



Predator avoidance, breeding experience and reproductive success in endangered cheetahs, *Acinonyx jubatus*

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I examine three hypotheses about predator avoidance behaviour: (1) avoidance increases an individual's reproductive success; (2) avoidance changes with breeding experience according to one of three described models; and (3) any reproductive or experience benefits accrued to individuals by avoidance are reflected in their spatial distribution. These hypotheses were tested on cheetahs which incur substantial juvenile mortality from predation by two larger competitors: spotted hyaenas, *Crocuta crocuta*, and lions, *Panthera leo*. To examine avoidance tactics, I played lion and hyaena vocalizations to individual female cheetahs. Lion avoidance increased with the statistical interaction between age and reproductive success, suggesting that it may be a learned behaviour, reinforced by successful reproductive events. This behaviour translated into a nonrandom spatial distribution of cheetahs with the most reproductively successful females found near lower lion densities than less successful females. Hyaena avoidance decreased with the interaction between age and reproductive success, suggesting that it is diminished by successful reproductive events, perhaps because a female cheetah switches from avoidance to using antipredator behaviours as she gets older. Hyaena avoidance behaviour translated into a spatial distribution with the most reproductively successful females found near lower hyaena densities than less successful females; however, younger females were found near lower hyaena densities than older females.

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Predator avoidance behaviour has attracted increasing interest during the last few years and has been documented for a wide variety of species (e.g. upland bullies, *Gobiomorphus breviceps*: Kennedy et al. 1994; bluegill, *Lepomis macrochirus*: Werner & Hall 1988; sand gobies, *Pomatoschistus minutus*: Forsgren & Magnhagen 1993; salamanders, *Desmognathus ochrophaeus*: Hileman & Brodie 1994; toads, *Bufo* spp.: Flowers & Graves 1997; hedgehogs, *Erinaceus europaeus*: Ward et al. 1997; rodents: Dickman & Doncaster 1984; Dickman 1992; lions, *Panthera leo*: McComb et al. 1993). However, while such behavioural tactics are often assumed to increase reproductive success through individual survival or reproduction, these effects have rarely been investigated. Neither have they been related to changes in the age or breeding experience of individuals. Finally, no study has shown how avoidance may shape the patterns of distribution of individuals within animal communities.

Older, and hence more experienced, individuals often have higher breeding success than younger individuals,

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which has been attributed to a number of factors, including foraging success and kleptoparasitism (Orians 1969; Quinney & Smith 1980; Sullivan 1988; Hesp & Barnard 1989; Gilardi 1994). Older individuals may also show stronger predator avoidance. In general, a behavioural tactic that is acquired with age and that enhances reproductive performance may be related to an individual's age as well as to its reproductive experience, since successful reproductive events may reinforce or diminish the behaviour. This relationship could take one of three forms depending on the mode of acquisition of the behavioural tactic. In the first model, an individual acquires a behaviour pattern at adulthood and this behaviour is fixed for life. Under these circumstances, an individual will show a positive relationship between the behaviour pattern and reproductive success; however, this relationship will not change with age. This will be reflected in a statistically significant positive relationship between the behaviour and reproductive success that is independent of age. In the second model, an individual matures with a certain level of the behaviour; however, as it grows older it enters a positive feedback loop, whereby it acquires stronger behavioural tactics with each successful reproductive

event. In this scenario young individuals may show a weak or nonexistent relationship between the behaviour and reproductive success, whereas old individuals show a strong relationship with reproductive success. This change between young and old individuals is most likely to take the form of a gradual improvement as individuals refine their behavioural tactics with experience. It will be reflected in a statistically significant positive interaction between age and reproductive success on the behaviour. The final model is similar to the second except acquisition of the behaviour operates in the opposite direction. Here the behavioural tactics weaken with each successful reproductive event, perhaps, in the case of predator avoidance, because the individual learns that a predator poses a lesser threat as it ages or because it learns successful antipredator behaviour and avoidance is no longer necessary. This will be reflected in a significant negative interaction between age and reproductive success on the behaviour. I used avoidance of lions and spotted hyaenas, *Crocuta crocuta*, by cheetahs in the Serengeti National Park in Tanzania to test these models.

