship to independence is nearly 50% which is common in mammals (Clutton-Brock, 1998a). After independence, cheetahs show a constant decrease in survival (5%) at each age rather than levelling off until survivorship decreases at the

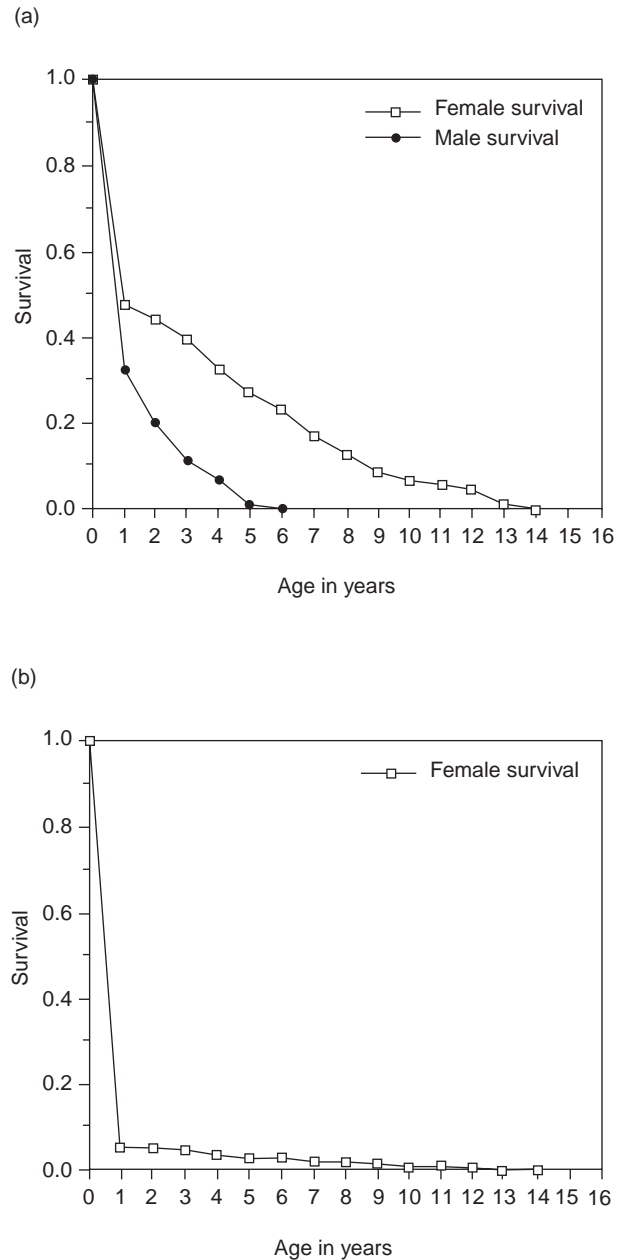


Fig. 1. (a) Survivorship curves for males and females born in the study area. Only emergent cubs (2–4 months or older) were counted which leads to an overestimate of survival in the 0–1 age class. However, differential survival of emergent males and females can be clearly seen. (b) Survival of females using Laurenson's (1994) data on survival of cubs to independence, which includes mortality in the lair, combined with data from this study for all other ages, shows much higher mortality from 0–1 years.

very old age classes. Our estimate, however, does not include the early cub mortality as this could not be determined from this study. We therefore used the Laurenson *et al.* (1992) data on early cub mortality in the lair and survivorship to independence to reconstruct the survivorship curve for females. This shows that, once female cheetahs survive to independence, they have a very high probability of surviving to old age compared

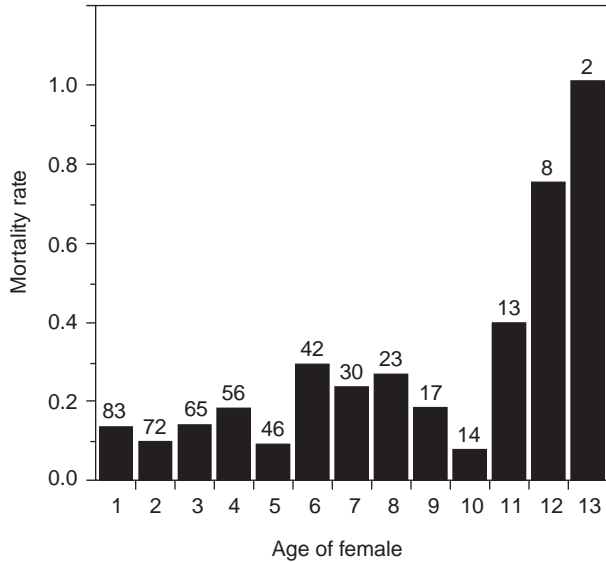


Fig. 2. Age specific mortality beyond one year old for female cheetahs born in the study area.

