Factors affecting life and death in Serengeti cheetahs: environment, age, and sociality

Sarah M. Durant,[a,b] **Marcella Kelly,**[c] **and Tim M. Caro**[b,d]
[a]Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK,
[b]Tanzania Wildlife Research Institute, Box 661, Arusha, Tanzania, [c]Department of Fisheries
and Wildlife, 106 Cheatham Hall, Virginia Polytechnic Institute and State University, Blacksburg,
VA 24061-0321, USA, and [d]Department of Wildlife, Fish and Conservation Biology and Center for
Population Biology, University of California, Davis, CA 95616, USA

We examined environmental and social factors affecting reproductive success across a 20-year data set of individually known cheetahs on the Serengeti Plains of Tanzania. Because cheetahs are seen infrequently and are not amenable to mark–recapture techniques, we devised a model to estimate time of death for individuals that disappeared from our records. We found that males had markedly lower survival than females. Recruitment was negatively affected by rainfall but positively affected by numbers of Thomson's gazelles, the cheetahs' chief prey. There was a negative association between recruitment and numbers of lions, demonstrating that the high rates of predation observed in previous studies have implications for the dynamics of cheetah populations. Recruitment was related to mother's age, peaking when she reached 6–7 years. Sociality affected survival in two ways. First, adolescents living in temporary sibling groups had higher survival than singletons, particularly males with sisters. Second, adult males living in coalitions had higher survival than singletons in periods when other coalitions were numerous, yet they had lower survival when other coalitions were rare. These results corroborate observations of enhanced prey capture by female adolescents and antipredator benefits for adolescents in groups, as well as competitive advantages for adult males in groups. Furthermore, our findings stress the importance of interactions between environmental and social factors in affecting reproductive success in mammals. *Key words:* Acinonyx jubatus, age, cheetahs, group living, predator avoidance, predator–prey relationships, reproductive success, sociality. *[Behav Ecol 15:11–22 (2004)]*

F actors affecting patterns of reproduction in animals can broadly be divided into environmental factors, including food and predators, and life-history characters, such as age and sex. Unfortunately, demonstrating the effects of these variables on fitness requires long-term data sets, and for long lived animals this necessitates years of study. In the last 15 years, however, a number of studies on factors affecting individual fitness in mammals have been published (Boyce and Boyce, 1988; Clutton-Brock et al., 1988; Packer et al., 1988; Wauters et al., 1994). Most have concerned either highly polygynous or monogamous mammals (e.g., le Boeuf and Reiter, 1988; Ribble, 1992; see also Clutton-Brock, 1988b), and far less is known about species with other mating systems (but see Creel and Waser, 1994). Moreover, factors affecting reproductive success have generally been explored in mammals that suffer little from predation because they are large (Smith and MacDougal, 1991), or mammals have been studied in areas where predators are absent or have been eliminated (Kônig, 1994). In contrast, the species that we study, the cheetah (*Acinonyx jubatus*), has a unique social system among mammals and suffers from extremely high predation-induced juvenile mortality. The principal factors affecting fitness in cheetahs may therefore differ considerably from those of other mammals.

Female cheetahs live alone or with dependent cubs, whereas males either live alone or in permanent coalitions of two or three individuals (Caro and Collins, 1987a). In the Serengeti National Park, Tanzania, females occupy huge annual home ranges (833 km[2] on average), whereas males either defend small territories (37 km[2] on average) where females collect, or else they wander over large ranges each year (777 km[2] on average; Caro, 1994). Male competition over territories is intense, and the superior fighting ability of coalitions enables them to compete for and take over occupied territories; while singletons are left to occupy vacancies or are forced to take on a floating lifestyle.

Cheetah cubs in the Serengeti suffer extraordinarily high mortality. A detailed behavioral study of radio-collared females showed that only 36% of cubs leave their lair at 2 months of age, and only 5% reach independence at 18 months. The chief source of this mortality is predation by lions (*Panthera leo*), which accounts for nearly 75% of known cub mortality (Laurenson, 1994, 1995).

Although we now have sufficient observational data on several environmental and social factors influencing cheetah reproduction or the correlates of reproduction, the consequences of these factors on fitness have received little attention (but see Kelly et al., 1998). This is unfortunate because the importance of these factors as selection pressures cannot be critically assessed without long-term data on individual reproductive success (Clutton-Brock, 1988a). In this study we used 20 years of demographic data on individually recognized cheetahs to investigate the effects of environmental factors: rainfall, prey availability, lion and cheetah numbers, and life-history variables—specifically age and grouping—on reproduction and survival of male and female cheetahs living in a 2200-km[2] region of the Serengeti plains of Tanzania.

METHODS

Study area and population

Cheetahs were studied on the Serengeti plains in the Serengeti National Park in Tanzania (see Sinclair, 1979, for

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Address correspondence to S. M. Durant. E-mail: s.durant@ucl. ac.uk.

Table 1

Numbers of individuals used in analyses (numbers in parentheses indicate the number of individuals whose age was known)

	Females	Males	Total
Adolescents (1−2 years)	82	69	141
Adults (>2 years)	177 (96)	121 (47)	298 (143)
Litters	116 (76)	−	−
Total no. individuals	202	161	363

By definition, the ages of all adolescents were known. Many individuals seen as adults were also seen as adolescents.

a full description of the study area). Rainfall follows a gradient from an annual 1000 mm in the northwest to 600 mm in the southeast of the study area (Campbell and Hofer, 1995), falling mostly in the wet season between November and June, with little falling in the dry season from July to October (Sinclair, 1979). Variation in seasonal rainfall drives the migratory patterns of the large herbivores in the ecosystem. Thomson's gazelle (*Gazella thomsoni*), the main prey species for cheetahs (Caro, 1994; FitzGibbon, 1990), move up to the woodland border to the north and west of the plains during the dry season and out onto the short-grass plains at the start of the rains (Bell, 1971; Durant et al., 1988; McNaughton, 1976). Female and nonterritorial male cheetahs follow this migration (Durant et. al., 1988).

During the period from 1975 to 1994, except for a 2-year gap in 1978 and 1979, cheetahs were usually located by driving to scan points and searching through 10 × 50 binoculars (see Caro, 1994, for details). Individuals can be recognized by distinctive spot patterns on their face and haunches (Caro and Durant, 1991; Caro and Kelly, 2001; Kelly, 2001). Cubs were defined as 0–1 year old, adolescents as 1–2 years old, and adults as >2 years. When cheetahs were first seen with their mothers as cubs or adolescents, their age could be estimated to within 1 month (Caro, 1994). When they were first seen as adolescents independent of their mother, their age was estimated as 18 months. This estimate had a maximum error of 6 months, based on the normal age composition of adolescent groups (Caro, 1994).

The analyses here concentrate on cheetahs judged to be resident in the study area. These were either individuals that were first seen as cubs or as adolescents and that were subsequently seen at least once after reaching adulthood or immigrants that were seen repeatedly in 2 or more years. Individuals seen during only 1 year of the study were designated as transients and were not used in analyses. Table 1 gives the numbers of different individuals in analyses. The years 1978 and 1979, when there was no resident cheetah researcher in the study area, were omitted from analyses.

