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The costs and benefits of predator inspection behaviour in Thomson's gazelles

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Summary. When Thomson's gazelles (*Gazella thomsoni*) detect stalking predators, such as cheetahs (*Acinonyx jubatus*) and lions (*Panthera leo*), they often approach and follow the predator for up to 72 min (average 14 min). Coursing predators are rarely approached. Gazelle groups were more likely to approach cheetahs if the groups were larger, if the vegetation was low, or if the cheetahs came closer to the group. Immature gazelles were more likely to approach than adults, and a higher proportion of group members participated in inspection behaviour in small groups than in large ones. Gazelles approached closer in less risky situations: if they were in larger groups or if the vegetation was low. Inspection behaviour caused cheetahs to move further between rests and between hunting attempts. Approaching cheetahs was risky, particularly for younger gazelles (probability of being killed while inspecting a cheetah was 1 in 5000 approaches for adults and 1 in 417 approaches for half-grown/adolescent gazelles), and the risks were higher than monitoring cheetahs from a distance. The time costs of predator inspection were also considerable (less than 4.2% of daylight time budget), suggesting that the benefits must be substantial to offset these costs. The results suggested that inspection behaviour was multifunctional, causing stalking predators to move out of the vicinity, enabling gazelles to monitor the predators' movements, and providing an opportunity, particularly for younger animals, to learn about predators. By approaching, gazelles also inform predators that they have been detected and alert other gazelles to the predators' presence.

Key words: Predator inspection – Mobbing – Predation

Introduction

Many prey animals, from a wide range of taxa, approach and follow predators, particularly when they are first encountered (see Curio 1978 for a review). Such behaviour, called predator inspection, mobbing, fascination or investigative behaviour depending on the circumstances, appears paradoxical. Rather than fleeing from approaching predators, individual prey reduce the distance between themselves and the predator, apparently increasing their chances of being attacked (Curio and Regelmann 1985, 1986; Dugatkin 1992). Since approaching predators is also costly, both energetically and in terms of lost opportunities for feeding and obtaining mates, participants are thought to benefit from a reduced risk of predation for themselves or their relatives. While a number of possible functions of approach behaviour have been proposed, such as deterring the predator from further attacks, gathering additional information, and warning other group members that a predator is present, few studies have attempted to distinguish between them (see Curio 1978; Dugatkin and Godin 1992 for reviews), mainly because of the difficulties of observing the reactions of predators to approach behaviour in the wild (but see Bildstein 1982; Buitron 1983; Ishihara 1987; Pettifor 1990). Recent studies of predator inspection behaviour have often focused on the extent of cooperation between inspecting individuals (e.g. Dugatkin 1991), rather than the reasons that individuals inspect. Although predator inspection behaviour has generally been studied in birds and fish, it is widespread in ungulates, and the aim of this paper is to determine the costs and benefits of predator inspection behaviour for Thomson's gazelles (*Gazella thomsoni*). The costs and benefits are assessed in terms of changes in the risk of predation, time lost from other essential activities, such as feeding, and energy expenditure.

The main benefits that gazelles may derive from predator inspection are:

A. Reducing the current risk of predation. Approaching the predator may reduce an individual's probability of being attacked, by causing the predator to move on to hunt elsewhere (Curio 1978; Bildstein 1982; Shedd 1982; Buitron 1983; Pettifor 1990), by confusing the predator, particularly if the prey approaches in a saltatory manner and as a member of a group (Hoogland and Sherman 1976; Curio 1978), by informing the predator that it has been detected and that its chances of a successful attack are therefore reduced (Harvey and Greenwood 1978; Owings and Owings 1979), or by keeping the predator in sight, thereby reducing the risk of ambush (Lipetz and Bekoff 1980; Schaller 1972).

B. Acquiring information about the nature of the potential threat. Many prey animals live in close proximity to their predators and encounter them frequently (e.g. fish, Pitcher 1980). On account of their low motivation to hunt, the predators will often pose little threat, rendering extreme evasive action by the prey unnecessary. By assessing the risk posed by a particular predator, a prey animal could modify its behaviour accordingly, and consequently conserve time and energy. Approaching and following predators may enable prey animals to gather such information. This has been proposed as an important benefit of predator inspection in fish (Csányi 1985; Magurran and Girling 1986; Pitcher 1986; Licht 1989; Dugatkin and Godin 1992), birds (Kruuk 1976; Curio 1978), and mammals (Walther 1969; Owings and Coss 1977; Robinson 1980; Rowe and Owings 1990). Inexperienced gazelles, in particular, may benefit from the opportunity to learn about predators in a relatively low-risk situation when the predators are out in the open (Altmann 1956; Kruuk 1972; Berger 1979).

C. Informing others of the potential threat. A number of studies have shown that individuals that have approached predators transmit information about the current threat of predation to conspecifics nearby (Pitcher et al. 1986; Magurran and Higham 1988). Usually they warn others of the presence of a predator in the vicinity, and consequently recruit more individuals to collectively approach the threat (Kruuk 1976; Curio 1978; Owings and Owings 1979; Tamura 1989). By observing conspecifics approaching potential predators, predator-naive individuals may also learn to recognise dangerous predators and to react to them accordingly (Curio et al. 1978a, b; Buitron 1983; Bartecki and Heymann 1987).

