

Competition refuges and coexistence: an example from Serengeti carnivores

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Summary

1. In the last two decades predator–prey models have shown that ‘refuges’, in which prey can seek respite from predation, are crucial for the persistence of prey and predator. This concept is equally applicable to interspecific competition and, in a heterogeneous environment, species with low competitive ability should seek out ‘competition refuges’ where competition is reduced.

2. Cheetahs have low competitive ability compared with their principal competitors, hyenas and lions, which are directly responsible for their low density. This study uses distribution data collected in the Serengeti National Park in Tanzania over a 4-year period to show that cheetahs are more strongly associated with each other than with their competitors and utilize areas with low-density prey.

3. Cheetahs exhibit local avoidance behaviour in both space and time with respect to lions and hyenas. This behaviour is facultative and is strongest when cheetahs are engaged in activities that might expose them to food loss or increase the risk of close interactions, such as when they are hunting or eating.

4. Lactating cheetahs, whose range is restricted, are more likely to have difficulties finding prey and come into more frequent contact with lions than free-ranging animals.

5. It is argued that although cheetahs always lose in direct competition, they persist in the ecosystem by seeking out ‘competition refuges’ with low densities of lions and hyenas and that their mobility is the key to their continued coexistence with these predators. This pattern of distribution may be generally applicable to other species which, although widely distributed, always occur at low densities.

Key-words: cheetahs, migration, spatial heterogeneity, predator avoidance, rarity.

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Introduction

Early models of interspecific competition predicted that coexistence of competing species is only possible if intraspecific competition is greater than interspecific competition, since otherwise one species always outcompetes the other (Lotka 1925; MacArthur & Levins 1967; Tilman 1982). Even when competitive coexistence does occur, very often the precise conditions needed under these simple models can be so restrictive that they are unlikely to occur in the real world (May 1975). Since many species undoubtedly do compete with each other and appear to do so more strongly with other species than with themselves and yet still manage to coexist (Creel & Creel 1996), another explanation is necessary.

Models have been developed to show that resource partitioning (MacArthur & Levins 1967; Roughgarden 1974) and fluctuating environments (Chesson & Warner 1981; Chesson & Huntly 1989) can promote

coexistence. However current thinking suggests that the key to coexistence relies on spatial heterogeneity (Chesson 1985; Hanski 1994). This can arise either as a consequence of variation in physical features, or because of aggregation in plant and animal communities. In these systems a competitively inferior species can escape competition by arriving at a patch first, by using a different kind of patch, or by finding empty patches which result from clumped distributions of competitors (Shorrocks 1991). In all cases this leads to a reduction in interspecific competition relative to intraspecific competition (Shorrocks 1991). Avoidance of competitors can greatly magnify this effect (Ives & Dobson 1987; Chesson & Rosenzweig 1991).

Studies are beginning to acknowledge the key role which habitat heterogeneity plays in promoting species coexistence (Chesson 1985). The concept of *predator refuges*, in which prey can seek respite from predation, is well known within predator–prey systems, and can be crucial for the persistence of both prey

and predator (Hassell & May 1973). This concept can equally be applied to interspecific competition and, in a heterogeneous environment, species with low competitive ability can persist by making use of *competition refuges* where competition is reduced. There is now ample evidence showing that heterogeneity can promote coexistence of predator–prey (Turchin & Kareiva 1989; White, Murray & Lewis 1996) and host–parasite systems (Murdoch *et al.* 1989; Lampo 1994; Schrag & Mittler 1996), however examples in competitive systems are rare (Hassell 1978), perhaps because of their complexity.

Temporal heterogeneity exerts a weaker stabilizing effect compared to spatial heterogeneity (Chesson 1985), but can also be important if it can be linked to spatial heterogeneity; for example, if species aggregate, move and aggregate again in different localities. Averaged over a long period, such a system might appear to have little spatial heterogeneity, yet at any particular moment may be extremely heterogeneous. Similarly, averaged over a large area there may appear to be little temporal heterogeneity, yet at any location there may be extensive temporal fluctuations. In this type of system, temporal heterogeneity acts in concert with spatial heterogeneity. In this paper an example is presented of such a system from a guild of large African carnivores.

In the Serengeti National Park in Tanzania cheetahs (*Acinonyx jubatus*) have low competitive ability compared with their principal competitors, spotted hyenas (*Crocuta crocuta*) and lions (*Panthera leo*), which are postulated to be directly responsible for their low density (Laurenson 1995). Cheetah cubs suffer a high mortality in their first 4 months of life due to direct predation by these carnivores (Laurenson 1994) and adult and adolescent cheetahs are chased from their kills by them (Caro 1994). Both these competitors are highly social and live in aggregated groups. Hyenas live in clans averaging 45 individuals (Hofer & East 1995) and lions live in social prides averaging 15 individuals (Schaller 1972).

All three predators, at least in part, rely upon migratory prey species. In the wet season the plains in the south-east of the park are flooded with white-bearded wildebeest (*Connochaetes taurinus*), common zebra (*Equus burchelli*) and Thomson's gazelle (*Gazella thomsoni*). This migration leads to large temporal and spatial variation in the availability of prey. The migratory herds attract large numbers of hyenas which, due to their commuting lifestyle, are able to exploit these prey (Hofer & East 1995). Lions, which are generally territorial, are less mobile and, except for a smaller number of nomadic lions, are concentrated in the woodland margins (Schaller 1972).

The niche overlap of all three predators is large and previous studies have found it difficult to explain their coexistence (Frame 1986). Lions depend on wildebeest, zebra, Thomson's gazelle, buffalo (*Syncerus caffer*) and warthog (*Phaecochoerus aethiopicus*) in

decreasing proportions (Scheel & Packer 1995), whereas hyenas depend on wildebeest, Thomson's gazelle and zebra and, to a lesser extent, Grant's gazelle (*Gazella granti*), topi (*Damaliscus korrigum*) and kongoni (*Alcelaphus buselaphus*) (Kruuk 1972). Cheetahs principally prefer Thomson's gazelle, then hares (*Lepus* spp.), wildebeest and Grant's gazelle (Caro 1994). However, there are differences in predator hunting behaviour. Hyenas prefer to hunt large groups of prey, generally selecting out target animals from rushing herds (Kruuk 1972). By contrast, cheetahs, which are stalking predators, prefer to target small groups of widely dispersed gazelle (FitzGibbon 1990). This is because small groups have lower vigilance levels than large ones and are less likely to detect an approaching predator (FitzGibbon 1988). Lions, which prefer to hunt at night and in groups (Schaller 1972), also prefer small herds of prey (Scheel 1992), but depend less on Thomson's gazelle than do cheetahs and hyenas (Kruuk 1972; Schaller 1972; Scheel 1992; Caro 1994). It is unlikely that these species are separated because of some other factor, as all three species make use of similar habitats (Frame 1986).

The patchy distribution of lions and hyenas may enable cheetahs to persist in the ecosystem if they are able to employ local avoidance behaviour. Evidence from playback experiments shows that cheetahs actively move away from calls of both lions and hyenas (Durant, unpublished). In addition, female cheetahs are extremely mobile. They are able to exploit migratory prey and move from the woodland edges in the dry season to the short grass plains in the wet season (Durant *et al.* 1988). Also, since they have higher hunting success when hunting small groups of prey, they are likely to be able to persist within *competition refuges*, where there are low densities of both prey and competitors. It is therefore hypothesized here that high mobility, coupled with a high hunting success on low density prey, is the key to the coexistence of cheetahs with lions and hyenas.

The following predictions which result from this hypothesis will be tested in this paper: (i) cheetahs are found in areas with lower densities of prey compared to their competitors; (ii) cheetahs are found in areas where competitors are at low density whilst other cheetahs are at similar or higher density; (iii) avoidance increases as the density of competitors increases through dry to wet season; and (iv) cheetahs with a restricted range, and hence reduced mobility, are more likely to come into contact with other predators. This last prediction will be tested by comparing lactating and non-lactating female cheetahs.