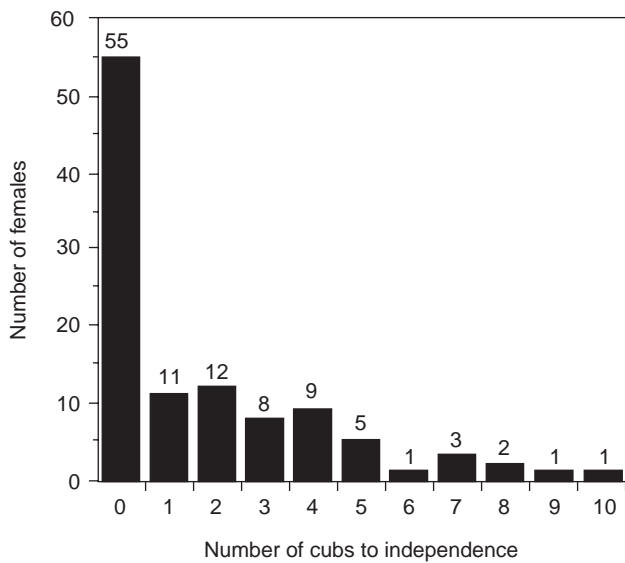


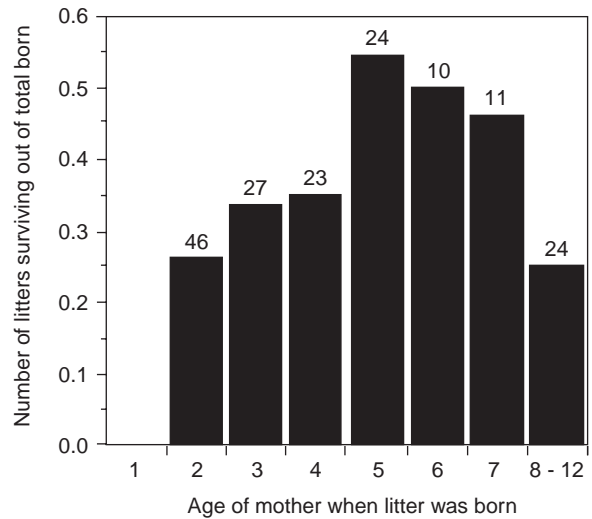
Fig. 3. Number of cubs raised to independence over a female's lifetime for the entire study (1969–1994). Numbers above histogram denote the number of females.

to the total number born (Fig. 1b). After one year of age, age-specific mortality for female cheetahs peaks at age 6 years with a slight decline at 7 and 8 years until a very high rate in old age from 11 years on (Fig. 2).

Reproductive success

Most female cheetahs of the Plains population raised no cubs at all to independence, while a few raised many (Fig. 3). The average number of cubs raised to independence per lifetime during the entire study was 1.72 ($n = 108$ females; S.D. = 2.35). The average reproductive rates were 0.36 cubs per year surviving to independence

a) Survival of litters as a function of mother's age



b) Average litter size as a function of mother's age

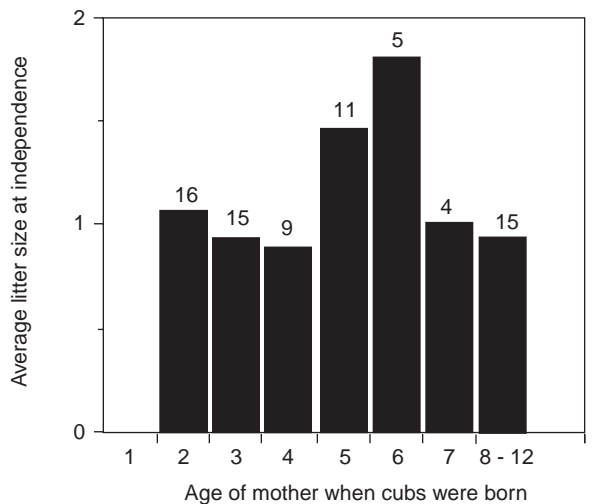


Fig. 4. (a) Proportion of litters surviving to independence out of those born as a function of mother's age when born. Any number of cubs surviving per litter constitutes a litter survival. (b) Average litter size to independence as a function of mother's age when cubs were born. Numbers above histograms denote number of litters. Ages 8 through 12 were pooled due to small sample sizes. Average litter size at independence was calculated from successful litters only.

($n = 103$; S.D. = 0.51) and 0.17 litters per year surviving to independence ($n = 103$; S.D. = 0.22).

Litter survival was constant for the first three litters at approximately 32% and then dropped off to 22% and 20% for the fourth and fifth litters. The combined category of litters six through nine had a survival rate of 38%. The number of cubs surviving per successful litter peaked at litter number three, although all sample sizes here are small.