The main competitors of cheetahs, lions and hyaenas, are also their main predators. Offspring survival is strongly affected by lion and hyaena predation. Over 90% of cheetah cubs die before reaching independence, predominantly from predation (Laurenson 1994). Adult cheetahs may be killed by lions (unpublished data) and they may also lose their kills to both predators (Schaller 1972; Caro 1994). Of the two species, evidence suggests that the lion is a more dangerous threat to the cheetah than the hyaena (Laurenson 1994; Durant, in press). There is also evidence that cheetah populations are limited by lion density (Laurenson 1995). Since cheetahs have small jaws and a light build, a mother has difficulty defending her cubs or kills against either predator, although cheetahs have occasionally been observed driving hyaenas away through aggressive displays (Caro 1994; personal observation). None the less such antipredator behaviours are likely to be risky. However, once a cheetah mother's cubs are mobile and have left their natal lair at 2 months, she can reduce both predation of her cubs and kleptoparasitism by adapting her behaviour and adopting an avoidance strategy (Caro 1987). It is this mobility that may enable cheetahs to coexist with lions and hyaenas (Durant 1998).

I tested the following three hypotheses to ascertain the mechanisms by which avoidance tactics may be acquired and the extent to which avoidance affects the distribution patterns of cheetahs within the Serengeti ecosystem. (1) Avoidance of potential predators by female cheetahs increases their reproductive success. (2) Avoidance changes with breeding experience according to one of the three models described above. (3) Any reproductive or experience benefits accrued to individual cheetahs by avoidance of predators are reflected in their spatial distribution.

METHODS

I tested the hypotheses on data from a long-term study population of cheetahs in the Serengeti National Park.

I used audio playback experiments to test for active avoidance of lions and hyaenas by cheetahs and counts of predators in timed scans to examine whether avoidance patterns were reflected in the spatial distribution of cheetahs across the study area.

The study area covers 2200 km² in the southeast of the Serengeti National Park (for full description see Caro 1994). Within this area, the habitat ranges from open woodland in the north and west, dissected with rivers, through long grass plains to short grass plains in the southeast. 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 on the open plains. The climate is seasonal with a wet season from November to 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 & Durant 1991) and complete life histories have been obtained for many individuals (Kelly et al. 1998; S. M. Durant, M. J. Kelly & T. M. Caro, unpublished data). Throughout the study, I located cheetahs 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). Active cheetahs can be seen up to and occasionally beyond 3 km away.

I used 65 females in the analyses. Of these, 34 had known reproductive histories, and were first seen as cubs, when their age can be estimated to within 1 month (Caro 1994). Another two females were first seen in an adolescent group when they were estimated to be 18 months old. This estimate could have a maximum error of 6 months, based on the normal age composition of adolescent groups (Caro 1994). The hunger state of each individual in the study was estimated by its belly size according to an increasing 14-point scale (Caro 1994).

Playback Experiments

I used audio playback techniques to quantify variation in avoidance behaviour between female cheetahs in a series of controlled experiments (Durant, in press). Between May 1993 and September 1996, I played lion and hyaena vocalizations to individual cheetahs and recorded their reactions. Recordings of lion roars and hyaena whoops were obtained with either a Panasonic SV250 or Sony TCD D7 digital audiotape recorder linked to a Sennheiser MKH816 microphone. Playbacks were played through a Sony XM 4020 Sony amplifier linked to a Sony TCD D3 digital audiotape 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 (peak pressures at 1 m of 116 dB for lions and 105 dB for hyaenas). I conducted experiments in the early morning between 0630 and 0930 hours when cheetahs are most active and are likely to hear lion and hyaena vocalizations (Kruuk 1972; Schaller 1972; East & Hofer 1991). The speaker was placed an average ± SD of 237 ± 11 m from the cheetah (the vehicle was used to

mask the observer when this was done) and observations made from a vehicle 100 m away. Cheetahs in this study were habituated to vehicles.

Lion playbacks consisted of a single bout of roars (McComb et al. 1994), whereas hyaena playbacks involved two bouts of whoops separated by a 5-min interval. Since hyaenas often whoop when moving (Kruuk 1972), playing two bouts gives the impression that a hyaena is stationary in the area. Playbacks alternated between two different hyaena recordings and five different lion recordings (Durant, in press). I conducted 26 hyaena playbacks to 18 individuals and 24 lion playbacks to 17 individuals. In addition, 12 'dummy' playbacks to 10 individuals where the equipment was set up but no sound was played were used for controlled comparisons.

For 1 h after playing recordings, I made instantaneous scans every 30 s to record whether the cheetah was looking at the speaker and whether she was moving. The number of scans when 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. In addition, for all except six experiments, data were collected for at least 5 min before the start of each playback experiment. I combined these data with data obtained from dummy playbacks to assess behaviour in the absence of lion or hyaena calls. At the end of the 1-h observation period the cheetah's location was noted using a Global Positioning System (GPS), accurate to within 100 m. Repeat lion and hyaena playbacks of the same type to the same individual were made a maximum of three times with a minimum of 1 month between repeats. No responses from lions or hyaenas were obtained after any of the playbacks.

