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Top-down population regulation of a top predator: lions in the Ngorongoro Crater

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Efforts to determine whether bottom-up or top-down processes regulate populations have been hampered by difficulties in accurately estimating the population's carrying capacity and in directly measuring food intake rate, the impacts of interspecific competition and exposure to natural enemies. We report on 40 years of data on the lion population in Ngorongoro Crater, Tanzania, which showed strong evidence of density-dependent regulation at 100–120 individuals but has remained below 60 individuals for the past decade despite consistently high prey abundance. The lions enjoy a higher *per capita* food-intake rate and higher cub recruitment at low population density, and interspecific competition has not increased in recent years. These animals have suffered from a number of severe disease outbreaks over the past 40 years, but, whereas the population recovered exponentially from a severe epizootic in 1963, three outbreaks between 1994 and 2001 have occurred in such rapid succession that the population has been unable to return to the carrying capacity. The Crater population may have become unusually vulnerable to infectious disease in recent years owing to its close proximity to a growing human population and a history of close inbreeding. The Crater lions may therefore provide important insights into the future of many endangered populations.

Keywords: population regulation; food limitation; infectious disease; interspecific competition; inbreeding depression

1. INTRODUCTION

Populations can be regulated either by 'bottom-up' processes (e.g. food limitation) that are inherently density dependent or by 'top-down' processes (e.g. 'natural enemies' such as predators or parasites) that operate independently of population density. In food-limited populations, reproductive output declines through reduced pregnancy rate, delayed maturity and/or lower survival as the population approaches the 'carrying capacity', and density-dependent effects directly contribute to population regulation through competition for food (e.g. Sinclair *et al.* 1985; Mduma *et al.* 1999). Although the incidence of infectious disease generally increases with population size (Anderson & May 1991), the incidence of multi-host pathogens can be essentially independent of population density in a given host species (Cleaveland *et al.* 2001). Infectious disease can have a significant impact on population size (Holmes 1982; Scott & Dobson 1989) and may persistently hold populations below carrying capacity (Sinclair 1979; Mitchell & Power 2003; Torchin *et al.* 2003).

Carnivore populations appear to be sensitive to all of these factors. Food shortages are known to play an important role in infant mortality through abandonment (Packer & Pusey 1984) and starvation (e.g. Packer & Pusey 1995); social behaviour can also have a considerable impact through infanticide (Packer 2001) and territoriality. Disease outbreaks can reduce population sizes by more than 35% (Fosbrooke 1963; Roelke-Parker *et al.* 1996; Sillero-Zubiri *et al.* 1996; Peterson *et al.* 1998), and competition with other carnivores can be severe, both through feeding competition (Cooper 1991; Mills & Biggs 1993) and predation (Kruuk 1972; Laurenson 1995; Crabtree & Sheldon 1999; Durant 2000). In small isolated populations, inbreeding may also play a part by reducing reproductive rates (Peterson *et al.* 1998) or render individuals more susceptible to disease (Acevedo-Whitehouse *et al.* 2003; Reid *et al.* 2003).

Although numerous inferences have been made about population regulation in carnivores, most studies have been too narrowly focused to provide comprehensive data on demography, ecology and genetics. The field has consequently been mired in controversy, for example in relation to the demise of the Serengeti wild dogs (Burrows *et al.* 1994 versus Creel 2001) and the genetic vulnerability of the cheetah (Caro & Laurenson 1994 versus O'Brien 1994). In this paper, we provide the first direct measurements of food availability, interspecific competition, infectious disease and infanticide in a well-defined population. The lions of the Ngorongoro Crater, Tanzania, have been monitored since the early 1960s, and there is virtually no immigration into the Crater population. These animals have a known history of close inbreeding (Packer *et al.* 1991), and lions are an excellent species for assessing the mechanistic role of food limitation (Krebs 1995), since recent food intake can be measured from both the size of their prey and the profile of their bellies (Bertram 1975; West & Packer 2002). Prey availability is also easily measured, since the Crater herbivores have been censused regularly for the past 40 years (Runyoro *et al.* 1995). We use all available data between 1963 and 2002 to assess long-term changes in prey abundance and the impact of disease outbreaks on the lion population, but our detailed

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data on diet and food intake were collected during two intensive study periods: 1982–1983, when the Crater population reached its all-time high and averaged 105 individuals (Cairns 1990), and 1999–2000, when the population averaged only 50 individuals and a severe drought temporarily boosted food availability (Kissui 2001).