Cheetah demography

Estimating survival rates for cheetahs is problematic because when an individual disappears from a population it may be dead or simply may not have been seen. Although Jolly-Seber mark–recapture models are designed to deal with this problem, they assume equal resighting probabilities (Jolly, 1965; Seber, 1965). This assumption does not apply to cheetahs because they range widely, and many individuals spend some of the year outside the study area, or individuals differ in habituation to vehicles. These factors lead to large individual differences in intersighting intervals and hence resighting probabilities (Figure 1). Although recent developments in mark–recapture techniques can account for a certain amount of heterogeneity in resighting probabilities (Kawata, 1996; Lebreton et al., 1992), they do not make full use of data sets where individuals are seen repeatedly within capture intervals.

Previously, two methods have been used to determine time of death for cheetahs. First, an individual's time of death was assumed to be equal to time of last sighting plus two standard deviations of that individual's intersighting interval (Caro, 1994). Second, time of death was assumed to correspond to the age at which an individual was last seen (Kelly et al., 1998). The former method overestimates time of death, whereas the latter underestimates it. Here we constructed a model that takes account of individual differences in mean intersighting interval and which should neither over- or underestimate time of death.

The model

First we assumed that both time of death from the last sighting and time between sightings are distributed exponentially, with means λ and μ, respectively. This assumption was tested against our data; however, there are sound theoretical reasons for expecting this distribution. For example, in mark–recapture analysis there is always an underlying assumption that from time of marking to time of recapture there is some probability of survival that, by definition, usually is a Bernoulli process, the discrete version of an exponential process (e.g., Seber, 1973).

Assuming the exponential distribution, in a time interval, t, the probability that a cheetah dies is given by $1 - e^{-t/\lambda}$, and the probability that a cheetah is seen, given that it is alive, is
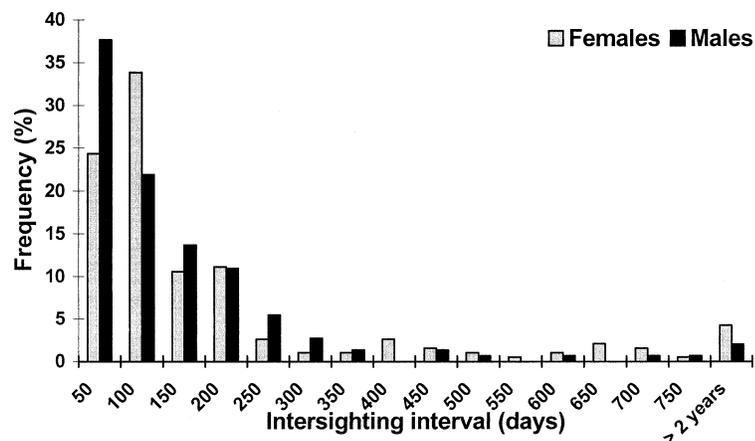
Figure 1
Frequency distribution of the mean time between sightings for males and females over the course of the study.

$1 - e^{-t/\mu}$. If D denotes the event of a cheetah's death and S denotes the event of a cheetah being seen, then D' and S', respectively, denote the event of D and S not happening. Then the probability that a cheetah is dead given that it is not seen is given by:

$$P\{D/S'\} = P\{D \cap S'\}/P\{S'\} = P\{S'/D\}P\{D\}/P\{S'\}$$

Now $P\{S'/D\}$ is the probability that a cheetah is not seen given that it is dead and is therefore equal to 1. So

$$\begin{aligned} P\{D/S'\} &= P\{D\}/P\{S'\} \\ &= P\{D\}/[P\{D\} + P\{D'\}P\{S'/D'\}] \\ &= \left(1 - e^{-t/\lambda}\right)/\left[1 - e^{-t/\lambda} + e^{-t/\lambda}e^{-t/\mu}\right] \end{aligned} \qquad (1)$$

For our analyses we wanted to be equally likely to under-estimate as to overestimate the time of death. Therefore we set Equation 1 to 0.5, giving:

$$1 - e^{-t/\lambda} + e^{-t/\lambda}e^{-t/\mu} = 2 - 2e^{-t/\lambda}$$
$$e^{-t/\mu} = e^{t/\lambda} - 1 \qquad (2)$$

This equation can then be solved iteratively for t, given estimates of μ and λ.

Calculation of time of death

In order to use Equation 2 to estimate time of death, it is first necessary to estimate the mean intersighting interval, μ, and the mean life span, λ. We estimated μ for each individual cheetah by calculating the mean time between sightings. For females, this was estimated across all sightings after the cheetah was first seen, both as a cub and an adult. For males, we calculated the estimate from sightings after the cheetah attained 2 years of age. We did this because some males are likely to disperse into and out of the study area at around this age (Caro, 1994), altering the distribution of the time between sightings for these individuals. When males were seen before reaching 2 years of age, the last sighting before 2 years was also included in the estimate.

Estimating λ, the mean life span, poses more of a problem because the true life span cannot be calculated unless the time of death is known. Instead, we approximated λ using the mean age at last sighting plus the mean intersighting interval. To test the validity of this approximation, we examined the time of death, t, for its sensitivity to changes in λ according to Equation 2. For low values of the intersighting interval (μ), t was insensitive to changes in the mean life span, but t became more sensitive as μ increased (Figure 2). However, even when μ was equal to 1 year, the error in estimating t was unlikely to be more than 2 months, and this error was only reached when the original estimate of life span had an inaccuracy of more than 1 year. Most estimates would have been much more accurate than this because for most cheetahs μ was much less than 1 year. We concluded that a more accurate estimate of life span would make little difference to the final estimation of time of death. It is beyond the scope of this article to examine the sensitivity of our estimate of time of death to our assumption of an underlying exponential distribution, but, given the sensitivities examined here, it is unlikely that a change in this assumption would have a major impact.

Although Equation 2 could be used to estimate time of death for all adult cheetahs as described above, we could not use this equation to estimate time of death during adolescence. This was because adolescents may range farther when they are newly independent than when they are with their mother, meaning that their intersighting intervals during this period may differ from their intersighting intervals as cubs.
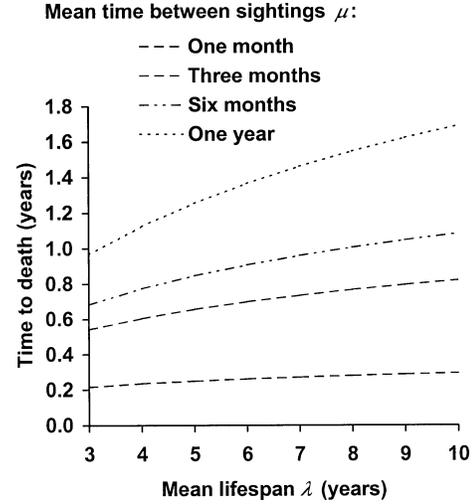
Figure 2
Sensitivity of the estimation of time between last sighting and time of death to variation in the estimates of the mean time between sightings and mean lifetime.

Instead we estimated whether an individual survived over its second year as follows: an individual was assumed to have died if it was never seen again, but its mother was seen within one year. The individual was known to have survived if it was later seen at 2 years or older. Individuals whose mothers were not seen within 1 year of the last sighting were excluded from this analysis.

In analyses of both adults and adolescents, we denoted survival using the binomial variate 0 and 1. A cheetah was denoted as surviving a particular year by setting this variate to 1 and as dying by setting the variate to 0. We estimated adult population size in a particular year from the number of individuals surviving that year.

