

Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti

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Predator avoidance is likely to play a strong role in structuring species communities, even where actual mortality due to predation is low. In such systems, mortality may be low *because* predator avoidance is effective, and if the threat of predation is lifted then entire community structures may be altered. Where competition is intense, then competitor avoidance may have a similar impact on communities. Avoidance behaviors have been documented for a wide range of species, but this is the first attempt to document avoidance behavior within a large carnivore community. Audio playback techniques are used to examine the risk perceived by cheetahs from their two main competitors that are also their main predators, lions and hyenas. The results from these experiments show that cheetahs actively moved away from lion and hyena playback experiments, compared with dummy playbacks where no sound was played. Cheetahs showed no differences in their responses to playbacks dependent on their sex or reproductive status, suggesting they were responding principally to a competition rather than a predation threat. However, cheetahs were much less likely to hunt after competitor playbacks than after dummy playbacks, and this resulted in a lower kill rate after competitor playbacks, demonstrating that the perceived presence of competitors had a noticeable impact on the foraging rate of cheetahs. Furthermore, while cheetahs moved just as far following lion playbacks as after hyena playbacks, they spent significantly more time looking at the loudspeaker and were less likely to make a kill after lion playbacks, suggesting that cheetahs perceive lions to be a greater threat than hyenas. *Key words*: anti-predator behavior, carnivores, competition, foraging strategy, kleptoparasitism, playback experiments, predator avoidance, predation risk. [*Behav Ecol* 11:624–632 (2000)]

Predator avoidance, whereby prey avoid encounters with predators, is one means by which prey are able to reduce the chance of predation. An avoidance behavior can be defined as any behavioral strategy that enhances the survivorship of prey by reducing the probability that they occur within the foraging range of potential predators (Brodie et al., 1991). Predator avoidance is likely to play a strong role in structuring species communities, even where actual mortality due to predation is low (Lima and Dill, 1990; Turner and Mittelbach, 1990). In such circumstances, mortality may be low precisely because predator avoidance is effective and, if the threat of predation is lifted, then entire community structures may be altered. Avoidance of predation has attracted increasing attention over recent years, however predation is not the only negative interspecific interaction which a species may want to avoid; competitor avoidance behaviors may also be important as a mechanism for shaping communities. Competitor avoidance can be defined similarly to predator avoidance, except enhancement of survival is through indirect rather than through direct mechanisms.

Both predator and competitor avoidance are likely to carry costs. For example, a reduction in activity or an increase in the use of refuges due to a perceived risk of predation can lead to a reduction in foraging rate (Kennedy et al., 1994; Ward et al., 1997). The relative balance between the costs and benefits of predator avoidance may differ between different species and between different age and reproductive classes within species, and can result in different avoidance strategies, even when the predator is identical (Peckarsky, 1996; Sih, 1992). In addition, some species may evolve an ability to adapt their avoidance tactics in response to a perceived predation risk (Loose and Dawidowicz, 1994; McIntosh and Townsend,

1994; Peckarsky, 1996). The evolution of such a flexible response will depend on the costs associated with gathering information about a potential predation threat (Dill, 1986; Sih, 1987). Selection will only favor flexibility in predator avoidance tactics when the cost of gathering information about the predation threat is relatively low, when the risk of predation fluctuates unpredictably, and when there are reliable cues for detecting predation risk (Harvell, 1986, 1990). Competitor avoidance is likely to be subject to weaker selective forces than predator avoidance, since the cost of not avoiding a competitor will generally be lower than the cost of not avoiding a predator, as the latter carries a risk of direct mortality.

To date most studies of predator avoidance have concentrated on aquatic and small mammal communities, while communities of large mammals have been neglected (but see Bshary and Noe, 1997). This article addresses this gap in our knowledge by examining avoidance of the two main predators, which are unusually also the main competitors, of the cheetah (*Acinonyx jubatus*)—lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*). In cheetahs, offspring survival is strongly affected by lion and hyena predation. Over 90% of cheetah cubs die before reaching independence, predominantly due to predation (Laurenson, 1994). Adult cheetahs may also lose their kills to these predators (Caro, 1994; Schaller, 1972), and may also be killed by lions (Durant SM, unpublished data). There are no published records of adult cheetahs being killed by hyenas, although this possibility cannot be completely discounted. The impact of lions on cheetah populations results in a negative relationship between cheetah population size and lion density both across and within different protected areas (Durant et al., under review; Laurenson, 1995b).

Since cheetahs have small jaws and a light build, a mother cannot defend her cubs or kills against lions and hyenas. However, she can reduce predation of her cubs by adapting her behavior and adopting an avoidance strategy (Caro, 1994). Cheetahs make use of various techniques in order to minimize direct interactions with lions and hyenas. They reduce visual and audio cues by killing silently by asphyxiation after a short

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chase, hunting during the day when many of their competitors are inactive, and dragging kills immediately into cover to avoid attracting vultures to carcasses (Caro, 1994). These behaviors minimize contact with competitors and may reduce rates of kleptoparasitism and cub mortalities. Cheetahs can further minimize direct contact by making use of any spatial heterogeneity in the distributions of lions and hyenas and seeking out “competition refuges”—areas with low densities of their competitors (Durant, 1998).

The risk of predation and kleptoparasitism to cheetahs is likely to be influenced by a number of predictable factors, therefore a flexible avoidance response may have evolved in this species. Cheetahs are more likely to be noticed by predators when they are active and hunting, when they are also vulnerable to kleptoparasitism, and so avoidance should be particularly marked at these times. Moreover, if cub vulnerability is the predominant cause of avoidance, avoidance should be more marked in females than in males, since the former are more frequently accompanied by dependent cubs and hence might perceive predators to be a greater threat. Female cheetahs should also show greater avoidance when they are accompanied by dependent cubs than when solitary. Finally, since young cubs are more vulnerable to predation than older cubs (Caro, 1994), the strength of avoidance by a mother should depend on the age of her cubs.