2. MATERIAL AND METHODS

The Ngorongoro Crater is a 250 km^2 caldera located at the western edge of the Gregory Rift, with walls 400–600 m high. The Crater floor enjoys a year-round supply of water from seasonal rainfall and permanent streams originating in the northern highland catchment forest, supporting large numbers of resident ungulates through persistent grass growth at the edges of marshes and swamps (Estes 2002). Individual lions are identified from whisker-spot patterns (Pennycuick & Rudnai 1970) and natural markings (Packer *et al.* 1991). Dates of birth are inferred from the characteristic behaviour of females around parturition (Packer *et al.* 2001). During the two intensive study periods, every individual in the population was located two or three times every 10 days, and prey selection and preferences were estimated from census data collected in 1978–1980 and 1998–2001. Major herbivore species have been censused by ground counts conducted in the wet and dry seasons in most years since 1964 (Runyoro *et al.* 1995; Estes 2002).

Diet and food intake were recorded between 06.30 and 18.30 with a 2–3 h gap in the afternoon. Carcass data included species and age–sex class (based on body size, size and shape of horns and coat colour; Sinclair 1977). 'Observed food intake rate' is the total biomass of carcasses obtained during each study period divided by the total number of 'female sightings'. 'Female sightings' are tabulated as follows: a lone female observed on 3 days contributes three female sightings, whereas a group of five females observed on 2 days contributes 10 female sightings.

As an upper limit of carcass biomass, we assume that the lions always consumed the entire carcass; as a lower limit, we assume that they consumed only the amount still available when first observed. Estimates are adjusted according to live weight, total carcass weight, proportion of lean meat and proportion of inedible matter (Sachs 1967; Packer *et al.* 1990). At the onset of each observation, the carcass was categorized as: 1, intact; 2, viscera partly absent but muscle tissue intact; 3, viscera absent but muscle intact; 4, three-quarters of muscle remaining; 5, one-half remaining; or 6, one-quarter remaining. We also estimated recent food intake from the standing profile of each lion (Bertram 1975), which provides a more complete measure of food intake, including night-time feeding when lions are most active, and indicates whether a lion has fed even when no carcass had been observed. The belly scale ranges from 1, indicating maximal distension, to 5 with increments of one-quarter (0.25). Bone-marrow condition reflects fat content and, hence, health at death (Sinclair & Arcese 1995). Samples were obtained from long bones and assigned to one of five categories according to texture and colour: solid white fatty, white opaque gelatinous, translucent gelatinous, red gelatinous and absent. For multiple carcasses, the median weight and health of the carcasses was used.

We estimated the selection ratio ($\hat{w}_i$) for a prey species i as (o_i/π_i), where o_i is the proportion eaten and π_i is the proportion in the prey population (Manly *et al.* 1993; Höner *et al.* 2002). The standardized selection ratio (B_i) is calculated as $\hat{w}_i/\left(\sum^{i=1}\hat{w}_j\right)$ and estimates the probability of a particular prey species i being selected if all prey types were equally available; standard errors and χ^2 statistics were determined following Manly *et al.* (1993). Statistical analyses used SAS for Windows v. 8, release 8.2; p-values are two-tailed.

3. RESULTS

In 1962, the Crater lion population crashed from 75–100 individuals to 12 individuals, coincident with an outbreak of blood-sucking stable flies (*Stomoxys calcitrans*) (Fosbrooke 1963; Packer *et al.* 1991). Subsequently, the population climbed rapidly to reach over 100 individuals by 1975 (figure 1*a*) then averaged *ca.* 100 individuals until 1983 when it went into a persistent decline, and it has generally remained below 60 animals since 1993, reaching a low of 29 animals in 1998. At a coarse level, these changes are not correlated with overall changes in prey availability on the Crater floor, in terms of the numbers either of medium-sized herbivores (wildebeest plus zebra) or of Cape buffalo (figure 2). We combine zebra with wildebeest because lions catch the two species with similar success, but buffalo are more formidable (see later in this section).

