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ECOLOGICAL DETERMINANTS OF SURVIVAL AND REPRODUCTION IN THE SPOTTED HYENA

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Large carnivores play a key role in the structuring and dynamics of many ecosystems, yet the factors influencing dynamics of carnivore populations themselves are often poorly understood. Spotted hyenas (*Crocuta crocuta*) are the most abundant large carnivores in many African ecosystems. We describe demographic patterns in a population of spotted hyenas observed continuously for 15.5 years, and assess the effects of per capita prey availability, interspecific competition, rainfall, anthropogenic disturbance, and disease on 2 key determinants of population dynamics: reproduction and survival. Annual reproduction, survival of juveniles (i.e., recruitment to adulthood), and mortality of adults varied among years of the study. Per capita prey availability and group size both had positive effects on reproduction, whereas interspecific competition with lions had a negative effect. Competition with lions and rainfall both had negative effects on survival of juveniles. We suggest that the negative effect of rainfall on survival may be mediated by increased rates of human–carnivore conflict during periods of heavy rain, although human population size did not influence survival or reproduction directly. Disease had no substantial effect on this hyena population, despite occurrence of at least 2 disease outbreaks among sympatric carnivores during the study. By focusing on demographic processes that determine population growth (i.e., survival and reproduction), this study highlights the importance of both top-down and bottom-up forces acting on populations of large carnivores. These findings also add to a growing literature suggesting that interspecific competition may be more important than previously recognized in the dynamics of populations of large carnivores.

Key words: anthropogenic disturbance, carnivore, *Crocuta crocuta*, demography, disease, interspecific competition, mortality, sociality

Mammalian carnivores play a key role in the structuring and dynamics of many terrestrial and aquatic ecosystems, and changes in carnivore populations can have strong effects on species at lower trophic levels. When large carnivores are lost from ecosystems, predator-mediated trophic cascades can lead to increases in herbivore populations, which in turn can cause habitat loss or modification (Beschta 2003; Estes et al. 1998; Hebblewhite et al. 2005). Alternatively, the loss of larger carnivores can result in increases in the populations of smaller carnivores, termed mesopredator release. Mesopredator release can cause declines in prey species such as birds, reptiles, rodents, and ungulates (Berger et al. 2008; Crooks and Soulé 1999; Henke and Bryant 1999). Wilmers and Getz (2005) have even suggested that the presence of populations of large carnivores might buffer ecosystems from effects of climate change.

Despite the importance of mammalian carnivores in many ecosystems, the factors influencing the dynamics of carnivore populations themselves are often poorly understood. In general, populations may be influenced by bottom-up forces (resources—White 1978), top-down forces (natural enemies—Hairston et al. 1960), or both. Bottom-up population control via prey availability has been suggested for a variety of carnivores (reviewed in Fuller and Sievert 2001). Reduced prey availability can cause carnivore populations to decline through starvation, increased susceptibility to disease, or increased risk of intra- and interspecific killing (Funk et al. 2001; Mech 1977; Schaller 1972). Reduced prey availability also can affect populations by reducing energy available for reproduction (Boertje and Stephenson 1992; Creel and Creel 2002).

Top-down forces, including disease and anthropogenic disturbance, also have been implicated in the dynamics of carnivore populations. Disease outbreaks can dramatically increase mortality rates among carnivores, leading to population declines (Roelke-Parker et al. 1996; Young 1994). Increased anthropogenic disturbance can reduce carnivore abundance as a result of direct killing of carnivores by humans (Woodroffe and Ginsberg 1998) as well as through indirect

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effects such as disruption of behavior leading to reduced foraging efficiency (Boydston et al. 2003b; Kerley et al. 2002; Wielgus and Bunnell 1994). Interspecific competition among carnivores, including intraguild predation (Holt and Polis 1997), also has been suggested to influence predator populations (Laurenson 1995). The effects of such competition may be complex. Interspecific competition can reduce access to food via exploitation or interference competition (bottom-up—Creel and Creel 2002), but it also can include interspecific killing (top-down—Palomares and Caro 1999). Furthermore, there is also potential for nonlethal “risk effects” (Creel and Christianson 2008) if the risk of intraguild predation induces costly behavioral changes in a subordinate predator.

Very few studies have examined the influence on carnivore populations of all of these factors simultaneously. One exception is the work of Kissui and Packer (2004), who found that disease, rather than prey availability or interspecific competition, has been the primary determinant of the dynamics of a lion population. However, the generality of their findings for other carnivores remains unknown. Here we describe long-term demographic patterns in a population of free-living spotted hyenas (*Crocuta crocuta*) under continuous observation since 1988. Spotted hyenas are the most abundant large carnivore in sub-Saharan Africa (Cardillo et al. 2004) and occupy a wide diversity of habitats including deserts, montane forests, woodlands, and savannas (Mills and Hofer 1998). Given the potential importance of spotted hyenas to a large number of ecosystems, enhanced understanding of their demographic responses to particular ecological variables should prove useful to those concerned with conservation and management of African wildlife. Therefore, in this study we assess effects of per capita prey availability, interspecific competition, anthropogenic disturbance, and disease on 2 key determinants of population dynamics: reproduction and survival.

