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The response of spotted hyaenas to long-term changes in prey populations: functional response and interspecific kleptoparasitism

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Summary

1. Over the last three decades the main prey species (wildebeest *Connochaetes taurinus*, zebra *Equus burchelli*, Thomson's gazelle *Gazella thomsoni*, and Grant's gazelle *Gazella granti*) of spotted hyaenas *Crocuta crocuta* in the Ngorongoro Crater, Tanzania, substantially declined in numbers, whereas buffalo *Syncerus caffer* numbers increased strongly. This provided a 'natural experiment' to investigate how a generalist predator such as the spotted hyaena responds to long-term changes in prey populations. Here we compare data on the feeding ecology of Crater hyaenas from the late 1990s (period II) with equivalent data from the late 1960s (period I).

2. Hyaenas showed strong hunting preferences for wildebeest calves and gazelle fawns during both periods I and II. Adult buffaloes, prey difficult to hunt for hyaenas, were rarely hunted in either period despite a large increase in buffalo numbers from period I to II.

3. Hyaenas exhibited a functional response to the changes in prey populations by killing more buffalo calves and adult wildebeest during period II, relatively easy prey categories for hyaenas to hunt.

4. The proportion of carcasses scavenged and acquired by kleptoparasitizing other predators increased from period I to II. This was facilitated by an increase in the relative number of lion kills available to hyaenas during the same period.

5. Hyaenas defended a similar proportion of their kills against kleptoparasitic attempts by lions during both periods. Since the ratio of kills hyaenas kleptoparasitized from lions in relation to kills lost to lions increased from period I to period II, hyaenas obtained more food resources from lions during period II than I.

6. The success of hyaenas kleptoparasitizing lions was influenced by the presence of male lions and the ability of hyaenas to recruit sufficient clan members to appropriate carcasses from lions.

7. This study is the first to demonstrate both a functional response of a predator to changes in the size of prey populations and an associated change in foraging behaviour of the predator.

Key-words: *Crocuta crocuta*, lion, predator–prey relationship, preference index, scavenging.

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Introduction

A number of studies have investigated the effect of short-term changes in prey populations on the

behavioural ecology of predators (e.g. lion *Panthera leo* (Linnaeus): Van Orsdol, Hanby & Bygott (1985); spotted hyaena *Crocuta crocuta* (Erxleben): Hofer & East 1993a,b,c). Studies of the effects of pronounced long-term changes in prey populations on their predators, however, are rare (Bergerud & Elliot 1986; Scheel & Packer 1995) despite the fact that such changes are likely to be common (Caughley 1970) and the investigation of their impact on predators

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is crucial for the understanding of predator–prey dynamics.

In the Ngorongoro Crater (hereafter referred to as Crater), a caldera in north-western Tanzania characterized by high densities of resident herbivores, significant long-term changes in vegetation and composition of large herbivore species were recorded over several decades. From 1963 to 1974, total numbers of wildebeest *Connochaetes taurinus* (Burchell), Thomson's gazelle *Gazella thomsoni* (Günther), Grant's gazelle *Gazella granti* (Brooke), kongoni *Alcelaphus buselaphus* (Pallas) as well as buffalo *Syncerus caffer* (Sparrman), a species virtually absent from the Crater in 1963, increased moderately (Runyoro *et al.* 1995). Plains zebra *Equus burchelli* (Gray) and eland *Taurotragus oryx* (Pallas) numbers remained stable. In 1974, Masai pastoralists and their livestock were removed from the Crater floor, which led to a significant change in vegetation species composition (Moehlman, Runyoro & Hofer 1997). Additionally, the composition of the herbivore community changed substantially: the buffalo population increased significantly while populations of all other species declined significantly (Runyoro *et al.* 1995). These changes provided a 'natural experiment' to assess the impact of a long-term change in prey populations on the ecology of the most numerous large predator in the ecosystem, the spotted hyaena.

Generalist predators such as spotted hyaenas may respond to a decline in their main prey species by switching to other prey species (Bergerud & Elliot 1986), increasing scavenging and kleptoparasitizing other predators (Jorde & Lingle 1988), and/or declining in numbers (White, Vanderbilt White & Ralls 1996). We compare data from the pioneering study of Crater hyaenas by Kruuk (1966, 1972) in the 1960s with our own to investigate the long-term functional response of the Crater hyaena population to the decrease of their main prey species and analyse the extent of scavenging and kleptoparasitism between spotted hyaenas and lions, their main competitors. Kruuk's study period (March 1965–December 1967; Kruuk 1972) hereafter is referred to as period I, our study period (April 1996–June 1999) as period II.

FUNCTIONAL RESPONSE

From period I to period II the populations of wildebeest, zebra and gazelles, the herbivores that comprised 96% of the prey hyaenas hunted during period I (Kruuk 1972), declined strongly, while buffaloes increased by two orders of magnitude (Runyoro *et al.* 1995). It might thus be expected that hyaenas would have switched to hunting buffaloes during period II. However, as adult buffaloes are difficult prey for spotted hyaenas (Kruuk 1972; Cooper 1990), we expected hyaenas to hunt buffalo vulnerable to hyaena predation, such as calves and individuals weakened by drought and disease. In addition, spotted hyaenas might have increased predation pressure on those

declining herbivore species that were preferred prey during period I.

SCAVENGING AND INTERSPECIFIC KLEPTOPARASITISM

Spotted hyaenas are effective hunters that acquire most of their food by hunting but they also scavenge (e.g. Kruuk 1972). The opportunity to scavenge is determined by the availability of carcasses, which depends on the number of animals dying from causes other than predation and the number of prey killed by other predators in the area.