The abundances of buffalo and wildebeest changed between the intensive-study periods: buffalo increased over 200% from 1280 individuals in the high-lion-population-density years (1978, 1980–1981) to 3982 individuals in the low-lion-population pre-drought years (1998–2000), whereas wildebeest decreased by *ca.* 20% from 13 924 animals (1978–1980) to 11 234 animals (1998–2000). Zebra remained nearly constant at *ca.* 4081 individuals (1977–1978, 1980) versus 4184 individuals (1998–2000). During the drought of 2000, the Crater buffalo fell by 45% to 2206 individuals by early 2001 (Estes 2002), but wildebeest (10 956 individuals) and zebra (3852 individuals) were largely unaffected. Table 1 presents selection ratios and prey preferences for the lions during 'high lion density' (1982–1983), 'low lion density–pre-drought' (1999–March 2000) and 'low lion density–drought' (April–November 2000). The standardized selection ratios (B_i) indicate that at high population density the lions selected buffalo more often than wildebeest and zebra, and both buffalo and zebra were taken more often than expected from their abundances. During both low-lion-density study periods, lions selected buffalo more than zebra and wildebeest, and buffalo were taken more often than expected from their abundance, but the selectivity for buffalo was far higher during the drought. We categorized prey into large (greater than 300 kg live weight: adult buffalo, eland, rhinoceros and hippopotamus), medium (100–300 kg: adult wildebeest, zebra and hartebeest, yearling buffalo, and hippopotamus and rhinoceros calves) and small (less than 100 kg: adult gazelle, reedbuck, warthog and ostrich, and wildebeest, zebra and buffalo calves) and found that the lions' diet contained a similar proportion of medium-sized prey during the high and low population (pre-drought) periods, whereas the proportion of large prey increased during the 2000 drought ($\chi^2 = 27.28$, d.f. $= 4$, $p < 0.01$, $n = 418$). Thus, the Crater lions showed an increasing preference for buffalo through the course of the three study periods, while buffalo increased in abundance until the end of the drought. Since buffalo are far larger than wildebeest or zebra, the lions had access to greater prey biomass in the two low-lion-density periods than at high population density.

The Crater lions enjoyed higher food intake rates at low population density than at high density (figure 3). *Per*

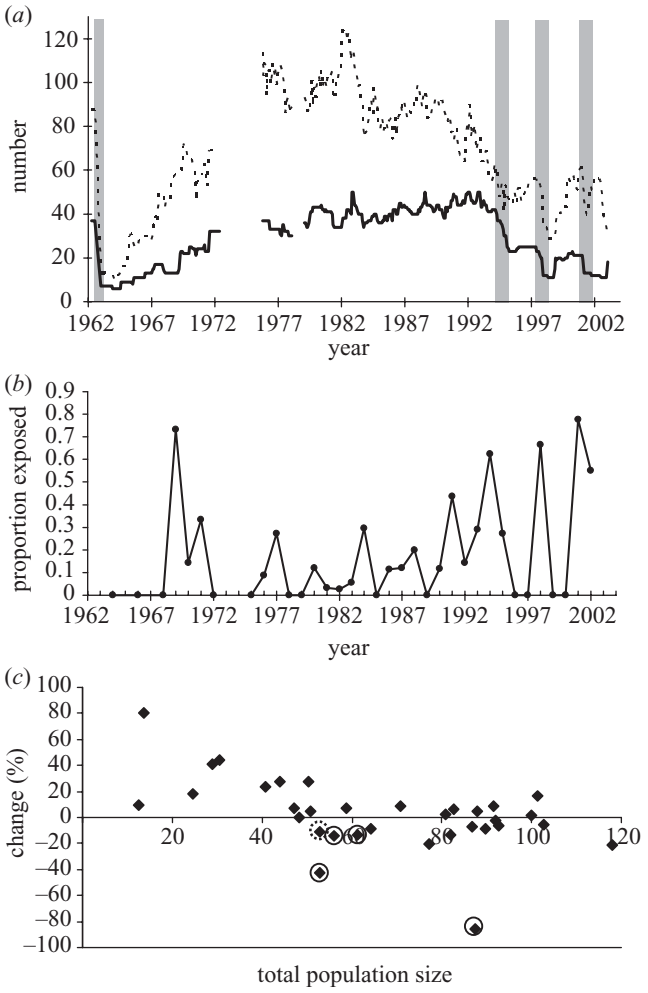

Figure 1. Demographic trends. (*a*) Total population size (dotted line) and the number of adults aged 4 years or older (solid line) for each month in the period 1963–2003; vertical bars indicate timing of die-offs. (*b*) Proportion of cubs less than 1 year old exposed to male takeovers each year. (*c*) Annual rate of population change as a function of population size. Data from outbreak years (1962, 1994, 1998 and 2001) are circled; the dotted circle is the second year of the 1994 die-off.

capita, females gained access to considerably more meat in the later study periods (figure 3*a*), owing both to a greater frequency of carcasses (0.10 per female per day in 1999–2000 versus 0.07 per female per day in 1982–1983) and to a greater proportion of large prey (especially buffalo) in the diet. Meat availability skyrocketed during the drought of 2000 (figure 3*a*) when the frequency of carcasses was 0.16 per female per day. Consistent with the overall trend, each age–sex class enjoyed substantially higher belly sizes (and hence food consumption) at low population density (figure 3*b*). However, belly sizes were no higher during the drought than in the preceding months, despite a much higher availability of meat, suggesting that the lions were already obtaining as much meat as they required during the low-density pre-drought period and that they did not completely consume the drought-stricken buffalo carcasses.