MATERIALS AND METHODS

The study was conducted in the Talek area of the Masai Mara National Reserve (hereafter, Mara), Kenya. Spotted hyenas are gregarious carnivores that live in social groups called clans. Here, 1 large clan was observed between 1 July 1988 and 31 December 2003. All individual hyenas were identified by unique spot patterns, and sex was determined based on penile morphology (Frank et al. 1990). Observations were made during 2 daily data-collection periods, between 0530 and 0900 h and between 1700 and 2000 h. During each data-collection period, the Talek area was searched by vehicle, and an observation session was initiated each time 1 or more hyenas was located. Observation sessions lasted from 5 min to several hours and ended when observers left that individual or group.

Spotted hyena clans are composed of multiple adult females, their immature offspring, and immigrant males. To assess clan composition, we considered females > 3 years old to be adults, as well as any younger female that had already conceived her 1st litter. Males were considered adults at 2 years of age. Resident natal males were adults born in the study clan that had not yet dispersed. Resident immigrant males had emigrated

from other clans and were present in the study clan for at least 6 months. Juveniles were all hyenas other than adults. Mean monthly clan size (i.e., the total number of juveniles, adult females, and both natal and immigrant adult males present) was calculated for each year of the study.

Determination of births, deaths, and other life-history events.—Spotted hyenas breed year-round (Holekamp et al. 1999; Lindeque and Skinner 1982), with females giving birth to cubs in protective dens. Cubs reside at dens until they are at least 8–9 months of age (Boydston et al. 2005). Here, den sites were visited daily throughout the study to monitor births and development of cubs. Ages of cubs were estimated to within ± 7 days when they were initially observed above ground (as in Holekamp et al. 1996). A cub was considered to be independent of the den when it was found more than 200 m from the den on at least 4 consecutive occasions (Boydston et al. 2005).

Most male spotted hyenas disperse from their natal clan after 2 years of age, but dispersal by females is very rare (Boydston et al. 2005; East et al. 2003; Frank et al. 1995; Höner et al. 2007). Occasionally clan fissions occur, in which several females emigrate together from their natal clan to form a new clan in a nearby territory (Holekamp et al. 1993; Mills 1990). Approximately one-half the adults of both sexes present in the study clan wore radiocollars at any given time during the study, and were tracked daily (details in Boydston et al. 2003a). Capture and handling procedures were approved by the All University Committee on Animal Use and Care at Michigan State University and followed the guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). Observations of radiocollared females indicate that disappearances by females from our study area are due to death rather than dispersal (Boydston et al. 2005). Therefore, we attributed the disappearances of all females, and males < 2 years old, to death in the current study, except in cases of clan fission (following Frank et al. 1995; Hofer and East 2003). Although radiotracking allowed us to determine the ages at which males dispersed from the study area, it was subsequently often difficult to track them regularly in their new home ranges. Therefore, only females were used in analyses of adult mortality.

Ecological variables.—Spotted hyenas prey primarily on ungulates they kill themselves, although they frequently compete with lions for food at kills (Kruuk 1972). The Talek area is composed of rolling grassland grazed year-round by resident ungulates; these are joined for 3–4 months each year by large migratory herds. To monitor prey availability in Talek, biweekly counts were conducted between 0800 and 1000 h of all ungulates within 100 m of two 4-km transect lines in different areas of the Talek home range; an additional 4-km transect was added in 2001. Transect counts were used to generate monthly estimates of prey density, which ranged from 21.3 to 1,917.5 animals/km², with a mean of 277.3 animals/km² \pm 21.0 SE ($n = 363$ counts). Per capita prey density, estimated by dividing prey density by the number of adult females present in the clan, was used as our measure of prey availability (Fig. 1a). Gregarious large carnivores, such as spotted hyenas, compete not only for live prey, but also for

carcasses, which are even more valuable to large carnivores than live prey (Creel 2001). Therefore, the use of a composite per capita measure was more appropriate than raw counts of prey animals, because it accounted for both the quantity of live prey available for hunting and the intensity of competition for carcass access once prey animals have been killed.

Although increasing group size may lead to increasing feeding competition, group size also might affect reproduction and survival independently of intraspecific feeding competition. Increasing group size might confer benefits such as reduced risk of predation or improved defense of resources, but it also might increase rates of disease transmission within groups. Therefore, clan size was included in our analyses in order to examine effects of intraspecific interactions on survival and reproduction, in addition to effects on feeding competition. To analyze the effect of clan size on reproduction, juveniles were excluded from calculations of clan size to avoid non-independence. Rate of reproduction and clan size were not correlated across years ($P = 0.27$).

The Talek study area is located on the reserve edge, adjacent to a growing human population (Boydston et al. 2003b). Human census data for the area, based on counts of huts, were available from periodic surveys conducted between 1950 and 2002 (Lamprey and Reid 2004). To obtain estimates of population size for the current study period, these census data were used to fit a polynomial equation describing population growth. This equation was then used to interpolate and extrapolate population estimates for each year of our study (1988–2003; Fig. 1b). Based on these estimates, the population grew from 1,225 huts in 1988 to 2,245 huts in 2003. We assumed that this measure of human population size would reflect overall levels of anthropogenic disturbance in the study area.