Direct observation of causes of mortality of cheetahs are rare (Caro, 1994), making it difficult to directly ascertain the extent of the relative threat that hyenas and lions pose to cheetahs. Moreover, observation of interactions between cheetahs and their competitors are highly variable in terms of the distance of nearest approach of the competitors and the time of day at which interactions occur (Caro, 1994). If more reproductively successful cheetahs are better at avoiding lions and hyenas (Durant, 2000), then data gathered by field observation alone would be biased towards less successful cheetahs, since these would most often be seen near other competitors. In this article I employ audio playback techniques to examine avoidance behavior by cheetahs. Such experiments allow the manipulation and standardization of naturally rare events.

I tested the following predictions in order to ascertain the extent of avoidance tactics by cheetahs and whether cheetahs adapt avoidance behavior according to the relative risk of predation or competition. First, I tested whether cheetahs avoid hyenas and lions. Second, I tested whether reactions are flexible, and are affected by various cues such as the hunger state of the cheetah in the experiment and the presence of prey. Third, I tested whether responses are dependent on sex or reproductive state. Finally, I tested whether avoidance has a real cost to cheetahs in terms of a reduced foraging rate. Henceforth lions and hyenas are referred to as “competitors,” however it should be borne in mind that they are also known predators of cheetah cubs and, in the case of lions, adult cheetahs.

METHODS

Study population

The hypotheses were tested on data from a long-term study population of cheetahs in the Serengeti National Park in Tanzania. The study area covers 2200 km² in the south east of the Serengeti (for 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 grass plains to short grass plains in the south east. The entire area is scattered with rocky outcrops known as “kopjes” which provide havens for trees and bushes and are often the only cover available

out on the open plains. The climate is seasonal with a wet season that starts in November and ends in June (Sinclair, 1979).

Cheetahs on the Serengeti plains have been studied intensively since the mid-1970s (Caro, 1994). Each cheetah can be individually recognized by distinctive spot patterns on its face and haunches (Caro and Durant, 1991). Cheetahs were located in the early morning and late afternoon when they are most active, by driving to high points with good visibility and scanning through binoculars (10 × 50 magnification). Active cheetahs can be seen up to and occasionally beyond a distance of 3 km. Upon approach each cheetah was identified and its hunger state estimated by its belly size according to an increasing 14 point scale (Caro, 1994). This scale has proven to be accurate and has a high reliability between different observers (Caro, 1994). Cubs were aged when they were first seen, when their age could be estimated to within an accuracy of 1 month (Caro, 1994).

Playback experiments

Audio playback techniques were used to quantify competitor avoidance behavior, in a series of controlled experiments. Between May 1993 and September 1996 lion and hyena vocalizations were played to individual cheetahs and their reactions recorded. Recordings of lion roars and hyena whoops were obtained within the study area using either a Panasonic V250, Sony TCD D3 or Sony TCD D7 digital audio tape recorder linked to a Sennheiser MKH816 microphone. Recordings were made from within 30 m of a single individual vocalizing lion or hyena. Lion recordings were of adult females, while the sex of the caller in the hyena recordings was not determined. Playbacks were played through a Sony XM 4020 Sony amplifier linked to a Sony TCD D3 digital audio tape recorder and a Martin Audio CT2 studio monitor loudspeaker. The volume of the playback experiments was standardized across experiments so that calls were played at natural sound pressure levels. Experiments were conducted in the early morning between 0630 and 0930 when cheetahs are most active and are likely to hear lion and hyena vocalizations (East and Hofer, 1991; Kruuk, 1972; Schaller, 1972).

The speaker was placed approximately 200 m from the cheetah and observations made from a vehicle at a distance of 100 m. The speaker was placed upwind of the cheetah to ensure that the sound carried with the wind. Since cheetahs rely principally on sight and hearing, rather than smell, it is unlikely that the fact that they were unable to smell a competitor despite being able to hear one would have influenced their reaction. The location of the loudspeaker and initial position of the cheetah were noted using a Global Positioning system (GPS) which was accurate to within 100m. This allowed verification of the initial distance between the speaker and the cheetah (mean and standard error 232 ± 8m). Wherever possible the speaker was hidden from the cheetah either in long grass, in a dip, behind a termite mound, or behind a bush. All playbacks were conducted in open habitat on the short or long grass plains, or at the woodland edges. Cheetahs in this study were well habituated to vehicles. A total of 45 individuals were used in the analyses presented in this article. Thirty-four of these were females and 11 males. In 55 out of the 79 playbacks made to females, females were accompanied by dependent cubs at the time of the experiment, 14, 20, and 21 of these were to females in dummy, hyena, and lion experiments respectively.