We have little evidence that lions suffered from increased competition with hyenas in recent years. Spotted hyenas are most successful in stealing carcasses from lions when they greatly outnumber them, and hyenas are far less successful at supplanting male lions than females. However, the relative abundance of hyenas was no higher in the 1990s than in earlier years, nor has there been a significant change in the adult sex ratio of the lion population. Despite the relatively small size of the lion population in recent years, the hyena–lion population ratio was only 4.2 : 1 in the late 1990s (Höner *et al.* 2002) compared with an estimated 14 : 1 in the late 1960s (Kruuk 1972) when the lion population was nevertheless able to grow rapidly (figure 1*a*).

Höner *et al.* (2002) report 22 cases in which hyenas obtained carcasses from lions during 1996–1999. However, during our low-density study periods in 1999–2000, we observed lions feeding from more than 260 carcasses, but hyenas never succeeded in supplanting the lions. We observed the hyenas waiting until the lions had finished the meat and scavenging the bones and skin only after the lions had moved off. Nevertheless, hyenas are sufficiently nocturnal that our sampling techniques might not reveal the true extent of competition between the two species. We therefore checked for feeding competition with hyenas by measuring the amount of meat already eaten and the amount still remaining when lions were first observed at a carcass. If lions suffered greater scavenging from hyenas in recent years, the lions should have eaten less meat from each carcass. The amount of meat already eaten when the lions were first encountered at a kill did not differ among the three periods (ANOVA: $F = 1.92$, $p = 0.15$, $n = 253$), but there was a significant difference in the amount of meat remaining (ANOVA: $F = 15.24$, $p < 0.01$, $n = 253$) with the highest amount remaining during the 2000 drought period (table 2*a*).

If the Crater lions suffered from greater levels of hyena scavenging in recent years, the lions should have consumed less meat at each kill—and had concomitantly smaller belly sizes for a given carcass size. We therefore used a generalized linear model (GLM) to compare the belly sizes of female lions (2 years old or older) observed at each carcass, adjusting for the amount of meat already eaten and the number of female lions present at the carcass (table 2*b*). The relationship between belly size and the amount of meat already eaten showed a significant interaction with study period: belly size depended on the amount of meat already eaten during both high population density ($t = -4$, $p < 0.01$, $R^2 = 0.20$) and pre-drought low population density ($t = -4.23$, $p < 0.01$, $R^2 = 0.20$), but not during the 2000 drought ($t = -0.52$, $p = 0.60$, $R^2 = 0.00$), suggesting that lions ate a comparable proportion of meat per carcass in the first two study periods, but maintained a more constant belly size when food was superabundant during the 2000 drought.

Finally, even though lions and hyenas specialize on the same prey species and might therefore be expected to suffer from exploitation competition, lions were significantly more likely to kill adults whereas hyenas took more juveniles ($p < 0.01$ for buffalo and $p < 0.02$ for wildebeest). Thus, the two species show a degree of niche separation by specializing on different age–sex classes.

Data from the Serengeti suggest that foraging-group size has a significant impact on food intake (Packer *et al.* 1990), and, in 1999–2000, the Crater lions showed a significant interaction between prey size and prey health for small (three or fewer individuals) versus large (four or more