Thomson's gazelles in the Serengeti, Tanzania, commonly approach and follow predators, sometimes for as long as 72 min, and usually in large groups (Kruuk and Turner 1967; Walther 1969; Kruuk 1972; Schaller 1972). By comparing situations when gazelles are more or less likely to approach, and determining the effect of inspection behaviour on the predator and on the behaviour of other gazelles nearby, I test the hypotheses outlined above.

Methods

Predator inspection behaviour in Thomson's gazelles is defined here simply as gazelles approaching and following a predator. Although a gazelle may approach just once, and then return to feed, it is usual for the behaviour to escalate, with many other gazelles being attracted to the disturbance, sometimes from distances of up to 800 m, and the gazelles milling around the predator, usually in a compact group (Walther 1969). It is similar to the mobbing behaviour of birds but there is no aggression against the predator (Walther 1969). Sometimes gazelles will run towards the predator, only turning away when 20–30 m from it. Other times they stand in front of the predator, only fleeing when it gets too close and then running away to watch from behind. Groups of up to 1000 individuals may be involved in following the predator at any one time. Gazelles sometimes emit short snorts while following the predator.

Thomson's gazelles interacting with four of their main predators, cheetahs (*Acinonyx jubatus*), lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*) and wild dogs (*Lycaon pictus*), were observed on the long-, intermediate-, and short-grass plains of the Serengeti National Park, Tanzania, between March 1985 and April 1987. I collected data only during daylight hours and mainly in response to cheetahs, diurnal predators whose main prey are Thomson's gazelles. In addition, I noted the reactions of gazelle groups to lions, wild dogs and spotted hyaenas opportunistically whenever I saw them interacting. These predators can be broadly categorised into two groups, coursers and stalkers, based on their main hunting technique (FitzGibbon and Fanshawe 1988). Stalkers, such as cheetahs and lions, tend to rely on surprise and very short fast chases for their success, while coursers, such as wild dogs and spotted hyaenas, tend to rely more on stamina, approaching their prey in full view and running them down over long distances.

Observations were made from a Landrover during daylight hours, using 10 × 50 binoculars, and were usually recorded onto tape for later transcription to data sheets. I followed cheetahs at a distance of 200–400 m and recorded the reactions of gazelle groups that detected them, noting whether they approached or simply monitored the predators from a distance. I only collected data in situations where I thought the cheetah had previously been undetected by all gazelles within 1 km, either because it had been lying down, had walked out of cover or from over a hill, or because it had approached through an area with no gazelles; otherwise the reactions of the focal group might have been influenced by the behaviour of other groups that had previously followed the cheetah. A group was categorised as having inspected if at least one group member approached and followed a predator. To measure the duration of inspection behaviour, I started a stopwatch when the first gazelle approached and stopped it when 50% of the inspecting group had returned to feed.

Whenever I saw a gazelle group inspect a cheetah, I recorded the following data: (i) the time of day, categorised as morning (0700–1100 hours), midday (1101–1500 hours) and afternoon (1501–1900 hours); (ii) the height of the vegetation through which the cheetah was walking when the first gazelle detected, estimated to the nearest 10 cm; (iii) the number of cheetahs [the majority of data were collected in response to single cheetahs (73% of cases), but data were collected in response to groups of two and three cheetahs in 14% and 13% of cases respectively; no data were collected from female cheetahs with cubs]; (iv) the cheetah's belly size, categorised as follows: 1: thin, 2: intermediate, 3: very full (belly size is a good indicator of how recently a cheetah has fed, and therefore its likelihood of hunting again within the next few hours; cheetahs in groups usually have similar belly sizes, so one of the broad categories described here could be used to describe the whole group); (v) the cheetah's behaviour when it was first detected by a gazelle in the focal group, categorised as follows: 1: walking towards the gazelle group that detects it, 2: walking parallel to the group, 3: walking away, and 4: stalking; (vi) the initial size of the gazelle group (individuals were defined as group members if they were within 50 m of each other) when the first group member detected the cheetah [defined as adopting the stare posture (Walther 1969) while looking in the cheetah's direction], and again when the group stopped inspecting or in the case of non-inspecting groups when 50% of group members had returned to feed; (vii) the shortest distance between the cheetah and the focal group before any group member approached, or in cases where no group member approached, the shortest distance the cheetah came to the group; (viii) the total number of gazelles within 1 km of the cheetah when it was first detected, and the percentage of these gazelles which had detected the cheetah 10 min after the first gazelle detected; (ix) the distance from the cheetah to the nearest gazelle at 1-min intervals during predator inspection, estimated to the nearest 5 m if less than 30 m and to the nearest 10 m if greater than this; (x) the percentage of group members that participated in predator inspection, approximately 5 min after the first gazelle had started to approach; and (xi) the age and sex of gazelles in both the part of the group that approached and in the part that remained behind. Gazelles were divided into five age categories, fawns, half-growns, adolescents, subadults and adults, on the basis of external physical characteristics (Walther 1973).