Lion playbacks consisted of a single bout of roars (McComb et al., 1994), where hyena playbacks involved two bouts of the same whoop recording separated by a 5 min interval. Since hyenas often whoop when moving (Kruuk, 1972), playing two

Table 1
Number of each playback type played to individual cheetahs participating in playback experiments

Cheetah	Gender	Playbacks			Location and hunting data
		Dummy	Hyena	Lion	
128	M	0	0	0	1
2180	F	0	1	0	0
2490	F	0	1	0	0
2549	M	0	0	1	0
Ame	F	2	2	1	3
Aud	F	1	3	1	0
Cam	F	0	0	1	0
Cat	F	1	1	2	1
Chan	F	0	1	0	0
Chr	F	1	0	0	1
Coc	F	0	0	0	1
Cur	M	0	0	0	1
Der	M	1	1	1	1
Fla	F	1	0	0	0
Flo	F	0	2	2	0
Fud	F	2	3	1	2
Gal	F	0	0	1	0
Gru	M	0	0	1	0
Haz	F	1	2	1	1
Jur	F	2	2	1	0
Kit	F	0	1	2	1
Lap	F	0	1	0	0
Lis	F	0	0	1	0
Luc	F	0	2	0	0
Mar	F	1	0	0	0
Mat	F	1	1	2	1
Mik	M	0	0	1	0
Mis	F	0	1	1	0
Mon	F	1	1	1	0
Mos	F	0	1	1	0
Oba	F	0	1	0	0
Pen	M	0	0	1	0
Rol	M	0	1	1	0
Sco	M	0	0	0	2
Sik	F	1	2	2	0
Sim	M	0	0	1	0
Ski	F	0	0	1	0
Spo	F	0	1	0	0
Squ	F	0	1	0	0
Suc	F	0	0	1	0
Syl	F	0	1	0	0
Tal	F	1	1	3	0
Tob	M	0	0	1	0
Twi	F	0	1	2	0
Wis	F	0	0	1	0
Total playbacks		17	36	37	16
Total Subjects		14	26	29	12

Location and hunting data supplemented data obtained from dummy playbacks in analyses of distance moved and hunting behaviour (see Methods).

bouts was intended to give the impression that a hyena is stationary in the area. Whooping is a long distance contact call and, once away from the den, is most commonly given by solitary hyenas (Kruuk, 1972), therefore it is unlikely that a cheetah, upon hearing two whoops, would perceive two hyenas as being present. Playbacks alternated between two different hyena recordings and five different lion recordings. A total of 36 hyena playbacks and 37 lion playbacks were conducted (Table 1). In addition 17 "dummy" playbacks where the equipment was set up but no sound was played were used for controlled comparisons. No responses by lions or hyenas were recorded in any of the experiments reported here.

The presence of prey (Thomson's or Grant's gazelle) within 1 km of the cheetah at the start of the experiment was noted. For 1 h after starting to play the first recording, instantaneous scans were taken every 30 s to record whether the cheetah was looking at the speaker and whether it was moving. The number of scans where a cheetah was looking at the speaker or moving was divided by the total number of scans when the cheetah was visible to give a proportion of time spent looking or moving. The latency or time to first movement was also recorded, if no movement occurred, as was the case in 20% of experiments, latency was set to 1 h, the duration of observation after experiments. In addition, for all except nine experiments, data were collected for at least 5 min before the start of each experiment. These data were used in paired *t* tests to assess changes in behavior before and after the three types of playbacks.

During the 1-h observation period the presence of any hunting activity was noted. A cheetah was defined to stalk if it placed its head below shoulder height, stared fixedly at prey and walked a minimum of two steps towards prey. A cheetah was defined to chase prey if it broke into a fast run after prey. At the end of the hour the cheetah's location was noted. Repeat lion and hyena playbacks of the same type to the same individual were made a maximum of three times with a minimum of 1 month between repeats. Data from dummy playback experiments were further supplemented by location and hunting data obtained on 16 occasions from cheetahs that were first sighted between 0630 and 0930am and subsequently followed for an hour (Table 1). These data were used in analyses of distance and hunting behavior.

Statistical analyses

A combination of paired *t* tests, ANCOVAs, and generalized linear models were used for analyses. The initial distance of the loudspeaker, hunger state, presence of prey and time at the start of the experiment were controlled for in all analyses except paired *t*-tests and those investigating hunting behavior. In the latter analyses these terms were initially included in the model and were then deleted stepwise by dropping the least significant terms one by one until all remaining terms had probability values less than 0.1. This process was also adopted in analyses investigating restricted data sets, that is those estimating effects of cub presence, cub age and litter size, and explains small differences in the degrees of freedom in reported statistics. Paired *t* tests implicitly controlled for all these variables.

In paired *t* tests, whenever an individual was involved in more than one experiment of the same type, responses were averaged for that individual. All other analyses, except where indicated, controlled for individual identity as a categorical variable whenever it exerted a significant effect. Terms were judged as statistically significant when probabilities were less than 5%, however all probabilities of less than 10% are reported. Because a number of statistical analyses are conducted on the same data set, Bonferroni statistical significance is indicated next to reported *p* values in the text and in Tables 3–5 by way of the following symbols: ¹ for *p* < .1; * for *p* < .05; ** for *p* < .01; and *** for *p* < .001 (Rice, 1989). It should be noted that Bonferroni corrections give an overly conservative result (Hsu and Nelson, 1998; Samuel-Cahn, 1996).

Three types of model were used:

1. Paired *t* tests and ANCOVAs for analyses of proportionate measures of cheetah activity (looking at the speaker or moving). Proportions were converted to a normal distribution before analysis using an arcsin transformation after first correcting for zero values (Sokal and Rohlf, 1981).
2. ANCOVAs for analyses of the latency of first movement and

Table 2
Effect of playback type on transformed measures of vigilance and movement during the first 30 min and the second 30 min after playback experiments in comparison with pre-playback levels