Estimation of recruitment

We estimated recruitment for each female in each year as the number of cubs that a female reared to 12 months of age. All cheetah cubs remain with their mother up to 12 months (Caro, 1994), and so deaths can be determined when the mother is seen but the cubs are not. If the fate of a female's cubs was unknown in a particular year, then she was omitted from the analysis for that year. Cheetahs occasionally adopt cubs from other mothers (Caro, 1994), but adopted cubs were not included in this analysis.

Group size

After leaving their mother, adolescent cheetahs of both sexes remain in a sibling group for an average of 6 months, at which point females leave the group, but brothers remain together throughout their lives (Caro, 1994). In this study we examined the effects of both adolescent group size and male coalition group size on survival. Adolescent group size was estimated as litter size at 12 months. Adolescents could be singletons, same-sex siblings, or male and female siblings or adopted cubs (three instances). We estimated male coalition size as the size of a male coalition at 2 years. Most coalitions were brothers (Caro and Durant, 1991), but unrelated males could also join up to form coalitions (Caro, 1994). All male coalitions had the same composition over two or more sightings. The number of coalitions in the population at any one time ranged from one to four.

Environmental factors

We calculated annual rainfall from monthly records obtained from a rain gauge at the Serengeti Wildlife Research Center, near Seronera (mean 740 mm, range 546–932 mm). Estimates for 15 missing months were calculated using the mean for that month over the years where data were available. Population estimates of Thomson's gazelle were available for the entire ecosystem until 1991 (Borner et al., 1987; Dublin et al., 1990). These were irregular, and estimates for intervening years were estimated through linear interpolation between estimates (mean 446,433, range 319,666–688,459; see Scheel and Packer, 1995). We estimated numbers of lions in the study area from the annual number of females in resident prides (mean 98, range 72–120 individuals; Hanby et al., 1995; Roelke-Parker et al., 1996).

Statistics

All analyses were conducted using generalized linear models. We used three types of model. (1) We analyzed survival using logistic regressions on the binomial variate denoting survival for each known individual. (2) We analyzed recruitment using a generalized linear model with Poisson errors. Recruitment, measured here as the number of surviving cubs per litter, deviated from the Poisson distribution, resulting in an overdispersed distribution with an excess of litters with no cubs or with several cubs. Therefore, analyses of this measure corrected for overdispersion by adjustment of the scale parameter using the methods outlined by McCullagh and Nelder (1989). (3) We analyzed the number of females per litter using a binomial distribution with a denominator equal to the total litter size.

To avoid some of the problems from pseudoreplication due to repeated survival data across years for the same individuals, individual identity was fitted as a factor in the analyses of adult survival. However, because of the large number of individuals in the study and the low number of repeats for the large number of individuals that died at a young age, it was necessary to reduce the number of individual categories before the full analyses could be performed. We did this by first fitting a generalized linear model to survival with individual identity as a factor and aggregating all those identities that had identical parameter estimates until further aggregations caused a significant change in deviance explained by the model. This reduced identity factor was then included in all analyses of adult survival except those looking at effects of sex, where, because identity was not replicated across sex, it was impossible to investigate these effects independent of identity. There were no significant effects of maternal identity on recruitment (effect of maternal identity: $\chi^2_{123} = 138.49$) or the number of females in a litter (effect of maternal identity: $\chi^2_{73} = 48.27$), and so analyses of these variables did not control for these factors.

Because whether an individual was resighted depended on search effort, we constructed survival models by first testing for search effort effects. Five different study goals over the 20-year span (see Kelly et al., 1998) resulted in differing amounts of time spent searching for cheetahs. We endeavored to account for this by statistically testing for the effects of study period as a categorical variable and for the number of months spent in the field in each year of the study as a continuous variable. Where significant, these effects were included in all subsequent analyses. Because our recruitment measure did not depend on the resighting probability, these search effort factors were not included in analyses of recruitment.

We tested the influence of sex followed by annual rainfall and Thomson's gazelle numbers because gazelle numbers were only available for 17 years of the 20-year study. Analyses then included cheetah and lion numbers, together with rainfall and Thomson's gazelle where significant, and all first-order interactions. Age effects were similarly tested separately initially and then in combination with lion and cheetah numbers. Models were constructed by first including all the explanatory variables and then deleting each term stepwise, according to the lowest change in deviance.

RESULTS

Intersighting interval

For adults that had a sufficient number of sightings for a goodness-of-fit test, 64.9% had an intersighting interval that fitted an exponential distribution at the $p = .05$ significance level. Whether the exponential distribution fitted the intersighting interval did not depend on the number of sightings for individual cheetahs ($t_{152} = .82$, ns), and so any lack of fit of the model to the data did not merely reflect a low number of sightings and a consequent reduction of power of the goodness-of-fit test. The less than 100% fit of the exponential distribution to the data is most likely to reflect the fact that sightings were slightly more regularly spaced than expected. This is because search efforts focused on finding new individuals each month. In this situation the mean intersighting interval is likely to be slightly overestimated; however, the error in this estimate is likely to be of the order of days, rather than months and hence is unlikely to have a major effect on the time of death estimates, which are estimated to the nearest year. The gamma distribution fitted the data only marginally better, with 70.6% of individuals having an intersighting interval that fitted this distribution. The normal distribution gave a very poor fit to the data; only 16.5% of individuals had intersighting intervals which fitted this distribution.

Demographic rates

We calculated mean survival rates for males and females across both individuals and years (Table 2). Adolescent survival for both females and males from 1 to 2 years of age was lower than survival for adults. Mean recruitment to 12 months was low. Assuming a stable age structure, these parameters gave an overall annual multiplicative growth rate of 1.00, reflecting a stationary population.

The predicted variance in annual adolescent and adult survival just under demographic stochasticity can be calculated for each year from standard equations for the binomial distribution (Sokal and Rohlf, 1981). Over the course of the study, the mean variance due to demographic stochasticity for this population was 0.0052 and 0.0035 for females and 0.053 and 0.0103 for males, respectively (see Kelly and Durant, 2000). Because observed rates are higher than these values, environmental stochasticity must also be exerting an effect on the population.

Survival of males was much lower than that of females, as might be predicted by the observed unequal adult sex ratios (Caro and Collins, 1987b; Kelly et al., 1998). However, this measure may be confounded by dispersal. In the early part of the study many individuals were first seen as adults and were therefore not necessarily traceable as cubs, but after the first 10 years it was possible, in most cases, to distinguish between individuals born in the study area and immigrants. After 1984, 72% of female cheetahs seen in the study area were known from birth, indicating immigration was low, but not insignificant. However, only 54% of males were known from birth, suggesting that many of the males in the population had immigrated into the study area. This confirms obser-

Table 2

Demographic rates: means and variances for both individual and annual rates of survival and recruitment

	Individual rates			Annual rates		
	Mean	Variance	n	Mean	Variance	n (years)
Females						
Adult survival	0.8532[a]	0.1254	797[b]	0.8516[c]	0.004085	18
Adolescent survival (1−2 years)	0.6790[c]	0.2207	81	0.6503[d]	0.08439	15
Recruitment	0.5303	1.0025	437[b]	0.5419[e]	0.08993	18
Minimum age of first reproduction	2.00		88			
Mean age	7.01	12.27	88			
Maximum longevity	11.8[f] (13.6)		88			
Males						
Adult survival	0.7012[a]	0.2101	338	0.6837[c]	0.04550	18
Adolescent survival (1−2 years)	0.3857[c]	0.2404	70	0.3556[g]	0.1336	17
Mean proportion of males recruited to 12 months	0.4346	1.0025	214			
Mean age	3.60	1.83	47			
Maximum longevity	7.8		47			

[a] Omits individuals that were estimated to die in 1978 and 1979 from calculation.