There has been one outbreak of rinderpest affecting buffaloes and eland in the Crater in 1982 since the beginning of herbivore counts in 1963 (Ngorongoro Ecological Monitoring Programme (NEMP) 1989). Mortality from rinderpest was moderate and of short-term benefit to the hyaenas as the buffalo population recovered quickly and doubled between 1980 and 1986 (Runyoro *et al.* 1995). In general, mortality in herbivores from causes other than predation are likely to provide only sporadic short-term increases in food supply.

Because buffalo were the only prey species that substantially increased from period I to period II, it is likely that the number of buffalo carcasses increased. Accordingly, we predicted that the proportion of scavenged buffalo carcasses in the total of scavenged carcasses should have increased from period I to II.

A predator may also compensate for a reduced food supply by scavenging carrion from or kleptoparasitizing other predators. The opportunity to do so is a function of the number of animals killed by other predators and their ability to retain their kills (Lamprecht 1978). The only predators likely to provide Crater hyaenas with a substantial amount of food on a regular basis are lions (Kruuk 1972). Work by Mills & Biggs (1993) suggests that the availability of lion kills to hyaenas should increase as the ratio of hyaenas to lions declines. Accordingly, hyaenas should scavenge more (less) from lions during period II than period I, particularly from large carcasses such as adult buffaloes, if the hyaena/lion ratio declined (increased) during this time.

The ability of carnivores to obtain and defend large carcasses from kleptoparasitism by competitors is likely to be influenced by a number of factors, including the respective group sizes during such encounters (Lamprecht 1978; Cooper 1991; Mills & Biggs 1993; Carbone, Du Toit & Gordon 1997). We will examine in detail factors that determine the outcome of such encounters between lions and spotted hyaenas in the Ngorongoro Crater and compare them with data from other studies.

Methods

The Ngorongoro Crater is a 250-km² large caldera situated at 3° South and 35° East in north-western

Tanzania. We studied the behaviour and ecology of the spotted hyaena population inhabiting the Crater floor between April 1996 and June 1999. Observations were conducted during more than 6200 h from a vehicle usually between 06.00 h and 12.00 h in the morning and 16.00 and 19.00 h in the evening. During period I, observations were also made mainly during daylight hours (Kruuk 1972). Members of Crater clans were well habituated to our presence.

DIET COMPOSITION AND PREY POPULATIONS

Data on the feeding ecology of hyaenas were obtained ad libitum while following individuals or when incidentally encountering hyaenas feeding. A 'kill' was defined as a prey killed by one or several hyaenas and a 'carcass' as a prey either killed by a predator other than spotted hyaenas or that had died of a reason unrelated to predation. We defined scavenging 'in the strict sense' as feeding from prey that was killed and abandoned by another predator or that had died of a reason unrelated to predation. Kleptoparasitism was defined as the aggressive acquisition of a carcass from another predator. Scavenging 'in the broad sense' included both scavenging in the strict sense and kleptoparasitism. The species, sex and approximate age (adult, sub-adult or juvenile) of carcasses was recorded. Prey populations and kills were divided into the categories adults (including sub-adults) and juveniles. The two gazelle species, Thomson's and Grant's gazelle, were merged into the category 'gazelles'. The carnivore species responsible for a kill was determined in most cases by direct observation or after inspecting the carcass and nearby tracks (Kruuk 1972; Mills 1990). When hyaenas and lions were observed together on a kill, fresh blood covering heads and full stomachs of animals were indicative of which species had killed and fed first. Cases where the cause of death of the carcass could not be determined were not considered for the comparison of the proportion of diet obtained by scavenging. Carcass states were estimated at the point of takeover or when observations were terminated while hyaenas and lions were still together at a kill, and classified as: 1, intact; 2, intestines and some other internal organs eaten, carcass otherwise intact; 3, abdominal cavity and rib cage open, all internal organs and most muscle eaten; 4, all internal organs and muscle eaten, leg(s) missing; 5, only head, backbone and part of the rib cage left. Fragments from carcasses (e.g. bones, pieces of skin) hyaenas chewed or carried were not considered for diet analysis.

Total mean population sizes of the herbivore species inhabiting the Crater during period II were available from total counts of all large herbivores conducted by the NEMP during the dry and wet seasons of 1996–99. For period I, numbers of herbivores presented in Runyoro *et al.* (1995) for the years 1965 and 1966 (wet season) and 1964 and 1969 (dry season) were used because no dry season censuses were conducted during

period I. If more than one census was conducted during a season, data were averaged to provide a mean estimate.

HUNTING PREFERENCES

The selection ratio \hat{w}_i for prey category i was calculated by dividing the proportion killed o_i by the proportion available in the herbivore population π_i (Manly, McDonald & Thomas 1993). To describe hunting preferences we used the standardized selection ratio α_i (Chesson 1978, 1983) as $\alpha_i = (o_i/\pi_i)/(\sum_{j=1}^m o_j/\pi_j)$, or in terms of selection ratios \hat{w}_i , $\alpha_i = \hat{w}_i/(\sum_{j=1}^m \hat{w}_j)$ (Manly *et al.* 1993). α_i gives the estimated probability that a randomly selected killed prey will be in category i if all categories are equally frequent in the original population of available resource units (Manly *et al.* 1993). Unlike many other measures of preference (e.g. Ivlev 1961), α_i does not change with prey density, i.e. it controls for density of prey type. It only changes with changes in the behaviour of predators and is thus the appropriate measure for detecting 'switching' behaviour (Chesson 1983). To separate preferences for adults and juveniles of each species, population sizes of adults and juveniles were calculated on the basis of estimates of the ratio of juveniles to adults and total population size for each prey species presented in Runyoro *et al.* (1995) and obtained by the NEMP (Table 1). Juvenile/adult ratios were calculated from transect counts conducted during period II (Höner 2001). For period I the same ratios were applied, except for zebra and wildebeest for which empirical estimates of the juvenile/adult ratio were available (Klingel 1969; Estes & Estes 1979). To assess changes in hunting preference, the selection ratios \hat{w}_i of the two periods were compared using estimates of standard errors, confidence limits and chi-squared statistics developed by Manly *et al.* (1993), and denoted by χ^2_M . Wildebeest, zebra, the two gazelle species, and buffalo were included to calculate hunting preferences of Crater spotted hyaenas.