Playback type	Pre-playback mean	First 30 min			Second 30 min		
		Mean	<i>t</i> -test	Significance	Mean	<i>t</i> -test	Significance
Looking at speaker							
Dummy playbacks	0.212	0.217	$t_{11} = 0.14$	ns	0.228	$t_{11} = 0.52$	ns
Hyena playbacks	0.169	0.417	$t_{25} = 7.99$	$p < 0.001$	0.248	$t_{25} = 3.02$	$p = 0.006$
Lion playbacks	0.205	0.504	$t_{22} = 6.68$	$p < 0.001$	0.289	$t_{22} = 2.63$	$p = 0.015$
Moving							
Dummy playbacks	0.531	0.165	$t_{11} = 1.22$	ns	0.327	$t_{11} = 1.30$	ns
Hyena playbacks	0.337	0.499	$t_{25} = 2.27$	$p = 0.032$	0.326	$t_{25} = 0.18$	ns
Lion playbacks	0.240	0.431	$t_{23} = 3.55$	$p = 0.002$	0.433	$t_{23} = 2.63$	$p = 0.015$

Means reported are from transformed data. Bonferroni corrections were not performed on these analyses as they are partially independent of later analyses.

the straight line distance from the speaker 1 h after the start of the playback. Since the logarithm of both latency and distance were distributed normally (goodness of fit test on the logarithm of latency and distance respectively: $\chi^2_5 = 6.54$, ns and $\chi^2_7 = 8.18$, ns), these variables were log transformed before analysis.

3. A logistic regression model for analyses of the binomial variate of the presence or absence of hunting behavior during the experiment.

All analyses were conducted using the GENSTAT 5 version 3.1 statistical package (Payne et al., 1987). Results from ANCOVAs were tested using the *t* and *F* distributions, while those from logistic regression models were tested using a χ^2 distribution (Sokal and Rohlf, 1981).

RESULTS

Cheetahs did not respond differently to different recordings of the same competitors in levels of vigilance (measured here as the proportion of time they spent looking at the speaker), movement patterns or hunting behavior. Cheetahs also did not respond significantly differently according to whether the speaker was visible to or was hidden from the cheetah at the start of the experiment. Finally, distance moved and hunting behavior after dummy playbacks did not differ according to whether the equipment was set up or not, allowing the use of these data in supplementing experimental data in subsequent analyses.

Reactions to predators

Cheetahs changed their behavior when a sound of a lion or hyena vocalization was played, but not when no sound was played (Table 2). Cheetahs were significantly more likely to look at the loudspeaker and spent significantly more time moving during the first 30 min after both lion and hyena playbacks than during the observation period prior to the experiments (Table 2). In the second half hour of observation vigilance was also significantly higher after both lion and hyena playback experiments than during the pre-playback period, but cheetahs only spent significantly more time moving after lion experiments. There was no difference in vigilance or movement before and after dummy experiments.

Comparing across the three different playback types over the entire 1-h observation period after experiments, cheetahs were significantly more likely to look at the loudspeaker after lion or hyena playbacks than after dummy playbacks (Figure 1, Table 3). Cheetahs looked at the loudspeaker most after

lion playbacks, and least after dummy playbacks. The latency to first movement did not differ between playback types (Table 4), however cheetahs spent significantly more time moving after lion or hyena playbacks than after dummy playbacks, moving most after a lion playback and least after a dummy playback (Figure 1, Table 4). In addition, at the end of the hour cheetahs were significantly farther from the loudspeaker after lion and hyena playbacks than after dummy playbacks (Figure 1, Table 4), suggesting that they were moving in a consistent direction and moved more quickly after competitor playbacks.

Despite an increase in activity, cheetahs were much less likely to hunt after a lion or hyena playback than after a dummy playback (Figure 1, Table 5). Cheetahs were also less likely to chase and kill prey after competitor playbacks than after dummy playbacks (Table 5). Of those cheetahs which did hunt, cheetahs were no less likely to chase prey after playbacks of competitors (effect of playback type, $\chi^2 = 0.80$, ns), but they were less likely to kill prey after playbacks of lions than after dummy or hyena playbacks (effect of playback type: coefficients for dummy, hyena and lion playbacks respectively 0.0, 0.94, -9.7 , $\chi^2_2 = 11.21$, $p = .004^*$). This suggests that once cheetahs started hunting, they were just as likely to chase prey after lion playbacks as after dummy playbacks, but they may not have invested as much energy into the chase, resulting in a lower kill rate, and indicating an avoidance of investing energetic effort into hunts once started.

Are reactions strongest to lions or hyenas?

Cheetahs were significantly more likely to look at the loudspeaker after lion playbacks than after hyena playbacks (effect of playback type, $F_{1,67} = 5.73$, $p = .019$). However the latency to first movement did not differ between lion and hyena playbacks (effect of playback type, $F_{1,68} = 1.71$, ns), neither did cheetahs spend more time moving (effect of playback type: $F_{1,68} = 1.47$, ns), nor move farther (effect of playback type, $F_{1,68} = 0.74$, ns). Cheetahs were also no less likely to hunt or chase prey after a lion playback than after a hyena playback (effect of playback type on hunting, $\chi^2_1 = 1.25$, ns, and on chasing: $\chi^2_1 = 0.70$, ns), however they were less likely to make a kill after a lion playback (effect of playback type, $\chi^2_1 = 4.05$, $p = .044$).