Methods

STUDY AREA

The study area covers a 2200 km² region in the south-east of the Serengeti National Park in Tanzania (for

a full description see Caro 1994). Within this area the habitat ranges from open woodland dissected with rivers in the north and west, through the long grasslands, to the short grass plains in the south-east. The area is scattered with rocky outcrops known as 'kopjes' which support trees and bushes, often the only available cover on the open plains. Rainfall follows a gradient from an annual 1000 mm in the north-west to 600 mm in the south-east (Campbell & Hofer 1995) and is concentrated in the wet season, starting in November and ending in June (Sinclair 1979). Very little rain falls in the dry season from July to October.

The variation in seasonal rainfall patterns drives the migratory patterns of the large herbivores in the ecosystem. Huge herds of wildebeest, zebra and Thomson's gazelle move onto the short grass plains when the rains start in November to make use of the nutritious short swards in this area (Maddock 1979; McNaughton 1976, 1988). When the rains stop in June the herds of wildebeest and zebra begin their long trek west and north, spending the end of the dry season in the Mara river catchment area in the north of the ecosystem. Thomson's gazelle follow a less extensive migration, moving only as far as the woodland borders to the north and west of the plains during the dry season (Durant *et al.* 1988). They move out onto the short grass plains prior to the arrival of the wildebeest, whilst their migration north and west lags behind that of the wildebeest (Bell 1971; McNaughton 1976). Their small mouths enable them to concentrate on the new shoots at the start of the rains and the short-mown grass left behind after the wildebeest have passed through at the end of the rains (Bell 1971; McNaughton 1976). Cheetahs in the study area have been studied intensively since the mid-1970s (Caro & Laurenson 1994). Each cheetah can be individually recognized by distinctive spot patterns on its face and haunches.

DATA COLLECTION

From October 1991 until October 1995, detailed data on vegetation cover, prey densities and predator distribution were collected at each cheetah sighting. In addition identical data were collected from 739 scan points distributed across the study area (Fig. 1). Scan points were used to locate cheetahs and were therefore centred on high vantage points with good all-round visibility. Cheetahs used similar vantage points for observing prey and potential competitors (Caro 1987). Scan point locations were therefore biased towards sampling upper catena habitats. Thirty-six scan points were visited at least once every 2 months throughout the year during the 42-month period covered by observers. The remaining scan points were visited depending on the season; for example, more scan points were visited in the north and west of the study area in the dry season when cheetahs were most concentrated in this area, whilst more scan points were

visited on the southern plains during the wet season. A total of 3997 scans were collected for this study, over half of which were collected by a single observer, the remaining by a further four observers. All data were entered directly into Psion Organisers (model LZ64), which also automatically timed each scan.

PHYSICAL FEATURES

During the first 19 months of the study locations of scan points were estimated to within 500 m from 1 : 50 000 maps published by the government of Tanzania. Afterwards locations were estimated by a geographical positioning system (Trimble Flightmate) to within an accuracy of 100 m. At each scan point visibility in four different directions, north, east, south and west, was graded by eye as 1, 2 or 3 km; this was then translated into two area measurements; area 1 to 2 km and area 2 to 3 km, defined as the number of directions (out of four—north, east, south and west) in which it was possible to see at least 2 km and 3 km, respectively. Heat haze was graded as 4 if none were present and as 1, 2 or 3 if it was possible to see a predator at 1, 2 or 3 km. Weather, which can affect visibility both directly and indirectly by affecting predator activity, was graded according to the following categories.

1. Sunny, when cloud did not pass overhead and obscure the sun during the entire period of the scan.
2. Light cloud, when cloud temporarily passed in front of the sun during the scan.
3. Medium cloud, when cloud obscured the sun throughout the scan.
4. Heavy cloud, when low, dark clouds obscured the sun throughout the scan.
5. Drizzle, when rain fell lightly at some time during the scan.
6. Rain, when rain fell heavily at some time during the scan.

Estimating prey and predator densities

Variable circular plots were used to count numbers of prey and predators seen from scan points (Buckland *et al.* 1993). Cheetahs living on the Serengeti plains rely on Thomson's gazelle as their major prey (Caro 1994). Therefore numbers of these gazelle within 1 km of the scan point were counted at each scan. Also, since hunting success of cheetahs varies with group size (FitzGibbon 1988), cheetahs may prefer particular densities of gazelle. Therefore between June and September 1996 a series of counts was made of both the number of gazelle within 1 km and the number of groups, defined to be any collection of individuals that were at least 100 m from any other gazelle. Mean group size was then calculated by dividing the number of gazelle seen by the number of groups. This data was then used to test whether an increase in the

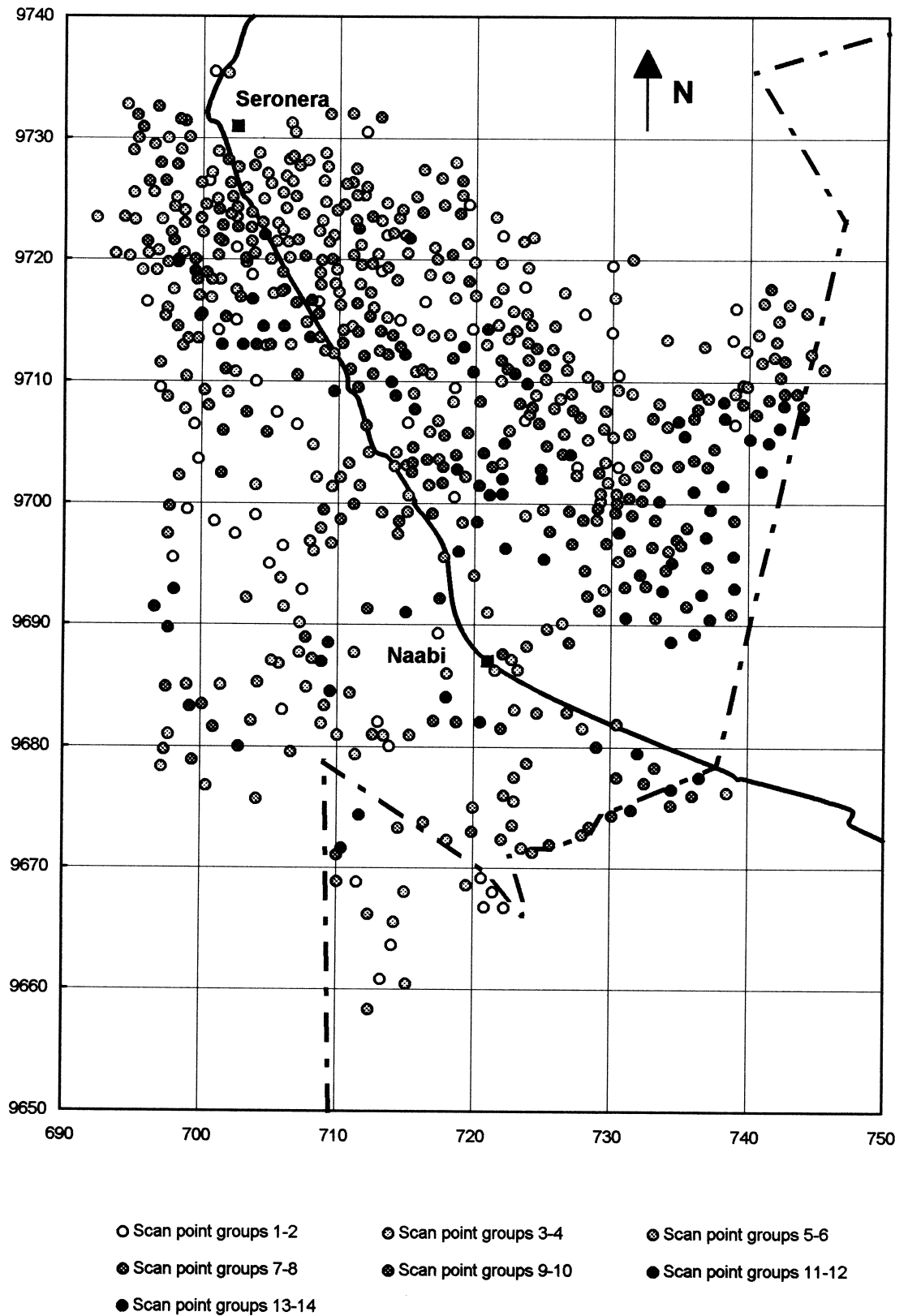


Fig. 1. Scan point locations. Each symbol indicates one of the 739 scan points used for this study. A generalized linear model with Poisson errors corrected for overdispersion was used to fit scan point location to the number of Thomson's gazelle seen in scans. Initially a full model, which fitted each location separately, was employed and was then reduced by aggregating together locations with statistically similar parameter estimates. Aggregation was halted when any further aggregation resulted in a significant change in deviance. The full model explained a deviance of 462 019, dispersion coefficient of 191, whilst the final model explained a deviance of 455 674, dispersion coefficient of 156. The difference between the two models gave $\chi^2_{20} = 40.67$, NS. The degree of shading of each symbol indicates the scan point group after points were aggregated. Each increase in shading represents an increase across two scan point groups (see legend). The x and y axes represent UTM co-ordinates where 10 map grid intervals represent 10 km.

number of gazelle seen during a scan resulted in an increase in mean group size.