[b] Samples sizes represent the number of cheetah-years (number of individual cheetahs multiplied by the number of years alive).

[c] Omits years 1978 and 1979 from calculation.

[d] Omits years 1975, 1978–1980, and 1982 from calculations because there were fewer than three female adolescents in these years.

[e] Omits years 1979 and 1980 because the recruitment rates were known for fewer than five females in these years.

[f] Although measured longevity was 13.6, the oldest female seen to produce cubs was 11.8 years.

[g] Omits years 1978–1980 from calculations because there were fewer than three male adolescents in these years.

vational data that shows that dispersal rates for this sex are high (Caro, 1994; Frame, 1984). Overall, numbers of adult cheetahs in the study area averaged 38.5 females (range 19–54 females) and 15.5 males (range 10–34 males).

Recruitment of cubs to 12 months of age was marginally biased toward females. Of the 0.530 cubs recruited per female, 43% of these were male. This sex ratio bordered on a significant difference from a 1:1 sex ratio (121 females and 93 males out of 214 cubs; goodness-of-fit test: $\chi^2_1 = 3.66$, $p = .056$). Cubs are born at equal sex ratios (Caro, 1990, 1994; Frame, 1984; Laurenson, 1992), and so any difference in the sex ratio of recruits is likely to reflect differential mortality before 1 year of age.
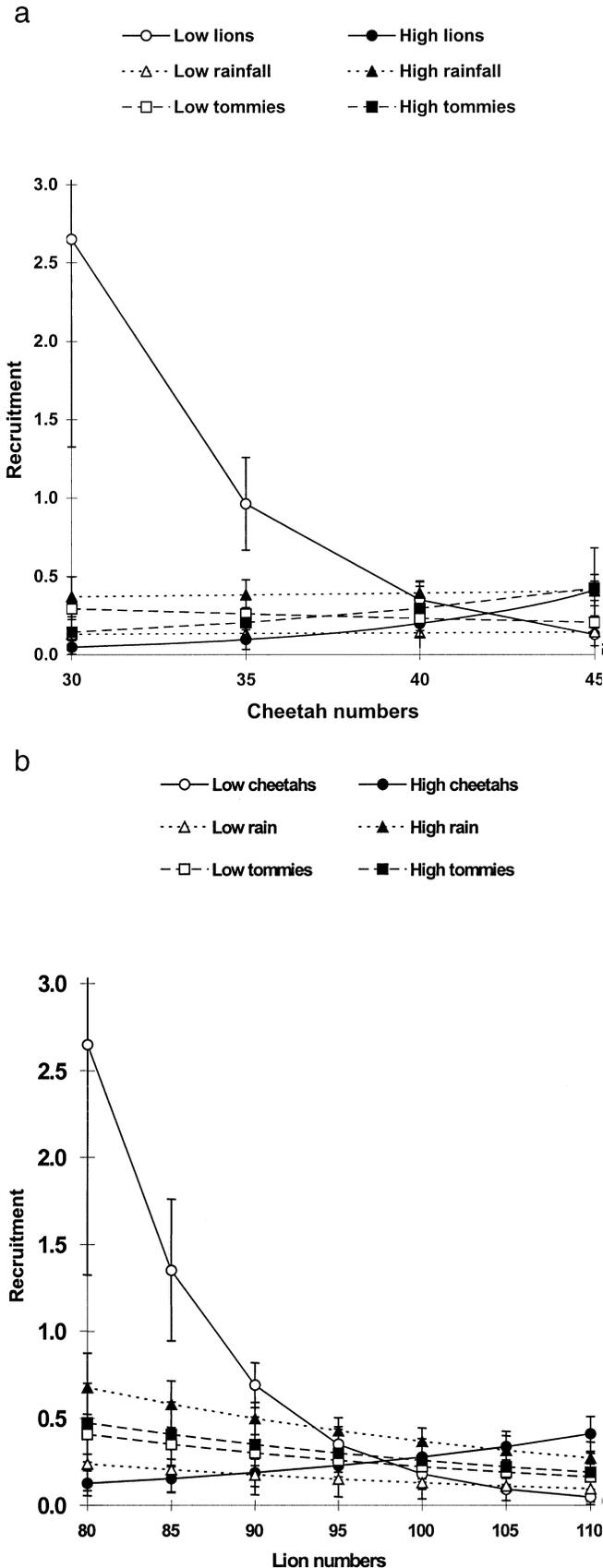
Recruitment

Recruitment of cubs to 12 months was negatively related to annual rainfall (effect of annual rainfall: coefficient = −0.0020, $\chi^2_1 = 6.29$, $n = 401$ cheetah years, $p = .012$). Recruitment also showed a strong positive relationship with numbers of Thomson's gazelle (effect of Thomson's gazelle, controlling for rainfall: coefficient = 0.24×10^{-5}, $\chi^2_1 = 8.01$, $n = 328$ cheetah years, $p = .005$).

Table 3

Effect of numbers of lions, cheetahs, Thomson's gazelles, and rainfall on recruitment

Independent variable	Coefficient	Deviance	Dispersion	χ^2	df	Significance (p)
Rainfall	−0.048	4.20	1.48	2.84	1	.092
Thomson's gazelle	−0.00011	0.39	1.47	0.27	1	ns
No. female cheetahs	−1.45	1.49	1.49	1.01	1	ns
No. lions	−0.49	0.20	1.49	0.14	1	ns
Rainfall × Thomson's gazelle	$+0.12 \times 10^{-6}$	9.65	1.47	6.56	1	.010
Rainfall × no. female cheetahs	$+0.16 \times 10^{-4}$	0.01	1.45	0.01	1	ns
Rainfall × no. lions	$+0.18 \times 10^{-3}$	1.38	1.45	0.96	1	ns
Thomson's gazelle × no. female cheetahs	$+0.65 \times 10^{-6}$	5.84	1.46	4.00	1	.046
Thomson's gazelle × no. lions	-0.81×10^{-7}	0.16	1.45	0.11	1	ns
No. female cheetahs × no. lions	+0.012	15.75	1.49	10.57	1	.001

Deviance of the full model was 502.54, $n = 328$.

a

b

Figure 3
Relationship between recruitment and cheetah and lion numbers.
Tommies indicates Thomson's gazelles. Results are predicted from the

In a full model (see Table 3), controlling for prey and rainfall effects, recruitment was significantly related to the estimated number of adult female cheetahs and lions within the population through interactions between cheetah and gazelle numbers and cheetah and lion numbers. In consequence, for average rainfall and Thomson's gazelle numbers, recruitment decreased as cheetah numbers increased when lion densities were low but increased slightly when lion densities were high (Figure 3a). Similarly, when gazelle numbers were low recruitment decreased slightly as cheetah numbers increased, whereas it increased with cheetah numbers when gazelle numbers were high. Generally, recruitment declined with increasing lion numbers, whether rainfall was high or low or whether gazelle numbers were high or low (Figure 3b). The only exception to this pattern occurred when the number of female cheetahs in the population was high, when there was an increase in numbers with lion numbers, suggesting that another factor, unmeasured in this study, could have been driving increases in numbers of both lions and cheetahs. The steepest increase in recruitment with decreasing numbers of lions occurred when numbers of cheetahs were low, implying that density dependence in recruitment may play a role. The models predicted a recruitment of 0.09 cubs per adult female cheetah at the maximum recorded number of lions during the study, but predicted 0.74 cubs per adult female at the minimum number of lions.