Factors affecting reaction

Cheetahs were not significantly more vigilant after playback experiments when they were hungry than when they were well fed (Table 3). However their latency to first movement was significantly greater if they were well fed (Table 4), and they

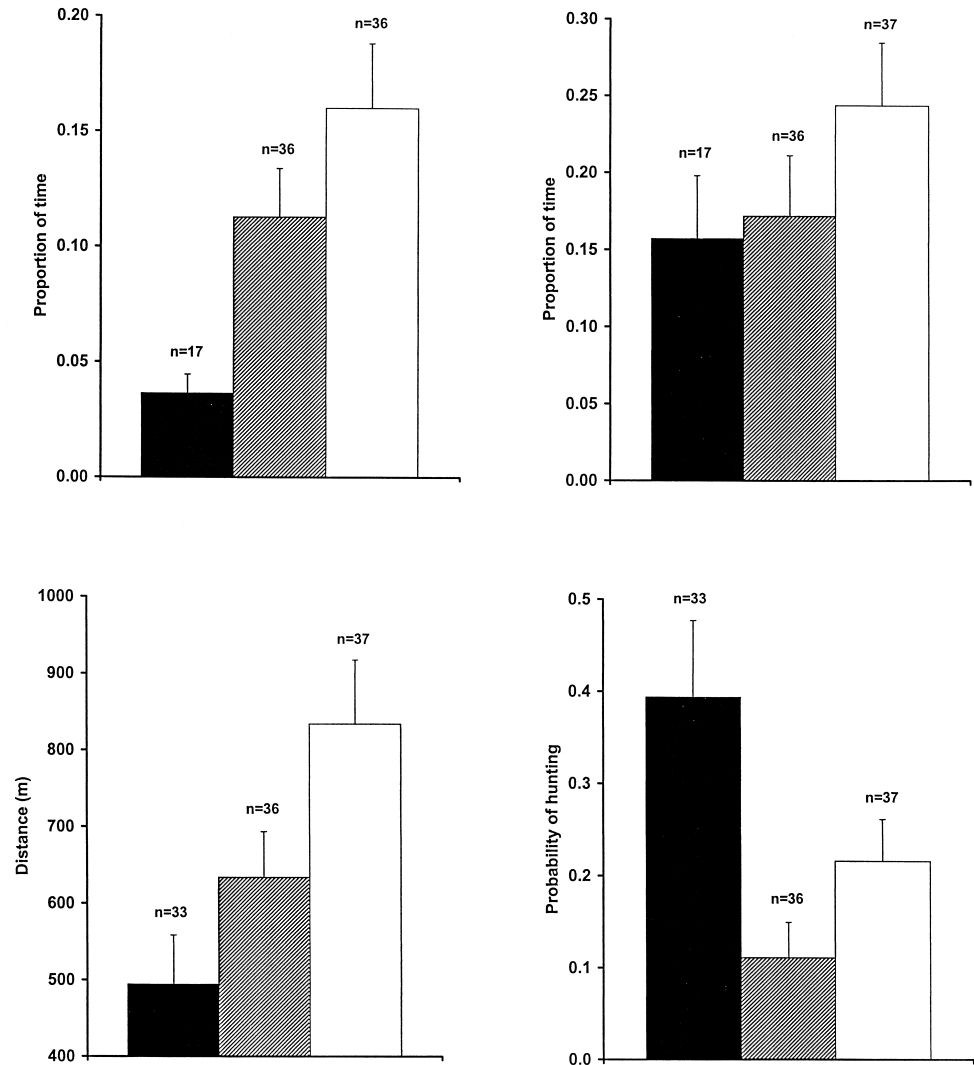


Figure 1

Responses of cheetahs over 1 h following dummy, hyena and lion playback experiments. Upper left, proportion of time spent looking at the loudspeaker; upper right, proportion of time spent moving; lower left, distance from loudspeaker; and lower right, the chance of hunting. Filled bars, dummy playback; hatched bars, hyena playback; open bars, lion playback. Means were calculated across all experiments, bars indicate standard errors.

spent significantly less time moving (Table 4), moved significantly less far (Table 4), were less likely to hunt, and were marginally less likely to chase prey, but were not significantly less likely to make a kill (Table 5).

If there were no prey present at the start of the experiment, cheetahs were marginally less vigilant (Table 3), spent significantly more time moving (Table 4), but were only marginally significantly farther from the loudspeaker at the end of the experiment than if prey were present (Table 4). They were no more likely to hunt if prey were initially present than if prey were absent (Table 5). This was partly because either prey would move into or cheetahs move out of the area during the 1-h observation, and partly because cheetahs often hunted prey, such as hares or gazelle fawns, which were initially not visible to the observer.

Other variables such as the time of day and the initial distance of the loudspeaker from the cheetah had some effect on responses. Cheetahs were less vigilant and had a greater latency to first movement when experiments were started later in the day (Tables 3 and 4), and were farther from the loudspeaker at the end of the experiment if they were farther from it at the beginning (Table 4). Individual identity did not have a significant effect on vigilance or movement patterns, but did affect hunting behavior (Tables 3–5).

Sex and reproductive status

Female cheetahs did not react more strongly to competitor playbacks than male cheetahs. Although females were significantly more likely to look at the loudspeaker than males (effect of sex, $t_{71} = 2.61$, $p = .011$), this effect was probably a result of a generally higher level of vigilance for females compared with males, since there was no significant interaction between sex and playback type (effect of interaction between sex and playback type: $F_{1,71} = 0.09$, ns). Females were not significantly more likely to move than males (effect of sex, $t_{72} = 0.09$, ns, interaction between sex and playback type, $F_{1,72} = 1.24$, ns), neither did they move farther (effect of sex, $t_{86} = 1.29$, ns, interaction between sex and playback type: $F_{2,88} = 1.61$, ns) and were no more likely to hunt, chase or kill after playback experiments (effect of sex for hunt, chase and kill respectively, $\chi_1^2 = 0.02$, ns, $\chi_1^2 = 0.01$, ns and $\chi_1^2 = 0.00$, ns, interaction between sex and playback type, $\chi_2^2 = 0.53$, ns, $\chi_2^2 = 0.60$, ns and $\chi_2^2 = 0.45$, ns). It should be noted that only two males were involved in hyena and only one in dummy playback experiments (but location and hunting data were available for a further four males—see Table 1), while eight males were involved in lion experiments. Therefore these analyses were largely dependent on a difference between the sexes in response to lion rather than hyena playback experiments.