The numbers of gazelle seen during scans were additionally allocated to nine 'number categories', as cheetahs might respond to particular densities of gazelle rather than absolute numbers. These categories were assigned as: 0, 1–10, 11–25, 26–50, 51–100, 101–250, 251–500, 501–1000 and > 1000 (Durant *et al.* 1988), and were later reduced to those categories that were statistically meaningful to cheetah distribution (see Results). In a small number of scans ($n = 222$), gazelle were not individually counted but were merely assigned a number category. These scans were excluded from analyses of total numbers of gazelle.

A mean and standard error of 1054 ± 8 s were spent searching for large predators in an intensive scan with 10×50 binoculars. When a predator was seen, its distance from the scan point was estimated by eye. Predators could be seen at distances of up to, and occasionally beyond, 3 km. Statistical analyses focused on the number of predators within 1 km, 2 km and the total number seen. Absolute numbers were used rather than density as these were more relevant to cheetah responses. However it should be noted that the proportion of predators seen at 2 or 3 km was lower than those seen at 1 km because detectability of predators declines with distance (Buckland *et al.* 1993). Therefore counts were indicative, but were not actual estimates, of absolute numbers. Nonetheless the numbers seen will correlate with the number present and with the number likely to be seen by cheetahs, and can be used for comparisons between scans.

If a cheetah was seen then the observer approached the cheetah slowly and in a zig-zag fashion to minimize disturbance (Caro 1994). The observer then conducted another scan centred on the cheetah's location. These scans were termed 'cheetah scans'. For statistical analyses of cheetah presence/absence, scans were divided into those in which no cheetahs were seen and *cheetah scans*, which were either centred on a cheetah or were scans in which a cheetah was seen within 500 m of the scan point (scans where cheetahs were seen beyond 500 m yet where none were seen within 500 m were excluded from these analyses). In most cases *cheetah scans* were centred on the location of the cheetah.

Cheetah sightings

Cheetahs were located by driving to scan points and searching through binoculars. Cheetahs are most active, and hence most easily seen, in the early morning and late afternoon and so most scans were made during these periods. Once located and approached, cheetahs were individually identified using their distinctive spot patterns. Scans conducted from cheetahs were classified into three categories according to the activity of the cheetah during the scan. Hunting scans

were those in which a cheetah was hunting or eating during the scan; moving scans were those in which a cheetah moved more than 500 m during the scan. All other scans were counted as resting/vigilant, when the cheetah could have been resting throughout the scan, sitting up, or could have moved less than 500 m.

Female cheetahs were classified as lactating if their mammary glands were full and the fur around their nipples was matted and brown (an indication that they had been recently suckling cubs). If a female was lactating and was seen alone, then she must have had dependent cubs hidden in a lair. The cubs remain in a lair for their first 2 months of life; their mother leaves every day in order to hunt, returning late in the evening (Laurenson 1992). During this period the mother's range is restricted to the region in the immediate vicinity of the den, generally within a mean distance of 3.3 km (Laurenson 1994).

Statistical analyses

Both prey and predator distributions were highly aggregated and skewed with high frequencies of zeros. Therefore a generalized linear model with Poisson errors was fitted to the distributions and all analyses were corrected for overdispersion using the methods outlined by McCullagh & Nelder (1989, pp. 121–124). Such correction was not necessary when analysing simple presence/absence measures, whose effects were analysed using logistic regression models. Analyses of Thomson's gazelle number categories were conducted using a multinomial model with Pearson errors.

Scan point locations were reduced for analysis by fitting a generalized linear model to each dependent prey and predator variable and aggregating those locations which had similar parameter estimates until further aggregations caused a significant change in the deviance explained by the model.

Analyses of Thomson's gazelle numbers and number categories controlled for observer, year and location. Analyses of predator counts also controlled for these factors where significant, but additionally controlled for other factors that were likely to affect predator visibility; for example, active predators were more likely to be seen than inactive ones, and activity varied through the day. Therefore factors included in these analyses were time spent scanning, time of scan, the quadratic of time of scan (since predator activity is high in the morning and evening and low at mid-day), heat haze, area 1 to 2 km, area 2 to 3 km and weather.

Most analyses of predator counts, which involved many independent variables, were conducted by deleting terms stepwise. This was achieved by first including all terms, then dropping the least significant terms one-by-one until all remaining terms were significant. Some analyses investigating effects of lactation and activity of cheetahs on the number of lions seen contained too few data for all terms to be initially included

in the model. Here, terms which explained the most deviance were added to the model one-by-one in a forwards regression until adding a further term caused a significant change in the deviance. If this approach was used rather than a backwards regression, it has been indicated in the text. Terms were judged as significant when deviance (corrected for overdispersion where necessary) gave a probability of less than 5% according to χ^2 tables. All statistical analyses were conducted using the GENSTAT 5 (version 3.1) statistical package (Payne *et al.* 1987).

Results

PREY SPECIES

Thomson's gazelle counts differed greatly according to scan point location, illustrating extensive spatial heterogeneity in prey distributions (Fig. 1). Scan points were aggregated into 14 groups that corresponded to areas with similar numbers of Thomson's gazelle when averaged over the study period. Points with high numbers of gazelle tended to be on the short grass plains in the south-east of the study area, while points with low numbers tended to be closer to the woodland borders.

Mean group size increased as the number of Thomson's gazelle seen within the 1 km counting radius during scans increased (correlation of the logarithm of mean group size on the logarithm of gazelle numbers $r^2 = 0.829$, $P < 0.001$). Therefore when few gazelle were seen in scans, groups tended to be smaller and gazelle were more scattered, whereas when many gazelle were seen, groups were larger and gazelle were more aggregated.

Thomson's gazelle numbers varied with predator presence. Significantly fewer gazelle were seen from cheetah scans than scans where no cheetah were seen (Table 1a). However, significantly more gazelle were observed from scans in which a hyena or lion was seen than were observed from scans where no hyena or lion was seen (Table 1b and c). This effect was particularly strong when analysing hyena presence.

In order to determine whether predators favoured particular densities of Thomson's gazelle, a generalized linear model was fitted to the binomial variate which described whether or not the numbers of gazelle seen in a scan fell under a particular number category; for example, for the 1–10 number category of gazelle, the binomial response variate was set to one if between one and 10 gazelle were seen in a scan, and zero if no gazelle or more than 10 gazelle were seen. This analysis showed that number categories seen in scans varied with cheetah presence (Table 2). In general, cheetahs avoided areas with no gazelle and concentrated around areas with low numbers of gazelle. When gazelle number categories were further aggregated into four categories (zero, low, intermediate and high, which corresponded to 0, 1–25, 26–250 and >250,

respectively) according to the sign and significance of the coefficient from this analysis, all number categories differed significantly between cheetah scans and scans in which no cheetahs were seen (Table 3). Cheetahs avoided areas with no gazelle or with high numbers of gazelle and showed a strong preference for low and intermediate numbers of gazelle.

Hyenas, like cheetahs, tended not to be seen when no gazelle were seen in scans. However, whereas cheetahs preferred low and intermediate numbers of gazelle, hyenas preferred intermediate and high numbers (Table 3). Lions were attracted to areas with the highest numbers of gazelle only (Table 3). They may have been less affected by Thomson's gazelle numbers than hyenas, either because of their territorial constraints or because they were less reliant on this species for prey (Schaller 1972).

Thomson's gazelle numbers varied markedly with season (controlling for year, observer and location; effects of season $\chi^2_1 = 27.64$, $P < 0.001$, interaction between location and season $\chi^2_{13} = 80.97$, $P < 0.001$). This is probably because this species is migratory and moves to the plains in the wet season and into the woodlands on the edge of the study area during the dry season (see also Durant *et al.* 1988).