Cheetah mothers were most successful at bringing litters and cubs to independence when they gave birth to

Table 3. Spearman correlation coefficients between reproductive rate of seven female cheetahs over their entire lifetimes and the proportion of sightings with predators and prey present while they had cubs of different ages, taken across the whole year. Correlation coefficients between reproductive success and average belly size over all sightings with cubs of different ages are also shown. * $P < 0.1$, ** $P < 0.05$

	LRS – cubs reared to independence per year	LRS – Litters reared to independence per year	LRS – cubs reared to independence per year	LRS – litters reared to independence per year
	Sightings with cheetah cubs ≤ 4 months old		Sightings with cheetah cubs of any age	
Presence of predators				
Lions	-0.685*	-0.901**	-0.643	-0.857**
Spotted hyenas	-0.036	0.071	-0.500	0.036
Other predators	-0.396	-0.721*	-0.357	-0.464
Other cheetahs	0.126	0.451	0.179	0.071
Presence of prey				
Thomson's gazelle = 0	0.107	0.640	0.107	0.530
Thomson's gazelle = 1–10	0.571	0.357	-0.250	-0.571
Thomson's gazelle = 11–50	0.143	-0.179	-0.214	0.214
Thomson's gazelle = 51–200	0.259	-0.126	0.500	0.071
Thomson's gazelle = 201–500	-0.778*	-0.334	-0.667	-0.396
Thomson's gazelle > 500	0.037	-0.519	-0.297	-0.630
Wildebeest ≥ 11	0.162	-0.270	0.107	-0.214
Grant's gazelle ≥ 11	-0.919**	-0.541	-0.536	0.107
Other prey ≥ 11	0.000	-0.536	0.321	0.000
Mother's belly size (14 point scale)				
Average belly size	0.214	-0.214	0.108	-0.476
Standard deviation of belly size	0.500	0.286	0.179	0.286

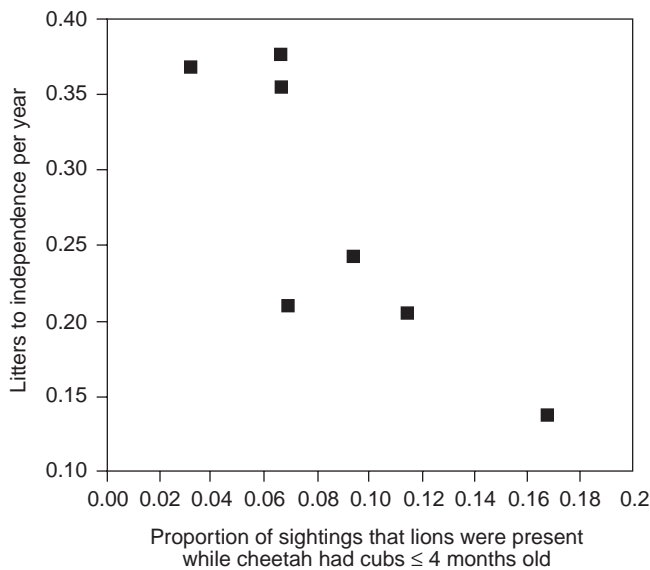


Fig. 5. Number of litters raised to independence per year calculated over the cheetah's lifetime plotted against the proportion of sightings that lions were present while cheetahs had cubs ≤ 4 months old.

them at 5 and 6 years of age (Fig. 4a,b), implying that females become more accomplished at raising litters with age and then perhaps get worse in old age. Since average longevity is 6.2 years (median = 5.8 years), and mortality is highest at 6 years (Fig. 2), a peak of litter or cub survival at 6 years of age shows that many cheetahs were dying at the same time they became most successful at raising cubs.

Longevity, number of sightings, and reproductive success

Not surprisingly, the number of cubs a female brought to independence over her whole lifetime was significantly correlated with her longevity ($n = 108$; $r^2 = 0.464$; $P = 0.0001$). There was, however, no correlation between her lifespan and reproductive rate in terms of cubs ($r^2 = 0.080$; $P = 0.593$) or litters ($r^2 = 0.0005$; $P = 0.820$) raised to independence.

The number of times a cheetah was seen did not affect estimates of her reproductive rates ($n = 106$ females; cubs/year: $r^2 = 0.000$, $P = 0.972$; litters/year: $r^2 = 0.004$, $P = 0.513$). The number of cubs a cheetah reared to independence over her lifespan was significantly correlated with the number of times she was seen ($n = 106$ females, $r^2 = 0.521$, $P = 0.0001$). This result, however, was most likely due to the strong association between longevity and the number of sightings ($r^2 = 0.647$, $P = 0.0001$). The longer a cheetah lived the more likely she was to be seen.