Rainfall was recorded daily within the Talek home range; monthly rainfall varied from 0 to 336 mm, with a mean of $89.5 \text{ mm} \pm 5.1 \text{ SE}$. Mean monthly rainfall was calculated for each year of the study (Fig. 1a). Rainfall might influence survival and reproduction through effects on disease dynamics (Altizer et al. 2006), flooding of hyena dens (Frank et al. 1995), effects on the behavior of other carnivores (Durant et al. 2004), effects on prey animals, or effects on rates of human–carnivore conflict. In our study area, rainfall is strongly and positively correlated with rates of livestock depredation (Kolowski and Holekamp 2006), a pattern that also has been found in other areas of Kenya (Patterson et al. 2004; Woodroffe and Frank 2005). Because local pastoralists will kill hyenas in response to livestock depredation (Kolowski and Holekamp 2006), rainfall may be an important predictor of hyena mortality rates. Rainfall also might influence prey abundance, but this variation should be reflected in our measure of prey availability. In order to test whether a negative relationship between rainfall and juvenile survival might be due to den flooding, the relationship between the ecological predictors and juvenile survival (i.e., recruitment to 2 years of age) also was analyzed separately for the period after den independence, when den flooding no longer poses a risk to youngsters.

Lions are the primary competitors of spotted hyenas. The 2 species have a high degree of dietary overlap (Hayward 2006;

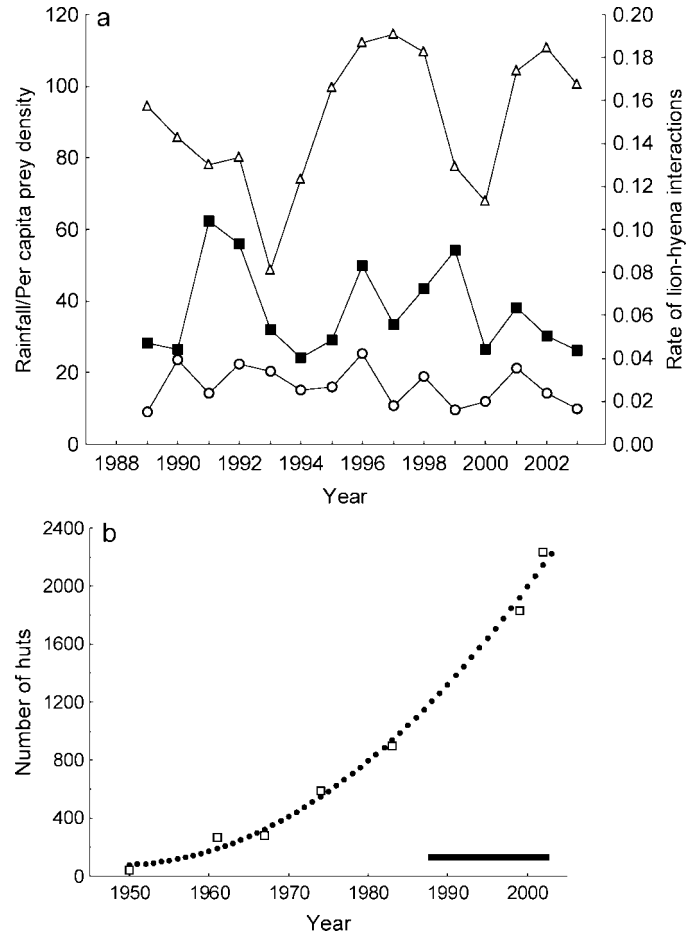


FIG. 1.—a) Mean monthly rainfall (mm; Δ), lion–hyena interaction rate (\blacksquare), and per capita prey availability (\circ) for each year of the study. Means for 1988 are not included because the study did not begin until July of that year. Rate of lion–hyena interactions is a measure of competition between the species. Per capita prey availability is prey density (prey animals/ km^2) per adult female in the clan. b) Estimated human population adjacent to the study area, based on the number of huts. A polynomial equation was fitted to census data (\square) from Lamprey and Reid (2004) to generate estimates (\bullet) for all years. Horizontal bar indicates the period of the current study.

Kruuk 1972); lions often steal food from hyenas, and they also represent a major source of hyena mortality (Frank et al. 1995; Kruuk 1972; Mills 1990). Therefore, the presence or absence of lions with hyenas was recorded in each observation session. The degree of competition between Talek hyenas and sympatric lions was estimated annually using the mean monthly rate of lion–hyena interactions, calculated as the number of observation sessions at which lions were present with hyenas during each month, divided by the number of twice-daily data-collection periods during that month (Fig. 1a). This measure controls for variation in intensity of observation effort.

Data analysis.—STATISTICA 6.1 (StatSoft 2002) and R (R Development Core Team 2007) were used for statistical analyses. The Kaplan–Meier method was used to estimate age-specific survivorship for all individuals born during the study. Individuals still alive at the end of the study were included as right-censored data. Life-table data are only available until 12 years of age,

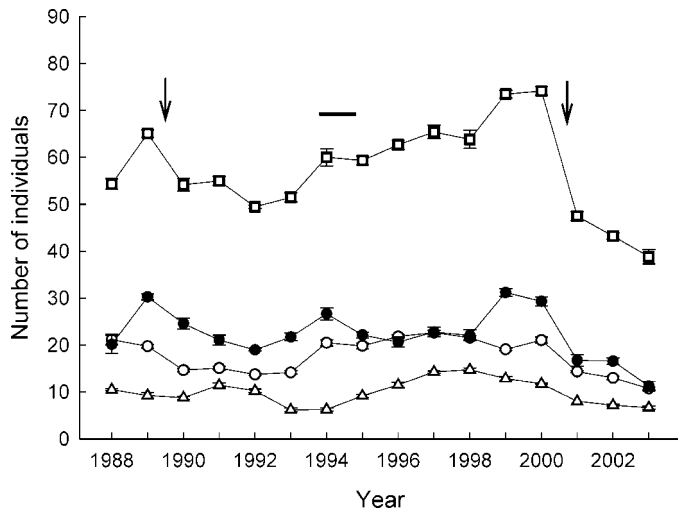


FIG. 2.—Mean clan size (□), number of adult females (○), number of resident immigrant males (△), and number of juveniles present (●) in the spotted hyena (*Crocuta crocuta*) study clan (\pm SE) for each year between 1988 and 2003. Arrows indicate 2 clan fission events. Horizontal line indicates canine distemper virus epizootic.

because few females born in our study had yet reached older ages. To determine whether survivorship varied with age in adulthood, a generalized linear mixed model (lmer function in R) was used with a binomial response variable indicating survival of an individual to the end of a given age class. Age was a fixed effect in the model, whereas individual identity was included as a random effect. Mean values are presented \pm 1 SE.