The frequency with which different number categories of gazelle were seen in scans also changed with season (Thomson's gazelle number category as the dependent multinomial variate, controlling for observer, year and location: effects of season $\chi^2_1 = 24.42$, $P < 0.001$; interaction between location and season $\chi^2_{13} = 158.07$, $P < 0.001$). The low and intermediate number categories preferred by cheetahs, were seen in scans more frequently in the dry season than in the wet season, whereas the zero and high number categories were seen less frequently (Fig. 2). This indicates that the gazelle distribution was more clumped in the wet season, which may be explained by the peak in the birth rate during these months (Caro 1994).

When numbers of Thomson's gazelle seen in scans were analysed within seasons, fewer gazelle were seen in cheetah scans compared with scans in which no cheetah was seen in both wet and dry seasons (controlling for observer, year and location, in the wet season: effect of cheetah presence $\chi^2_1 = 9.56$, $P < 0.01$ and in the dry season: effect of cheetah presence $\chi^2_1 = 13.48$, $P < 0.001$). The frequency of different number categories of gazelle also varied with cheetah presence within seasons. During the wet season cheetahs were less likely to be seen in scans with zero or high numbers of gazelle, and more likely to be seen around low and intermediate numbers (Table 4a). In the dry season cheetahs were less likely to be present in scans with high numbers of gazelle and more likely to be present in scans with low numbers. However they were no more likely to be present or absent in scans with zero or intermediate numbers of gazelle (Table 4b).

Table 1. Variation in the number of Thomson's gazelle with predator presence. A generalized linear model with Poisson errors and corrected for overdispersion was fitted to the numbers of Thomson's gazelle seen in scans. The table gives changes in deviance explained by each term in the model: observer identity, aggregated location, and year for: (a) cheetah ($n = 3569$); (b) hyena ($n = 3203$); and (c) lion ($n = 3557$) presence. Analyses for each predator species do not include scans where the predator concerned was seen beyond 1 km but was not seen within 1 km

Parameter	Coefficient estimate	Deviance	Dispersion	d.f.	χ^2	<i>P</i>
(a)						
Location	–	404 904	260	13	1557.32	<0.001
Year	–	18 055	152	4	118.78	<0.001
Observer	–	5734	148	4	38.74	<0.001
Cheetah presence	–0.24	2215	147	1	15.07	<0.001
(b)						
Location	–	309 820	228	13	1358.86	<0.001
Year	–	12 771	135	4	94.60	<0.001
Observer	–	7529	134	4	56.19	<0.001
Hyena presence	+0.44	14 335	136	1	105.40	<0.001
(c)						
Location	–	401 946	260	13	1545.95	<0.001
Year	–	21 436	153	4	140.10	<0.001
Observer	–	7409	149	4	49.72	<0.001
Lion presence	+0.26	1558	147	1	10.60	<0.01

The number of gazelle seen in cheetah scans showed a weak relationship with cheetah activity during scans in the wet season (Table 4a). Most gazelle were seen from resting cheetahs and fewest from hunting cheetahs. However there was no relationship between the number category of gazelle seen and cheetah activity in either the wet season (Thomson's gazelle number category as the dependent multinomial variate, controlling for observer, year and location: effects of cheetah activity $\chi^2_2 = 1.66$, NS) or the dry season (Thomson's gazelle number category as the dependent multinomial variate, controlling for observer, year and location: effects of cheetah activity $\chi^2_2 = 1.01$, NS).

PREDATORS

Counts of predators strongly depended on the time spent looking and on factors affecting visibility (Tables 5 and 6). These effects, where significant, were controlled for in all analyses. Analyses of numbers of lions and hyenas additionally controlled for location by following a procedure identical to that used to aggregate scan points for Thomson's gazelle. This procedure reduced scan points to ten groups for lions and nine groups for hyenas.

The visibility of predators declined markedly with distance. Across all scans analyses predicted an average of 0.567 hyenas, 0.124 lions and 0.064 cheetahs within 1 km, 0.324, 0.080 and 0.047 between 1 and 2 km and 0.191, 0.038 and 0.026 beyond 2 km. This decline was partly because distances of beyond 1 km were not always visible across the entire 360° of a scan. On average, it was only possible to see up to a

distance of 2 km over 79%, and beyond 2 km over 61% of this angle. When counts were corrected for these differences and for the ratio of the area visible for each distance (ratio of area visible within 1 km to the area between 1 and 2 km and to the area between 2 and 3 km is 1:4:9), hyenas were 18% less likely to be seen between 1 and 2 km than within 1 km and 6% less likely to be seen beyond 2 km. The corresponding visibility figures for lions were 20% and 6%, and for cheetahs 23% and 7% respectively, both similar to those for hyenas.

This sharp decline in visibility of predators with distance is explained, in part, by the low visibility of inactive predators beyond 1 km, where recumbent predators were rarely seen. However, from the point of view of the cheetah, visibility of other predators is likely to show a similar decline with distance, and so the numbers of predators seen by an observer remains relevant to cheetah responses, despite the decrease in the detection of predators.

Significantly more hyenas were seen in scans in the wet season than in the dry season (Table 5), whereas lion numbers did not differ between seasons (Table 6). The number of hyenas and lions seen in scans varied significantly with the interaction between season and location, indicating that particular areas or habitats were favoured in different seasons by both species (Tables 5 and 6). This effect became less marked within large distances for lions, losing significance for the total number of lions seen, implying that preferred areas were more locally distributed than for hyenas, as might be expected for this territorial species.

The higher densities of hyenas seen in the wet season indicate that cheetahs should be most strongly

Table 2. Variation in particular number categories of Thomson's gazelle with cheetah presence. A logistic regression was fitted to the binomial variate describing the presence of each number category of Thomson's gazelle across 3769 scans where cheetahs were either within 500 m of the scan point or were not seen at all. The table gives the amount of deviance explained by each term in the model: observer identity, aggregated location, year and cheetah presence

Parameter	Coefficient estimate	Deviance	d.f.	P
(a) Frequency of scans with zero Thomson's gazelle				
Location	–	577.89	13	<0.001
Year	–	100.13	4	<0.001
Observer	–	58.57	4	<0.001
Cheetah presence	–0.63	32.31	1	<0.001
(b) Frequency of scans with 1–10 Thomson's gazelle				
Location	–	234.09	13	<0.001
Year	–	14.12	4	<0.01
Observer	–	9.79	4	<0.05
Cheetah presence	+0.29	7.12	1	<0.01
(c) Frequency of scans with 11–25 Thomson's gazelle				
Location	–	71.68	13	<0.001
Year	–	3.23	4	NS
Observer	–	8.02	4	NS
Cheetah presence	+0.42	9.64	1	<0.01
(d) Frequency of scans with 26–50 Thomson's gazelle				
Location	–	109.65	13	<0.001
Year	–	18.47	4	<0.001
Observer	–	9.63	4	<0.05
Cheetah presence	+0.26	3.40	1	NS
(e) Frequency of scans with 51–100 Thomson's gazelle				
Location	–	124.38	13	<0.001
Year	–	4.44	4	NS
Observer	–	0.98	4	NS
Cheetah presence	+0.28	3.65	1	NS
(f) Frequency of scans with 101–250 Thomson's gazelle				
Location	–	277.82	13	<0.001
Year	–	8.10	4	NS
Observer	–	15.14	4	<0.01
Cheetah presence	+0.06	0.23	1	NS
(g) Frequency of scans with 251–500 Thomson's gazelle				
Location	–	271.40	13	<0.001
Year	–	7.65	4	NS
Observer	–	7.25	4	NS
Cheetah presence	–0.38	3.51	1	NS
(h) Frequency of scans with 501–1000 Thomson's gazelle				
Location	–	337.24	13	<0.001
Year	–	8.23	4	NS
Observer	–	25.58	4	<0.001
Cheetah presence	–0.39	2.68	1	NS
(i) Frequency of scans with > 1000 Thomson's gazelle				
Location	–	150.00	13	<0.001
Year	–	15.77	4	<0.01
Observer	–	3.34	4	NS
Cheetah presence	–0.87	2.44	1	NS

influenced by hyenas at this time. This prediction was supported by the data collected in this study, summarized in Table 4. In the wet season significantly fewer hyenas were seen in cheetah scans than in scans where no cheetah was seen (Table 4a), but in the dry

season there was no difference between these two scan types (Table 4b).