To determine whether inspection behaviour affected the movements of cheetahs, I carried out 23 all-day (daylight only) follows of cheetahs, recording the distances they walked and the time between rests (i.e. sitting or lying down), whether they were approached or not during each move, and the distances between successive hunting attempts. Series of moves by individual cheetahs were not independent. Therefore, in the final analysis to determine the effect of inspection behaviour on the distance and duration of moves, I included only the first move recorded during the follow of each cheetah when it was/was not being inspected (i.e. two records/cheetah). The distances between rests were recorded from the Landrover odometer to the nearest 100 m, or estimated by eye if less than 200 m. All the cheetahs followed had belly sizes 1 or 2.

From my follows of cheetahs, I knew the average number of gazelle groups that approached cheetahs each day, the size of these groups, and the average length of time for which they followed the cheetah. The approximate size of the gazelle (Campbell et al. 1990) and cheetah (Caro 1993) populations in the Serengeti are also known, and therefore I could estimate the percentage of an average gazelle's daily time budget spent following cheetahs (mean number of gazelles that approach a cheetah each day × mean duration of approach × number of cheetahs/number of gazelles in ecosystem). Gazelles also follow lions, but not having data on the behaviour of gazelles in response to these predators, I used the percentage of time spent following cheetahs, as calculated above, to calculate the amount of time spent following lions, multiplying it by 5.6 to take into account the relative size of the cheetah (500) and lion (2800) populations (see Caro 1993 for derivation of predator population estimates), and by 39/52 because of the differences in the probability of groups approaching cheetahs and lions (Table 1).

Analysis. I used logistic regression models (Cox 1970) to determine the factors that influenced whether or not a group approached and followed cheetahs (see Albon et al. 1986 and Clutton-Brock et al. 1992 for more detailed descriptions of this method). The parameters of the model were estimated by maximum likelihood, which provides an index of the goodness-of-fit of a model including a particular set of parameters, and can be used to determine whether the inclusion of extra parameters in the model significantly improves the fit. All likely explanatory variables were fitted as terms in the model, and terms were dropped until the model contained only those terms whose elimination would significantly decrease the explanatory power of the model. The "percent total deviance" provides an index of the goodness-of-fit of the term compared to a model which would explain all of the variation in the dependent variable.

Results

The probability that a gazelle group detecting a predator in daylight would approach and follow it varied according to the predator species (cheetahs > lions > wild dogs > spotted hyaenas, Table 1). Walther (1969) also noted that inspection behaviour was most common in response to cheetahs, and also leopards, while Schaller (1972) noted that it rarely occurred in response to wild dogs or hyaenas, but was common to lions. Inspection behaviour was never observed in response to jackals (*Canis* sp.). Predators vary in rarity in the study area with wild dogs currently being the rarest, and spotted hyaenas the most common, with lions and cheetahs intermediate (Table 1). In terms of the threat posed by the different predator species, spotted hyaenas kill the most gazelles/individual predator, followed by cheetahs, lions and wild dogs in that order (Table 1). However, spotted hyaenas and lions primarily hunt at night (Kruuk 1972; Schaller 1972; Van Orsdal 1984), wild dogs also hunt at night but to a lesser extent (Frame 1986), and cheetahs hunt almost entirely during the day, so that the risk posed by these predator species encountered during daylight hours is probably in the order cheetahs > wild dogs > hyaenas > lions. The incidence of inspection behaviour does not therefore simply reflect the rarity of the predator or the risk it poses to the gazelles, but is far more common in response to stalking predators than coursers.

Inspection behaviour in response to cheetahs

The percentage of group members which approached a cheetah varied from 0 to 100, but there were relatively few cases where only a proportion of the group approached (19.1% of groups). In the majority of cases either all group members approached (in 35.8% of groups) or none did (in 45.1% of groups, Fig. 1), and therefore the probability of an individual group member approaching a cheetah was not independent of the behaviour of other group members. As a result, in order to determine the factors that influenced the incidence of predator inspec-

Table 1. The incidence of predator inspection in response to four predator species, as measured by the percentage of groups detecting the predators that approach, the relative abundance of each predator in Serengeti National Park, the relative importance of gazelles in the diet of each predator (measured in terms of the number of adult gazelles killed/individual predator) and the relative probability that the predator will hunt gazelles during the day (1 = highest, 4 = lowest)

Predator species	Hunting method	% Groups inspecting	Relative abundance	Importance of gazelles in diet	Probability that predator will hunt
Cheetahs	Stalker	52 ($n=173$)	3	2	1
Lions	Stalker	39 ($n=52$)	2	3	4
Wild dogs	Courser	3 ($n=176$)	4	4	2
Spotted hyaenas	Courser	0 ($n=38$)	1	1	3

The data on relative abundance of the four predators, and killing rates are from Caro 1993