A large number of females in this study were of known age, and so, within this data subset, we tested for a relationship between recruitment and age. On this reduced data set some factors found to be significant in earlier analysis lost significance; however, all previously significant variables were included in this analysis. There was a significant quadratic and cubic effect of age on recruitment, but higher order effects were not significant (Table 4). Therefore, as the age of a cheetah increased, there was an initial increase in recruitment, reaching a peak at 6–7 years, and then a decline into later years (Figure 4a). There were no effects of the interaction of age with the other factors shown earlier to influence recruitment: rainfall and numbers of Thomson's gazelle, lions, and female cheetahs (Table 4).

The sex composition of litters reaching 12 months did not differ from a random binomial distribution. Of those litters with one female cub or more, 66% contained one female cub, 31% contained two, 2% contained three, and 1% four contained females, while 70% of litters contained one male, 28% contained two males, and 1% of litters contained three males. Thus, the number of females and males surviving in litters of different sizes fitted a random binomial distribution (goodness-of-fit test assuming a 1:1 sex ratio $\chi_6^2 = 5.83$, ns, and assuming sex ratio as observed $\chi_5^2 = 3.73$, ns). There was no relationship between the number of females surviving in a litter and the mother's age (effect of age: $\chi_1^2 = 0.08$; effect of age^2: $\chi_1^2 = 0.00$; effect of age^3: $\chi_1^2 = 0.09$).

←

model described in Table 3. Lines are depicted for low and high rainfall (600 mm and 850 mm, respectively), low and high numbers of gazelles (400,000 and 550,000, respectively), and, where appropriate, low and high numbers of adult female cheetahs (30 and 45, respectively) and low and high numbers of adult female lions (80 and 110, respectively). For each set of predictions, all other variables are held at their average values of 446,433 gazelles, 740 mm rainfall, 39 cheetahs, and 98 lions. Standard error bars are predicted from the model and are therefore approximate. (a) Predicted recruitment with increasing population size of adult female cheetahs. (b) Predicted recruitment with increasing population size of adult female lions.

Table 4

Effect of numbers of lions, cheetahs, Thomson's gazelles, rainfall, and age on recruitment

Independent variable	Coefficient	Deviance	Dispersion	χ^2	df	Significance (p)
Rainfall	−0.036	2.95	1.27	2.33	1	ns
Thomson's gazelle	−0.000090	3.29	1.28	2.60	1	ns
No. female cheetahs	−1.43	5.12	1.29	4.36	1	.037
No. lions	−0.46	5.71	1.29	4.51	1	.034
Rainfall × Thomson's gazelle	$+0.86 \times 10^{-7}$	2.58	1.27	2.04	1	ns
Thomson's gazelle × No. female cheetahs	$+0.75 \times 10^{-6}$	2.62	1.27	2.07	1	ns
No. female cheetahs × No. lions	+0.011	6.24	1.29	4.93	1	.026
Age	+2.83	9.46	1.31	7.48	1	.006
Age^2	−0.35	7.69	1.30	6.08	1	.014
Age^3	+0.013	6.11	1.29	4.83	1	.028
Age × rain	+0.00060	1.80	1.26	1.43	1	ns
Age × Thomson's gazelle	-0.14×10^{-7}	0.00	1.27	0.00	1	ns
Age × no. female cheetahs	−0.0041	0.43	1.27	0.34	1	ns
Age × no. lions	−0.0048	1.38	1.26	1.09	1	ns
Age × rainfall × Thomson's gazelle	$+0.32 \times 10^{-9}$	0.42	1.27	0.33	1	ns
Age × Thomson's gazelle × no. female cheetahs	-0.50×10^{-8}	0.11	1.27	0.09	1	ns
Age × no. female cheetahs × no. lions	−0.000049	1.26	1.27	0.99	1	ns

Deviance of the full model was 297.01, $n = 212$.

Adolescent survival

Survival of adolescents from 1 to 2 years was related to the study period (effect of study period $\chi^2_4 = 11.06$, $n = 150$, $p = .026$). All analyses described in this section therefore controlled for this variable.

Adolescent survival was significantly higher for females than for males (Table 2; effect of sex: coefficient = −1.22, $\chi^2_1 = 12.32$, $p < .001$). Treating males and females separately,
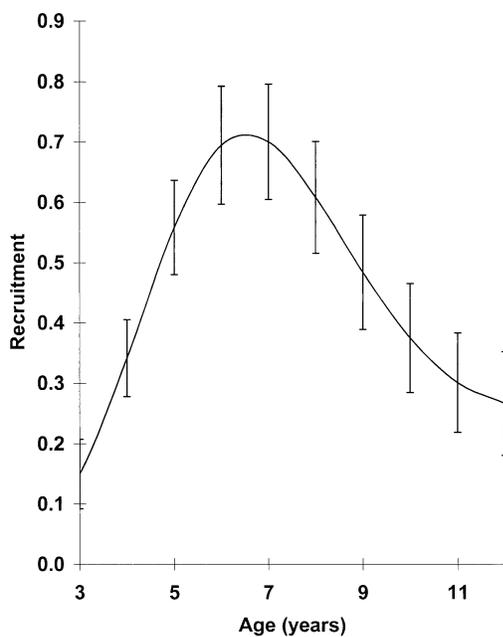
Figure 4
Relationship between recruitment of male and female cubs and the mother's age. Values are predicted from a generalized linear model with Poisson errors corrected for overdispersion. Standard error bars are as predicted from the model and are therefore approximate.

adolescent female survival was unrelated to rainfall (effect of annual rainfall: $\chi^2_1 = 0.07$, $n = 69$), but was significantly related to Thomson's gazelle numbers, although this latter relationship was in a negative direction (effect of Thomson's gazelle numbers: coefficient = -0.41×10^{-4}, $\chi^2_1 = 5.53$, $n = 60$, $p = .019$).

Because of the small number of data points for adolescents, the effects of lions and cheetahs on female survival were tested separately. There was no effect of lions on survival (effect of lion numbers; $\chi^2_1 = 0.14$; interaction of Thomson's gazelle numbers with lion numbers: $\chi^2_1 = 2.50$), but there was an effect of the number of female cheetahs in the study area through its interaction with Thomson's gazelle numbers (effect of number of cheetah females: coefficient = 0.97, $\chi^2_1 = 2.64$, ns, interaction of Thomson's gazelle numbers with female cheetah numbers: coefficient = -0.18×10^{-5}, $\chi^2_1 = 11.12$, $p < .001$). This negative interaction resulted in a decline in adolescent survival as Thomson's gazelle and cheetah numbers increased.

Male adolescent survival was unrelated to the annual rainfall (effect of annual rainfall: $n = 69$, $\chi^2_1 = 1.11$), numbers of gazelles (effect of Thomson's gazelle numbers: $n = 56$, $\chi^2_1 = 0.01$), cheetah (effect of male cheetah numbers, $\chi^2_1 = .79$), or numbers of lions (effect of lion numbers: $\chi^2_1 = 0.53$).