General linear models (lm function in R) were used to examine variation in annual rates of reproduction, with the ecological variables as predictors. The rate of reproduction was calculated as the total number of hyena cubs born during the year of interest, divided by the mean number of adult females in the clan during that year. To examine effects of ecological variables on annual recruitment and adult mortality, we used generalized linear models (glm function in R) with binomial errors and a logit link function (Crawley 1993). Recruitment was quantified as the number of juvenile hyenas that survived to reach 2 years of age from the total number of individuals in the cohort born in a given year. This measure of recruitment reflects variation in juvenile survival, and does not reflect variation in birthrates. Adult mortality was quantified as the total number of deaths of adult females during a given year relative to the total number of adult female hyenas present at the beginning of that year. To check for overdispersion in generalized linear models, the ratio of residual deviance to residual degrees of freedom was examined. The amount of variation explained by these models was estimated using Nagelkerke's (1991) calculation for R^2 . For general and generalized linear models, residuals were inspected, and Cook's distance was used to identify influential data points (either extreme values or values close to 1) for further examination (Cook and Weisberg 1982). We used Akaike information criterion adjusted for small sample size (AIC_c) for model selection (Burnham and Anderson 2002). For each dependent variable we 1st fit a model that included all 5 ecological

predictors (i.e., global model), and subsequently removed parameters whose removal minimized AIC_c . The model with the lowest AIC_c value was considered the best model, and models that differed in AIC_c value from the best model (ΔAIC_c) by <2 were considered equally parsimonious (Burnham and Anderson 2002). Statistical hypothesis testing was then carried out on selected models. For generalized linear models, we report both the z statistic for parameter estimates and the chi-square statistic for deletion tests (Crawley 1993). In making inferences about the influence of the ecological variables on our dependent variables, we consider results both from model selection and statistical hypothesis testing.

RESULTS

Demographic patterns.—Clan size during the study ranged from 27 to 79 hyenas with a mean of 57.5 ± 0.8 (Fig. 2). The clan underwent 2 fission events. The 1st occurred during a 7-month period between late 1989 and early 1990 (Holekamp et al. 1993). The 2nd occurred gradually over a period of years, and was complete by late 2001 (J. Smith and K. Holekamp, pers. obs.). All animals leaving the clan during both fissions were subsequently observed elsewhere. Onset of both fission events coincided with peaks in numbers of juveniles and overall clan size (Fig. 2).

Reproductive output did not vary significantly with maternal age once females reached reproductive maturity ($n = 34$ females, Kruskal–Wallis $T = 8.60$, $d.f. = 7$, $P = 0.28$; Table 1). Therefore, data for all mature females were pooled for subsequent analysis of annual reproduction. Mortality in the first 2 years of life was 63% and declined thereafter (Table 1; Fig. 3). This drop in mortality at 2 years coincides with the age at which spotted hyenas begin to reach reproductive maturity. After 2 years of age, survivorship did not vary with age ($n = 241$ from 55 females, $\chi^2 = 6.07$, $d.f. = 9$, $P = 0.73$). Therefore, mortality was subsequently examined separately for hyenas < 2 years old (juveniles) and those older than 2 years (adults). Survivorship did not vary with sex in the first 2 years of life ($n = 329$; Gehan's Wilcoxon test = -0.183 , $P = 0.86$; Fig. 3).

It was possible to determine the cause of 73 deaths (Fig. 4). The greatest source of mortality was lions, accounting for 27% of deaths with known causes. Humans and starvation of cubs after death of the mother were each responsible for 18% of deaths. Other important sources of mortality were illness (11%), infanticide (8%), siblicide (5%), and den flooding (4%). Because most deaths were attributed to sources of mortality that are likely to be independent of sex, males and females were grouped together to examine mortality of juveniles. Mortalities of juveniles ($n = 49$) were well represented in all source categories, whereas mortalities of adults ($n = 24$) were caused almost exclusively by lions and humans, with less than 2% in each other category (Fig. 4).

Ecological influences.—The best model for annual reproduction ($n = 15$ years; Fig. 5a) included clan size, per capita prey availability, and competition with lions ($F = 3.67$, $d.f. = 3, 11$, $P = 0.047$; Appendix I), and explained 50% of the variation in

TABLE 1.—Life table for female spotted hyenas (*Crocuta crocuta*) born during the study.