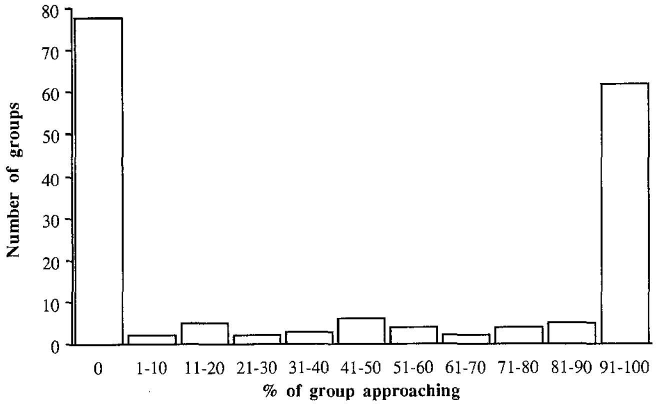

Fig. 1. Frequency distribution of the percentage of group members approaching cheetahs

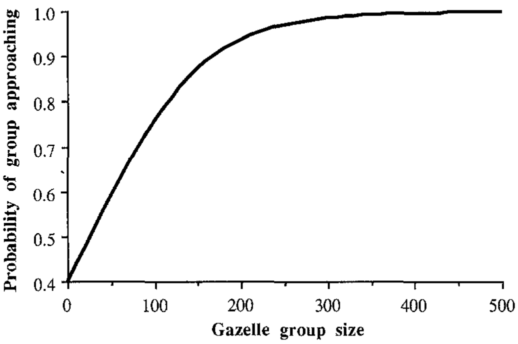

Fig. 2. Logistic curve fitted to the probability of gazelle groups of varying sizes approaching cheetahs. The height of the vegetation and the closest distance from the gazelle group to which the cheetah came before inspection started are set at their means of 40 cm and 193 m respectively

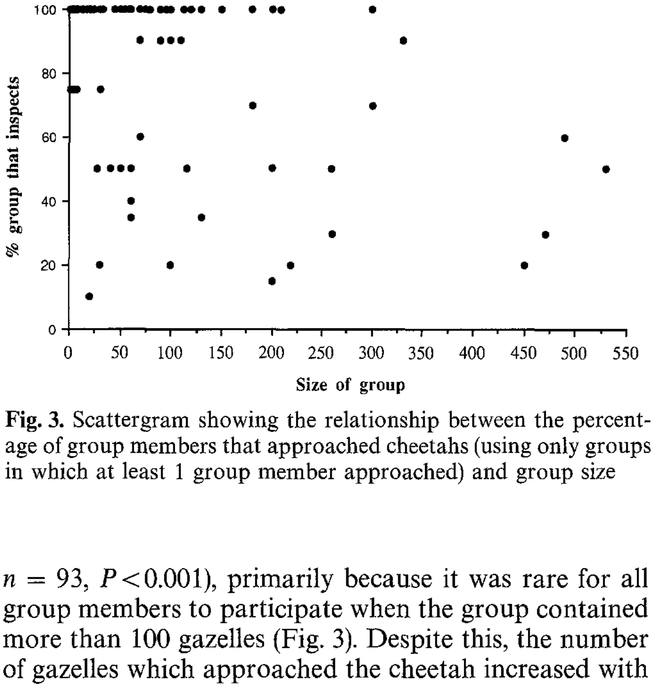

Fig. 3. Scattergram showing the relationship between the percentage of group members that approached cheetahs (using only groups in which at least 1 group member approached) and group size

tion behaviour, I used the probability of the group approaching as the dependent variable. Although a group was defined as having approached if at least one group member approached the predator, in most cases (66%) of inspection behaviour, all group members participated. The results of the logistic regression analysis showed that a gazelle group was more likely to approach and follow cheetahs if the group was larger, if the vegetation was lower, or if the cheetahs came closer to the group (Table 2, Fig. 2). The size of the gazelle group could be replaced in the model by the number of gazelles within 1 km ($\chi^2 = 9.0$, $df = 1$, $P < 0.01$, deviance explained = 6.8%), but once gazelle group size had been put into the model, the number of gazelles within 1 km did not significantly improve the goodness of fit ($\chi^2 = 1.3$, $df = 1$, NS). The time of day, and the number of cheetahs, their behaviour, and their belly size had no effect on the probability of the group approaching the predator (Table 2).

Considering data only from groups in which at least one group member approached, the probability of a gazelle participating in predator inspection varied according to the initial size of the group and the gazelle's age. The percentage of group members participating in inspection behaviour decreased with increasing size of the group (when it first detected the predator, $r = -0.458$, $n = 93$, $P < 0.001$), primarily because it was rare for all group members to participate when the group contained more than 100 gazelles (Fig. 3). Despite this, the number of gazelles which approached the cheetah increased with the initial size of the gazelle group ($r = 0.819$, $n = 93$, $P < 0.001$). Immature gazelles (subadults, adolescents and

Table 2. Logistic regression models examining the factors influencing whether a group approaches and follows a cheetah or not

Term	Coefficient	χ^2	*df*	*P*	% Total deviance
Constant	2.580				
Gazelle group size	0.01555	14.9	1	$P < 0.01$	8.6
Shortest cheetah gazelle distance	−0.00976	14.2	1	$P < 0.01$	8.2
Vegetation	−0.2743	11.6	1	$P < 0.05$	6.7
Rejected terms					
Time		4.8	2		
Number of cheetahs		1.6	2		
Cheetah's belly size		0.2	2		
Cheetah's behaviour		6.1	3		