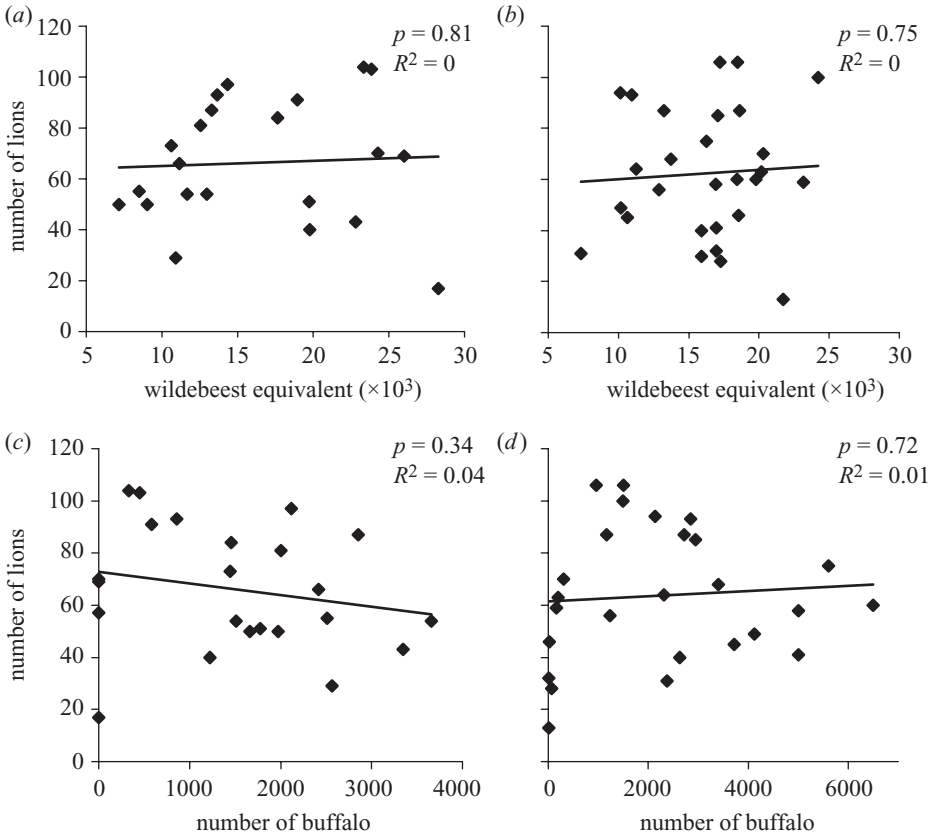

Figure 2. Relationships between herbivore and lion population sizes, 1964–2001. (*a*) Number of zebra and wildebeest, combined into a single measure with 1 zebra = 1.35 wildebeest, each dry season. (*b*) Wildebeest equivalents each wet season. (*c*) Number of buffalo each dry season. (*d*) Buffalo each wet season.

Table 1. Estimated selection indices and prey preferences for the Ngorongoro Crater lions during the three intensive study periods. Scavenged carcasses were excluded from this analysis.
(Thomson's gazelle and Grant's gazelle are combined as 'gazelle'; w/beest, wildebeest).

prey species	prey population (n)	population proportion (π_i)	carcasses (u_i)	carcass proportion (o_i)	selection ratio ($\hat{w}$)	standardized ratio (B_i)	s.e. ($\hat{w}$)	χ^2	p-value	preference
1982–1983 (high lion density)										
zebra	4258	0.159	34	0.234	1.471	0.287	0.191	6.10	0.01	+
w/beest	18450	0.691	85	0.586	0.849	0.166	0.056	7.41	0.01	−
buffalo	1498	0.056	18	0.124	2.214	0.432	0.341	12.69	0.00	+
gazelle	2507	0.094	8	0.055	0.588	0.115	0.258	2.55	0.11	0
total	26713	1	145	1	5.121	1				
March 1999–April 2000 (low lion density–pre-drought)										
zebra	4604	0.189	17	0.145	0.769	0.203	0.192	1.45	0.23	0
w/beest	12175	0.499	57	0.487	0.975	0.257	0.093	0.07	0.79	0
buffalo	4593	0.188	39	0.333	1.769	0.467	0.192	16.07	0.00	+
gazelle	3004	0.123	4	0.034	0.277	0.073	0.247	8.59	0.00	−
total	24375	1	117	1	3.791	1				
May–November 2000 (low lion density–drought)										
zebra	5465	0.247	24	0.180	0.731	0.089	0.151	3.16	0.08	0
w/beest	12338	0.557	34	0.256	0.459	0.056	0.077	49.10	0.00	−
buffalo	1778	0.080	74	0.556	6.926	0.847	0.293	408.01	0.00	+
gazelle	2553	0.115	1	0.008	0.065	0.008	0.240	15.15	0.00	−
total	22134	1	133	1	8.181	1				

individuals) feeding groups. Feeding-group size is the number of females (2 years or older) present at the kill, and prey size is the average live weight of prey. Compared to smaller groups, large groups were better able to include large healthy prey in their diet (*t*-test, $t_{0.05}$: d.f. = 67, $p < 0.01$). Thus, small groups may be restricted to large