Table 3
Factors affecting vigilance during the full hour of observation after playback experiments

	Coefficient	Statistic	Significance
Playback type			
Dummy	0.00	$F_{2,83} = 11.37$	$p < 0.001$ ***
Hyena	0.15		
Lion	0.22		
Hunger state	0.0060	$t_{81} = 0.98$	ns
Time	-1.09	$t_{81} = 2.17$	$p = 0.033$
Proportion of time spent moving	-0.12	$t_{81} = 2.03$	$p = 0.046$
Distance from speaker at start of experiment	-0.16×10^{-4}	$t_{81} = 0.17$	ns
Presence of prey	-0.067	$t_{81} = 1.69$	$p = 0.096$
Individual identity ^a	—	$F_{39,81} = 1.24$	ns

The proportion of time spent looking at the loudspeaker was fitted as the dependent variate in an ANCOVA after an arcsin transformation. The model explained 31.4% of the total variance. Probability symbol after Bonferroni corrections: ¹ for $p < .1$; * for $p < .05$; ** for $p < .01$; and *** for $p < .001$ (Rice, 1989).

^a Not included in final model.

Female cheetahs did not react more strongly to competitor playbacks if they had cubs than if they were solitary. Solitary females were marginally less likely to look at the loudspeaker after competitor playbacks than females with cubs (effect of cub presence, $t_{67} = 1.74$, $p = .086$), but this effect was independent of playback type (effect of interaction between cub presence and playback type, $F_{1,66} = 0.15$, ns) and therefore probably reflected higher overall levels of vigilance for cheetah mothers (Laurenson, 1995a). Females with cubs were not significantly more likely to move after experiments than were females without cubs (effect of cub presence, $t_{65} = 1.01$, ns, interaction between cub presence and playback type, $F_{1,64} = 0.40$, ns), neither did they move farther (effect of cub presence, $t_{76} = 0.58$, ns, interaction between cub presence and playback type, $F_{2,74} = 0.83$, ns). Furthermore, females were not less likely to hunt, chase or kill prey after playback experiments if they had cubs (effect of cub presence, $\chi_1^2 = 0.71$, ns; $\chi_1^2 = 0.09$, ns and $\chi_1^2 = 0.04$, ns, and interaction between cub presence and playback type: $\chi_2^2 = 1.78$, ns; $\chi_2^2 = 2.39$, ns and $\chi_2^2 = 0.32$, ns on hunts, chases, and kills respectively).

Reactions of females with cubs did not depend on the cubs' age or number. Females did not look at the speaker more often, spend more time moving, move farther or hunt more frequently as their litter size increased or the age of their cubs decreased, regardless of playback type (Table 6).

DISCUSSION

These results demonstrate that cheetahs actively moved away from lions and hyenas once they perceived them to be present through an auditory stimulus. Perception of the presence of a competitor through playbacks also had a measurable impact on foraging rates of cheetahs, since cheetahs were much less likely to hunt after competitor playbacks than after dummy playbacks, resulting in a lower kill rate. Cheetahs appeared to perceive lions as a greater threat than hyenas since they were significantly more vigilant and were less likely to make a kill after lion playbacks than after hyena playbacks, although they did not move significantly farther. These differences are likely to be particularly marked given that two calls were played dur-

Table 4
Factors affecting movement and distance moved during the full hour of observation after playback experiments

	Coefficient	Statistic	Significance
Latency to first movement ^a			
Playback type			
Dummy	0.00	$F_{2,101} = 0.81$	ns
Hyena	-0.43		
Lion	0.18		
Hunger state	0.28	$t_{99} = 3.05$	$p < 0.01$ **
Time	19.23	$t_{99} = 2.38$	$p < 0.05$ *
Distance from speaker at start of experiment	-0.0024	$t_{99} = 0.99$	ns
Presence of prey	0.43	$t_{99} = 0.71$	ns
Individual identity ^d	—	$F_{40,99} = 1.15$	ns
Movement ^b			
Playback type			
Dummy	0.00	$F_{2,85} = 4.54$	$p = 0.013$ ¹
Hyena	0.16		
Lion	0.22		
Hunger state	-0.045	$t_{83} = 4.32$	$p < 0.001$ ***
Time	-1.50	$t_{83} = 1.61$	ns
Distance from speaker at start of experiment	0.00055	$t_{83} = 2.06$	$p = 0.042$
Presence of prey	-0.16	$t_{83} = 2.22$	$p = 0.029$
Individual identity ^d	—	$F_{40,83} = 1.15$	ns
Distance from speaker ^c			
Playback type			
Dummy	0.00	$F_{2,101} = 6.51$	$p = 0.002$ *
Hyena	0.50		
Lion	0.64		
Hunger state	-0.13	$t_{99} = 4.19$	$p < 0.001$ **
Time	-2.05	$t_{99} = 0.77$	ns
Distance from speaker at start of experiment	0.0020	$t_{99} = 2.47$	$p = 0.015$
Presence of prey	-0.37	$t_{99} = 1.84$	$p = 0.069$
Individual identity ^d	—	$F_{44,99} = 1.14$	ns

Probability symbol after Bonferroni corrections: ¹ for $p < .1$; * for $p < .05$; ** for $p < .01$; and *** for $p < .001$ (Rice, 1989).

^a The time to first movement was fitted as the dependent variate to an ANCOVA after a logarithmic transformation. The model explained 10.4% of the total variance.

^b The proportion of time spent moving was fitted as the dependent variate to an ANCOVA after an arcsin transformation. The model explained 21.6% of the total variance.

^c The distance from the loudspeaker at the end of the 1-h observation period was fitted as the dependent variate after a log transformation to an ANCOVA. The model explained 24.3% of the total variance.