Correlates of reproductive success

Presence of predators

Significant negative correlations were found between reproductive success of cheetahs and the presence of lions nearby whether cheetahs had cubs ≤ 4 months old or cubs of any age (Table 3, Fig. 5). There was no significant correlation between the presence of spotted hyenas or other cheetahs and reproductive success. A marginally significant negative correlation was also found between

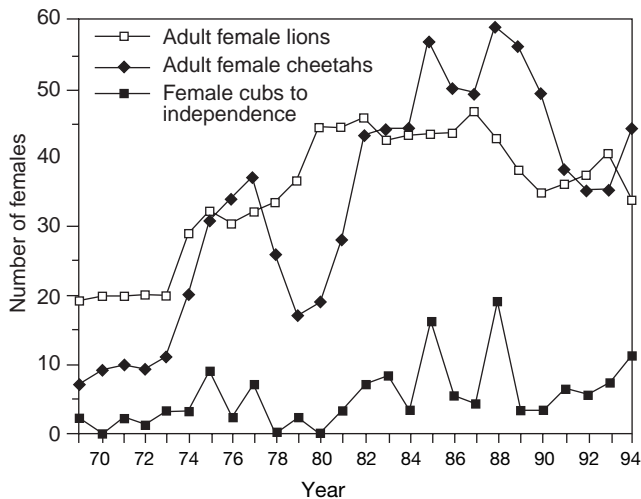


Fig. 6. Population size estimates for cheetahs and lions over 25 years on the Serengeti Plains. Cheetahs exhibit high variance in the numbers of female cubs raised to independence on an annual basis. Increasing numbers of cheetahs until 1975 reflects intermittent or irregular search effort; the apparent decline in 1978 and 1979 was due to absence of observers. Search area was most consistent from 1981 to 1990. Search effort for lions was low before 1974.

reproductive success and the presence of all other predators while cheetahs had cubs under 4 months.

Presence of prey

When Thomson's gazelles, the preferred prey of female cheetahs, were absent, or were present in very small (1–10), small (11–50), or medium-sized herds (51–200), there was no significant correlation with cheetah reproductive success. There was a marginally significant negative correlation between the presence of large herds of Thomson's gazelle (200–500) and one out of the four measures of cheetah reproductive success. This was primarily the result of Thomson's gazelle presence in the wet season ($n=7$ females, $r_s = -0.757$, $P = 0.060$) rather than dry. Presence of Grant's gazelles while cheetahs have cubs under four months was significantly negatively correlated with reproductive success.

Belly size

There was a marginally significant correlation between the standard deviation of mother's belly size (a measure of the variability of food intake) and her reproductive success in the wet season while cubs were ≤ 4 months ($n=7$ females, $r_s = 0.714$, $P = 0.080$).

Annual cheetah population size, rainfall, and lion numbers

Adult female cheetah population size and number of cubs to independence are plotted in Fig. 6. The smaller

search area in the early 1970s and the absence of consistent observers between 1978 and 1980 most likely led to unrealistically low population size numbers in those years. Between 1981 and 1990, search method and area searched were most consistent, therefore, the following statistical analyses are restricted to those 10 years.

No significant associations were found between the number of adult female cheetahs and the total number of cubs or total number of female cubs raised to independence per year ($n=10$ years and hereafter; $r_s = 0.349$, $P = 0.296$; $r_s = 0.440$, $P = 0.186$, respectively). In fact, a nearly significant positive correlation was found between total adult cheetahs (males and females) and the number of cubs reared to independence ($r_s = 0.547$, $P = 0.101$). This implies that density-dependent mechanisms were not limiting cheetah population size. Nor were correlations found between adult female population size and average number of cubs per female to independence ($r_s = 0.134$; $P = 0.687$) per year.

Average yearly rainfall during this 10-year period had no effect on total adult cheetah numbers ($r_s = 0.346$; $P = 0.300$), the number of cubs to independence ($r_s = 0.729$, $P = 0.827$), female cubs to independence ($r_s = -0.006$, $P = 0.985$), or average cubs to independence per year ($r_s = -0.067$, $P = 0.842$). There was a significant association between yearly rainfall and adult female cheetah numbers ($r_s = 0.701$, $P = 0.035$). No significant correlations were found between these annual cheetah numbers and average wet season or average dry season rainfall either. Numbers of adult transients or adult female transients did not show an association with rainfall ($r_s = 0.086$, $P = 0.798$); ($r_s = 0.366$, $P = 0.272$).

Lastly, no significant correlations were found between numbers of adult female lions on the Plains and adult female cheetah population size on the Plains ($r_s = -0.354$, $P = 0.289$), annual cubs to independence ($r_s = 0.103$, $P = 0.757$), annual female cubs to independence ($r_s = 0.131$, $P = 0.694$) or average annual cubs to independence ($r_s = 0.224$, $P = 0.501$). Female lion numbers were not associated with the total number of transient cheetahs ($r_s = 0.215$, $P = 0.518$) or number of transient female cheetahs ($r_s = 0.006$, $P = 0.985$).