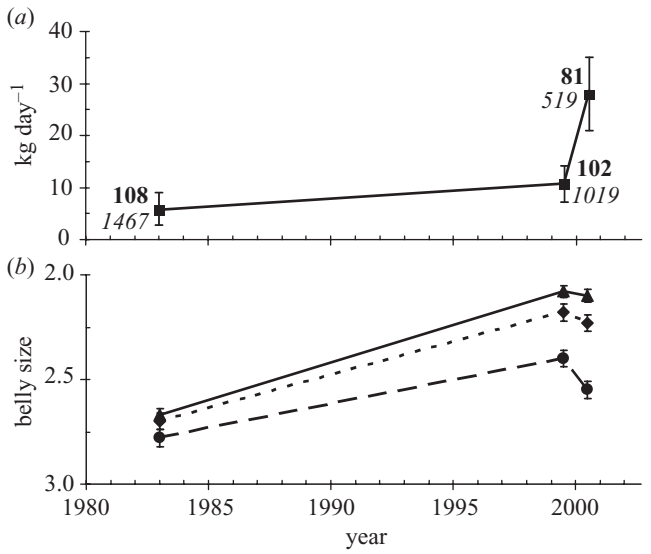

Figure 3. Measures of food intake. (*a*) Food acquisition calculated as described in § 2. Upper dashes indicate maximum food available; lower dashes represent the minimum; squares are the midpoints between the two limits. Bold numbers indicate the numbers of carcasses; italics indicate the number of female sightings. (*b*) Mean ± s.e. for belly-size measurements during 1982–1983 and 1999–2000. Smaller numbers indicate more distended bellies and, hence, higher food intake. Cubs are designated by triangles and solid line, females by circles and dashed line, and males by diamonds and dotted line. Lions had significantly higher belly sizes in 1999–2000 than in 1982–1983 ($p < 0.01$ for all tests).

prey in poor health, and any difference in foraging success between high and low population densities might result only from differences in foraging-group size. However, the number of females per carcass was greater at high population density than at low densities (table 2*a*). Thus the lions gained less food at high density despite foraging in larger groups, perhaps as a result of greater within-group feeding competition.

The long-term data suggest that the lions have been struck by four deadly disease outbreaks over the past 40 years. During the *Stomoxys* plague of 1962 more than 80% of the estimated population disappeared (Fosbrooke 1963). In 2001, six Crater lions were found dead between 7 January and 18 February, and 34% of the total population (population size before any disappearances, $n = 61$) had died or disappeared by 5 April. Veterinary investigation determined that the die-off resulted from a combination of tick-borne disease and canine distemper virus (CDV) (T. Mlengeya, R. Koch, L. Munson and C. Packer, unpublished data). The population suffered similar declines in 1994 and 1997 (figure 1*a*), and figure 4 shows that the age-specific annual mortality for each of the three time periods was the same as for the 1994 CDV outbreak in the Serengeti (Roelke-Parker *et al.* 1996). Unfortunately, no veterinary investigations were permitted in the Crater between 1991 and 2001, so we lack diagnostic data from 1994 and 1997.

Incoming males typically kill small cubs, and the proportion of cubs exposed to male takeovers varied each year (figure 1*b*). Owing to the small size of the Crater floor, there have been several periods when one or two large coalitions controlled the entire population, resulting in periods of extreme instability when they were finally replaced. Consequently, the overall population showed short-term drops during these peak-replacement years. For example, the strong upward trend in the population in the 1960s was temporarily reversed in 1968 when a large proportion of cubs was exposed to takeovers. Similarly, several takeovers occurred shortly after the population reached its all-time high in 1983, and the overall population dropped by 1984 though the adult population remained unchanged (figure 1*a*). The proportion of cubs exposed to takeovers has increased in recent years as a result of the high adult mortality in 1994, 1997 and 2001. Several resident-male coalitions were ousted shortly after being reduced by disease; thus social factors amplified the effects of epidemics by increasing the incidence of infanticide.

Table 2. (*a*) Amount of meat already eaten, amount remaining and the mean number of females observed at each carcass during each study period. Values are mean ± s.e. (*b*) GLM for female belly sizes during the high-population-density and the two low-population-density periods.