Adult survival

Survival of adult males was lower than that of females (Table 2; effect of sex: coefficient = −0.84, $n = 1167$, $\chi^2_1 = 28.81$, $p < .001$). The oldest female seen in the study was last seen at 13.6 years, markedly older than the oldest male seen at 7.8 years (Table 2). Survival of females was unaffected by annual rainfall ($n = 761$, $\chi^2_1 = 0.01$) or prey (effect of Thomson's gazelle numbers: $n = 629$, $\chi^2_1 = 0.25$). However, female survival was influenced by the number of lions in the study area through its interaction with numbers of female cheetahs (effect of numbers of female cheetahs: coefficient = −0.40, $\chi^2_1 = 4.31$, $p = .038$, numbers of lions: coefficient = −0.17, $\chi^2_1 = 3.76$, $p = .053$, interaction of lion numbers and female cheetah numbers: coefficient = 0.0043, $\chi^2_1 = 4.19$, $p = .041$).

a

b
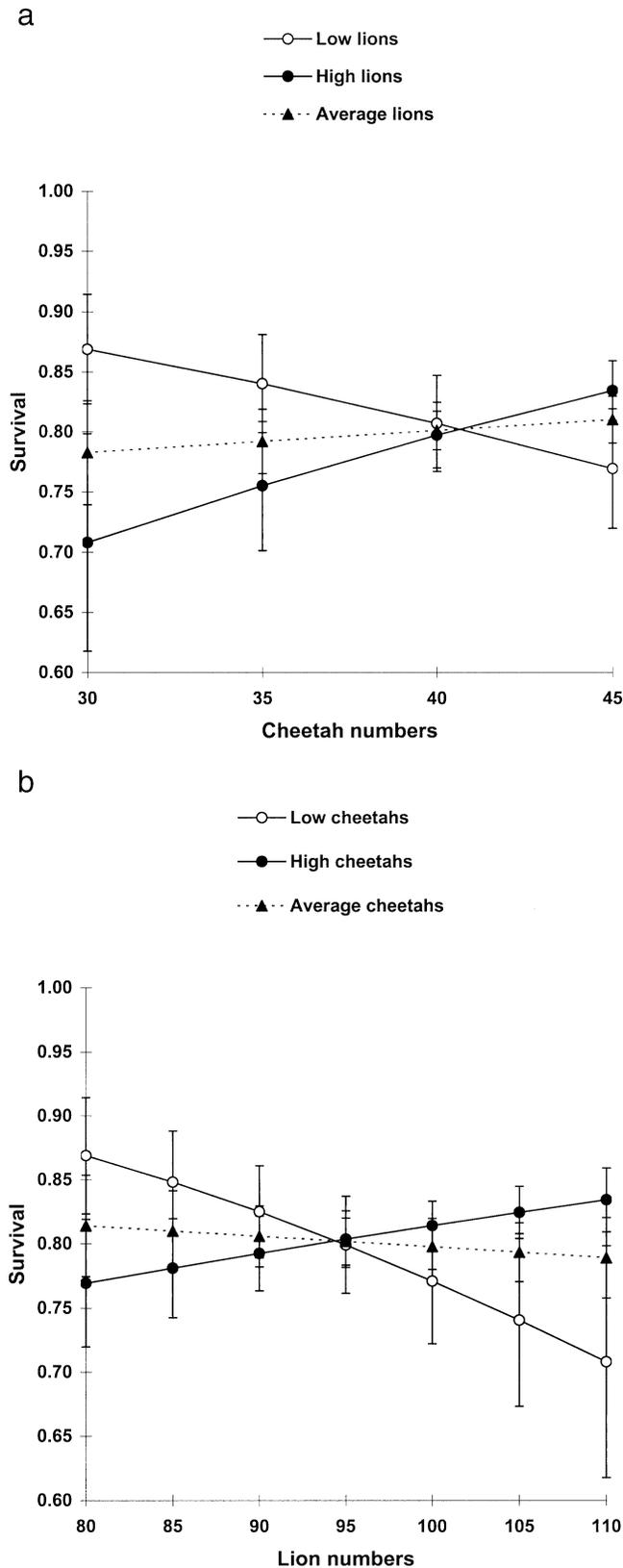
Figure 5
Relationship between adult female survival and cheetah and lion numbers. Results are predicted from a logistic regression model with survival as the dependent variate. Low and high values are as reported in Figure 3. Standard error bars are as predicted from the model, and are therefore approximate. (a) Predicted survival with increasing

Thus, adult female cheetah survival declined with cheetah numbers when lion numbers were low and declined with lion numbers when cheetah numbers were low (Figure 5). However, when lion numbers and cheetah numbers were high, survival increased with cheetah and lion numbers, respectively.

Survival of those females whose age was known changed in relation to a polynomial expression of age, where the cubic of age was the highest power showing significance (Table 5). As females grew older their survival dropped nonlinearly with their age, showing an initial decline in their early years, a leveling off at around 8–10 years, and then a steep drop beyond this age (Figure 6a). This has the effect of causing the cumulative survival curve to level out slightly at 8–10 years. There were no significant interactions between age and the number of female cheetahs or lions in the study area (Table 5). Interestingly, in this reduced data set, the effect of the interaction between numbers of adult female cheetahs in the study area and adult lions disappeared completely, suggesting this effect may have been related specifically to females in the study area of unknown age that were not included in this analysis. These females were immigrants to the study area.

Survival of adult males was unaffected by measures of rainfall (effect of annual rainfall: $n = 337$, $\chi_1^2 = 0.95$) or prey numbers (effect of Thomson's gazelle numbers: $n = 274$, $\chi_1^2 = 0.06$). Neither was it affected by numbers of male cheetahs or lions in the study area, although the effect of male cheetahs bordered on significance (effect of male cheetah numbers: coefficient $= +0.10$, $\chi_1^2 = 3.05$, $p = .081$, effect of lion numbers: $\chi_1^2 = 1.03$, interaction of lion numbers with cheetah numbers: coefficient $= +0.00076$, $\chi_1^2 = 2.52$).

As with female survival, male survival showed a relationship with age (effect of age: coefficient $= -8.91$, $\chi_1^2 = 33.69$, $p < .001$, effect of age^2: coefficient $= +0.69$, $\chi_1^2 = 21.68$, ns; insufficient data to test for higher order effects, $n = 78$). Male survival declined dramatically until 5 years, then it leveled off (Figure 6). Predictions were not possible beyond 7 years because no male lived to 8 years in this study. There were no significant interactions among age and rainfall and numbers of Thomson's gazelles, lions, and male cheetahs.

Living in groups

Males who started adulthood as singletons did not suffer lower survival than those who lived in groups (effect of group size: coefficient $= -0.15$, $\chi_1^2 = 0.62$, ns). If the apparent lower survival rates of adult males compared with females reflect intramale aggression (Caro, 1994), then survival of males within coalitions should be related to the number of coalitions in the population. That is, the advantages of living in groups should increase when more males in the population live in groups. In agreement with this prediction, male survival was marginally related to both the number of coalitions and coalition size through the interaction between these two variables (effect of coalition size: coefficient $= -0.41$, $\chi_1^2 = 3.42, p = .064$, number of coalitions: coefficient $= -0.89$, $\chi_1^2 = 1.51$, ns, interaction: coefficient $= 0.28$, $\chi_1^2 = 2.78$, $p = .095$). This relationship had the effect that, when there were a large number of coalitions resident in the population, males in coalitions had higher survival than singletons,

←

population size of adult female cheetahs. (b) Predicted survival with increasing population size of adult female lions.