Since lion density did not change with season, there should be no difference in the influence these predators have on the movements of cheetah with season. How-

Table 3. The relationship between numbers of Thomson's gazelle and presence of predators. The table shows the sign and significance of the effect of the presence of cheetahs, hyenas or lions on total numbers and different number categories of Thomson's gazelle seen in scans. + = a positive relationship, - = a negative relationship. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Analyses of total numbers of Thomson's gazelle fitted a generalized linear model with Poisson errors and corrected for overdispersion. Analyses of number categories of Thomson's gazelle fitted a logistic regression to the presence of each number category. All analyses controlled for observer, year and location

	Presence of predator		
	Cheetah	Hyena	Lion
Number of Thomson's gazelle	-***	+***	+**
Scans with no Thomson's gazelle	-***	-***	NS
Scans with 1-25 Thomson's gazelle	+***	NS	NS
Scans with 26-250 Thomson's gazelle	+**	+**	NS
Scans with more than 250 Thomson's gazelle	-**	+***	+*

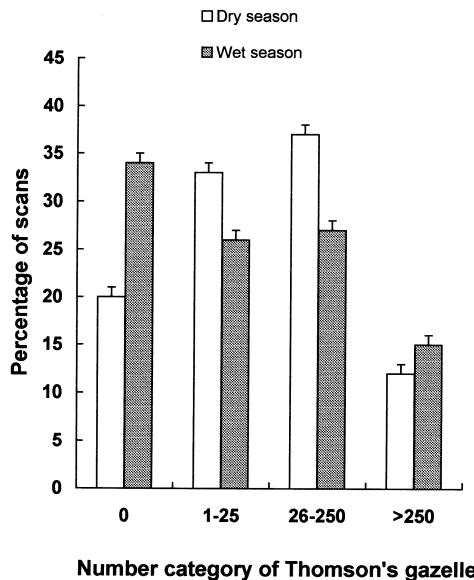


Fig. 2. Number of scans with different number categories of Thomson's gazelles separated by season. Bars indicate standard error estimates. Logistic regressions across 3974 scans controlling for observer, year and location, showed that scans with zero gazelle (effects of season $\chi^2_1 = 81.94$, $P < 0.001$; interaction between location and season $\chi^2_{13} = 61.89$, $P < 0.001$) and more than 250 gazelle (effects of season $\chi^2_1 = 8.79$, $P < 0.01$; interaction between location and season $\chi^2_{13} = 49.01$, $P < 0.001$) were significantly less common in the dry season. Whilst scans with 1-25 gazelle (effects of season $\chi^2_1 = 16.00$, $P < 0.001$; interaction between location and season $\chi^2_{13} = 61.78$, $P < 0.001$) and 26-250 gazelle (effects of season $\chi^2_1 = 35.63$, $P < 0.001$; interaction between location and season $\chi^2_{13} = 40.34$, $P < 0.001$) were significantly more common.

ever, although significantly fewer lions were seen within 1 km of cheetahs in the wet season, in the dry season no more lions were seen within 1 km from cheetah scans than from scans in which no cheetah was seen (Table 4). In addition, the number of lions seen within 2 or 3 km was higher from cheetah scans than from scans in which no cheetah was seen. At this time cheetahs are highly concentrated around the

Seronera River in the north-west of the study area (Durant *et al.* 1988), which is also the home of several large lion prides. In this area the chance of seeing a lion from any scan point was high, which could make it difficult for cheetahs to avoid lions. Hyenas were much more highly aggregated than lions, as illustrated by their markedly higher dispersion coefficients (Tables 5 and 6), making avoidance of these predators easier. In both seasons cheetahs were more likely to be seen from cheetah scans than from scans in which no cheetah was seen (Table 4).

Cheetahs were more likely to be moving and less likely to be hunting if there were many lions in the vicinity in both seasons (Tables 4a and b), indicating that their behavioural responses to these predators did not differ with season. In the wet season, when hyena density was highest, cheetahs responded to hyenas in a pattern similar to their response to lions (Table 4a). The highest numbers of hyenas were seen from scans centred on moving cheetahs, whilst the lowest from scans centred on hunting cheetahs. However, in the dry season, when overall observed hyena numbers were low, cheetahs were most likely to be hunting if high numbers of hyenas were seen within 1 or 2 km (Table 4b). Cheetahs altered their activity according to the number of cheetahs in the vicinity only in the dry season, when they tended to be less likely to hunt and most likely to move if there were cheetahs nearby (Table 4b).

The observed numbers of hyenas within a 1 km radius predicted by this analysis in the wet and dry season were 0.61 ± 0.02 and 0.51 ± 0.02 , respectively. These numbers indicate that there was a relative change in hyena density between seasons. Hunting behaviour of cheetahs was negatively correlated with hyena numbers at the higher density and not at the lower density, suggesting that they switch on this behavioural response when hyena densities reach a level somewhere between these two densities. Observed numbers of lions predicted by the analysis were 0.12 ± 0.01 in the wet season and 0.13 ± 0.01 in the dry season. These numbers were much lower than those for hyenas and they were similar in both seasons.

Table 4. The relationship between prey and predator numbers with cheetah presence and activity. The table shows the sign and significance of the effect of the presence and activity of cheetah on the total number and number categories of Thomson's gazelle and the number of predators seen from scans in the (a) wet and (b) dry season. In the cheetah presence column + = a positive relationship, - = a negative relationship. In the cheetah activity columns + = the activity most strongly correlated and - = the activity least correlated with gazelle or predator numbers. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ indicate respective levels of significance. Analyses of total numbers of Thomson's gazelle and predators fitted a generalized linear model with Poisson errors corrected for overdispersion. Analyses of number categories of Thomson's gazelle fitted a logistic regression to the presence of each number category. Analyses of gazelle numbers controlled for observer, year and location. Analyses of predator numbers also controlled for significant effects of these variables and additionally controlled for significant effects of time spent scanning, area 1 to 2 km, area 2 to 3 km, heat haze, weather, time of scan and time of scan²

		Presence of cheetah	Activity of cheetah		Moving
			Hunting	Resting	
(a) Wet season					
Prey					
Total number of Thomson's gazelle		-**	-*	+*	
Scans with no Thomson's gazelle		-***		NS	
Scans with 1-25 Thomson's gazelle		+**		NS	
Scans with 26-250 Thomson's gazelle		+***		NS	
Scans with more than 250 Thomson's gazelle		-*		NS	
Predators					
Number of cheetahs within	1 km	+***		NS	
	2 km	+***		NS	
	3 km	+***		NS	
Number of hyenas within	1 km	NS	-*		+*
	2 km	-*	-**		+**
	3 km	-*	-**		+**
Number of lions within	1 km	-***	-***	+***	+***†‡
	2 km	NS	-***		+***
	3 km	NS	-***		+***
(a) Dry season					
Prey					
Total number of Thomson's gazelle		-***		NS	
Scans with no Thomson's gazelle		NS		NS	
Scans with 1-25 Thomson's gazelle		+**		NS	
Scans with 26-250 Thomson's gazelle		NS		NS	
Scans with more than 250 Thomson's gazelle		-**		Insufficient data	
Predators					
Number of cheetahs within	1 km	+***	-*		+*
	2 km	+***		NS	
	3 km	+***	-***		+***
Number of hyenas within	1 km	NS	+**	-**	
	2 km	NS	+**	-**	
	3 km	NS		-*	+*
Number of lions within	1 km	NS	-***		+***†
	2 km	+***	-***		+***
	3 km	+***	-***		+***

† Because of the low number of lions seen within 1 km in cheetah scans, these analyses used forward regressions and did not control for year and weather.

‡ Cheetahs were just as likely to be resting as moving in this analysis.

CONSEQUENCES OF RANGE RESTRICTION

Scans taken from lactating females (who were constrained to the vicinity of a lair) were compared with scans from females that had accompanying cubs (who were not constrained in mobility) and used to test whether cheetahs with a restricted range were more likely to be found in areas with no prey and with higher densities of competitors. This comparison was chosen rather than one where territorial male cheetahs

were compared with nonterritorial males for two reasons: (i) floating male ranges are likely to be restricted because they are likely to try to avoid resident males (Caro 1994); and (ii) whilst nearly all lactating females become females with accompanying cubs, many floating males do not become territorial (S.M. Durant, personal observation).