χ^2 values refer to dropping the term from the full model in the case of terms included in the model and to adding the term to the full model in the case of rejected terms

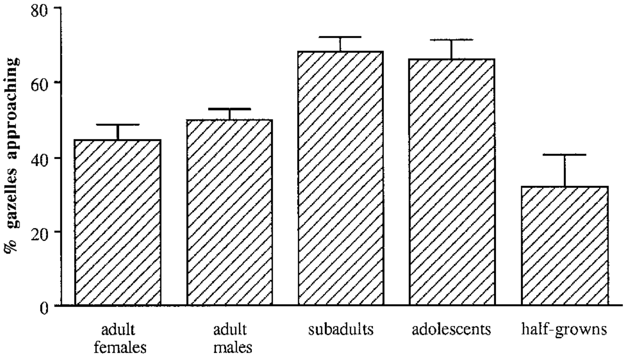

Fig. 4. The percentage of gazelles in five age/sex classes that approached the cheetah, using data from 39 gazelle group/cheetah interactions in which not all group members approached. Fawns were never observed to participate in predator inspection

half-growns combined) were more likely to approach the cheetah than adults (percentage of adults approaching using data from 39 cheetah/gazelle group interactions in which not all group members approached, mean $\pm$SE $= 49.7 \pm 2.6$, mean percentage of immatures approaching $\pm$SE $= 62.6 \pm 3.7$; $t = 2.85$, $P < 0.01$). Dividing up the age classes, sub-adults and adolescents were more likely to approach than adult males and adult females, while half-growns were less likely to (ANOVA, $F_{4,167} = 7.73$, $P = 0.001$, Fig. 4). Fawns were never observed to approach cheetahs; on detecting these predators, mothers of fawns usually led their fawns away or the fawns adopted the prone position, lying flat with their heads on the ground (FitzGibbon 1990).

Larger groups of gazelles followed cheetahs for longer (correlation between group size at end of inspection and duration of inspection, $r = 0.604$, $n = 90$, $P < 0.001$). The duration of inspection was not significantly correlated with vegetation height ($r = -0.192$, $n = 90$, NS) and did not vary with cheetahs' belly size (ANOVA, $F_{2,88} = 0.61$, NS). The duration of predator inspection was weakly correlated with the length of time for which the cheetah walked ($r = 0.243$, $n = 86$, $P < 0.05$), but it was not clear whether gazelles followed for longer because cheetahs kept walking or whether cheetahs kept walking for longer because inspection continued for longer.

The distance to which gazelles were prepared to approach depended on the risk involved; they approached closer when in large groups (correlation between shortest cheetah-gazelle distance and group size, $r = -0.355$, $n = 90$, $P < 0.01$ and between average cheetah-nearest gazelle distance and group size, $r = -0.400$, $n = 90$, $P < 0.01$) and when in low vegetation, when the cheetah was in full view and the risk of ambush reduced (correlation between shortest cheetah-gazelle distance and vegetation height, $r = 0.490$, $n = 89$, $P < 0.01$ and between average cheetah-nearest gazelle distance and vegetation height, $r = 0.262$, $n = 90$, $P < 0.05$).

Effects of predator inspection on gazelles

The size of the gazelle group increased dramatically during predator inspection, compared with groups that detected the cheetah but simply watched from a distance [t-test, $t = 3.80$, $P < 0.001$, mean increase in group size in groups that did approach $= 53.4 \pm 13.6$ gazelles, $n = 90$, and in groups that simply watched a cheetah (increase during time cheetah in view) $= 0.1 \pm 0.1$ gazelles, $n = 83$]. Predator inspection resulted in a high percentage of the gazelles in the vicinity being alerted to the predator's presence. The percentage of gazelles within 1 km of the cheetah that detected it, 10 min after the first gazelle detected it, was greater when a group approached and followed the cheetahs than when it simply stared ($t = 2.87$, $P < 0.005$, mean percentage that detected when group inspects $= 99.4 \pm 0.6$, $n = 90$, and when no group <1 km inspects $= 83.0 \pm 2.3$, $n = 80$).

Effect of predator inspection on cheetahs

Cheetahs moved further between rests when they had been approached and followed by gazelles (mean distance moved $= 483 \pm 86$ m, $n = 18$) than in cases where no inspection behaviour occurred (mean distance moved $= 199 \pm 47$ m, $n = 18$; $t = 2.93$, $P < 0.01$). To discount the possibility that the effect of predator inspection on cheetahs' movements resulted from the fact that cheetahs which moved further were more likely to be inspected, I only included "inspected moves" when cheetahs were inspected during the first 5 min of the move (5 min is the mean duration of "non-inspected" moves). They also walked for longer and faster when gazelles approached and followed them during the move (mean duration and speed of moves $= 9.0 \pm 1.2$ min and 52.5 ± 4.8 m/min respectively) than when gazelles simply watched (mean duration $= 5.3 \pm 1.4$ min, $t = 2.01$, $P < 0.05$ and 39.4 ± 4.4 m/min, $t = 2.03$, $P < 0.05$ respectively). The height of the vegetation did not influence the distances that cheetahs moved (correlation between vegetation height and distance moved, $r = 0.195$, $n = 36$), but they moved further when more gazelles were alert nearby (correlation between number of gazelles alert within 1 km and distance moved, $r = 0.663$, $n = 36$, $P < 0.01$, Fig. 5). Cheetahs also moved further when being