Since no significant effects of age or reproductive success on distance moved were obtained from the dummy playback experiments, these data were further supplemented by location data from six observations of five female cheetahs with known reproductive histories who were first sighted between 0630 and 0930 hours and subsequently followed for 1 h. These data did not differ significantly from measures obtained in experiments (Durant, in press) and were used for analyses of distance moved.

Scan Data

Between November 1991 and October 1996, five research assistants and I collected detailed data on prey densities and predator distribution at each cheetah sighting. All data were entered directly into Psion organizers (model LZ64) which also automatically calculated the search time (see Durant 1998 for a full description of data collected). The number of predators seen within 2 km of the scan point was estimated by eye. Because of differences in the success of sighting predators and in distance estimation between different observers, observer was entered as a factor in all analyses. At each scan point, visibility in four 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 1–2 km and Area 2–3 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 and 3 km, respectively. For example, if at one scan point it was possible to see 1 km north, 2 km east and 3 km south and west, Area 1–2 km was graded as 3, as it was possible to see at least 2 km in three directions, whilst Area 2–3 km was graded as 2, as it was possible to see 3 km in only two directions (south and west). Heat haze was graded according to whether it was present, or whether it was possible to see a predator at 1, 2 or 3 km. The time of day influenced the number of predators seen and was entered both as a linear and a quadratic variate (denoted as time of scan² in the tables in the Results), the latter to account for predators being less easy to see, owing to a reduction in activity, during the middle of the day. A total of 34 female cheetahs were involved in scan data analyses investigating effects of reproductive success. A further 29 individuals were included in analyses of age effects alone.

Reproductive Success

For each female cheetah, the number of surviving cubs was defined as the number reared to 12 months or more at the time of playback or scan, after which time mortality is low. If a mother was accompanied by dependent cubs of less than 12 months, as was the case in 40 of the 62 experiments, then I calculated the contribution of these cubs to her reproductive success by dividing the cub age by 12 months and multiplying by the number of cubs that were known to have subsequently survived to 12 months. This figure was then added to the number of cubs reared previous to the current litter. I calculated cubs produced per year by dividing this total by the mother's reproductive life span (her age minus 2 years). For example, a female of 6 years old, who had successfully reared two cubs to 12 months and was accompanied by three 2-month-old cubs, only one of which subsequently survived, would have a total reproductive success of $2+1 \times (2/12)=2.17$. Her annual reproductive success was $2.17/4=0.54$. Only those females that were at least 2 years (thus were old enough to have produced cubs (Kelly et al. 1998) at the time of playback) were included in analyses. Female ages ranged between 2.1 and 12.8 years in playback experiments, and across a marginally greater range in scans.

Statistical Analyses

I used multiple regression and generalized linear models since all analyses involved many independent variables. In each analysis, all 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. Two-tailed tests were used throughout. Results from playback experiments are reported for reproductive success, age and the interaction between these two variables. Three types of model were used.

(1) Multiple linear regressions for analyses of proportionate measures of cheetah activity (looking at the

speaker or moving). Proportions were converted to a normal distribution before analysis under an arcsine transformation (Sokal & Rohlf 1981). Each proportion was first multiplied by 120 (the number of instantaneous scans in the experiment) and added to 1 and divided by 122 to account for the small number of experiments where the individual did not look at the speaker or move throughout the experiment. Variables included in these analyses were the start time of the experiment, the cheetah's belly size score, the presence of prey within 1 km at the start of the experiment, the initial distance from the loudspeaker, the presence of cubs, the number of cubs produced per year, the age of the cheetah and the interaction between the latter two variables.

(2) Multiple regression for analyses of the distance from the speaker 1 h after the start of the playback. Distance was converted to a normal distribution using a log transformation before analysis (goodness-of-fit test: $\chi^2_7=8.18$, NS). The same variables listed above were included in these analyses.

(3) A generalized linear model with Poisson errors corrected for overdispersion (McCullagh & Nelder 1989) for analyses of the number of lions and hyaenas seen in scans. The variables included in these analyses are listed above, under scan data. Analyses additionally controlled for the identity of the cheetah at the centre of the scan, since there were a large number of repeat scans for most individuals.

All analyses were conducted with the Genstat 5 version 3.1 statistical package (Payne et al. 1987).

RESULTS

Playback Experiments

Average age and reproductive success of cheetahs in the playback experiments were evenly distributed across different years of playback experiments (linear regression on log-transformed data controlling for playback type: effect of year on age: $F_{3,65}=0.43$, NS; effect of year on reproductive success: $F_{3,65}=0.81$, NS). Female cheetahs showed no aggression towards the loudspeaker after any of the experiments. Instead, when a cheetah heard the sound of a predator, she was most likely to pause, watch the loudspeaker, then move off.