In this study there were significantly fewer sightings of lactating females in the dry season compared to the wet season (10 sightings in the dry season compared

Table 5. Variation in the number of hyenas with location and season. A generalized linear model with Poisson errors and corrected for overdispersion was fitted to the number of hyenas seen within (a) 1 km, (b) 2 km and (c) 3 km of scan points. The table gives changes in deviance explained by each term in the model across 3955 scans. The final model includes all terms which significantly affect changes in deviance, and leaves out those terms which do not. Therefore deviances given refer to changes in deviance obtained when dropping significant terms from the model or from including nonsignificant terms. Variates included in the model are area visible between 1 and 2 km, area visible between 2 and 3 km, time spent scanning, time of scan, quadratic effect of time of scan and heat haze. Factors included in the model are observer identity, aggregated location, year, weather, location, season and the interaction between location and season

Parameter	Coefficient estimate	Deviance	Dispersion	d.f.	χ^2	<i>P</i>
(a) Number of hyenas within 1 km						
Year	–	12.38	1.44	4	8.60	NS
Observer	–	96.25	1.46	4	65.92	<0.001
Time spent scanning	+0.00045	91.59	1.46	1	62.73	<0.001
Time of scan	–0.052	51.97	1.45	1	35.84	<0.001
Time of scan ²	+0.0026	1.12	1.44	1	0.78	NS
Area between 1 and 2 km	+0.085	8.17	1.44	1	5.67	<0.05
Area between 2 and 3 km	+0.0092	0.15	1.44	1	0.10	NS
Heat haze	+0.21	78.28	1.46	1	53.62	<0.001
Weather	–	20.84	1.44	5	14.47	<0.05
Location	–	3099.84	2.23	9	1390.06	<0.001
Season	–	12.61	1.45	1	8.70	<0.01
Location × season	–	27.15	1.44	9	18.85	<0.05
(b) Number of hyenas within 2 km						
Year	–	68.50	2.18	4	31.42	<0.001
Observer	–	157.30	2.20	4	71.50	<0.001
Time spent scanning	+0.00064	289.84	2.24	1	129.39	<0.001
Time of scan	+0.038	5.60	2.16	1	2.59	NS
Time of scan ²	–0.0022	89.31	2.18	1	40.97	<0.001
Area between 1 and 2 km	+0.094	10.75	2.16	1	4.98	<0.05
Area between 2 and 3 km	+0.067	12.86	2.17	1	5.93	<0.05
Heat haze	+0.24	168.71	2.20	1	76.69	<0.001
Weather	–	29.60	2.17	5	13.64	<0.05
Location	–	2294.36	2.75	9	834.31	<0.001
Season	–	37.06	2.18	1	17.00	<0.001
Location × season	–	63.17	2.17	9	29.11	<0.001
(c) Total number of hyenas seen						
Year	–	59.01	2.51	4	23.51	<0.001
Observer	–	273.96	2.57	4	106.60	<0.001
Time spent scanning	+0.00067	415.98	2.61	1	159.38	<0.001
Time of scan	+0.031	4.28	2.50	1	1.71	NS
Time of scan ²	–0.0024	146.07	2.54	1	57.51	<0.001
Area between 1 and 2 km	+0.070	7.21	2.50	1	2.88	NS
Area between 2 and 3 km	+0.17	125.01	2.53	1	49.41	<0.001
Heat haze	+0.26	282.30	2.57	1	109.84	<0.001
Weather	–	27.52	2.50	5	11.01	NS
Location	–	2021.14	3.02	9	669.25	<0.001
Season	–	63.31	2.53	1	25.02	<0.001
Location × season	–	72.51	2.52	9	28.77	<0.001

to 50 in the wet season, goodness-of-fit test $\chi^2_1 = 7.50$, $P < 0.01$). In both wet and dry seasons fewer Thomson's gazelle were seen from scans taken from lactating female cheetahs than from those taken from nonlactating females (Fig. 3a). In addition, although number categories of gazelle seen in scans showed no significant independent variation with lactational status, there was a significant interaction between this variable and season (Thomson's gazelle number category dependent multinomial variate controlling for observer, year, location: effects of lac-

tation $\chi^2_1 = 1.63$, NS; interaction between lactation and season $\chi^2_1 = 7.24$, $P < 0.01$).

When scans were analysed within season, significantly fewer gazelle were seen in scans taken from lactating female cheetahs compared with scans taken from nonlactating females in both wet and dry seasons (Table 7). However, there were disparities between seasons in the number categories of gazelle seen from lactating females. The number category of gazelle seen in scans did not vary with lactational status in the wet season (Thomson's gazelle number category as

Table 6. Variation in the number of lions with location and season. A generalized linear model with Poisson errors and corrected for overdispersion was fitted to the number of lions seen within (a) 1 km, (b) 2 km and (c) 3 km of scan points. The table gives changes in deviance explained by each term in the model across 3955 scans. The final model includes all terms which significantly affect changes in deviance, and leaves out those terms which do not. Therefore deviances given refer to changes in deviance obtained when dropping significant terms from the model or from including nonsignificant terms. Variates included in the model are area visible between 1 and 2 km, area visible between 2 and 3 km, time spent scanning, time of scan, quadratic effect of time of scan and heat haze. Factors included in the model are observer identity, aggregated location, year, weather, location, season and the interaction between location and season

Parameter	Coefficient estimate	Deviance	Dispersion	d.f.	χ^2	<i>P</i>
(a) Number of lions within 1 km						
Year	–	24.72	0.50	4	49.44	<0.001
Observer	–	28.41	0.50	4	56.82	<0.001
Time spent scanning	+0.00024	4.46	0.49	1	9.10	<0.01
Time of scan	+0.092	0.64	0.49	1	1.31	NS
Time of scan ²	–0.0026	18.14	0.50	1	36.28	<0.001
Area between 1 and 2 km	+0.16	5.49	0.49	1	11.20	<0.001
Area between 2 and 3 km	–0.095	3.54	0.49	1	7.22	<0.01
Heat haze	+0.29	31.71	0.50	1	63.42	<0.001
Weather	–	21.01	0.50	5	42.02	<0.001
Location	–	1349.46	0.84	8	1606.50	<0.001
Season	–	1.16	0.50	1	2.32	NS
Location × season	–	24.18	0.50	8	48.36	<0.001
(b) Number of lions within 2 km						
Year	–	26.68	0.95	4	28.08	<0.001
Observer	–	38.71	0.95	4	40.75	<0.001
Time spent scanning	+0.00052	43.02	0.96	1	44.81	<0.001
Time of scan	+0.047	1.81	0.95	1	1.91	NS
Time of scan ²	–0.0029	35.85	0.95	1	37.74	<0.001
Area between 1 and 2 km	+0.16	10.30	0.95	1	10.84	<0.001
Area between 2 and 3 km	–0.067	2.94	0.95	1	3.09	NS
Heat haze	+0.23	35.25	0.95	1	37.11	<0.001
Weather	–	35.62	0.95	5	37.49	<0.001
Location	–	909.00	1.18	8	770.34	<0.001
Season	–	2.56	0.95	1	2.69	NS
Location × season	–	20.90	0.95	8	22.00	<0.01
(c) Total number of lions seen						
Year	–	20.54	1.08	4	19.02	<0.001
Observer	–	63.14	1.09	4	57.93	<0.001
Time spent scanning	+0.00062	73.23	1.10	1	66.57	<0.001
Time of scan	+0.068	4.15	1.08	1	3.84	<0.05
Time of scan ²	–0.0055	12.22	1.08	1	11.31	<0.001
Area between 1 and 2 km	+0.16	12.74	1.08	1	11.80	<0.001
Area between 2 and 3 km	–0.063	3.10	1.08	1	2.87	NS
Heat haze	+0.30	69.69	1.10	1	63.35	<0.001
Weather	–	36.30	1.09	5	33.30	<0.001
Location	–	845.98	1.29	8	655.80	<0.001
Season	–	0.12	1.08	1	0.11	NS
Location × season	–	13.23	1.08	8	12.25	NS

dependent multinomial variate controlling for observer, year and location: effects of lactation $\chi^2_1 = 0.10$, NS), yet varied significantly in the dry season (Thomson's gazelle number category dependent multinomial variate controlling for observer, year and location: effects of lactation $\chi^2_1 = 8.90$, $P < 0.01$). This was because lactating females were more often found in areas with zero gazelle than were nonlactating females (presence of Thomson's gazelle as dependent binomial variate controlling for observer, year and location: effects of lactation $\chi^2_1 = 5.19$, $P < 0.05$, all other number categories were not significant).