HYAENA/LION RATIOS AND LION SEX RATIOS

The Crater hyaena/lion ratio for period II was calculated using the mean of the number of adult and sub-adult hyaenas and lions present on 1 December of each study year. We determined hyaena population size (Höner 2001) on the basis of individual recognition (Hofer & East 1993a). Lion population sizes were estimated by individually identifying lions by their vibrissae spots (Pennycuik & Rudnai 1970) using photographs taken when lions were involved in interactions with hyaenas, particularly at kills, and when encountered incidentally. Our estimates were similar to those obtained by scientists monitoring the lion population in the Crater (G. Hopcraft & B. Kisui, personal communication). The age of lions was estimated following Packer *et al.* (1991). The hyaena/lion ratio for period I was calculated using Kruuk's (1972) minimum

Table 1. Hunting preferences of spotted hyaenas in the Ngorongoro Crater during period I (1965–67) and period II (1996–99). Preferences of period I were calculated on the basis of data from Kruuk (1972)

| Species | <i>n</i> available | Proportion available π_i | <i>n</i> kills | Proportion hunted o_i | Selection ratio \hat{w}_i | SE (\hat{w}_i) | Standardized selection ratio α_i | χ^2_M | <i>P</i> | Sign of preference |
|----------------|-----------------------|---------------------------------|-------------------|----------------------------|--------------------------------|--------------------|--|------------|-----------|--------------------|
| Period I | | | | | | | | | | |
| Wildebeest ad | 12 611 | 0.556 | 109 | 0.464 | 0.83 | 0.06 | 0.031 | 8.16 | 0.0043 | – |
| Wildebeest juv | 2 121 | 0.094 | 69 | 0.294 | 3.14 | 0.20 | 0.118 | 110.87 | < 0.00001 | + |
| Zebra ad | 3 725 | 0.164 | 29 | 0.123 | 0.75 | 0.15 | 0.028 | 2.87 | 0.09 | 0 |
| Zebra juv | 1 038 | 0.046 | 18 | 0.077 | 1.67 | 0.30 | 0.063 | 5.10 | 0.024 | + |
| Gazelles ad | 3 100 | 0.137 | 1 | 0.004 | 0.03 | 0.16 | 0.001 | 34.95 | < 0.00001 | – |
| Gazelles juv | 52 | 0.002 | 8 | 0.034 | 14.84 | 1.36 | 0.557 | 103.49 | < 0.00001 | + |
| Buffalo ad* | 18 | 0.001 | 1 | 0.004 | 5.36 | 2.31 | 0.201* | 3.55 | 0.06 | (+) |
| Buffalo juv | 1 | 0.000 | 0 | 0.000 | 0.00 | 9.82 | 0.000 | 0.01 | 0.92 | 0 |
| Total | 22 666 | | 235 | | | | | | | |
| Period II | | | | | | | | | | |
| Wildebeest ad | 6 097 | 0.356 | 38 | 0.463 | 1.30 | 0.15 | 0.045 | 4.11 | 0.043 | + |
| Wildebeest juv | 1 017 | 0.059 | 21 | 0.256 | 4.31 | 0.44 | 0.150 | 56.77 | < 0.00001 | + |
| Zebra ad | 2 854 | 0.167 | 10 | 0.122 | 0.73 | 0.25 | 0.025 | 1.18 | 0.28 | 0 |
| Zebra juv | 266 | 0.016 | 2 | 0.024 | 1.57 | 0.88 | 0.055 | 0.42 | 0.52 | 0 |
| Gazelles ad | 2 932 | 0.171 | 2 | 0.024 | 0.14 | 0.24 | 0.005 | 12.47 | 0.00041 | – |
| Gazelles juv | 49 | 0.003 | 4 | 0.049 | 17.04 | 2.06 | 0.592 | 60.57 | < 0.00001 | + |
| Buffalo ad* | 3 673 | 0.215 | 1 | 0.012 | 0.06 | 0.21 | 0.002 | 19.93 | < 0.00001 | – |
| Buffalo juv | 230 | 0.013 | 4 | 0.049 | 3.63 | 0.95 | 0.126 | 7.73 | 0.0054 | + |
| Total | 17 118 | | 82 | | | | | | | |

*If very few animals of a prey type with small population size are killed, selection ratios should be treated with caution (Manly *et al.* 1993).

ad, adult; juv, juvenile; SE (\hat{w}_i), standard error of \hat{w}_i ; sign of preference: + overselected, – underselected, 0 selected according to expectation based on proportion of prey available.

estimates of sub-adult and adult hyaenas, and the mean of the numbers of adult and sub-adult lions on the 1 December 1965, 1966 and 1967 calculated from Fig. 2 in Packer *et al.* (1991). This minimum ratio made tests of our predictions conservative. Lion sex ratios during period I were calculated from Fig. 2 in Packer *et al.* (1991).

DATA FROM OTHER STUDIES

We extracted data on scavenging and hyaena/lion kleptoparasitism from other relevant studies. As in this study, we excluded feeding events on single bones, scraps, old desiccated carcasses, unidentified pieces and carcasses of unknown origin from the analysis and recalculated the respective percentages of carcasses that hyaenas scavenged from lion kills and acquired by kleptoparasitizing lions. These data were compared with results from the Crater.