No effect of reproductive success on movement or on distance from the loudspeaker was detected over 1 h after dummy playback experiments (Table 1). These variables also showed no relationship with age or with the interaction between age and reproductive success. However, vigilance (measured here by the proportion of time a cheetah spent looking at the loudspeaker) was significantly positively related to age. In addition, the interaction between age and reproductive success was negative. This led to a slight decrease in vigilance with increasing reproductive success for older females. None the less, cheetahs spent much less time looking at the speaker after dummy playbacks than after lion or hyaena playbacks (Durant, in press).

Vigilance after hyaena playbacks was unrelated to age or reproductive success (Table 1). However, movement

increased with both these variates, and there was a significant negative interaction between age and reproductive success. This interaction reversed the relationship between movement and reproductive success for older (8-year-old) cheetahs compared with younger (4-year-old) cheetahs (Fig. 1a). Therefore, whilst movement increased with reproductive success for young females, it declined with reproductive success for old females. Distance moved after experiments followed a similar pattern, indicating that movement was in a consistent direction (Table 1). After 1 h, the distance from the loudspeaker increased with reproductive success for young females; however, the significant negative interaction between age and reproductive success meant that this relationship was reversed for older females (Fig. 1b).

After lion playbacks, there was a similar relationship between vigilance and reproductive success and age as after dummy playbacks (Table 1), although overall vigilance was much higher. The interaction term resulted in lower vigilance in older than in younger females. The most likely explanation for this pattern is that older females were more likely to be moving than younger females (see below), and a moving cheetah is less likely to be able to look at the speaker than a stationary cheetah. Neither reproductive success nor age exerted an independent effect on movement patterns, but there was a significantly positive effect of the interaction between age and reproductive success for both movement and distance from the speaker. The direction of this interaction meant movement and distance from the loudspeaker at the end of the experiment were positively related to reproductive success and this relationship became stronger as females aged (Fig. 1).

Scan Data

Generally the longer an observer spent looking for predators, the more predators were seen (Table 2). In addition, various other physical factors, such as the time of the scan and heat haze, also influenced the number of predators seen. No more predators were seen from cheetahs without cubs than from those accompanied by dependent cubs; neither were more seen from cheetahs that were well fed than from cheetahs that were hungry. The number of hyaenas seen in scans was positively related to the age of the cheetah in the scan (Table 2). However, the interaction between age and reproductive success exerted a significantly negative effect on the number of hyaenas seen from a particular cheetah. This meant that although more hyaenas were seen from older cheetahs, as a cheetah aged, the negative relationship between the number of hyaenas seen and her reproductive success became more marked (Fig. 2a). The number of lions seen from scans declined with increasing reproductive success, but showed no relationship with age (Table 2, Fig. 2b).

When scan data were analysed across a larger number of scans where the age, but not necessarily reproductive success, was known for individual female cheetahs, there was no independent relationship between the number of hyaenas seen and age (generalized linear model with

Table 1. Vigilance and movement patterns after playback experiments

	Number of cubs/year				Age				Number of cubs/year×Age				Full model		
	Coefficient	df	t	P	Coefficient	df	t	P	Coefficient	df	t	P	Constant	Sum of squares	df
Dummy experiments*															
Looking at speaker	+0.087	46	1.76	0.085	+0.016	46	2.69	0.010	-0.024	46	2.41	0.020	+0.04	0.26	52
Moving	+0.043	54	0.75	NS	-0.005	54	0.54	NS	-0.003	54	0.03	NS	+0.39	2.03	56
Distance from speaker	+0.230	16	0.49	NS	-0.031	16	0.41	NS	-0.020	16	0.21	NS	+6.02	12.80	17
Hyaena experiments†															
Looking at speaker	+0.010	24	0.24	NS	-0.008	24	1.42	NS	-0.004	24	0.56	NS	+0.35	0.19	25
Moving	+0.790	19	2.78	0.012	+0.066	19	2.32	0.032	-0.160	19	2.67	0.015	+0.53	1.08	25
Distance from speaker	+2.740	19	2.85	0.010	+0.210	19	2.18	0.042	-0.500	19	2.51	0.021	+6.18	12.09	25
Lion experiments‡															
Looking at speaker	+0.180	19	1.98	0.062	+0.014	18	0.84	NS	-0.027	19	2.10	0.049	-0.27	0.60	23
Moving	-0.110	19	0.73	NS	+0.005	19	0.26	NS	+0.046	20	2.95	0.008	+1.76	1.60	23
Distance from speaker	-0.035	19	0.09	NS	-0.013	19	0.26	NS	+0.120	20	2.81	0.011	+10.70	12.04	23

Results are reported from multiple regression analyses of the proportion of time cheetahs spent looking at the speaker or moving and the total distance moved during 1 h after playback experiments. The final model includes all terms listed in the methods that affected the model with $P < 0.1$ and leaves out those terms that did not.