(a)

period	mean kg meat already eaten	mean kg meat remaining	mean number of females (⩾ 2 years old) observed
1982–1983 ($n = 75$)	95.64 ± 11.89[a]	53.63 ± 11.72[a]	6.23 ± 0.43
March 1999–April 2000 (pre-drought) ($n = 72$)	72.85 ± 8.64[a]	70.02 ± 11.12[a]	2.65 ± 0.17[a]
May–November 2000 (drought) ($n = 106$)	104.78 ± 12.46[a]	138.93 ± 12.37	2.69 ± 0.13[a]

(*b*)

parameter	sum of squares	F	p
number of ⩾ 2-year-old females feeding at carcass	0.00	2.02	0.89
amount eaten before observer's arrival at carcass	3.72	18.49	< 0.01
study period	2.42	6.01	< 0.01
total females at carcass × time period	0.33	0.83	0.44
amount eaten before observer's arrival × time period	2.00	4.97	0.01

[a] Means not significantly different.

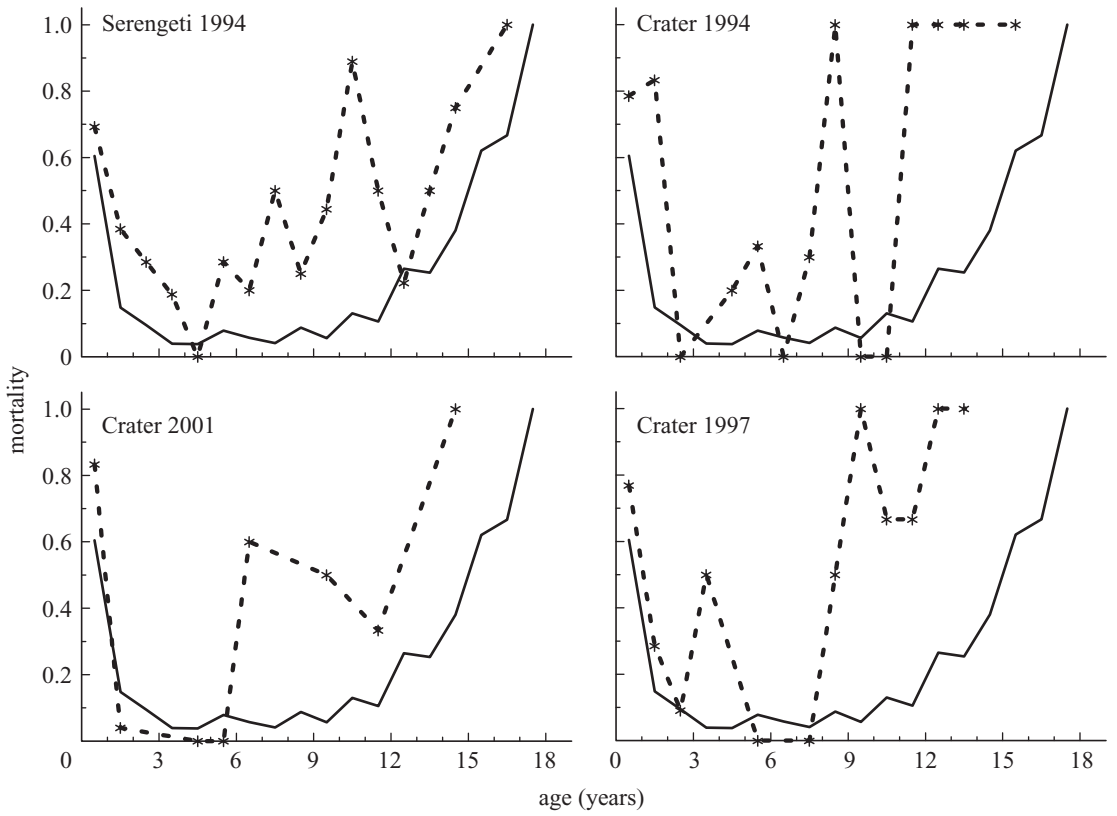

Figure 4. Age-specific annual mortality during known and presumed disease outbreaks. Dotted lines indicate annual mortality during the 1994 CDV outbreak in the Serengeti, the 2001 CDV outbreak in Ngorongoro and the undiagnosed outbreaks in 1994 and 1997. The solid line in each graph shows the background age-specific mortality of the Serengeti and Ngorongoro lions for the period 1966–1995.

The lion population showed clear signs of density-dependent reproductive performance (figure 1*c*). Except for disease-outbreak years, population growth was always positive when the population was less than 60 individuals, but negative in nine out of 16 years when the population exceeded 60 animals. The population showed no sign of lowered reproductive performance over the past 10 years, increasing at the same density-dependent rate (in the absence of disease) as during the post-*Stomoxys* recovery period in the 1960s.