^d Not included in final model.

ing hyena experiments while only one call was played during lion experiments.

It could be argued that the results obtained in this study might have been obtained if a cheetah avoids any loud sound regardless of whether it is the sound of a competitor. However, although some might argue that the sounds of ungulates such as wildebeest might be a more appropriate control than that used here, it might have also been argued that cheetahs may have been attracted to these sounds, and hence any differences between controls and predator playbacks were driven by prey attraction rather than competitor avoidance. In fact,

Table 5
Factors affecting hunting behaviour during the full hour of observation after playback experiments

	Coefficient	Statistic	Significance
Stalking or chasing prey^a			
Playback type			
Dummy	0.00	$\chi_2^2 = 14.65$	$p < 0.001^*$
Hyena	-4.61		
Lion	-4.37		
Hunger state	-1.05	$\chi_1^2 = 5.29$	$p = 0.021$
Time	-22.7	$\chi_1^2 = 1.17$	ns
Distance from speaker at start of experiment	0.0030	$\chi_1^2 = 0.20$	ns
Presence of prey	2.37	$\chi_1^2 = 1.27$	ns
Individual identity		$\chi_{44}^2 = 69.47$	$p = 0.009^{\dagger}$
Chasing prey^b			
Playback type			
Dummy	0.00	$\chi_2^2 = 6.01$	$p = 0.050$
Hyena	-1.66		
Lion	-1.15		
Hunger state	-0.26	$\chi_1^2 = 3.74$	$p = 0.053$
Time	-22.7	$\chi_1^2 = 4.45$	$p = 0.035$
Distance from speaker at start of experiment	0.00011	$\chi_1^2 = 0.00$	ns
Presence of prey	0.28	$\chi_1^2 = 0.09$	ns
Individual identity		$\chi_{44}^2 = 49.43$	ns
Killing prey^c			
Playback type			
Dummy	0.00	$\chi_2^2 = 11.48$	$p = 0.003^*$
Hyena	-1.09		
Lion	-9.30		
Hunger state	-0.17	$\chi_1^2 = 0.96$	ns
Time	-14.1	$\chi_1^2 = 1.29$	ns
Distance from speaker at start of experiment	0.0017	$\chi_1^2 = 0.18$	ns
Presence of prey	0.18	$\chi_1^2 = 0.04$	ns

The binomial variate of whether a cheetah exhibited hunting behaviour during the 1-h observation period after playback experiments was fitted as the dependent variate in a logistic regression model. The final model includes all factors which affected the model with $p < .1$ and leaves out those terms which do not. Probability symbols after Bonferroni corrections: [†] for $p < .1$; * for $p < .05$ (Rice, 1989).

^a The final model explained a deviance of 85.62 with 47 df out of a total deviance of 115.80 with 105 df.

^b The final model explained a deviance of 69.47 with 4 df out of a total deviance of 93.34 with 105 df.

^c The final model explained a deviance of 11.48 with 2 df out of a total deviance of 66.24 with 105 df. There was insufficient variation to be able to fit individual identity as a factor in this analysis.

a prior study is necessary to find a suitable control, and this was not feasible within the constraints of time and resources in this study. However while it is not possible to completely discount the loud noise hypothesis, it is most likely that the cheetahs were responding to the perceived presence of a competitor, especially given that cheetahs responded differently in terms of vigilance and kill rates to lion compared with hyena playbacks.

The stronger reaction of cheetahs to playbacks of lion calls than to hyena calls could have one of two explanations. First, cheetahs may perceive lions to be a greater threat than hye-

nas. Second, cheetah responses may vary because lions and hyenas have different hunting strategies, as lions are stalking and hyenas coursing predators. Unfortunately it is difficult to distinguish between these two explanations. Previous studies have shown that prey are more vigilant and have a longer flight distance (i.e., retreat further) to stalking predators compared with coursing predators (FitzGibbon and Lazarus, 1995). However whether this is because the stalking predator is a greater threat than a coursing predator, or is due to a different response pattern to alternative predator tactics is difficult to determine.

Were cheetahs responding to a perceived predation or a competition threat? Cheetahs did not adapt their behavior to their reproductive status. This result is surprising, given the high cub mortality due to predation (Laurenson, 1994), and could result from one of three explanations. First, cheetahs may be more at risk when they have dependent cubs but, if the cost of avoidance is low, selection may be too weak for cheetahs to adapt their behaviors to the relative predation risk. Second, cheetahs may themselves be at risk with or without dependent cubs, and by responding to predators they are avoiding a real threat to themselves as well as their cubs. Third, cheetahs may continue to respond to predators even when they have no cubs, because they are still vulnerable to kleptoparasitism. Since this study showed that cheetahs suffered a measurable reduction in foraging intake when they perceived other competitors to be present, the first explanation is unlikely. Distinguishing between the last two explanations depends on determining the relative threat that lions and hyenas pose to adult cheetahs.

While adult cheetahs have been known to be killed by lions within the Serengeti (Durant SM, unpublished data), there are no records of predation by hyenas within this ecosystem. Therefore, while there might be no reason for cheetahs to adapt their behavioral responses to lions according to the presence of dependent cubs, there may be a strong reason for cheetahs to adapt their responses to hyenas, yet this pattern was not reflected in the results reported here. Alternatively, since cheetahs lose kills to both lions and hyenas (Caro, 1994), they are vulnerable to kleptoparasitism from both these competitors. Hence there are probably indirect costs to not responding to the presence of a competitor even when an individual's survival is not directly threatened. Given this, it seems likely that cheetahs would benefit from avoiding both these competitors regardless of their reproductive status, through an avoidance strategy. Further evidence for this hypothesis is provided by the results obtained in this study, where cheetahs moved farther from competitor playback experiments when they were hungry than when they were well fed and were least vulnerable to kleptoparasitism.