STATISTICAL ANALYSIS

Statistical analyses were performed on a personal computer using SYSTAT 9.0, following Sokal & Rohlf (1981) and Lamprecht (1992). Manly *et al.* (1993) provided an approximate test for the significance of the selection ratio \hat{w}_i , and differences between selection ratios from the two periods with critical values approximately distributed according to the χ^2 distribution with one degree of freedom. Unless otherwise indicated, results are quoted as means with standard deviations, and *P*-values for two-tailed tests.

Results

During period II, spotted hyaenas were observed to feed on 124 carcasses for which the cause of death could be determined. Of these, 69% ($n = 85$) were killed by hyaenas, and 31% ($n = 39$) were scavenged in the broad sense (both kleptoparasitized carcasses and those scavenged in the strict sense). During period I, hyaenas were observed feeding on 262 carcasses of which 93% ($n = 244$) were killed by hyaenas and 7% ($n = 18$) were scavenged from other predators or died from causes other than predation (Kruuk 1972). Scavenging in the broad sense thus significantly increased from period I to period II ($\chi^2 = 37.63$, $P < 0.001$, $n = 386$).

HUNTING PREFERENCES

Of 85 prey animals killed by spotted hyaenas during period II (1996–99), wildebeest, zebra, Thomson's gazelle and Grant's gazelle comprised 90.6%, buffalo 5.9% (Table 1) and other species 3.5% ($n = 3$ kills). Of 244 prey killed by hyaenas during period I (1965–67), wildebeest, zebra and gazelles comprised 95.9%, buffalo 0.4% (Table 1) and other species 3.7% ($n = 9$ kills) (Kruuk 1972). The assessment of hunting preferences in Table 1 and the comparison between the two study periods excluded the 'other species' category.

During period II, hyaenas hunted significantly higher proportions of adult wildebeest and juvenile wildebeest, juvenile gazelles and juvenile buffaloes than would have been expected from the herbivores' respective abundances (Table 1). Adult zebra and zebra

Table 2. Changes in hunting preference of spotted hyaenas between period I and period II in the Ngorongoro Crater

| Species | Difference between selection ratios $\hat{w}_{i \text{ Period II}} - \hat{w}_{i \text{ Period I}}$ | Variance | χ^2_M | <i>P</i> | Direction of change in preference |
|----------------|---|----------|------------|----------|-----------------------------------|
| Wildebeest ad | 0.47 | 0.03 | 8.00 | 0.0047 | – to + |
| Wildebeest juv | 1.17 | 0.76 | 1.81 | 0.18 | No change |
| Zebra ad | –0.02 | 0.06 | 0.01 | 0.94 | No change |
| Zebra juv | –0.10 | 1.35 | 0.01 | 0.93 | No change |
| Gazelles ad | 0.11 | 0.01 | 1.14 | 0.29 | No change |
| Gazelles juv | 2.20 | 95.86 | 0.05 | 0.82 | No change |
| Buffalo ad | –5.30 | 28.93 | 0.97 | 0.32 | No change |
| Buffalo juv | 3.63 | 3.13 | 4.21 | 0.04 | 0 to + |

ad, adult; juv, juvenile; direction of change in preference: + overselected, – underselected, 0 selected according to expectation based on proportion of prey available.

foals were hunted according to their abundance, and adult gazelles and adult buffaloes were hunted less often than expected from their abundance.

During period I, hyaenas hunted juvenile wildebeest, zebra, and gazelles, more often than expected and adult wildebeest and gazelles less often than expected from their abundance (Table 1). Hyaenas were not observed killing old, sick or weak adult buffaloes, during either period II or period I.

FUNCTIONAL RESPONSE

The numerical composition of hunted prey in the categories ‘adult wildebeest’, ‘juvenile wildebeest’, ‘adult zebra’, ‘juvenile zebra’ and ‘adult and juvenile gazelles’ did not differ between the two periods ($\chi^2 = 4.71$, d.f. = 4, NS, $n = 311$).

A comparison of hunting preferences by hyaenas during period I and II demonstrates a significant change in behaviour for two prey categories (Table 2). Adult wildebeest changed from being taken less often than expected during period I to being over-represented as hyaena prey during period II. Buffalo calves changed from being selected according to their abundance during period I to being hunted more often than expected during period II.

SCAVENGING IN THE BROAD SENSE

Hyaenas scavenged (in the broad sense) from 22 carcasses from lions, four from jackals *Canis* spp., and a carcass from both a cheetah *Acinonyx jubatus* (Schreber) and a leopard *Panthera pardus* (Linnaeus). Eleven carcasses from which hyaenas fed were not apparently killed by any predator. Of the 39 carcasses scavenged in the broad sense, 25 (64%) were kleptoparasitized from other predators, whereas 14 carcasses either died from causes unrelated to predation or were killed and abandoned by another predator (scavenging in the strict sense). Buffalo comprised 26% ($n = 10$) of all carcasses scavenged during period II, significantly more than during period I when hyaenas were not observed to scavenge from buffalo carcasses (Fisher exact test, $P < 0.05$, $n = 57$).

SCAVENGING IN THE STRICT SENSE

Fourteen of 124 carcasses (11.3%) were scavenged in the strict sense and came from a variety of species. Adult wildebeest and adult buffaloes were the most important, with three carcasses each. There was no difference in the proportion of buffaloes that were scavenged in the strict sense by hyaenas in the total of scavenged carcasses between period I and period II ($n = 0$ of 18 carcasses of all species during period I and $n = 3$ of 39 carcasses of all species during period II; Fisher exact test, NS, $n = 57$).

TEMPORAL CHANGES IN SCAVENGING AND KLEPTOPARASITISM FROM LIONS

The ratio of hyaenas to lions in the Crater was 4.2 : 1 during period II and 14 : 1 during period I. These two ratios significantly differed, with relatively fewer hyaenas during period II ($\chi^2 = 18.95$, $P < 0.001$, $n = 544$). The mean adult sex ratio of female to male lions during period II was 2.1 : 1 and did not significantly differ from the ratio of 1.3 : 1 during period I ($\chi^2 = 0.62$, NS, $n = 42$).