Comparison of RS at two different times

As the previous analysis is restricted to the 10 years with the most uniformly collected data, it is not possible to examine adult cheetah population size in times of low versus high numbers of lions. For this reason, and in light of Laurenson's (1995a) data showing a decrease in litter size at independence from the 1970s to the 1980s, we examined lifetime reproductive success in times of low versus high lion numbers. Separating adult females into two groups that lived during different periods of lion abundance, we found that litter size at emergence from the lair (4 months old) decreased significantly from an average of 2.9 in the 1970s to 2.1 in the 1980s and

Table 4. Reproductive variables for female cheetahs in time periods of low (1969–1979) versus high (1980–1994) lion abundance on the Serengeti Plains. Low abundance: an average of 26.5 adult female lions on the Plains per year; high abundance: an average of 42.5 adult female lions. We present mean values for cheetah reproductive parameters, numbers of females in parentheses, U values for Mann-Whitney U-test and *P*-values

Reproductive variable	1969–1979	1980–1994	U	<i>P</i> -value
Litter size at emergence (4 months)	2.9 (23)	2.1 (58)	486	0.046
Litter size at independence	2.5 (22)	2.0 (83)	690	0.060
Cubs to independence over entire life				
All females	2.1 (22)	1.6 (87)	992.5	0.780
Breeders only	4.6 (10)	3.2 (44)	132	0.046
Reproductive rate (cubs to indep./year)				
All females	0.42 (20)	0.36 (84)	812.5	0.806
Breeders only	3.54 (10)	1.45 (44)	143.5	0.088
Reproductive rate (litters to indep./year)				
All females	0.16 (20)	0.18 (84)	792	0.668
Breeders only	0.93 (10)	0.83 (44)	167	0.238

early 1990s (Table 4). In addition, litter size at independence declined over the same period from an average of 2.5 to 2.0 and confirms previous analyses of changes in litter size over time (Laurenson, 1995a).

Average numbers of cubs reared per lifetime also decreased across the two time periods (Table 4). Examining the subset of successful breeders only (those cheetahs that reared one or more cubs to independence) we found that the number of cubs raised to independence declined significantly from the 1970s to the 1980s and early 1990s.

A similar pattern was seen in reproductive rates. Average number of cubs reared to independence per year over all females in the 1970s was 0.42, while in the 1980s and early 1990s it was 0.36. Again, taking only successful breeders, there was a marginally significant difference in cubs reared to independence per year between the two periods, although no significant difference was observed in the number of litters reared per year per female (Table 4).

Lifespan of cheetahs did not differ across the two time periods. Females of known age in the 1970s did not live longer on average than the 1980–1994 known age animals ($n = 17$, 62 females, respectively, $\bar{x}s = 5.7$, 6.0 years: $U = 481.5$, $P = 0.59$), nor was there a difference in longevity between the cheetahs of estimated age in the two time periods ($n = 24$, 55; $\bar{x}s = 6.4$, 6.2; $U = 619.5$, $P = 0.67$).

Male cheetahs of known age during 1980–1994 lived slightly longer than the 1970s known age males ($n = 31$, 18; $\bar{x}s = 2.9$, 2.6, respectively; $U = 195.5$, $P = 0.08$). Average lifespans for males of estimated ages in the earlier and later time periods were 5.5 years and 5.1 years, respectively, which did not differ significantly ($n = 64$, 14; $U = 381.5$, $P = 0.39$).

DISCUSSION

Demographic summary

This study used the largest data set so far employed for Serengeti cheetahs to determine baseline demographic and reproductive parameters. Cheetahs reached independence at 17.1 months, one month earlier than that estimated in a previous study of the same population using a smaller sample size (Laurenson *et al.*, 1992). Females first gave birth at an average of 2.4 years, similar to previous estimates (Adamson, 1969; Schaller, 1972; Laurenson *et al.*, 1992).

Interbirth interval was 20.1 months, one month longer than previously estimated (Caro, 1994). A large percentage of females in this study (44–70%) were already pregnant before their previous litter had left. This confirms that females usually come into oestrus and breed while still accompanied by their old cubs (Laurenson *et al.*, 1992), and lends support to the hypothesis that it is the mothers, not their cubs, who break up the family group because mothers need to increase food intake and find a lair before the birth of the next litter (Caro, 1994). No time estimates were made on resumption of oestrus after loss of an unweaned litter, but previous studies of radio-collared animals have shown that females mated on average 19 days after losing a litter but could conceive as early as 2–5 days after the loss (Laurenson *et al.*, 1992). In comparison with other large cats, cheetahs reproduce early and rapidly (Caro, 1994).

Litter size at independence was 2.1, intermediate between previous estimates of 2.6 for the mid 1970s (Frame, 1976) and 1.9 for the late 1980s (Laurenson *et al.*, 1992), based on a subsample of this data set.

Average lifespan for females that reached independence was 6.2 years, only 8.4 months shorter than Laurenson's (1994) estimate which was admittedly biased towards older females.

Male longevity, dispersal, and survivorship

There was a marked difference between the average longevity of known age males and estimated age males. This difference is most likely explained by the dispersal of the known age male cheetahs from the Plains. The average longevity for known age males is unrealistically low at 2.8 years considering that age at maturity is approximately 2.5 years. In addition, longevity of estimated age males at 5.3 is probably an underestimate as well, since these cheetahs were assigned the minimum age corresponding to their physique.