4. DISCUSSION

The comprehensive long-term data on the Crater lions provide a unique opportunity to evaluate the importance of food limitation in population regulation. The maximum of 124 individuals in 1983 almost certainly reflects the upper limit of the carrying capacity. If the lion population subsequently declined owing to a drop in carrying capacity, the lions should have shown similar rates of food intake and demographic performance in the low-population-density years of 1999–2000 as in the high-density years of 1982–1983. However, the lions enjoyed higher food intake and improved reproductive performance at lower population densities. In fact, the lions may have already fed at their maximum requirement in 1999, since their belly sizes were just as large as when meat was superabundant in the drought of 2000 (figure 3*b*).

Kruuk (1972) found that the Crater lions stole more food from spotted hyenas than vice versa in the 1960s, and Hanby *et al.* (1995) found that the Crater lions obtained 21% of their prey biomass from hyenas while losing no *edible* biomass to hyenas in 1976–1977. Höner *et al.* (2002) suggested that the situation had changed by the late 1990s, but our data do not support their proposition. While large groups of hyenas may occasionally take kills from the Crater lions, we observed hyenas feeding on scraps only after the lions had left voluntarily. In fact, Höner *et al.*'s data confirm that lions usually surrender a carcass only after they have eaten their fill. In the hyena 'takeovers' that Höner *et al.* observed in detail, the lions had already eaten at least 13 kg *per capita* in 11 out of 16 cases. Since lions eat 8 kg per day when prey is superabundant (Packer *et al.* 1990) hyenas prevented lions from exceeding their daily requirement only five times during Höner *et al.*'s entire study. More importantly, if lions lost significant food to hyenas, lion belly sizes should have declined in recent years, but belly sizes were significantly greater in 1999–2000 than in 1982–1983, and the relationship between belly size and the amount of carcass eaten was the same in 1982–1983 as in the pre-drought 1999–2000 period. Further, hyenas were far more numerous than lions in the 1960s (Kruuk 1972), yet the lion population increased eightfold from 1963 to 1975. Finally, there is scant evidence of 'exploitation competition' between lions and hyenas: lions preferentially feed on buffalo versus wildebeest for hyenas, and lions mostly capture adult buffalo and wildebeest whereas hyenas specialize on juveniles of these two species.

Disease therefore appears to be the only factor that has held the Crater lion population below its carrying capacity

for the past 10 years. The importance of disease is emphasized by the effects of the severe drought of 2000, which enabled the lions to gain access to extraordinary quantities of meat, but the population nevertheless suffered a dramatic decline at the beginning of 2001 owing to the CDV outbreak. The adult population declined strikingly during three distinct periods: 1994, 1997 and 2001. The 1994 die-off coincided with the severe CDV outbreak in the Serengeti (Roelke-Parker *et al.* 1996). The 1997 die-off coincided with the El Niño floods in East Africa; the Crater floor was impassable for approximately three months, thus we lack direct observations of morbidity and mortality. During each interim period, reproductive rates were sufficiently high that the population would have recovered at a similar rate to the recovery in 1963–1975 but for the sharp decline at the next die-off.

What could have caused disease to become more prevalent and/or harmful than in the 1970s and 1980s? We suggest two possibilities. First, the human population in the Ngorongoro Conservation Area has grown considerably over the past 20 years, especially in the highlands immediately surrounding the caldera. Larger human populations result in higher numbers of domestic dogs, the presumed reservoir of CDV in Northern Tanzania (Cleaveland *et al.* 2001), and larger populations can more readily sustain the infection. Second, the weather in East Africa was more variable in the 1990s than in the 1970s and 1980s, and all four lion die-offs coincided with drought or flood. The 1962 *Stomoxys* plague coincided with heavy floods that immediately followed a severe drought in 1961. The 1994 die-off followed a severe drought in 1993; the 1997 die-off coincided with the El Niño floods, and the 2001 CDV epidemic followed the drought of 2000. Drought may bring different host species into contact at water-holes, and flood may create conditions favourable for pathogens. Regardless of the precise cause, these frequent outbreaks provide important insights into the likely future of many other small genetically vulnerable carnivore populations. While natural geographical barriers have largely isolated the Crater lions, most other carnivore populations have only recently become fragmented owing to habitat loss. Our data clearly show that endangered populations can remain at serious risk even with a large stable food supply and no real threats from competing species.

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