During period II, hyaenas and lions simultaneously fed from a carcass or fed shortly after each other on 40 occasions. Excluding five cases when the predator responsible for the kill was unknown, hyaenas killed the victim in 54% ($n = 19$) and lions in 46% ($n = 16$) of cases. During period I, of 55 carcasses on which both lions and hyaenas fed, the victim was killed by hyaenas in 93% ($n = 51$) of cases and lions in only 7% ($n = 4$) (Kruuk 1972). Thus, when both hyaenas and lions were present at a carcass, lions were more likely to have killed the prey during period II than during period I ($\chi^2 = 18.41$, $P < 0.001$, $n = 90$).

Of the 16 lion kills during period II at which hyaenas and lions simultaneously fed, three carcasses were adult buffaloes, whereas during period I, hyaenas and lions were not observed together at an adult buffalo killed by lions (Kruuk 1972). There was no difference between the two periods in the probability of hyaenas and lions being present at buffaloes killed by lions (Fisher exact test, NS, $n = 20$).

Table 3. Hyaena/lion kleptoparasitism in the Ngorongoro Crater during period II

| Lion kills | | | | Spotted hyaena kills | | | | |
|--|-------------------------------|-----------------------------|-----------------------------|---|-------------------------------|-----------------------------|-----------------------------|-------------------------|
| Prey species | State of carcass ^a | No. LI present ^a | No. HY present ^a | Prey species | State of carcass ^a | No. HY present ^a | No. LI present ^a | Carcass obtained by LI? |
| <i>Takeover by hyaenas observed</i> | | | | <i>Takeover by or arrival of lions observed</i> | | | | |
| WI juv | 1 | 1af | 7 | WI juv | 3 | 6 | 2am | Yes |
| WI ad | 2 | 1af | 3 | EQ ad | 3 | 10 | 1am | Yes |
| WI ad | 2 | 1af | 12 | WI ad | 4 | 11 | 1am, 1af | Yes ^b |
| WI ad | 1 | 1af | 13 | BU juv | 4 | 11 | 1am, 2af | Yes ^b |
| WI ad | 3 | 2sm | 11 | WI juv | 5 | 17 | 2am | No |
| WI ad | 2 | 3af | 9 | <i>Lions had already arrived</i> | | | | |
| WI ad | 2 | 3af, 1sm | 17 | WI juv | 2 | 1 | 1af | Yes |
| EQ ad | 3 | 2af | 9 | WI juv | 3 | 3 | 1am, 1af, 1sm, 3cu | Yes |
| EQ ad | 1 | 2af | 24 | WI ad | 5 | 1 | 1sm | Yes |
| BU ad | 2 | 2sm, 2sf | 14 | WI ad | 4 | 3 | 1am | Yes |
| WI ad | 3 | 1am, 1af | 11 ^c | WI ad | 2 | 9 | 1am | Yes |
| WI ad | 4 | 2am | 13 ^c | WI ad | 4 | 15 | 1am | Yes |
| WI ad | 5 | 2am, 2af | 14 ^c | WI ad | 3 | 20 | 2af | Yes |
| BU ad | 4 | 1am, 1af | 7 ^c | WI ad | 3 | 12 | 2am | Yes |
| WI ad | 4 | 1sm | 1 ^d | WI ad | 4 | 12 | 2am | Yes |
| BU ad | 3 | 5af, 1sm | 14 ^d | WI ad | 4 | 28 | 2am, 1af, 1sm | Yes |
| <i>Carcass obtained by hyaenas but details of acquisition not observed^e</i> | | | | WI ad | 4 | 14 | 2am, 2af | Yes |
| BU ad | 4 | ? | ? | WI ad | 5 | 8 | 2am, 2af, 2sm | Yes |
| BU ad | 4 | ? | ? | WI ad | 4 | 27 | 2am, 3af, 1sm | Yes |
| BU ad | 4 | ? | ? | EQ juv | 3 | 6 | 4af | Yes |
| BU ad | 5 | ? | ? | EQ ad | 3 | 28 | 1am, 1af | Yes |
| HY juv | 4 | ? | ? | WI ad | 4 | 10 | 2sm | No |
| HY ad | 3 | ? | ? | WI ad | 3 | 11 | 1am | No |
| <i>Outcome unknown because observation terminated</i> | | | | | | | | |
| OS ad | 3 | 3af, 2cu | 1 | | | | | |
| WI ad | 3 | 1sm | 1 | | | | | |
| WI ad | 3 | 2af | 1 | | | | | |
| WI ad | 2 | 1am, 1af | 10 | | | | | |
| WI ad | 3 | 3am, 1af | 4 | | | | | |
| BU ad | 3 | 1am | 12 | | | | | |
| BU ad | 1 | 3am, 1af | 3 | | | | | |
| BU ad | 3 | 2am, 3af | 4 | | | | | |
| BU ad | 3 | 2am, 3af, 1sf | 16 | | | | | |

^aState of carcass or number of predators present determined when kill was obtained or when observation was terminated, respectively.

^bLions took over carcass when adult male lion approached.

^cHyaenas waited until adult male lions left and then obtained carcass.

^dLions left carcass because of reasons unrelated to hyaenas (approach by buffalo herd and tourist vehicle, respectively) and hyaenas acquired carcass.

^eAcquisition of carcass by hyaenas observed by other scientist or rangers, respectively.

HY, spotted hyaena; LI, lion; WI, wildebeest; EQ, zebra; BU, buffalo; OS, ostrich *Struthio camelus* (L.); ad, adult; juv, juvenile; af, adult female; am, adult male; cu, cub; sf, sub-adult female; sm, sub-adult male.