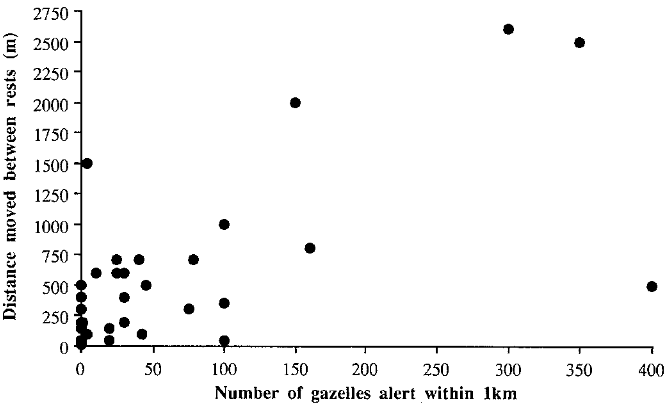

Fig. 5. Scatterplot showing the relationship between the number of gazelles alert within 1 km of the cheetah at the beginning of the move and the distance subsequently moved before the next rest, including both "inspected" and "not-inspected" moves ($r = 0.663$, $n = 36$, $P < 0.001$)

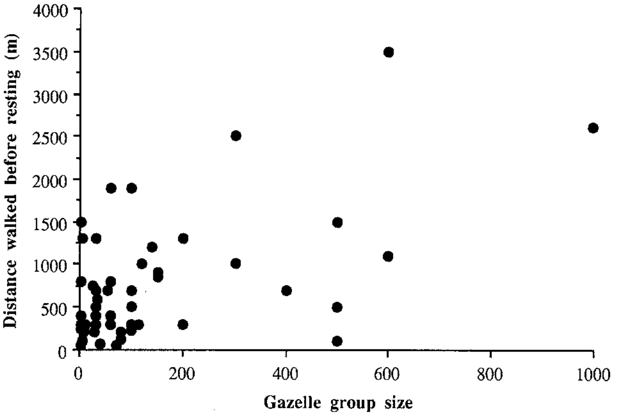

Fig. 6. Scatterplot showing the relationship between the size of the gazelle group at the start of inspection behaviour and the distance the cheetah subsequently moved (measured from the point at which the cheetah was first approached, $r = 0.545$, $n = 50$, $P < 0.001$)

followed by larger groups (correlation between distance moved from start of inspection behaviour to next resting point and gazelle group size, using all cases of inspection behaviour observed, $r = 0.545$, $n = 50$, $P < 0.001$, Fig. 6), suggesting that larger groups are more effective at keeping cheetahs moving.

Whether gazelles followed cheetahs or not also influenced the distances they moved between successive hunts. Having hunted but failed to kill, cheetahs moved further before trying again if they had been inspected than if they had not (mean distance between hunts = 1.86±0.35 km and 0.85±0.24 km respectively, $t = 2.50$, $P < 0.05$). While I could not discount the possibility that cheetahs which moved further were more likely to be inspected, in most cases included in the analysis gazelles approached cheetahs soon after the initial hunting attempt.

Costs of predator inspection

The costs of predator inspection for gazelles result from three main factors, the time and energy involved, and the risks of predation. While each predator inspection bout is fairly long (average 14 min, range 2–72 min), and much of the time is spent running, cheetahs are relatively rare and gazelles are estimated to spend only 0.8% of their daily daylight time budget inspecting these predators. Lions are 5.6 times more common than cheetahs, but gazelles are 25% less likely to approach them, so gazelles are estimated to spend 3.4% of their day inspecting these predators. While this is likely to be an overestimate, since lions are less active during the day than cheetahs, it suggests that gazelles spend less than 4.2% of their daily daylight time budget in inspection behaviour.

By approaching cheetahs, adults risk an increased probability of being attacked, although the risk is low. I only saw one adult gazelle being attacked and killed during 90 cases of groups following cheetahs (average size of inspecting groups = 65 gazelles, 73% of which are adults, so the risk of predation for adults = $1/(90 \times 65 \times 0.73) = 1/4271 = 0.0002$ or 1 in every 5000 approaches). None of the groups that monitored cheetahs from a distance were hunted during the 23 follows (83 groups, containing a mean of 38 gazelles of which 84% are adults = 0/2649 cheetah/gazelle interactions). In addition, outside of follows, I recorded a further 211 groups, containing a total of 7385 gazelles, that detected cheetahs without approaching, and were not attacked. Consequently the probability of being killed by a cheetah if the group detects but does not approach is less than 1 in 8926, considerably lower than the risk of being killed by approaching the cheetah.