*Results from 12 dummy playback experiments to 10 cheetahs. Analyses of the proportion of time spent looking at the speaker and moving were additionally supplemented by observations taken before initiating 45 hyaena and lion playback experiments to an additional 12 cheetahs. Analyses of the final distance moved were supplemented by data taken on six occasions where the direction of the cheetah's gaze was not recorded.

†Results from 26 hyaena playback experiments to 18 cheetahs.

‡Results from 24 lion playback experiments to 17 cheetahs.

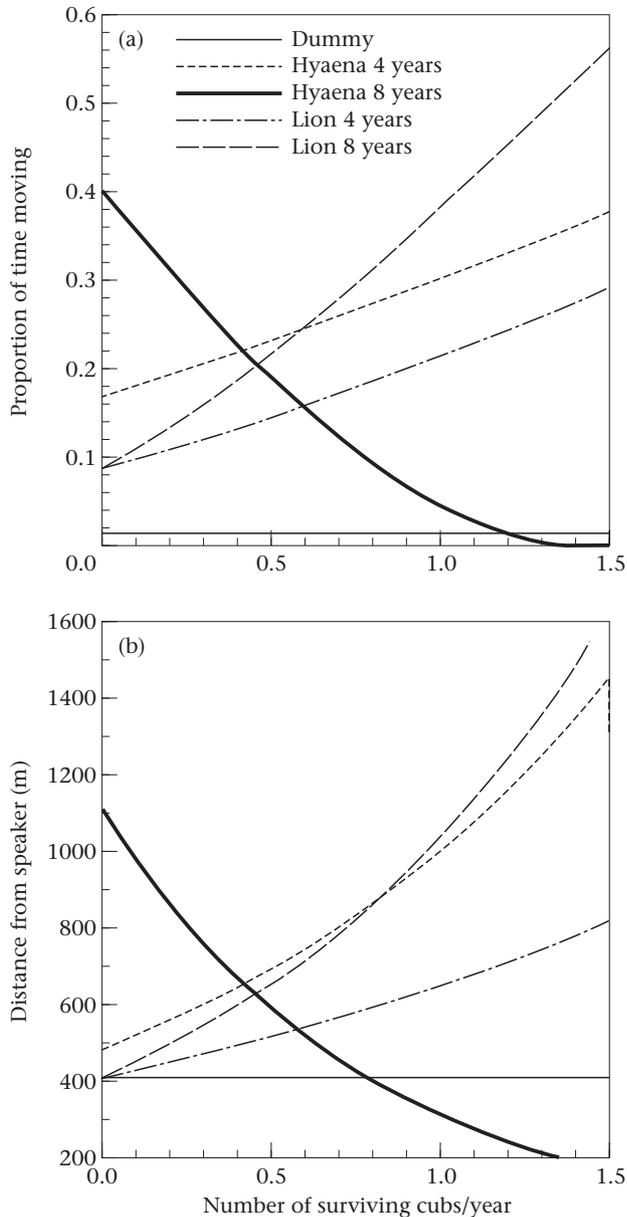


Figure 1. Variation in response to playback experiments with reproductive success. Values were predicted from the multiple regression models presented in Table 1. The curved graphs reflect the transformation of values for analysis. Playbacks were dummy or hyaena or lion vocalizations. Two age groups are depicted for illustration (young cheetahs at 4 years old and old cheetahs at 8 years old). Standard error bars are not shown because data were transformed for analysis. (a) Proportion of instantaneous scans taken every 30 s where cheetahs were moving during playback experiments. (b) Distance of cheetahs from the loudspeaker 1 h after the start of playback experiments.

Poisson errors: effect of age $+0.093$; $\chi_1^2=0.98$, 531 scans, 65 cheetahs, NS). However, for this larger number of scans, there was a significant negative effect of age on the number of lions seen (generalized linear model with Poisson errors: effect of age -0.28 ; $\chi_1^2=5.39$, 531 scans, 65 cheetahs, $P<0.05$). This effect could have been obtained if young females that were frequently found