Hyaenas scavenged (in the broad sense) from 22 lion kills during period II (Table 3). Kruuk (1972) did not specify the cause of death for the 18 carcasses hyaenas fed from during period I, but at least four carcasses were lion kills (see above). Even if all other 14 carcasses were also lion kills, hyaenas scavenged (in the broad sense) more often from lions during period II than during period I ($\chi^2 = 9.99$, $P < 0.01$, $n = 386$). Of the 22 lion kills hyaenas obtained during period II, 19 (86%) were adult large herbivores and seven (37%) of these were buffaloes. During period I, hyaenas were not observed to scavenge from adult buffalo carcasses (Kruuk 1972).

DYNAMICS OF HYAENA/LION ENCOUNTERS AT KILLS

Adult male lions were absent from the majority (60%, $n = 15$) of lion kills during period II at which hyaenas were also present (Table 3). Hyaenas (mean group size = 11.9 ± 5.8 , range = 3–24) aggressively acquired the carcass from lions (mean group size = 2.1 ± 1.2 , range = 1–4) in all 10 cases where adult male lions were absent (Table 3). In contrast, hyaenas never took over lion kills when adult male lions were present ($n = 4$). Thus, presence or absence of adult male lions significantly affected the chance of hyaenas acquiring a

carcass from lions (Fisher exact test, $P = 0.001$, $n = 14$). Hyenas acquired lion kills when the hyaena/lion ratio was on average 6.8 ± 4.0 (range = 3–13).

When there were no adult male lions present, hyenas acquired carcasses from lions before the lions had consumed the majority of the carcass (state 1, state 2 and state 3; Table 3). In contrast, when at least one adult male lion was present the hyenas only obtained the carcass after the male lions had left the carcass. In these cases a larger proportion of the carcass had been consumed (state 3, state 4, state 5; Table 3). Thus, hyenas obtained a significantly smaller amount of food from lion kills when adult male lions were present (Fisher exact test, $P = 0.01$, $n = 14$).

How severe was lion kleptoparasitism at hyaena kills? During period II, lions were attracted to 26% ($n = 22$) of hyaena kills ($n = 85$) and took over 22% ($n = 19$) of kills. When lions approached a hyaena kill ($n = 5$), the hyenas abandoned the kill when at least one adult male lion arrived, no matter how many hyenas were present (Table 3). In one case the hyenas retreated from two approaching male lions but the lions did not attempt to acquire the remains of a wildebeest calf. In 15 cases (18%) lions fed from a hyaena kill while the hyenas remained in the vicinity. During period I, lions were attracted to 21% ($n = 51$) of hyaena kills and lion kleptoparasitism occurred in 19% ($n = 47$) of cases (Kruuk 1972). There was no significant change between period I and period II in the probability of lions arriving at hyaena kills ($\chi^2 = 0.88$, NS, $n = 329$) or lions kleptoparasitizing hyenas ($\chi^2 = 0.37$, NS, $n = 329$). Also, hyenas were equally successful in retaining their kills from lions during period II (14%) and period I (8%) (Fisher exact test, NS, $n = 73$).

During period II, hyenas obtained 22 kills from and lost 19 to lions. During period I, hyenas lost 47 kills to lions, 2.6 times more than the maximum number of kills they could have obtained from lions ($n = 18$). The ratio of kills hyenas obtained from lions vs. kills lost to lions was significantly higher during period II than during period I ($\chi^2 = 7.18$, $P < 0.01$, $n = 106$), i.e. hyenas profited more from lions during period II than during period I.

TOTAL DIET

Considering all carcasses consumed by hyenas (including cases where the cause of death was unknown), wildebeest, zebras, Thomson's and Grant's gazelles comprised 75% of the total diet during period II compared to 94% during period I. The contribution of adult wildebeest, juvenile wildebeest, adult zebra, juvenile zebra, adult gazelles and juvenile gazelles did not differ between the two periods ($\chi^2 = 3.88$, d.f. = 5, NS, $n = 401$). During period II, the diet of hyenas included a larger proportion of buffaloes (0.13, $n = 21$) than during period I (0.003; $n = 1$) ($\chi^2 = 38.44$, $P < 0.001$, $n = 458$). Despite this increase, the proportion of buffaloes consumed during period II was lower than the proportion of buffaloes available.

HYAENA/LION KLEPTOPARASITISM IN DIFFERENT STUDY SITES

Table 4 summarizes results on hyaena/lion kleptoparasitism from seven studies. There was no relationship between the hyaena/lion ratio in these populations and the percentage of lion kills from which hyenas fed (Spearman rank correlation for low values of percentage of lion kills in hyaena diet: $\rho = 0.257$, NS, $n = 7$; for high values of percentage of lion kills in hyaena diet: $\rho = 0.236$, NS, $n = 7$).

The hyaena/lion ratio in our study population (period II) and that studied in Chobe National Park (Cooper 1990, 1991) were the same (Table 4). The population sex ratio of adult female to male lions in Chobe was 5.7 : 1, which was 2.5 times higher than the sex ratio in this study. In Chobe, 32% ($n = 34$; calculated from Cooper 1991) of lion feeding groups on lion kills with hyenas present had no adult male lion nearby. This value was significantly lower than that in our study ($\chi^2 = 6.74$, $P < 0.01$, $n = 131$). Chobe hyenas were significantly less likely (27%) to displace adult female and sub-adult lions from their kills than Crater hyenas (Fisher exact test, $P < 0.001$, $n = 43$). The mean lion group size in the Crater was 2.3 ± 1.5 adult female and sub-adults at a kill (range = 1–6, $n = 15$), 2.5 times lower than the mean of 5.6 ± 2.7 (range = 1–10, $n = 29$) in Chobe (calculated from Fig. 2 in Cooper 1991).