I did not see cheetahs attacking any sub-adults from inspecting groups but one half-grown and one half-grown/adolescent were chased and killed (risk = $2/(90 \times 65 \times 0.14) = 0.0024$ or 1 in 417 half-grown/adolescent approaches). No half-growns or adolescents were chased from the groups that detected but did not approach, which contained on average 9% half-growns and adolescents. Consequently, including the 211 groups recorded outside follows, the chances of being killed if the gazelle did not approach but monitored the cheetah from a distance were less than 1 in 949 gazelle/cheetah interactions, again far lower than the risk from approaching. Although I saw fawns being killed while cheetahs were being followed, the fawns were never members of the approaching group. Fawns have been observed to approach and be killed (O. Newman, pers. comm.), probably because they were disturbed out of hiding by the commotion, and in the absence of their mothers, followed other gazelles. Cheetahs have also been observed to kill wildebeest that approached them (T.M. Caro, pers. comm.).

Discussion

The inspection behaviour of Thomson's gazelles described in this paper differs from the inspection behaviour of fish and the mobbing behaviour of birds in a number of ways. In gazelles, normally all the group approaches (or a high proportion of it) together and then follows the predator for considerable periods of time, while in fish, usually one or two group members approach the predator for 1–2 s only, and then return to the group which is monitoring the predator from a distance (Magurran and Pitcher 1987). Alternatively, all the group approaches, but again only for a short time. The mobbing behaviour of birds, on the other hand, is normally accompanied by aggression, with birds flying directly at and sometimes hitting the predator, and is often accompanied by loud calling (Curio 1978). Despite these differences, there is accumulating evidence that approaching individuals may derive similar benefits despite approaching in very different ways. For example, the approach behaviour of birds, fish and ungulates may cause predators to move on (Ishihara 1987; Pettifor 1990; this study), and in a variety of species, it may also enable prey animals to gather information about the predator (for example, in fish: Csányi 1985, in birds: Kruuk 1976, and in mammals: Owings and Coss 1977, this study). In gazelles, approach behaviour may also enable individuals to monitor the movements of predators to ensure they do not ambush them at a later stage, inform the predator that it has been detected and alert other gazelles in the vicinity (see below).

The costs of predator inspection

Approaching predators is generally assumed to be risky, although the evidence is almost entirely circumstantial, consisting of anecdotal observations of predators killing mobbing individuals (e.g. Kruuk 1972; Poiani and Yorke 1989; Sordahl 1990). Dugatkin (1992) has shown a negative correlation between probability of survival and tendency to inspect in guppies (*Poecilia reticulata*), but it is not clear how this increased risk of mortality arises. The results of this study showed that by approaching and following predators, Thomson's gazelles incur an increased risk of predation. While the risk was low for adults and sub-adults, it was substantially higher for adolescents and half-growns, and apparently so high for fawns that they almost never approach.

That approaching predators was risky was supported by the finding that the probability that a gazelle group approached and followed cheetahs was influenced by the risks involved. Gazelle groups were more likely to approach in short vegetation, where the chances of being ambushed were lower, and when the group was larger. Gazelles also risked approaching closer when in safer situations, namely when in lower vegetation and in larger groups (although the negative correlation between cheetah-gazelle distance and group size may have arisen because larger groups were more likely to contain bold individuals simply by chance). The fact that gazelles were far more likely to approach stalking predators than coursing predators could also be argued to be a risk reduction tactic. Stalking predators are rarely successful once their prey is alerted to their presence, and are very dependent for their success on getting close to their prey before chases are initiated. In contrast, coursing predators are less dependent on surprise, and at least in wild dogs their probability of success is not influenced by predator-prey distance at the start of the chase (Fanshawe and FitzGibbon 1993). Consequently, approaching stalking predators may be less risky. These data support findings from other studies of a variety of species that approachers modify their behaviour according to the perceived risk (Curio et al. 1983; Curio and Regelmann 1985; Pitcher et al. 1986; Magurran and Pitcher 1987).

In addition to the risks involved, gazelles approaching predators also incurred time costs of less than 4% of their daylight time budget (less than 30 min each day). While 4% seems high and would reduce the amount of time available for feeding, parental care, territorial defence and other activities, it is difficult to assess the significance of this time cost without knowing the extent to which time is at a premium for this species, and how time lost from other essential activities affects survival and fecundity.

The benefits of predator inspection

Inspection behaviour is certainly multifunctional, gazelles deriving benefits in a number of different ways, each of which is discussed below. However, while many examples of prey approaching predators involve parental defence (e.g. Andersson et al. 1980; Curio et al. 1985; Montgomerie and Weatherhead 1988; Tamura 1989), it is unlikely that it plays such a role in this case. Inspection behaviour is performed by young gazelles as well as old, and includes non-reproductive individuals, such as subadult bachelor males, which are unlikely to be associated with close relatives.