In both wet and dry seasons numbers of lions seen within 2 km were higher in scans taken from lactating females than from those taken from nonlactating females (Fig. 3c). However, fewer hyenas were seen in the vicinity of lactating females compared to nonlactating females (Fig. 3b). When scans were analysed within season these effects still held, except for the number of hyenas seen in the dry season, when there were no significant differences between the number of hyenas seen from lactating and nonlactating females (Table 8).

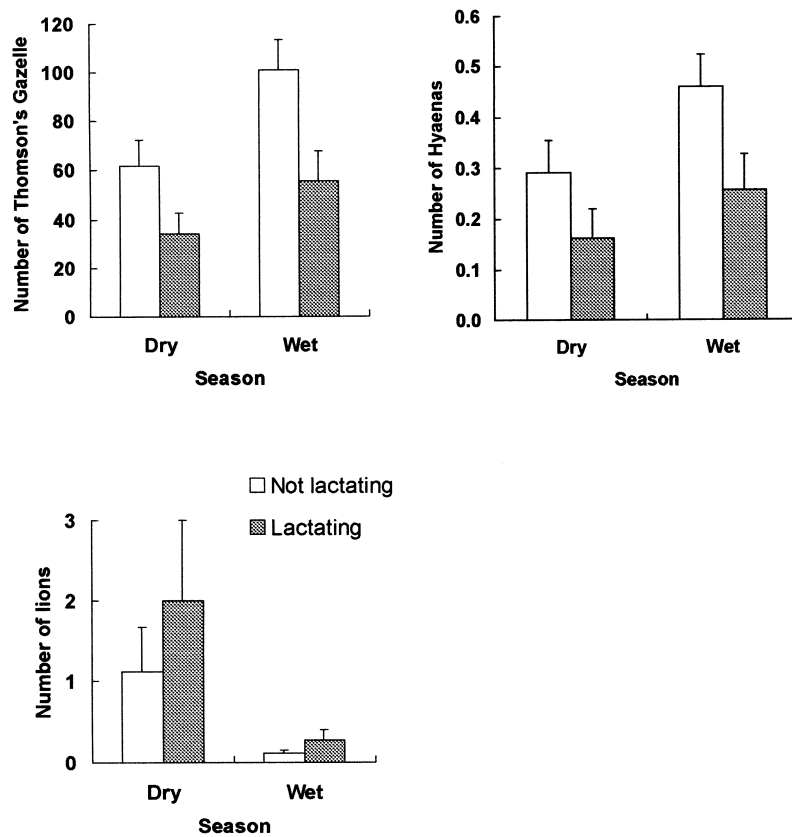


Fig. 3. Number of prey and predators seen from scans taken from lactating females compared with those taken from females accompanied by dependent cubs. Results are values predicted from a generalized linear model with Poisson errors, corrected for overdispersion fitted to 286 scans. Bars indicate standard error estimates. (a) Number of Thomson's gazelle seen within a 1 km radius of scans controlling for observer, year, location and season (effects of lactation $\chi^2_1 = 9.47$, $P < 0.01$; interaction between lactation and season $\chi^2_1 = 4.00$, $P < 0.05$). (b) Number of hyenas seen within a 2 km radius of scans controlling for significant effects of observer, year, location, time spent scanning, time of scan, time of scan², heat haze, proportion of area visible between 1 and 2 km, between 2 and 3 km, weather and season (effects of lactation $\chi^2_1 = 4.29$, $P < 0.05$; interaction between lactation and season $\chi^2_1 = 18.64$, $P < 0.001$). (c) Number of lions seen within a 2 km radius of scans controlling for significant effects of observer, year, location, time spent scanning, time of scan, time of scan², heat haze, proportion of area visible between 1 and 2 km, between 2 and 3 km, weather and season (effects of lactation $\chi^2_1 = 4.49$, $P < 0.05$; interaction between lactation and season $\chi^2_1 = 0.12$, NS).

Table 7. Variation in the number of Thomson's gazelle seen from lactating female cheetahs and from females accompanied by dependent cubs. A generalized linear model with Poisson errors and corrected for overdispersion was fitted to the numbers of gazelle seen within 1 km in (a) 181 scans in the wet season, and (b) 111 scans in the dry season. The table gives changes in deviance explained by each term in the model: aggregated location, year, observer identity and lactational status

Parameter	Coefficient estimate	Deviance	Dispersion	d.f.	χ^2	P
(a) Wet season						
Location	–	8708.87	160	11	54.43	<0.001
Year	–	1345.67	122	4	11.03	<0.05
Observer	–	1126.29	123	2	9.16	<0.05
Lactation	–0.49	520.47	120	1	4.34	<0.05
(b) Dry season						
Location	–	4626.38	102	13	45.36	<0.001
Year	–	7.19	60	3	0.12	NS
Observer	–	10.77	60	3	0.18	NS
Lactation	–2.21	700.72	68	1	10.30	<0.01

Discussion

Of all the large predator species in the Serengeti, cheetahs are one of the rarest (Caro & Durant 1995). In

1993 about 200–250 cheetahs were estimated to live in the entire Serengeti ecosystem, compared to estimates of 800–1000 leopards (*Panthera pardus*), 2800 lions and

Table 8. Variation in the number of hyenas and lions seen from lactating female cheetahs and from females accompanied by dependent cubs. A generalized linear model with Poisson errors and corrected for overdispersion was fitted to the number of predators seen within 2 km in 181 scans in the wet season and 108 scans in the dry season. The table gives the amount of deviance explained by each term in the model. The final model includes all terms which significantly affect changes in deviance, and leaves out those terms which do not. Therefore deviances given refer to changes in deviance obtained when dropping significant terms from the model or from including nonsignificant terms. Variates included in the model are area visible between 1 and 2 km, area visible between 2 and 3 km, time spent scanning, time of scan, quadratic effect of time of scan and heat haze. Factors included are aggregated location, year, observer identity and lactational status. Data was insufficient for inclusion of weather as a factor in all analyses. A forwards regression was used to analyse the number of lions seen in the wet season. This analysis did not include observer and year as factors

Parameter	Coefficient estimate	Deviance	Dispersion	d.f.	χ^2	P
(a) Number of hyenas within 2 km in the wet season						
Location	–	79.57	1.55	8	51.34	<0.001
Year	–	7.22	1.13	4	6.39	NS
Observer	–	3.08	1.15	2	2.68	NS
Time spent scanning	+0.00094	6.84	1.18	1	5.80	<0.05
Time of scan	+0.004	0.00	1.16	1	0.00	NS
Time of scan ²	–0.0057	13.59	1.22	1	11.14	<0.001
Area between 1 and 2 km	–0.001	0.00	1.16	1	0.00	NS
Area between 2 and 3 km	–0.20	3.11	1.14	1	2.73	NS
Heat haze	+0.41	16.65	1.24	1	13.43	<0.001
Lactation	–1.32	19.00	1.26	1	15.08	<0.001
(b) Number of lions within 2 km in the wet season						
Location	–	95.77	0.83	7	115.39	<0.001
Year	–	–	–	–	–	–
Observer	–	–	–	–	–	–
Time spent scanning	–0.00023	0.05	0.30	1	0.17	NS
Time of scan	–0.055	0.00	0.30	1	0.00	NS
Time of scan ²	–0.048	50.27	0.60	1	83.78	<0.001
Area between 1 and 2 km	+0.94	9.79	0.36	1	27.19	<0.001
Area between 2 and 3 km	–0.45	5.08	0.33	1	15.39	<0.001
Heat haze	–1.25	37.11	0.52	1	71.37	<0.001
Lactation	+1.54	8.17	0.35	1	23.34	<0.001
(c) Number of hyenas within 2 km in the dry season						
Location	–	27.38	1.08	6	25.35	<0.001
Year	–	15.12	0.99	3	15.27	<0.01
Observer	–	21.06	1.05	3	20.06	<0.001
Time spent scanning	+0.0014	9.55	0.95	1	10.05	<0.01
Time of scan	+2.13	4.30	0.89	1	4.83	<0.05
Time of scan ²	–0.12	5.56	0.91	1	6.11	<0.05
Area between 1 and 2 km	+0.21	0.46	0.86	1	0.53	NS
Area between 2 and 3 km	–0.15	0.29	0.86	1	0.34	NS
Heat haze	+0.98	5.53	0.91	1	6.08	<0.05
Lactation	+0.12	0.03	0.87	1	0.03	NS
(d) Number of lions within 2 km in the dry season						
Location	–	41.25	2.04	7	20.22	<0.01
Year	–	27.87	1.96	3	14.22	<0.01
Observer	–	1.31	1.79	3	0.73	NS
Time spent scanning	+0.00094	4.81	1.72	1	2.80	NS
Time of scan	+2.23	18.37	1.93	1	9.52	<0.01
Time of scan ²	–0.099	18.77	1.93	1	9.73	<0.01
Area between 1 and 2 km	+0.26	0.70	1.76	1	0.40	NS
Area between 2 and 3 km	+0.99	20.77	1.95	1	10.65	<0.01
Heat haze	+0.52	4.17	1.72	1	2.42	NS
Lactation	+1.62	10.34	1.84	1	5.62	<0.05