Table 5

Effect of numbers of lions, cheetahs, and age on adult female survival

| Independent variable	Coefficient	χ^2	df	Significance
Individual identity	—	175.94	4	<.001
Observer	—	11.28	4	.024
Age	−6.99	14.55	1	<.001
Age^2	+0.78	10.11	1	.001
Age^3	−0.029	9.25	1	.002
No. lions	+0.010	0.00	1	ns
No. female cheetahs	−0.087	0.06	1	ns
No. female cheetahs × no. lions	+0.00069	0.04	1	ns
Age × no. lions	−0.0091	1.80	1	ns
Age × no. female cheetahs	−0.0025	0.07	1	ns
Age × no. lions × no. female cheetahs	$−0.64 \times 10^{-4}$	0.64	1	ns

All significant environmental terms were included in this analysis; however, there were insufficient data to test for any interactions with higher orders of age. Deviance of the full model was 356.52, $n = 447$.

whereas when there were only a few coalitions, singletons had higher survival than males in coalitions (Figure 7).

Adolescents showed only marginally higher survival as adolescent group size increased (effect of litter size, controlling for sex: coefficient = 0.31, $\chi^2_1 = 2.79$, $p = .099$). However, survival was more strongly related to the presence of a sibling than overall group size (effect of sibling presence, controlling for sex: coefficient = 1.09, $\chi^2_1 = 4.82$, $p = .028$). The sex of an accompanying sibling was important. Adolescent female survival was marginally related to the presence of a brother within a litter (effect of brother presence: coefficient = 0.96, $\chi^2_1 = 3.00$, $p = .083$) but was unrelated to the presence of a sister (effect of sister presence: $\chi^2_1 = 0.38$). Adolescent male survival was strongly related to the presence of a sister within a litter (effect of sister presence: coefficient = 2.09, $\chi^2_1 = 9.95$, $p = .002$) but was unrelated to the presence of a brother (effect of brother presence: $\chi^2_1 = 0.38$).

DISCUSSION

This study demonstrates that recruitment in cheetahs is influenced by a wider range of environmental factors than are adolescent or adult survival. In addition, both recruitment and female survival vary greatly with age. Recruitment was highest for females of 6–7 years, whereas adult female survival was highest for young cheetahs of 2–3 years and declined as cheetahs aged. Adult male survival was substantially lower than that of females and also showed a decline with age, dropping off sharply through the first 5 years, and then leveling off to a very low level from 6–7 years. Finally, the semi-sociality observed in cheetahs had marked effects on survival. Adolescents had a much higher survival rate when they were in litter sizes larger than one. Adult male survival was related
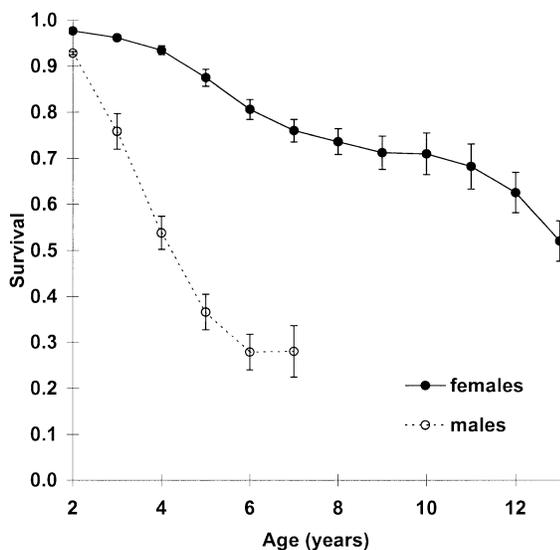
Figure 6
Relationship between annual survival and age for adult female and male cheetahs. Values are predicted from a logistic regression model with survival as the response variate on a polynomial expression of age, where a cube term was the highest significant power for female survival and a square term for male survival. Standard error bars are as predicted from the model and are therefore approximate.
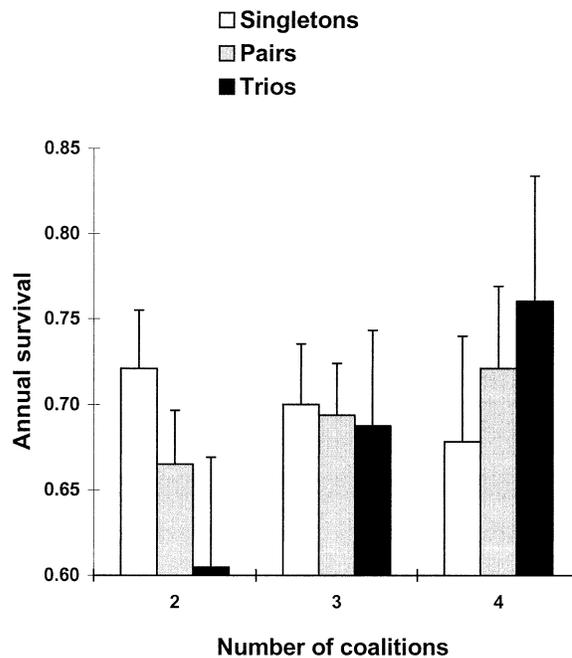
Figure 7
Relationship between adult male survival and coalition size and the total number of coalitions consisting of two or three males within the study area. Values are predicted from a logistic regression model with survival as the response variate. Standard error bars are as predicted from the model and are therefore approximate.

to the size of a male's coalition, together with the number of male coalitions in the study area.

Unfortunately, the measures of survival used here cannot completely distinguish between death and dispersal. In previous studies of radio-collared male and female cheetahs, it has been found that permanent dispersal of adult cheetahs out of the study area is unusual (Caro, 1994; Laurenson, 1992). Nonetheless, there was immigration of new adults into the study area, particularly males; therefore it is probable that dispersal does form a component of measured disappearances of adult cheetahs. Adult dispersal is likely to happen for similar reasons as adult mortality, since cheetahs are more likely to both move out of and die in poor areas. Therefore, although our measure of survival may include a dispersal component, an increase in survival is still likely to reflect an improvement in ecological conditions for cheetahs. Adolescent dispersal is likely to be more common than adult dispersal, as adolescents move out of their natal home range in many species (e.g., gorillas: Harcourt et al., 1976, vervet monkeys: Cheney and Seyfarth, 1983). However, unlike adult dispersal, adolescent dispersal may happen for reasons that do not necessarily indicate inferior conditions in the natal range (e.g., avoidance of inbreeding or competition with relatives; Greenwood, 1980), and so the results here should be interpreted with caution.

Environmental factors

Generally, recruitment and adolescent survival are expected to be more sensitive to environmental perturbations than adult survival (Eberhardt, 1977), and this was the pattern we observed in cheetahs. In this study recruitment in cheetahs was influenced by a wider range of environmental factors than was adolescent or adult survival. Recruitment was the only demographic parameter influenced by rainfall, but this relationship was in a negative direction. It is possible that low rainfall may benefit cheetahs indirectly because it forces lions, which are water dependent, to remain near water sources, thus restricting their range. Cheetah mothers may therefore be able to avoid lions more easily in years of low rainfall (see Durant, 2000b). Additionally, exposure to rain has been shown to account for a proportion of cheetah cub mortality in the lair (Laurenson, 1994).