A greater proportion of males than females on the Plains are of unknown origin (0.60 vs. 0.50) and male mortality (i.e. disappearance) between 1 and 2 years is higher for males, implying that males chiefly disperse. This confirms preliminary reports that male cheetahs disperse from their natal home ranges in the Serengeti (Frame, 1980). In theory, limited dispersal and inbreeding might be the cause of the extreme lack of genetic variation observed in cheetahs (Caro, 1994). However, the high percentage of male cheetahs dispersing out of the study area suggests that philopatry is not a cause of low heterozygosity.

Previous analyses of longevity of territorial versus floater males based on small sample sizes suggested that territorial males lived longer and that floater males had a lower chance of surviving due to poor health or competitive ability (Caro, 1994). We have shown, however, that longevity did not seem to differ between territorial and floater males. Our sample sizes for known age animals, however, were also very small. Although our sample sizes for estimated age males are much larger, it is known that males that have established a territory are older (Caro & Collins, 1987) and individuals have been shown to float for a while before becoming resident (Caro, 1994), a factor not considered when assigning ages to unknown cheetahs in this analysis.

Although longevity for known age males is an underestimate, the survivorship curve for males is an accurate portrayal of the fate of males born within the study area and clearly shows a different pattern from the females. Males born on the Plains disappear from the population by about 6 years old, either by death or dispersal, while females stay up to twice this long.

Reproductive success

Because of the difficulty of following individual animals over their entire lifespans, few studies of mammals have been able to measure lifetime reproductive success.

There is great theoretical interest in lifetime reproductive success (LRS) in animal populations, however, because the upper limit on the magnitude of natural selection is set by the magnitude of the variance in lifetime reproductive success (Arnold & Wade, 1984; Barrowclough & Rockwell, 1993). Following Crow (1958) and Arnold & Wade (1984), many studies of reproductive success use the ratio of the variance to the mean (s^2/\bar{x}) in LRS as an estimate of variability of success (see Clutton-Brock, 1988b). This ratio, called the standard variance (I), is a measure of the opportunity or potential for selection on any character or group of characters (Arnold, 1986), and influences the effective size (N_e) of a population (Crow & Kimura, 1970; Barrowclough & Rockwell, 1993). N_e has important implications for maintaining genetic variation in managed populations of threatened species (Lande & Barrowclough, 1987).

Variation in the reproductive success of female cheetahs is similar to other mammals (Table 5). Compared to related lions and tigers (*Panthera tigris*), however, variance in LRS is lowest for the cheetah. Nevertheless, certain problems in comparisons across taxa should be noted. All studies of mammals presented in Table 5, this one included, suffer to varying degrees from problems of defining a breeding adult, differences in the stage or age of offspring included in the female's reproductive success, emigration and immigration, disappearance of individuals for unknown reasons, and the inclusion of truncated lifespans (Clutton-Brock, 1988b). For example, this study shows that cheetahs are most reproductively successful at 5 and 6 years old, while from 8–12 they may have lower success. Animals first seen at 5 years versus at 9 years old may therefore have very different reproductive success if only these portions of their lives are included in estimates. From this, it is clear that inclusion of truncated lifespans could lead to an overestimate of variance in reproductive success in a population (Clutton-Brock, 1983).

The genetic basis for variance in reproductive success in mammals is largely unknown. Variance in components of reproductive success in a genetically diverse population could be a reflection of genetic variation, environmental variation, or both (Murray, 1992). Interestingly, the notoriously monomorphic cheetah (O'Brien *et al.*, 1985) has a variance equivalent to more genetically diverse species, possibly implying that environmental variation might still play a strong role in varying the cheetah's reproductive success and indirectly supporting the importance of predation in juvenile mortality (Caro & Laurenson, 1994).

Correlates of reproductive success

Three lines of evidence support the idea that lions are detrimental to cheetah population increase. First, Laurenson's (1994) observations of radio-collared cheetahs revealed that 73% of cubs die from predation and that

Table 5. Mean, variance, and standard variance in lifetime reproductive success for females across 14 different species. Blank spaces indicate missing data. Breeders include only those females which have successfully reared at least one young