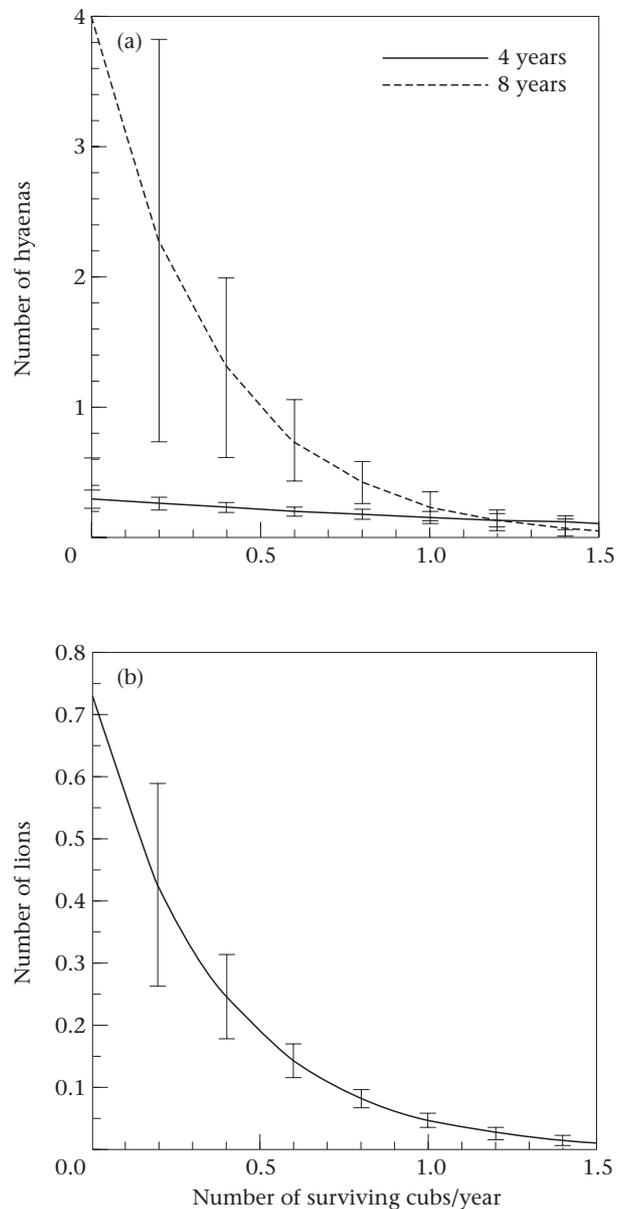


Figure 2. Variation in number of predators seen in proximity to cheetahs with reproductive success. Values were predicted from the generalized linear models presented in Table 2. Standard error bars were predicted from these models and are depicted as a guide. In (a) two age groups are depicted for illustration (young cheetahs at 4 years old and old cheetahs at 8 years old). In (b) there was no significant variation with age and sex and so the age groups are combined. (a) Number of hyaenas and (b) number of lions seen within 2 km.

near lions were less likely to survive. This is unlikely, however, because the effect remained when the analysis was restricted to females known to have lived to a minimum of 6 years (generalized linear model with Poisson errors: effect of age -0.26 ; $\chi_1^2=4.43$, 340 scans, 26 cheetahs, $P<0.05$). Six years is the average longevity for a female once she reaches independence (Kelly et al. 1998).

Table 2. The number of predators seen from cheetah scans

Factor or variate	Coefficient	Change in deviance	Coefficient of dispersion	df	χ^2	P
Number of hyaenas†						
Identity of cheetah	—	127.63	1.32	33*	96.69	<0.001
Time spent scanning	+0.002	34.08	1.17	1	29.13	<0.001
Observer	—	33.14	1.16	5	28.57	<0.001
Time of scan ²	-0.006	17.02	1.13	1	15.06	<0.001
Area 1–2 km	-0.230	4.44	1.09	1	4.07	0.044
Heat haze	+0.320	13.57	1.12	1	12.12	<0.001
Age	+0.460	10.43	1.11	1	9.40	0.002
Number of cubs/year	+1.560	3.48	1.08	1	3.22	0.073
Number of cubs/year×age	-0.210	5.92	1.10	1	5.38	0.020
Number of lions‡						
Identity of cheetah	—	96.66	0.94	33*	102.83	<0.001
Time spent scanning	+0.001	7.52	0.78	1	9.64	0.002
Observer	—	14.07	0.79	5	17.81	0.001
Time of scan	-0.120	8.21	0.78	1	10.53	0.012
Heat haze	+0.260	4.58	0.77	1	5.95	0.015
Number of cubs/year	-2.720	23.88	0.82	1	29.12	<0.001

Results are reported as deviance tables for terms affecting the number of predators seen within 2 km of known cheetahs across 406 scans. The number of predators seen in each scan was fitted to a generalized linear model with Poisson errors and corrected for overdispersion. Explanatory variates are described in the Methods. The final model includes all terms that affected the model with $P < 0.1$ and leaves out those terms that did not.

*Degrees of freedom reduced due to collinearity, where the explanatory variables for one individual are a linear combination of the other 33.