Age (years)	No. exposed (<i>n</i>) ^a	No. dying	Mortality rate	Proportion surviving	No. births	Offspring per female ^b
0–1	162.5	78	0.48	0.52	0	0
1–2	83.0	24	0.29	0.37	0	0
2–3	57.0	5	0.09	0.34	17	0.33
3–4	47.0	2	0.04	0.32	47	1.24
4–5	41.5	3	0.07	0.30	38	1.09
5–6	34.5	4	0.12	0.27	25	0.86
6–7	25.0	5	0.20	0.21	30	1.36
7–8	17.0	2	0.12	0.19	18	1.2
8–9	13.5	1	0.07	0.17	9	0.9
9–10	11.0	2	0.18	0.14	9	1.29
10–11	7.5	1	0.13	0.12	3	0.6
11–12	3.5	0	0.14	0.11	2	1

^a Censored data points account for fractions in number of individuals exposed.

^b Females that were censored in an age interval without giving birth were excluded from this calculation.

reproduction. Clan size and per capita prey availability had a positive effect on reproduction, whereas competition with lions had a negative effect (Table 2). Four other models were considered equally parsimonious and included combinations of all 5 ecological variables (Appendix I). When all variables from these models were included (i.e., the global model), clan size (estimate = 0.026, *t* = 2.69, *P* = 0.02), competition with lions (estimate = -7.28, *t* = -2.56, *P* = 0.03), and per capita prey availability (estimate = 0.029, *t* = 2.62, *P* = 0.03) had significant effects, but human population size (*P* = 0.41) and rainfall (*P* = 0.21) did not. Together, these results indicate that reproduction was influenced by clan size, per capita prey availability, and competition with lions.

The best model for annual recruitment (Fig. 5b, *n* = 13 years) of juveniles to 2 years of age included competition with lions and rainfall, but not clan size, per capita prey availability, or human population size (Table 2; Appendix I; model residual deviance = 8.39 on 9 *d.f.*). This model explained 68.6% of the variation in annual recruitment. No other models were strongly

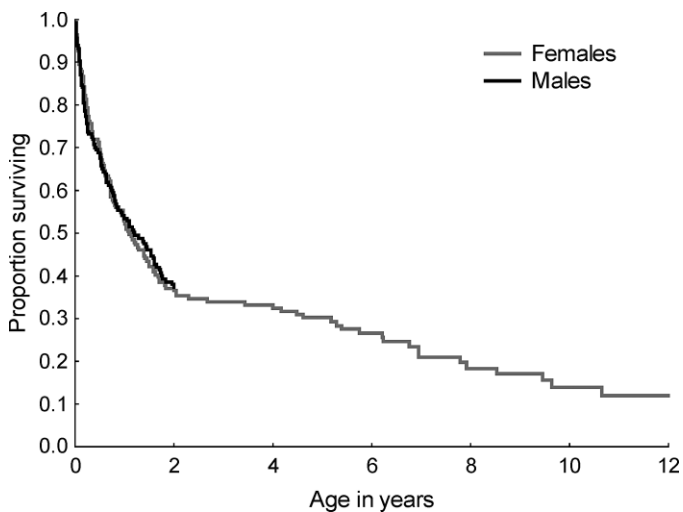


FIG. 3.—Survivorship curves for female (*n* = 164) and male (*n* = 165) spotted hyenas (*Crocuta crocuta*). Male survivorship is only known until 2 years of age. The proportion of females surviving does not reach 0 because some females were still alive at the end of the study (i.e., right-censored data points).

supported based on ΔAIC_c . Both competition with lions and rainfall had negative effects on recruitment (Table 2). The year 2000 was influential in the model (Cook's distance = 0.85); however, removal of this point did not change the results. Focusing strictly on recruitment between den independence and 2 years of age, the results were very similar to those from the previous analysis. The most-parsimonious model included competition with lions and rainfall, but no other variables (Appendix I; model residual deviance = 10.89 on 10 *d.f.*, R^2 = 0.63); recruitment of den-independent cubs was negatively related to both competition with lions (estimate = -27.01, *SE* = 9.05, *z* = -2.98, *P* = 0.003, χ_1^2 = 9.70, *P* = 0.002) and

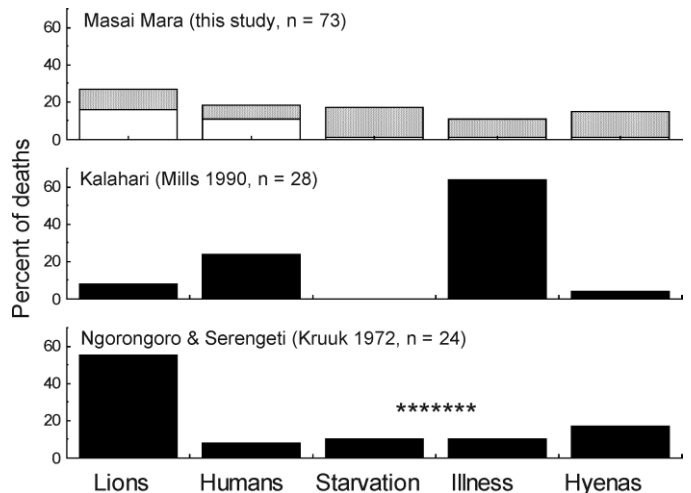


FIG. 4.—Percent of deaths caused by the major mortality sources for 3 spotted hyena (*Crocuta crocuta*) populations. Sample sizes for each population are indicated. Deaths caused by disease are included as illness. Most deaths caused by hyenas were either siblicide or infanticide. Kruuk (1972) lumped deaths caused by starvation and illness; together they accounted for 21% of deaths. Asterisks indicate that those deaths are divided equally between the 2 mortality sources here for representation only. Age categories are indicated for the Masai Mara population only. Juveniles were less than 2 years of age at death (hatched bars). Adults were older than 2 years (open bars). Almost all deaths due to illness in the Kalahari were likely due to rabies (Mills 1990).