Species	Measurement used	Breeders only			Non-breeders included			Source
		Mean LRS	Variance LRS	Standard variance	Mean LRS	Variance LRS	Standard variance	
Cheetah (<i>Acinonyx jubatus</i>)	cubs in independence	3.49	4.92	0.40	1.72	5.52	1.87	1
Lion (<i>Panthera leo</i>)	cubs to 12 months	3.44	5.43	0.47		5.86		2
Tiger (<i>Panthera tigris</i>)	cubs to dispersal	4.54	11.48	0.56				3
Vervet monkey (<i>Cercopithecus aethiops</i>)	young to 1 year	3.26	3.56	0.31				4
Elephant seal (<i>Mirounga angustirostris</i>)	pups weaned				0.75	2.95	5.23	5
Red deer (<i>Cervus elaphus</i>)	calves to breeding age	5.03	9.09	0.36	4.01	11.40	0.71	6
Dama gazelle (<i>Gazella dama</i>)	survival to 1 month				1.74			7
Dorcas gazelle (<i>Gazella dorcas</i>)	survival to 1 month				0.82			7
Cuvier's gazelle (<i>Gazella cuvieri</i>)	survival to 1 month				1.51			7
Prairie dog (<i>Cynomys ludovicianus</i>)	yearlings produced				2.14	5.20	1.14	8
Red squirrel (resident) (<i>Sciurus vulgaris</i>)	young weaned	5.33	6.15	0.22				9
Deer mouse (<i>Peromyscus californicus</i>)	young weaned				4.70	7.95	0.35	10
House mouse (monogamous) (<i>Mus domesticus</i>)	young weaned	12.50	114.73	0.73	11.25	117.46	0.93	11
Common vole (<i>Microtus arvalis</i>)	breeding daughters produced				3.17–5.19			12

Sources: 1. This study; 2. Packer *et al.*, 1988; 3. Smith & McDougal, 1991; 4. Cheney *et al.*, 1988; 5. Le Boeuf & Reiter, 1988; 6. Clutton-Brock, 1988c; 7. Alados & Escos, 1991; 8. Hoogland, 1995; 9. Wauters, Matthysen & Dhondt, 1994; 10. Ribble, 1992; 11. Konig, 1994; 12. Boyce & Boyce, 1988.

lions account for 78% of this mortality. Although it has been argued that the observer (MKL) attracted predators to the den (O'Brien, 1994), this is highly unlikely due to the precautions taken (Laurenson & Caro, 1994; Laurenson, Weilebnowski & Caro, 1995). Second, in areas where lions and other predators have been removed, cheetahs exhibit signs of predator release. For example, cheetah average litter size at 10 months old in areas of Namibia, where lions and hyenas have been exterminated, was extremely high at 4.0 (McVittie, 1979), double that of the Serengeti. Third, Laurenson (1995a) found that lion biomass was negatively associated with cheetah biomass across nine African protected areas. Our long-term demographic records provide a fourth and independent test of this hypothesis. Our strongest and most consistent finding is the negative correlation between lion presence and cheetah reproductive success. Measured over a cheetah's lifespan, the more often lions were present while she had cubs, the lower her reproductive rate. It should be noted that these results were obtained from non-invasive, observational data only.

Spotted hyenas also kill cheetah cubs (Laurenson, 1994) and our findings indicate that other predators may play a role in reducing cheetah reproductive success, especially when cheetah cubs are under 4 months old. Perhaps the lesser visibility of hyenas on the Plains accounts for the lack of association between reproductive success and hyena presence in this study. Jackals, particularly golden jackals, were the most commonly seen predator in our 'other predator' category and their interactions with cheetah cubs deserve further attention.

Although availability of food is known to be an important factor limiting the size of many vertebrate populations (Sinclair, 1989), this study found no significant positive correlation between abundance of prey and reproductive success. Laurenson (1995a) has argued that the biomass of appropriate prey in the Serengeti is higher than that required to support an equivalent biomass of cheetahs elsewhere in Africa. Moreover, her analysis did not include small prey such as hares which have been shown to be an important component in the cheetah's diet (Caro, 1994). On a local scale, scarcity of Thomson's gazelles led to litter abandonment on only a small percentage of the occasions, accounting for 7.7% of total cub mortality (Laurenson, 1994). Cheetah mothers are highly mobile, leaving the lair and travelling as far as 12 km in a day to hunt (Laurenson, 1994). Cubs begin to accompany their mothers in search of food when they are 2 months old and by 4 months followed their mothers on most hunts (Caro, 1994). Thus the high mobility of the cheetah is the most likely reason why local scarcity of gazelles did not affect cheetah reproductive success in this study. Lack of a positive association between reproductive success and prey availability in the current analysis is consistent with this argument.

A significant negative correlation was found between reproductive success and large herds of Thomson's

gazelle (200–500) in one out of four measures of reproductive success. There are at least two hypotheses for this result. Durant (In press) has found that cheetahs avoid areas of high Thomson's gazelle concentration (>250), preferring intermediate herd sizes (1–250). Other predators, especially lions and hyenas, are attracted to large congregations of prey. Since cheetahs always lose in direct competition with these competitors, cheetahs exhibit local avoidance behaviour. A second hypothesis is that there is a decline in hunting success with increasing prey group size (reviewed in Pulliam & Caraco, 1984) because large groups detect approaching predators further away and warn other group members. FitzGibbon (1989, 1990) examined cheetah predation on herds of Thomson's gazelle of up to 100 animals and has shown that gazelle in larger groups were less vulnerable to predation than solitary ones or small groups of 2–10 gazelles.