†Total deviance was 672.18. The following terms were not significant and hence were omitted from the analysis: time of scan; Area 2–3 km; season; belly size; presence of cubs.

‡Total deviance was 446.24. The following terms were not significant and hence were omitted from the analysis: time of scan²; Area 1–2 km; Area 2–3 km; season; belly size; presence of cubs; age; number of cubs per year×age.

DISCUSSION

When no sound was played in a playback experiment, cheetahs showed very little response in terms of movement patterns. However, when a lion call was played their response was best described by model 2, whereas when a hyaena call was played their response was best described by model 3 (see Introduction). Avoidance of lions by cheetahs increased with an individual's reproductive success. Furthermore, this avoidance increased as an individual grew older. This translated into a pattern of distribution in which the most successful cheetahs were found least often near lions. Avoidance of hyaenas by cheetahs showed a different relationship with age and reproductive success; here reproductive success of young cheetahs was positively related to hyaena avoidance, whereas for older females it was negatively related. This translated into a pattern of distribution in which older females tended to be found near higher densities of hyaenas, although the number of hyaenas seen from cheetahs of all ages continued to decrease with reproductive success. Here, young cheetahs appeared to recognize hyaenas as a greater threat than did older cheetahs. Whilst it cannot be discounted that my results might have been obtained if a cheetah avoided any loud sound regardless of whether it is the sound of a competitor, it is likely that my interpretations are reasonable, especially given that cheetahs responded differently to lion and hyaena playbacks.

A previous study has shown that cheetahs avoided lions and hyaena calls in playback experiments, but was unable to detect any changes in response when cheetah females were alone or were accompanied by dependent cubs (Durant, *in press*). My present results show that female cheetahs have a flexible response to predators, since their behaviour changes as they age, and they also reap reproductive benefits from this response. It may not be worthwhile for a female cheetah to cease avoiding lions and hyaenas when she is alone and is not accompanied by dependent cubs, since she may face a small, but not insignificant, risk of predation herself, as well as a risk of kleptoparasitism if she makes a kill when these predators are near by.

Other studies have demonstrated behavioural avoidance of predators. These studies are mainly restricted to aquatic species and the behaviours observed more commonly involve a use of a physical refuge and a reduction rather than an increase in activity (e.g. zooplankton: Li & Li 1979; isopods: Holomuzki & Short 1988; odonate larvae: Werner 1991; tadpoles: Semlitsch & Reyer 1992; Kiesecker et al. 1996; shrimps: Main 1987; hedgehogs: Ward et al. 1997). Examples of avoidance through an increase in activity, or escape or movement away from the threat are more unusual (e.g. zooplankton: Li & Li 1979). However, although no form of predator avoidance has yet been unambiguously related to reproductive success and age, there is some evidence that suggests that such a link exists. Mech & McRoberts (1990) showed that

older white-tailed deer, *Odocoileus virginianus*, have higher calf survival and hypothesized that this is related to an increase in the success of predator avoidance or anti-predator behaviour in older mothers. McComb et al. (1993), in a series of elegant playback experiments, showed that a female lion can recognize strange male lions that pose an infanticidal threat to her cubs, and move away, thus almost certainly reaping reproductive benefits.

Avoidance patterns observed in these playback experiments translated directly into distribution patterns of cheetahs in relation to lions and hyaenas. Four hypotheses could explain these patterns. First, if conditions changed during the study, the response of cheetahs to playback experiments may have changed in response to these conditions and not as cheetahs have aged. Assuming the estimated annual decline of 7.5–8.5% for the hyaena population close to Seronera is valid for the entire study area (Hofer et al. 1993), hyaenas declined by ca. a quarter during this study, whilst the lion population decreased by one-third in 1994, owing to a canine distemper epidemic (Roelke-Parker et al. 1996). This epidemic did not, in itself, affect the cheetah population (unpublished data). However, both the average age and reproductive success of the cheetahs in the playback experiments showed no relationship with the year of the study. Therefore the changes of behaviour with age and reproductive success observed were not merely an artefact of any changes in predator density.

Second, the observed distribution of cheetahs in relation to lions may arise because those cheetahs that come least into contact with lions suffer the least predation. This hypothesis does not require a mechanism of active avoidance to explain the distribution patterns observed. However, it does not provide a full explanation of my results for several reasons. (1) Active avoidance behaviour was observed during playback experiments. (2) Both cheetahs and their predators are highly mobile. Therefore, it is unlikely that a particular cheetah would be less likely to come into contact with a lion or a hyaena simply as a consequence of the location of its home range. (3) A previous study showed that cheetahs were more likely to be moving rather than resting or hunting if nearby lion numbers were high (Durant 1998) again supporting a mechanism of active avoidance.