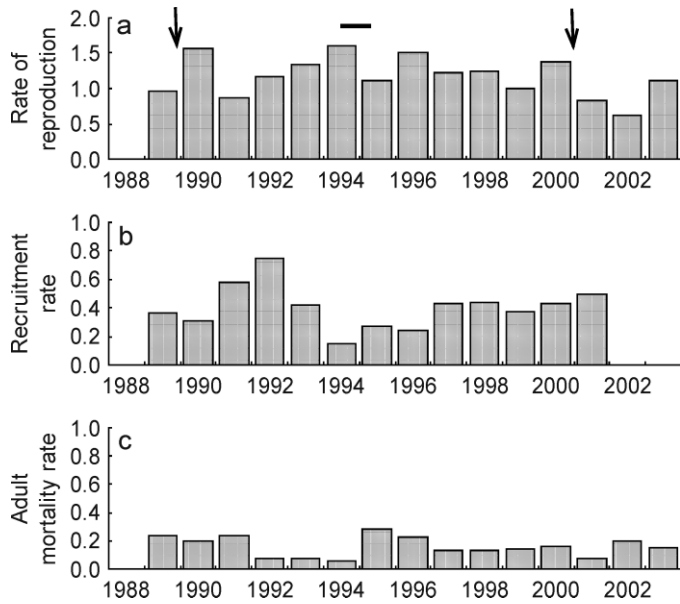


FIG. 5.—Annual a) rate of reproduction, b) recruitment rate, and c) adult mortality rate for spotted hyenas (*Crocuta crocuta*) in the Masai Mara from 1989 to 2003. The rate of reproduction is the number of cubs born per adult female. The recruitment rate is the proportion of individuals born in a given year that survive until 2 years of age. Rates are not given for 1988 because the study did not begin until July of that year. Recruitment data for individuals born in 2002 and 2003 were not yet available. Arrows indicate 2 clan fission events. Horizontal line indicates canine distemper virus epizootic.

rainfall (estimate = -0.034 , $SE = 0.011$, $z = -3.02$, $P = 0.003$, $\chi^2_1 = 7.48$, $P = 0.006$).

Using the ecological predictor variables examined here, we were unable to adequately fit a model to explain variation in annual mortality rates of adults ($n = 15$ years; Fig. 5c). The global model explained only 28.0% of the variation in mortality of adults, although there was no overdispersion (residual deviance = 6.66 on 9 *df.*). Further, the 2 most-parsimonious models were the null model (Appendix I), in which only the intercept was fitted, and the model containing only rainfall ($R^2 = 0.12$; Appendix I). Thus, no model was better supported than the null model.

The relationship between rainfall and human–carnivore conflict in this population may result from seasonal changes in prey distribution with rainfall. Although rainfall and prey density were not correlated among years ($r = 0.21$, $P = 0.45$, $n = 15$ years), there was a trend toward a negative correlation between quarterly rainfall and quarterly prey density ($r = -0.22$, $P = 0.09$, $n = 62$ quarters). There were no significant correlations among the other ecological variables, measured yearly ($P > 0.1$).

We found no evidence of high mortality of adults (Fig. 5c) coincident with epidemics of either canine distemper virus, which infected hyenas and other carnivores in the ecosystem in late 1994 and early 1995 (Roelke-Parker et al. 1996), or rabies that infected sympatric wild dogs (*Lycaon pictus*) in late 1989 (Kat et al. 1995). However, recruitment of juveniles was lowest for the cohort born in 1994 (Fig. 5b). Between July 1994 and

TABLE 2.—Parameter estimates for the best-fit models of annual rate of reproduction and annual recruitment of juveniles in spotted hyenas (*Crocuta crocuta*). A general linear model was used for reproduction (cubs born per female), whereas a generalized linear model was used for recruitment (survival to 2 years of age; see text for details).

	Estimate	SE	df.	t or z ^a	P	χ^2 ^b	P
Reproduction							
Intercept	0.256	0.435	11	0.59	0.57		
Clan size	0.024	0.010	11	2.28	0.04		
Lion competition	-6.77	3.08	11	-2.20	0.05		
Per capita prey availability	0.031	0.012	11	2.62	0.02		
Recruitment							
Intercept	2.51	0.75	12	3.33	0.0008		
Lion competition	-16.36	6.18	12	-2.65	0.008	7.32	0.007
Rainfall	-0.021	0.007	12	-3.13	0.002	10.15	0.001

^a *t*-values are presented for the reproduction model; *z*-values are presented for the recruitment model.

^b Chi-square (χ^2) and *P*-values for deletion tests are presented for the recruitment model only; *df.* = 1 for all tests.

March 1995, 3 juvenile hyenas died from illness. Although postmortem tests were not performed to confirm canine distemper virus infection, 2 exhibited symptoms consistent with canine distemper virus. These 3 deaths account for 50% of all deaths due to illness during the entire study (Fig. 4). Monthly mortality rates during the canine distemper virus epizootic (July 1994 to June 1995) were compared with mortality rates during months before and after the epizootic (January–June 1993 and July–December 1996), but there was no significant difference in mortality between canine distemper virus and non–canine distemper virus periods for either juveniles (Mann–Whitney *U*-test; $U = 64.0$, $P = 0.64$, $n = 12$ per group) or adults (Mann–Whitney *U*-test; $U = 71.0$, $P = 0.95$, $n = 12$ per group).