The strong negative correlation between reproductive success and presence of Grant's gazelle most likely occurs for a different reason. Grant's gazelle are moderately heterothermic and hence able to vary their internal body temperature approximately six degrees so they can withstand very hot and dry conditions (Taylor, 1972). They stay out on the Plains after other, less heat-tolerant species (e.g. Thomson's gazelle) have left. It is possible therefore, that cheetahs found near Grant's gazelle are in consistently dry areas without their favoured prey. Lack of water or food could play a role in reducing the number of cubs cheetahs can raise under these conditions.

Annual population size and comparison of reproductive success over time

Although it has been argued that lion predation may be limiting the cheetah population (Laurenson, 1994) and that cheetahs may be suffering substantially higher predation rates since the increase in lions beginning in the late 1970s (Laurenson, 1995a), this hypothesis has not been tested empirically. Our data provide evidence that cheetah reproductive success has significantly declined between the 1970s, and the 1980s and early 1990s, and that a most likely cause is the increase in lion numbers. In the 1970s, average lifetime reproductive success for female cheetahs was 2.1 cubs to independence – a self-sustaining population. Through the 1980s and early 1990s, the population was apparently failing to replace itself as females produced an average of only 1.6 cubs during their lifetime. It is not clear if the decrease in lifetime reproductive success has led to a decrease in the overall population size of cheetahs on the Serengeti Plains. In 1980, TMC expanded the search effort for cheetahs and hence, what appears to be an increase in cheetah numbers in the early 1980s is the likely result of this expanded search effort. Likewise, after 1990, the search area was shifted, again making it unclear if the apparent decrease in cheetah numbers in the early 1990s was due to this shift. In addition, our

analysis of annual cheetah numbers was restricted to the 1980s, hence we were not able to compare cheetah population size before and after the increase in lion numbers which occurred during the late 1970s and early 1980s. Monitoring changes in cheetah population size and reproductive success during the recent dramatic but temporary decline in lion numbers due to the canine distemper virus (Roelke-Parker *et al.*, 1996), may shed light on the relationship between adult cheetah and lion population sizes on the Plains.

It is also possible that annual cheetah numbers were not negatively associated with annual lion population size during the 1980s because the Plains cheetah population is not closed. Cheetah numbers vary widely from year to year and most animals in this study were of unknown origin. Only half of the females and 40% of the males were known to be born in the study area. Adult cheetahs from outside the national park immigrate and establish residence on the Plains. This implies that the Serengeti Plains may be a sink for cheetahs and not a source. Furthermore, preliminary work suggests that woodland habitat may be favourable for cheetahs (SMD, pers. obs.).

It is unlikely that environmental factors (aside from increased lion predation) caused the decrease in cheetah reproductive success. The total source population of spotted hyenas increased between 1966–1968 and 1977, but those hyenas of most concern to the cheetah, the short grass Plains residents, did not increase over the same period (Hofer & East, 1995). Although the total source population of hyenas increased between the 1977 census and the 1986 census (Hofer & East, 1995), it is unclear if the resident Plains hyenas increased. Hofer & East (1995) argue that clans in the central study area have remained constant or declined between 1986 and 1992.

Variation in rainfall has been shown to affect prey numbers and movement such that wet years drive prey on to the Plains (Scheel & Packer, 1995). This is probably the reason for our positive correlation between rainfall and adult female cheetahs on the Plains. However, rainfall did not increase cheetah reproductive success in this study. In terms of overall prey abundance, Thomson's gazelle numbers were estimated to have declined from 1972 to 1985 (Borner *et al.*, 1987), but a subsequent appraisal indicated that gazelle numbers remained constant over that same time period (Dublin *et al.*, 1990). Our results and those of previous studies (Laurenson, 1994, 1995a), however, indicate that gazelle scarcity is not currently affecting cheetah reproductive success.

Since no negative correlation was found between annual cheetah numbers and the total or average number of cubs they rear to independence, it is unlikely that cheetahs have reached their carrying capacity on the Plains. Density dependence, therefore, is unlikely to have caused the decline in cheetah reproductive success.

Lastly, the decrease in cheetah reproductive success over time is unlikely to be due to changes in the number of cubs born per litter. Although no estimate

of average litter size at birth exists for Serengeti cheetahs, Laurenson *et al.*'s (1992) estimation of litter size at an average of 2 weeks of age between 1987–1990 was not significantly different from Frame's estimate at under 4 weeks for 1969–1976 (Laurenson, 1995a). Moreover, both figures are comparable to captive litter sizes (Marker & O'Brien, 1989). Nor was there a high percentage of inviable cubs (possibly 3.8%) in recent times (Laurenson, 1995a), implying that inbreeding depression is not a major factor. Rather, our findings of a decreased litter size at emergence (4 months) in recent times and Laurenson's (1995a) of a decreased litter size at independence, reconfirmed by this analysis, suggests that more cubs died between birth and independence due to partial litter mortality in recent times than in the past. Since predation is the chief source of juvenile mortality in Serengeti cheetahs, increased predation seems the most plausible candidate for the cheetah's declining reproductive success in recent years.

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