A third hypothesis can be termed a 'fail-move' hypothesis where, if her litter is killed by lions, a female moves away from the site of failure. Females that succeed might not move or might move a shorter distance. This hypothesis fits the movement patterns of female red-winged blackbirds, *Agelaius phoeniceus*, which are more likely to move to new nest sites if their previous one is unsuccessful (Beletsky & Orians 1991). However, it is unlikely to be true for cheetahs because of their extreme mobility, and the large temporal variation in the distributions of lions and hyaenas. Cheetahs in the study area migrate across large home ranges averaging 800 km² (Caro 1994), an area that encompasses an average of four lion territories (Hanby & Bygott 1979), moving from the woodland edges in the dry season to the short grass plains in the wet season (Durant et al. 1988; Caro 1994). Furthermore,

lions and hyaenas are also mobile and move large distances daily (Kruuk 1972; Schaller 1972). If a cheetah loses her cubs and moves, she cannot move into an area devoid of lions and hyaenas, because soon these predators will also move through this area. Thus, for a fail-move strategy to work, a cheetah would have to learn to associate lions or hyaenas with her failure and recognize them rather than their location. This explanation then reduces to one that is identical to the final hypothesis below.

The final and most likely explanation for the distribution pattern is as follows. Whether a young female manages to rear cubs may be largely related to chance. However, as a female ages and becomes more experienced, if she is to be consistently successful at rearing her cubs, she begins to avoid their main predators. If avoidance behaviour is acquired in this way, it could enable a proportion of cheetah females to achieve high reproductive success. Successful females move away quickly from dangerous predators when they are seen or heard, allowing them to fill spatiotemporal refuges as and when they appear. This could enable cheetahs to coexist alongside superior competitors. In support of this hypothesis, lions and hyaenas were less likely to be seen near cheetahs in the wet season, when densities of competitors were highest whilst cheetahs were positively associated with each other in both seasons (Durant 1998).

How might such a behaviour pattern be acquired? No study to date has investigated the interactive role that age and reproductive success exert on behaviour patterns. Semlitsch et al. (1992) suggested that a species has a fixed innate response to low-level predation which can be modified by environmental factors that, in the case of their study species, tadpoles, appeared to be chemical in origin. However, in many organisms such modifications could originate through learning and experience, although these have only rarely been related to reproductive success. Learning is best put forward as an unambiguous explanation of changes in individual behaviour with age when data are collected longitudinally and an individual modifies its response after repeated exposure to a particular stimulus. However, for many long-lived vertebrates, if learning relates to an individual's success at rearing offspring, the time frames within which these behaviours are learnt are too long for longitudinal study. In these situations, studies have to rely on cross-sectional data, such as that from playback experiments. My scan data, which were collected over a longer period and involved many repetitions for each individual, were analysed longitudinally by controlling for individual identity. These data showed a similar relationship with age and reproductive success for the number of hyaenas seen near cheetahs to that of the avoidance response of cheetahs to hyaena playback experiments. The relationship for the number of lions seen was slightly different in that it showed no relationship with age; however, lions were rarely seen near cheetahs. When I increased the sample size by including females whose age, but not reproductive success, was known, there was a significant negative relationship between the number of lions seen and the cheetah's age. This relationship remained even

when the analysis was restricted to females known to survive beyond the average age for the population, and so was not due to higher mortality of those females seen most often near lions.

Therefore it seems most likely that cheetahs acquire or lose avoidance behaviour through learning according to models 2 and 3. Upon independence, cheetahs are wary of both lions and hyaenas. However, older and more successful cheetahs show stronger avoidance of the more dangerous predator, the lion, and weaker avoidance of the less dangerous spotted hyaena. Whilst antipredator behaviours against lions are extremely risky and largely ineffective, they can occasionally be effective against spotted hyaenas (Caro 1994; personal observation). Therefore as cheetah mothers become more experienced, they may be switching from avoidance to antipredator behaviours against hyaenas, but retain and extend avoidance behaviours for use against lions.

These results are particularly pertinent since cheetahs are endangered and declining throughout their range (Myers 1975) and the species is often considered a case study within conservation biology (O'Brien et al. 1983, 1985; Caro & Laurenson 1994; Caughley 1994). My results suggest that variation in potentially adaptive behaviour patterns between individuals can be crucial to population persistence. Indeed, predator naiveté has been cited as a factor in the failure of reintroduction programmes (May & Lyles 1987; Short et al. 1992) and it is easy to imagine a sudden increase in lion numbers driving a predator-naïve population of cheetahs extinct. A population with a diverse suite of potentially adaptive behaviour patterns is more likely to be protected against the consequences of demographic and environmental stochasticity.

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