DISCUSSION

Our analysis of long-term data from spotted hyenas revealed significant effects of several ecological factors on survival and reproduction. Per capita prey availability and clan size had positive effects on spotted hyena reproduction, whereas increased rainfall and competition with lions had negative effects on hyenas. Both rainfall and competition with lions reduced recruitment of juvenile hyenas, and competition with lions also decreased hyena reproduction.

The positive effect of per capita prey availability on annual reproduction is consistent with other studies of spotted hyena that have found correlations between prey availability and seasonal (Cooper 1993; Holekamp et al. 1999) or individual (Hofer and East 2003; Holekamp et al. 1996) variation in reproduction. Indeed, studies across a wide range of mammals have found effects of food availability on reproduction and survival (e.g., Altmann and Alberts 2003; Dobson 1995b; Mduma et al. 1999). However, prey availability did not influence survival in spotted hyenas. Although nursing cubs starved to death after the loss of their mother, only 1 adult hyena was ever observed to die of starvation, and that

individual had a broken leg, leaving it unable to hunt. Compared to other habitats occupied by spotted hyenas, the Mara is relatively prey-rich, with a year-round resident ungulate population (Ogutu and Dublin 2002). Consequently, prey availability may rarely reach levels low enough to cause hyenas to starve. In other hyena populations with lower prey abundance or greater fluctuations in prey abundance (e.g., Hofer and East 1993; Mills 1990), we might expect prey availability to have a greater effect on survival.

The positive effect of clan size on reproduction suggests that group living, and living in large groups in particular, confers significant benefits for spotted hyenas. In other gregarious mammals reproductive success is variously maximized in large groups (*L. pictus*—Creel and Creel 2002; *Suricata suricatta*—Russell et al. 2003), intermediate-sized groups (*Panthera leo*—Packer et al. 1988), or small groups (*Papio cynocephalus*—Altmann and Alberts 2003; *Cervus elaphus*—Clutton-Brock et al. 1982). These differences likely reflect variation in the trade-offs associated with group living in each species (e.g., predator defense and feeding competition); for spotted hyenas these trade-offs are expected to center around inter- and intraspecific competition. High prey density in the Mara supports high densities of lions (Ogutu and Dublin 2002) and hyenas (Trinkel et al. 2006). High density of lions should favor large groups of hyenas in order to protect cubs, or to acquire and defend carcasses. Here the positive effect of clan size on reproduction, but not on recruitment, suggests that the advantage of large group size lies in enhanced access to food rather than protection of cubs. Similarly, high density of hyenas is likely to favor large clan size to facilitate the defense of territories and individual carcasses from conspecifics in the ecosystem. Clan size ranges widely among spotted hyena populations from 10 to 80 hyenas (Kruuk 1972; Mills 1990). This likely reflects variation in the prevailing ecological conditions, particularly with respect to lion populations and prey densities.

The negative effect of rainfall on recruitment cannot be explained solely by den flooding during periods of heavy rain. Such events are quite rare (Frank et al. 1995; this study), and the negative relationship between rainfall and recruitment was observed even among older cubs that no longer resided at dens. Rainfall might have a negative effect on recruitment because of increased rates of disease infection, but disease does not seem to be of primary importance in this hyena population (see below). It seems most likely that rainfall influenced recruitment as a result of deliberate killing of hyenas by local pastoralists, in response to livestock depredation during wet periods. Juveniles are vulnerable to direct killing by humans, as well as to starvation if their mothers are killed. Livestock depredation is thought to increase during periods of high rainfall because abundance of natural prey species fluctuates with rainfall; when natural prey are scarce, conflicts increase between predators and livestock (Polisar et al. 2003; Saberwal et al. 1994; Woodroffe and Frank 2005). In the Mara, wider availability of free water and green vegetation during periods of rain leads to a more dispersed distribution of prey.

Using local human population size as an estimate of anthropogenic disturbance, we found no effect on measures

of survival or reproduction. However, this estimate of human population size fails to capture either changes in human behavior or smaller scale patterns of disturbance that might affect hyenas. Given that the local human population is known to influence both daily activity patterns and space use in this hyena population (Boydston et al. 2003b; Kolowski et al. 2007), it will be important to determine whether these behavioral changes are buffering the hyena population from more severe (i.e., demographic) effects of human disturbance, or whether they signal demographic changes that we have yet to detect. Consistent with the former hypothesis, studies in other mammals to date have failed to detect demographic changes in response to human-induced stress (Creel et al. 2002) or behavioral changes (Griffin et al. 2007).

Disease played a relatively minor role in the population dynamics of spotted hyenas during this study. The 2 epizootics that occurred in this ecosystem during the study period had no noticeable impact on mortality rates of adults. Although the canine distemper virus epizootic may have influenced survival of juveniles, the effect was not statistically significant. The magnitude of any effect of the canine distemper virus and rabies epizootics on the spotted hyena population was small in comparison to their respective effects on the populations of lions and wild dogs in this ecosystem. The canine distemper virus epizootic killed lions in all age classes and resulted in a loss of approximately 30% of the population (Roelke-Parker et al. 1996), and the rabies epizootic killed roughly one-third of the local wild dogs (21 dogs—Kat et al. 1995). Indeed, the finding that disease has had a minor role in the dynamics of this spotted hyena population stands in contrast to the predominant influence that disease has had on populations of other carnivores (Kissui and Packer 2004; Thompson et al. 2005; Woodroffe and Ginsberg 1999) and several other large mammals (Dobson 1995a; Gross et al. 2000; Walsh et al. 2003). This discrepancy may reflect a general difference in disease resistance between hyenas and other mammals. Greater disease resistance may have evolved in spotted hyenas and other hyaenids in the same subfamily because of their heavy reliance on carrion and scavenging; a similar hypothesis has been suggested for scavenging birds (Blount et al. 2003).