9000 spotted hyenas (Caro & Durant 1995). Wild dogs (*Lycaon pictus*) are the only predator species which is rarer than cheetahs, numbering only about 50 individuals in 1993 (Caro & Durant 1995). The main prey species of cheetah, the Thomson's gazelle, is numerous

at an estimated 441 000 animals (Campbell 1989) and is unlikely to be limiting cheetah population size (Caro 1994). Cheetahs are likely to be limited instead by other predators, principally lions and hyenas (Laurenson 1995). Both hyenas and lions are predators of

Thomson's gazelle (Kruuk 1972; Schaller 1972; Scheel & Packer 1995) and could potentially compete directly with cheetahs over this prey. In addition, both are directly responsible for cheetah cub mortalities (Laurenson 1994) and both steal kills from cheetahs (Caro 1994). In fact, cheetahs appear to be continually outcompeted by these larger predators. How then do cheetahs manage to coexist alongside hyenas and lions?

The data presented here showed that cheetahs were found in lower density prey areas compared to their competitors. This result could have two explanations: either cheetahs were avoiding areas with high density prey, or gazelle were avoiding areas with cheetahs. If the latter explanation were true, then a similar pattern of distribution should have been observed for the numbers of Thomson's gazelle seen around lions, another stalking predator, but this was not so. In addition, wildebeest and zebra, prey which were also commonly taken by lions, were seen at higher densities when lions were seen in scans compared with when lions were absent (S.M. Durant, unpublished data). Again, this result is unlikely if prey were actively avoiding predators. Instead the first explanation is the most likely. Cheetahs can benefit from concentrating on areas with low densities of gazelle since gazelle in these areas had a lower mean group size. These small groups are less likely to become alerted to a hunting cheetah, and hence the hunting success of cheetahs is higher than on larger groups (FitzGibbon 1990). During the wet season, when there is a birth peak in Thomson's gazelle, cheetahs might be more likely to concentrate in areas with high densities of gazelle as these herds are more likely to contain hidden fawns, which are easy prey for cheetahs (Caro 1994). However, this study showed no such relationship.

Cheetahs are mobile cats, and are able to move long distances in search of prey. Furthermore, their hunting technique, consisting of a long stalk followed by a short, fast chase, is most successful if they exploit the low densities of prey among which they are found. It thus allows them to avoid the high densities preferred by their competitors. Lions and hyenas, although they are found around larger herds of gazelle, typically prefer the wildebeest herds (Scheel 1992). These features mean that cheetahs could potentially avoid the high densities of hyenas that occur around the dense migrant herds and exploit the sparsely distributed gazelle at the edge of this distribution. However, cheetahs were not systematically found in areas with low densities of their competitors. Instead they were found near lower densities of hyenas and lions only in the wet season, whilst there was a tendency for them to be found close to lions in the dry season. Nonetheless they were more likely to be found close to other cheetahs in both seasons, suggesting that competition with competitors was more intense than competition with conspecifics.

If lions were in the vicinity, cheetahs were more

likely to be moving during scans in both seasons. However, they were only more likely to be moving away from hyenas in the wet season, and from other cheetahs in the dry season. Since lions are territorial (Schaller 1972), their range is restricted and hence their distribution is not as highly aggregated as that of hyenas. This meant that it may have been difficult for cheetahs to avoid lions on a large scale, and so avoidance was facultative. Cheetahs tended to avoid lions at a local scale and when the situation demanded it, such as when hunting. This may have been particularly true in the dry season, when both Thomson's gazelle and lions tended to concentrate around the few remaining supplies of permanent water. At this time cheetahs were concentrated in the same area as lions and were thus positively associated with this species within a 2 km radius.

In the dry season, when hyena densities were relatively low, cheetahs did not need actively to avoid hyenas, and so they were not more likely to respond to hyenas. However, in the wet season, when the plains were inundated by large numbers of hyenas, there were fewer gaps in their distribution, and cheetahs were forced to become more active in their avoidance of these predators. Cheetahs adjusted their activity patterns in response to much lower densities of lions than hyenas, which indicates that cheetahs were more strongly influenced by lions than by hyenas, as predicted by previous studies (Caro 1994; Laurenson 1994). In the dry season cheetahs were more likely to be moving if cheetah densities were high and were less likely to be moving if hyena densities were high. This suggests that at this time, when hyena density is lower, competition with conspecifics becomes more important than competition with hyenas, and avoidance of other cheetahs becomes a higher priority.

Lactating females, with restricted mobility, were found near lower density prey areas and higher lion densities. Furthermore, in the dry season, lactating females were found more frequently in areas with no gazelle. In this study cheetahs were less frequently seen lactating in the dry season, which could be a consequence of these harsher conditions. Laurenson (1994) showed evidence that if the nearest gazelle herds were 11.5 km from a mother's den location, then she would abandon her cubs, suggesting that low densities of prey in the vicinity of the den site have real reproductive consequences for cheetahs. The results presented here support the prediction that mobility is the key to the ability of cheetahs to coexist alongside lions.

The data presented here cannot completely exclude the possibility that some other factor might explain the avoidance observed in this study. It is possible that such a factor, not measured in this study, might be preferred by lions and hyenas but is avoided by cheetahs. However, it is difficult to envisage what such a factor might be. All three species are attracted to cover in the form of kopjes and bush (Schaller 1972;

Frame 1986; Caro 1994). Furthermore, the observation that cheetahs were more likely to be moving if hyena or lion density was high and evidence from playback experiments, where cheetahs moved away from calls of lions and hyenas, also supports the argument that avoidance was active (Durant, unpublished).

This study shows that a less able competitor can utilize areas with low density prey and avoid its higher ability rivals, seeking out spatio-temporal refuges in an ever-changing predator environment. Furthermore avoidance is probably facultative. Whether a low ability competitor responds to a high ability rival depends on the relative density of its rival and the extent of competition between the two species. If the competitor is at a sufficiently low density or has a relatively weak effect, then there is no great need to adjust behaviour to its presence. However, at high densities a response becomes necessary. By not responding a low ability competitor risks lower feeding rates or even its own mortality. This can affect the overall density of the population and may make persistence impossible.

Cheetahs therefore form the final layer in a spatio-temporal hierarchy of prey and predators, fitting into vacant niches in an ever moving and changing system. This is a position that they may share with other species, which are likely to be characteristically rare. A large number of species falling under the 'everywhere small but widespread' category of rarity laid out by Rabinowitz, Cairns & Dillon (1986) may fill a similar position in the ecological hierarchy. An alternative African carnivore example is that of wild dogs, as, like cheetahs, they have high mobility and low competitive ability (Creel & Creel 1996). Such species may only be able to persist in areas that are large enough to maintain sufficient spatial heterogeneity. If we are to be able to ensure the future survival of these species, it is critical for us to understand the dynamics of these systems while they still function in the wild.

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