Discussion

FUNCTIONAL RESPONSE

As predicted, spotted hyenas in the Crater exhibited a functional response to the long-term decline of their main prey species and the increase in the buffalo population. Adult wildebeest that were hunted less often than expected during period I were taken more often than expected during period II, and buffalo calves that were hunted according to expectation during period I were hunted more often than expected during period II. These changes in hunting preferences were significant even though the overall contribution of the major prey items to the numerical composition of the diet changed little between periods I and II. Wildebeest calves and gazelle fawns were preferred prey during both periods. Despite their population increase adult buffaloes were hunted less often than expected during period II. These findings suggest that hyenas responded to the prey population changes by switching to and increasing their hunting preference for categories of prey that were relatively easy to hunt.

SCAVENGING AND INTERSPECIFIC KLEPTOPARASITISM IN THE CRATER

Spotted hyenas are well adapted to utilize food sources left by other large carnivores: their molars are specifically designed to crack large bones and their

Table 4. Hyaena/lion ratio, percentage of lion kills in hyaena diet, and relative amount of food hyaenas scavenged from lion kills and acquired by kleptoparasitising lions in six different study sites

| Study site | Hyaena/lion ratio | Percentage of lion kills in hyaena diet | Relative amount of food hyaenas obtained from lion kills | Daytime of observations ^c | Reference |
|--|-------------------|---|--|--------------------------------------|---|
| Ngorongoro Crater, Tanzania, period I | 14 : 1 | 2–7 ^a | Not specified | Mainly daytime | Kruuk 1972 |
| Ngorongoro Crater, Tanzania, period II | 4 : 1 | 18 | A lot in 80%, medium in 20% | Mainly daytime | This study |
| Chobe National Park, Botswana | 4 : 1 | 24–33 ^b | A lot in 25%, little in 75% | Only night | Cooper 1990, 1991 |
| Masai Mara National Reserve, Kenya | 3 : 1 | 2 ^c | Little in 100% | Mainly daytime | Ogutu & Dublin 1998; Cooper, Holekamp & Smale 1999 |
| Etosha National Park, Namibia | 2 : 1 | 0–17 ^a | Little in 100% (only leftovers) | Only night | Gasaway, Mossestad & Stander 1991 |
| Kruger National Park, South Africa | 1 : 1 | 25 | Medium to little (only leftovers) | Mainly night | Henschel & Skinner 1987, 1990; Mills & Biggs 1993 |
| Southern Kalahari, Botswana/South Africa | 0.6 : 1 | Low ^d | Mainly leftovers | Day and night | Mills 1990 |

^aThe cause of death was not specified for some carcasses. A minimum and a maximum percentage was calculated by treating these carcasses as carcasses with unknown cause of death (and thus excluding them from the analysis) or by allocating them to lion kills, respectively.

^bFor carcasses that did not originate from predator kills it was not stated whether the cause of death was unknown (and thus should be excluded from the analysis) or the animals died of reasons unrelated to predation. Cooper (1991) stated that most of these carcasses consisted of bones, i.e. were carcasses we excluded from our analysis. We thus excluded 50% plus one carcass from the analysis. With the remaining ones a minimum and a maximum value was calculated by allocating them to carcasses with unknown cause of death or to carcasses that died from reasons other than predation, respectively.

^cThe cause of death for carcasses that did not originate from predator kills was not stated. Minimum and maximum values calculated as in note b yielded the same percentage.

^dNo value supplied, but Mills (1990) noted that interference competition between spotted hyaenas and lions was very rare because of the low densities of both predators.

^eObservations during daytime tend to overestimate the amount of food scavenged by spotted hyaenas (Mills 1990). Thus, when daytime observations were made, percentage of lion kills in hyaena diet are maximum estimates.

digestion system extracts 90% of the food including bones (Kruuk 1972; Houston 1988). In the Crater, their main food competitors are lions since other large predators such as wild dogs *Lycaon pictus* (Temminck), cheetahs and leopards are either not present or occur at very low densities.

Studies on hyaena/lion kleptoparasitism in other ecosystems suggested that the availability of carcasses to hyaenas and their chance to acquire carcasses from lions is influenced by: (a) the ratio of hyaenas to lions in the ecosystem (Mills & Biggs 1993), and (b) the ratio of adult male to female lions (Cooper 1991) in the ecosystem. In the Crater the hyaena/lion ratio declined significantly from period I to period II whilst the ratio of adult male to female lions did not change appreciably. Despite this decrease in the hyaena/lion ratio, lions were present at hyaena kills and kleptoparasitized hyaenas at the same rate during both periods which suggests that the relatively less numerous, and probably more widely spaced hyaena kills during period II were more difficult for lions to detect or more costly for them to attend in terms of travel distance. Hyaenas were also equally able during periods I and II to retain their kills from challenges by lions, indicating that hyaenas during period II recruited sufficient clan members to defend kills despite the decrease in the hyaena/lion ratio.

Crater hyaenas aggressively took over a lion kill when they outnumbered female or sub-adult lions by a factor of at least 3, but retreated when at least one adult male lion appeared. These results suggest that (i) the ratio of the number of hyaenas to the number of female or sub-adult lions at a lion kill, and (ii) the presence of a male lion may determine whether lions can prevent kleptoparasitism by hyaenas or acquire kills from hyaenas, rather than the sex ratio in the lion population at large.