Although lions and humans were the major causes of mortality for adult spotted hyenas in the current study (Fig. 4), we were unable to explain variation in mortality rates of adults using these and other ecological predictors. Perhaps adult hyenas are less susceptible than juveniles to the effects of ecological variation, as is the case in many large herbivores (Gaillard et al. 1998). Certainly, mortality of adults varied considerably less between years of our study than did recruitment of juveniles. It is also possible that both human disturbance and competition with lions are influencing mortality of adults, but not in an easily predictable manner. For example, killing of hyenas by local pastoralists can occur in clumped events such as mass poisonings (Holekamp et al. 1993). Similarly, being killed by a lion may be a chance event for an adult hyena, because adults regularly come into close contact with lions without dying. Such random events can potentially have significant and rapid effects on hyena demographics (Holekamp

et al. 1993), and we hypothesize that stochastic events contribute greatly to mortality of adults in this species.

Interspecific competition with lions was the only ecological factor found to influence both reproduction and recruitment. The effect of interspecific competition on reproduction is likely due to competition for food (either interference or exploitation—Watts and Holekamp 2008), whereas the effect on recruitment could be due indirectly to feeding competition or directly to intraguild predation on juveniles. Although further research will be needed to assess the potential effects of feeding competition on survival, lions were the single leading cause of mortality of hyenas in this study and in at least 3 other hyena populations (Ngorongoro, Serengeti, and Etosha—Kruuk 1972; Trinkel and Kastberger 2005). This suggests that direct killing is an important mode of competition between these species. Further, it is possible that lions influence hyena populations by inducing behavioral changes in hyenas (i.e., risk effects). Although initially described in invertebrate and plant species (Tollrian and Harvell 1999), risk effects have recently been documented in mammalian herbivores (Creel et al. 2007). Observations of predator-induced behavioral changes in carnivore species, such as cheetahs (*Acinonyx jubatus*—Durant 2000) and coyotes (*Canis latrans*—Switalski 2003), indicate the potential for such effects even among large carnivores.

Interspecific competition between carnivores can be particularly intense relative to competition within other guilds, because carnivores have both morphological and behavioral adaptations for killing (Creel et al. 2001; Palomares and Caro 1999). Our study adds to a growing literature (lions [Cooper 1991], wild dogs [Creel and Creel 2002], and cheetahs [Durant et al. 2004; Laurenson 1995]) suggesting that interspecific competition may be more important than previously recognized in the dynamics of populations of large carnivores.

Because our results derive from data on a single large social group, additional studies are necessary to assess whether the effects we have observed can be generalized across spotted hyena groups and populations. Examination of the data in Fig. 4 suggests that the relative importance of specific ecological variables to population dynamics is likely to vary among populations. Interestingly, reduced competition with lions also had a positive effect on the rate of reproduction in a spotted hyena population in Amboseli National Park, Kenya, although there was no effect on juvenile survivorship (Watts and Holekamp 2008). Ecological conditions in the Mara and Amboseli are quite similar, but it is reasonable to assume that the magnitude of any particular ecological effect may be influenced by other prevailing ecological conditions across the wide variety of ecosystems inhabited by spotted hyenas. For example, the high susceptibility of Kalahari hyenas to disease (Fig. 4) may be related to low prey availability in that ecosystem. Thus, data from a diverse range of ecosystems are still needed.

Both top-down and bottom-up forces influenced spotted hyena demography. We found effects on survival and reproduction of per capita prey availability, group size, rainfall, and interspecific competition. These data are consistent with the growing consensus that both top-down and bottom-up mechanisms are important in population dynamics and community

structure (e.g., Hunter and Price 1992; Menge 2000). Among spotted hyenas survival was most strongly influenced by top-down forces, whereas reproduction was more strongly influenced by bottom-up forces. These results demonstrate the utility of examining the underlying demographic processes (i.e., survival and reproduction) that determine population growth, in order to better understand the mechanisms by which top-down and bottom-up forces influence population dynamics.

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APPENDIX I

Results of model selection for a) annual reproduction, b, c) recruitment of juveniles, and d) mortality of adults in spotted hyenas (*Crocuta crocuta*). The variables included in each model are indicated by x, and are described in the text. The Akaike information criterion adjusted for small sample size (AIC_c), the difference in AIC_c between a given model and the best model (ΔAIC_c), and the Akaike weight (w_i) are provided for each model. The best model, based on AIC_c , is indicated in bold. Only models that were equally parsimonious with the best model ($\Delta AIC_c < 2$) are shown.

Clan size	Human population	Lion competition	Prey availability	Rainfall	AIC_c	ΔAIC_c	w_i
a) Reproduction							
x		x	x		7.42	0	0.182
x		x	x	x	7.67	0.25	0.160
x			x		9.05	1.63	0.080
x	x	x	x		9.25	1.83	0.073
		x	x		9.41	1.99	0.067
b) Juvenile recruitment							
		x		x	60.21	0	0.529
c) Juvenile recruitment after den independence							
		x		x	50.41	0	0.565
d) Adult mortality							
					51.33	0	0.457
				x	52.94	1.61	0.205