Recruitment was generally positively related to numbers of Thomson's gazelles. Increased prey availability is likely to affect the amount of food provided to cubs. For example, cheetah cubs may be abandoned by their mothers when gazelles move far from their lairs (Laurenson, 1994). Surprisingly, adolescent female survival was negatively related to gazelle numbers. Adolescent females have low hunting success because prey often see them approaching (Caro, 1994), and we might therefore expect that their hunting success to be especially poor against large groups of gazelle, which show more vigilance than small groups. Large groups may be more common when the size of the gazelle population is high.

The relationship between cheetahs and gazelles is likely to be complex because within an area cheetahs appear to prefer areas with low densities of gazelle (Durant, 1998a), and females most often found near low densities of gazelle have higher lifetime reproductive success (Kelly et al., 1998). High densities of gazelles attract other predators, which can directly threaten cheetahs and usurp their kills (Durant, 1998a). Therefore, cheetah recruitment and survival may also depend on the distribution of gazelles within their environment in addition to overall numbers. Furthermore, we are cautious of our gazelle estimates for several reasons (see Scheel and Packer, 1995): estimates were calculated across the whole

ecosystem, rather than within the study area; one of these estimates was an average between two different methods of estimating population size (Borner et al., 1987; Dublin et al., 1990); and linear interpolation was used between estimates.

The complexity of the relationship between cheetahs and their environment became apparent when more ecological variables are included in the analysis. Cheetah recruitment showed a strong negative association with numbers of female cheetahs when numbers of lions were low. This result contrasts with our earlier simpler analysis that did not take other factors into account (Kelly et al., 1998). Although previous calculations show that cheetahs live at densities far lower than would be expected to cause competition over prey (Caro, 1994; Laurenson, 1995), this result may be misleading. Cheetahs are known to avoid other large carnivores in the ecosystem (Durant, 2000a) and to concentrate their hunting in areas where carnivore densities are low (Durant, 1998b). Therefore, although overall cheetah density may be low, local densities within carnivore-free areas depend on the distribution of prey and other carnivores and hence may be high, leading to high levels of competition within these areas. This is supported by our results: recruitment and survival were affected by the interaction between lion and cheetah numbers rather than by these variables independently.

Overall, there was a negative association between cheetah recruitment and numbers of lions that confirms both observational (Laurenson, 1994) and demographic data (Kelly et al., 1998) showing that lions are an important source of mortality for cheetah cubs in Serengeti (see Caro, 2000). Adult female survival appeared to be related to numbers of lions and cheetahs such that survival increased with numbers of cheetahs when numbers of lions were high. However, this relationship disappeared completely in later analyses of females of known age, suggesting that it was driven by immigrant females that were always of unknown age. Such a result could be obtained if adult females were more likely to move into the study area when lion densities were high in the woodlands. Because the plains habitat in our study area is not the preferred habitat of lions (Hanby et al., 1995), we might expect emigration of cheetahs from the surrounding woodlands onto the plains and into the study area when numbers of lions increase.

Age

The relationship between recruitment and age followed a similar pattern to that for many long-lived vertebrates (Clutton-Brock, 1984; Packer et al., 1988; Pianka and Parker, 1975). Recruitment followed a cubic relationship with age, peaking when females reached 6–7 years (a similar peak to that found by Kelly et al., 1998). Survival declined with age, more dramatically through the early years for males than for females, but leveled out briefly in later life, at between 8 and 10 years for females and between 6 and 7 years for males. The sharp drop after 10 years for females may be indicative of physiological deterioration through senescence (Packer et al., 1988), although we have no data to support this. There was no comparable decline for males. Instead, the decline in survival for males may be indicative either of increasing male-male competition or dispersal (see above) or a combination of these factors.

In this study there was no evidence that females of peak reproductive age differentially recruited sons (Trivers and Willard, 1973); neither did mothers differentially recruit litters containing more brothers, as might be expected in species where brothers cooperate (Clutton-Brock and Iason, 1986). An earlier study of cheetahs found that mothers disproportionately provisioned litters containing two or more

sons compared to those containing one during the period that cubs were dependent on their mother for solid food, whereas there was no such effect for daughters (Caro, 1990). Both that study and the one here similarly found that sex ratios were not skewed toward males in large litters, in contrast to lions living in the same area, where brothers also cooperate (Packer and Pusey, 1987). The reasons for these species differences are unknown.

Sociality

We found that both the transient sociality observed in adolescent cheetahs and the permanent coalitions formed by adult males affected survival. Adolescents had higher survival if they were in litters with at least one sibling. Caro (1994) has shown that spotted hyenas (*Crocuta crocuta*) and male cheetahs were less likely to approach groups of cheetahs than singletons, and hence may have been less likely to attack groups of adolescents than solitary adolescents. In addition, adolescents did not pay foraging costs by being in groups because they caught larger prey than singletons. Higher survival of adolescent groups was mainly driven by an increase in survival of adolescent males when they had a sister. Observational data showed that adolescent males rely strongly on their sisters to catch prey for the group (Caro, 1994).

Once reaching adulthood, cheetah brothers remain in coalitions for life, where they are likely to reap reproductive benefits (Caro, 1994). This study did not find that adult males in larger coalitions had a higher overall survival than singletons, replicating results reported by Caro (1994). However, we found that males in coalitions had higher survival than singletons when more coalitions were in the study area. This may be explained by territoriality: if territorial males live longer than nonterritorial males, and coalitions are more likely to obtain and retain territories (Caro, 1994), then, in years of low numbers of coalitions, singletons may be able to hold territories and hence boost their survival. Increased competition when the number of coalitions is high probably prevents singletons from taking up territories and similarly reduces their survival chances, as found in this study.

All-male groups are uncommon in mammals, probably because male reproductive success is related to intrasexual competition (Trivers, 1972). Such groups are particularly unusual when they are permanent and long-lasting as in cheetahs. The results in this study demonstrate that cheetah males reap survival benefits from living in groups when coalitions are common and hence when competition for territories is likely to be intense. Males will therefore benefit most from remaining in coalitions when more coalitions are present. However, such a system is unstable if it depends entirely on survival benefits because when there were few coalitions, this study showed that a male would benefit most as a singleton. Instead, males are likely to reap additional reproductive benefits from living in coalitions because they are able to more easily takeover and retain territories than singletons, and territory tenure is almost certainly related to male reproductive success (Caro and Kelly, 2001).

Conclusions

Findings presented in this paper draw attention to two general issues in studies of correlates of reproductive success. First, there are relatively few studies that have examined the effects of environmental factors on recruitment or survival (but see Packer et al., 1988). We found that rainfall, prey numbers, and cheetah and lion numbers all affected recruitment in cheetahs; moreover, cub survival, which is a component of recruitment, has an important impact on

the viability of populations of this species (Kelly and Durant, 2000). Second, we uncovered a number of interactions between factors affecting reproductive success. For example, recruitment was related to an interaction between lion and cheetah numbers, while male survival was influenced by coalition size only in situations where coalitions were numerous. These interactions indicate that certain factors become influential only under particular environmental or social circumstances. Such interactions are fundamental to our understanding of selection and long-term dynamics of ecological systems and are only likely to be uncovered in long-term field studies where data are simultaneously collected on many candidate variables.

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