A number of other studies have demonstrated behavioral avoidance of predators (Chivers and Smith, 1995; Dickman and Doncaster, 1984; Flowers and Graves, 1997; Hileman and Brodie, 1994; Holomuzki and Short, 1988; Kiesecker et al., 1996; Li and Li, 1979; Loose and Dawidowicz, 1994; Main, 1987; Peckarsky, 1996; Semlitsch and Reyer, 1992; Ward et al., 1997; Werner, 1991), however, in most of these examples avoidance is due to a visual, scent or chemical stimulus. There are few examples of avoidance due to an auditory stimulus (but see Bshary and Noe, 1997). Avoidance of infanticide, a behavior that is directly related to avoidance of cub predation, has been documented for lions, where female lions are able to recognize strange male lions that pose an infanticidal threat to her cubs, and move away from playbacks of their calls (McComb et al., 1992). Examples of avoidance of kleptoparasitism are rare.

Avoidance through active movement away from a potential predation or competitive threat is only likely to be worthwhile

Table 6

Effect of playback type, cub age and litter size on measures of vigilance, patterns of movement and hunting behaviour during the full hour of observation after playback experiments

Effects	Cub age		Cub age × playback type		Litter size		Litter size × playback type	
	Statistic	Significance	Statistic	Significance	Statistic	Significance	Statistic	Significance
Looking at speaker	$t_{50} = 0.12$	ns	$F_{2,48} = 0.11$	ns	$t_{50} = 0.86$	ns	$F_{2,48} = 0.25$	ns
Moving	$t_{50} = 0.20$	ns	$F_{2,48} = 0.13$	ns	$t_{50} = 0.03$	ns	$F_{2,48} = 0.23$	ns
Distance from speaker	$t_{57} = 0.40$	ns	$F_{2,55} = 0.16$	ns	$t_{57} = 0.50$	ns	$F_{2,55} = 0.28$	ns
Hunt	$\chi_1^2 = 2.09$	ns	$\chi_2^2 = 0.37$	ns	$\chi_1^2 = 1.96$	ns	$\chi_2^2 = 0.87$	ns
Chase	$\chi_1^2 = 0.14$	ns	—	—	$\chi_1^2 = 2.85$	ns	$\chi_2^2 = 2.36$	ns
Kill	$\chi_1^2 = 0.00$	ns	$\chi_2^2 = 0.02$	ns	$\chi_1^2 = 0.57$	ns	$\chi_2^2 = 1.10$	ns

Statistics are reported from the final model, which includes all factors which affected the model with $p < 0.1$ and leaves out those terms which did not. F statistics were obtained from ANCOVAs, while χ^2 statistics were obtained from logistic regression models. Dash indicates insufficient variation for inclusion in the model.

if predators or competitors are rare or aggregated (Colegrave, 1997). Thus prey, by moving away from a predator once seen, are more likely than not to be moving to an area where predators are at lower densities. This, in effect, means the prey is making use of a spatio-temporal refuge, in a similar way to a physical refuge fixed in time and space. Both lions and hyenas have an aggregated distribution (Durant, 1998), and so a cheetah which moves away from these competitors once seen has a better than average chance of moving into an area with lower competitor densities.

Predator avoidance is also only likely to be a useful strategy if anti-predator tactics are ineffective, since individuals will not choose to bear the energetic costs of avoidance when they are unlikely to be at any real risk. Anti-predator tactics are more likely to be employed by social species, since they are more effective when a large number of individuals are involved and individual risks of predation can be spread across the group (Stanford, 1995). In addition, social species are more likely to be the target of predator attacks because of the increased conspicuousness of large groups (Cowlshaw, 1997; Lima and Dill, 1990). These principles are also valid when an individual faces a kleptoparasitism threat rather than a predation threat. Cheetahs are generally solitary or in small groups and are unlikely to benefit from anti-predator behavior, since they are much smaller than lions and hyenas and are nearly always displaced by these competitors at kills (Caro, 1994; Durant SM, personal observation).

If a cheetah is spotted by a lion or hyena it will often be approached (Durant SM personal observation). At this point a cheetah can stay put and risk attack, or flee and risk fleeing into the path of another competitor, since both hyenas and lions live in social groups. Both these options are risky, and so it is likely to be better for a cheetah to move away before the threat becomes real, preferably before it is sighted by other competitors. In this study cheetahs generally moved a few hundred m from competitors (Figure 1), distances easily covered by lions and hyenas, but which make the difference between detection or no detection of a resting cheetah by competitors. However, the activity associated with hunting is more easily detectable over these distances, which might explain the reduction in hunting activity after competitor playbacks.

Does avoidance have implications for the distribution of cheetahs within the ecosystem? A previous study has shown that whenever cheetahs are found near high densities of lions or hyenas they are less likely to be hunting and more likely to be moving than at low densities (Durant, 1998). Furthermore, both lions and hyenas are found near high densities of gazelle, the main prey of cheetahs on the Serengeti plains (Caro, 1994; FitzGibbon, 1990a), where cheetahs are more frequently found near low densities of gazelle, while avoiding

areas with no gazelle at all (Durant, 1998). By avoiding competitors, cheetahs might move away from areas with high prey densities to areas of lower prey densities, where they are able to survive because of their higher hunting success on small groups or isolated individuals (FitzGibbon, 1990b). The mobility of cheetahs and their ability to avoid direct competition in an ever-changing landscape of competitors and prey may be the key to their coexistence with lions and hyenas.

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