As the sex ratio of the adult lion population was similar during period I and II, no difference between the periods would be expected in the ability of hyaenas to acquire lion kills or deter lions from their kills. This was the case for hyaenas deterring lions. Interestingly, hyaenas acquired more kills from lions during period II than period I, and the ratio of kills that hyaenas obtained from lions vs. kills they lost to lions also increased. Thus, hyaenas benefited more from lions during period II than period I, possibly due to an increase in the number of lion kills per hyaena and sufficient recruitment of hyaenas to challenge lions. The overall proportion of carcasses hyaenas scavenged from and acquired by kleptoparasitizing lions was higher during period II than period I. In particular, hyaenas fed from a higher proportion of adult buffalo carcasses. This was chiefly due to an increase in the number of buffaloes killed by lions and obtained by hyaenas.

This study is, to our knowledge, the first to demonstrate that a functional response of a predator population to changes in its prey populations occurs in conjunction with a change in foraging mode.

HYAENA/LION KLEPTOPARASITISM

In the Crater, spotted hyaenas scavenged from and took over more lion kills when the population hyaena/lion ratio was relatively low (period II) than when it was high (period I). However, across all study sites there was no relationship between this ratio and the proportion of lion kills from which hyaenas fed (Table 4).

To investigate the factors that determine the outcome of hyaena and lion encounters at kills and the effect of the adult lion population sex ratio on hyaena kleptoparasitism we compared two studies (Crater period II vs. Chobe) with the same hyaena/lion ratio but different adult lion sex ratios. In Chobe the population sex ratio of adult female to male lions was 5.7 : 1 and Cooper (1991) stated that female and sub-adult lions seriously suffered from kleptoparasitism by spotted hyaenas. Among Crater lions the ratio of adult females to males was considerably lower than in Chobe, suggesting that Crater hyaenas should be more likely to encounter lion kills with an adult male lion present and thus should have less access to lion kills than Chobe hyaenas. The data available, however, show a significant difference in the opposite direction. This finding indicates that factors other than the sex ratio of the adult lion population influence the ability of hyaenas to kleptoparasitize lions.

Cooper (1991) stated that the ability of hyaenas to kleptoparasitize lions not only depends on the sex ratio of the adult lion population but also on (i) the ratio of hyaena foraging group size to female and sub-adult lion feeding group size at kills, and (ii) female and sub-adult lion feeding group size at kills. Cooper (1991) found that Chobe hyaenas acquired lion kills when there was a mean ratio of 3.7 hyaenas per lion at the kill, and considered this to be the critical ratio required for takeover. In the Crater, the mean ratio was 6.8 hyaenas per lion when takeovers occurred. These differences either suggest that Crater hyaenas were more effective in recruiting clan members to lion kills than Chobe hyaenas, or that the mean ratio required for a takeover was higher in the Crater than in Chobe.

Crater hyaenas aggressively took over 100% of lion kills when adult male lions were absent, whereas Chobe hyaenas took over only 27% of such kills. This suggests that Crater hyaenas were more effective in recruitment than Chobe hyaenas and that the number of female and subadult lions present was not a factor that limited the probability of Crater hyaenas acquiring a lion kill.

What threshold hyaena group size is required to guarantee displacement of female and sub-adult lions from their kills, and what level of recruitment in terms of total clan size does this represent? Applying the Chobe ratio of 3.7 hyaenas per lion (when the success of displacement was only 27%) and the mean Chobe lion foraging group size of 5.6, yields a threshold group size of 20.7, representing 41% of the mean clan size in Chobe. Using parameter values from the Crater

(ratio of 6.8 hyaenas per lion and mean foraging group size of 2.3), then the threshold group size of hyaenas is 15.6 hyaenas, or 61% of the mean total clan size in the Crater. These rough estimates suggest that Chobe clans should have been able to recruit a larger proportion of clan members to lion kills. Why did Crater hyaenas succeed and Chobe hyaenas fail?

First, we know that in the Crater actual group sizes at takeover corresponded or exceeded the estimated threshold group sizes. Data from Chobe on actual hyaena group sizes at takeover are not available, but the lower success rate in Chobe suggests that these threshold group sizes were less often reached. We suggest that the difference between Crater and Chobe lie in the efficiency by which clan members can be recruited to a kill.

The smaller mean territory size of Crater clans of 27 km² corresponds to a circular area with a radius of 2.9 km, whereas the larger territories of more than 100 km² in Chobe would be equivalent to a circle with a radius exceeding 5.6 km. Previous hyaena studies have shown and argued that recruitment over a distance of up to 4–5 km by loud calls is possible (Mills 1990; East & Hofer 1991). This suggests that recruitment in the Crater is more likely to be successful than in Chobe.

We thus conclude that the factors that determine the outcome of hyaena and lion encounters at kills in the Crater are the presence of adult male lions at the kill and the ability of hyaenas to recruit sufficient clan members for an aggressive takeover.

KLEPTOPARASITISM AND THE EVOLUTION OF GROUP SIZE

In contrast to small predators such as jackals, large predators need large prey to satisfy their requirements, and thus their hunts tend to be conspicuous (Lamprecht 1978). An increase in foraging group size is likely to result in a more successful defence of kills against interspecific competitors (Lamprecht 1978). Caraco & Wolf (1975) found that group sizes of lions at kills were usually larger than would be predicted on the basis of maximum foraging efficiency. Several explanations have been suggested to interpret this finding including kin selection (Rodman 1981; Giraldeau 1988), minimizing the risk of starvation (Clark 1987), per capita pay-offs for solitary and group animals (Giraldeau 1988), and co-operative cub defence, territorial defence and female reproductive patterns (Packer, Scheel & Pusey 1990). Our data suggest that kleptoparasitism by spotted hyaenas may be another factor influencing group size patterns in lions (see also Cooper 1991). Studies that investigated hunting and foraging group sizes of wild dogs (Fanshawe & FitzGibbon 1993; Carbone, Du Toit & Gordon 1997) similarly found that the success of wild dogs to defend carcasses against kleptoparasitism by hyaenas increased with wild dog group size at kills.

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