Deterring predators

Moving on the predator. Cheetahs moved further between rests and between successive hunts when they had been approached and followed by gazelles, particularly when followed by large groups, suggesting that inspection behaviour causes stalking predators to move out of the local area. Kestrels (*Falco tinnunculus*) have also been shown to move further between hunting positions when they were mobbed compared to when they were not mobbed (Pettifor 1990), although why the kestrels moved was not clear. Similarly fish predators tend to leave the immediate area having been mobbed by damselfish (*Pomacentrus coelestis*) (Ishihara 1987). The most likely reason that cheetahs reacted to the gazelles approaching in this way was that, once gazelles had started to follow them, all the gazelles in the vicinity were alerted to their presence and therefore their chances of hunting successfully were much reduced (FitzGibbon 1989). Consequently, the cheetahs moved elsewhere to find less wary prey. Such approach behaviour would be less effective against coursing predators, since they do not rely on surprise and therefore their hunting success is relatively unaffected by high levels of prey alertness, and they would have less reason for moving on.

Keeping predator in sight. Since gazelle groups were far more likely to approach stalking predators than coursing predators, one possibility is that gazelles follow cheetahs and lions to keep them in view, ensuring that they do not take them unawares at a later stage. Once the cheetah has moved out of the local area, the gazelle can return to feed, or in cases where the predator lies down, it can continue to monitor the predator to ensure that it is does not start to stalk. However, it is unlikely that gazelles would need to approach the predator so closely, since they could probably reduce their risk of being attacked to the same extent by following at a distance. Consequently, while gazelles will certainly benefit from keeping track of the predator's movements, it is unlikely to be the primary function of predator inspection behaviour.

Signalling perception. Stalking predators are extremely sensitive to the level of alertness of their prey, usually abandoning stalks once the prey has detected their presence and often selecting the less wary individuals available (FitzGibbon 1989). As Bildstein (1982) points out, it is unlikely that the prey would need to move repeatedly towards the predator, nor approach very closely, to inform the predator that it has been detected. Such information could probably be signalled more cheaply and just as effectively by snorting. Certainly gazelles would not need to devote up to 72 min, and an average of 14 min, convincing a cheetah that it has been detected, so this is unlikely to be the main function of approach behaviour. However, it will certainly be a supplementary benefit.

Confusing the predator. Cheetahs rarely hunt gazelles once the gazelles are alert to their presence (FitzGibbon 1989), so it is unlikely that predator inspection would function solely to confuse the predator. In this case it would be expected to be far more common in response to coursing predators which do not rely on surprise and could start to chase anytime.

Acquiring information about the predator

Gazelles could be approaching predators to identify them, improve their recognition skills and/or to acquire additional information, such as the predator's motivation to hunt. Animals often approach objects that are unusual (e.g. displaying Kori bustards in the case of gazelles, Walther 1969, and predator models in the case of fish, Magurran and Girling 1986), suggesting that the behaviour enables individuals to obtain information. While it is clear, from the varying responses of gazelle groups to the four predator species studied here, that gazelles can usually recognise the different predators without having to approach and follow them, the fact that younger gazelles were more likely to approach than older animals suggests that they may be using the opportunity to learn more about the predators. However, it is also possible that both adults and juveniles are equally keen to learn about predators but juveniles are less able to assess the risks associated with different situations. The additional information gathered might enable the gazelles to improve their ability to recognise predators in more difficult circumstances (e.g. partially concealed in dense cover) at a later stage. Although gazelles were no more likely to approach and follow rare predators, such as wild dogs, than more common species, such as lions, it may be more important to collect information on stalking predators, as compared with coursing predators, since these predators rely so much more on concealment and surprise for their success. It could also be argued that it was more important to gain information about common predators because they are encountered, and therefore have to be identified, more often.

Evidence, mainly from fish, suggests that predator inspection enables approachers to gather information about the predator's motivation to hunt (see Introduction). In this case, approachers should modify their behaviour according to the information they gather (Magurran and Girling 1986), but there was no evidence from this study that hungry cheetahs were followed for longer than full ones. In addition, one would expect gazelles to approach all predators, at least to some extent, and gazelles would only be expected to inspect for a relatively short time. Gazelles often followed cheetahs for long periods, occasionally up to 72 min, far longer than would be needed to determine the predator's belly size and thus motivation to hunt. Since it is more difficult to assess belly size and motivation to hunt from predators that are further away, gazelles should also be more likely to approach predators that are some distance from them. In fact, gazelle groups were more likely to approach and follow cheetahs if they passed closer to the group. Overall, it seems unlikely that acquiring information about predators is the primary reason for predator inspection in gazelles, although younger animals may be making use of the opportunity to improve their predator recognition skills.

Informing others of potential threat

While it is clear that, by approaching, a gazelle alerts conspecifics nearby to the cheetah's presence, and that these gazelles consequently benefit, it is less certain whether the approacher derives any benefits from alerting them. If the first gazelle to detect the predator simply monitored it from a distance, other gazelles would be less likely to detect and consequently have a higher probability of being attacked (FitzGibbon 1989). However, if the attack was successful, the cheetah would be more likely to remain in the area to hunt again, while if all gazelles are alerted, the cheetah may move elsewhere in search of less wary prey. Since larger groups are more successful at keeping cheetahs moving than smaller ones, it would be beneficial to alert as many gazelles as possible. In addition if a gazelle benefits in other ways from following a predator, for example by keeping track of its movements, by recruiting other gazelles, the approacher dilutes its own risk (Kruuk 1976; Curio 1978; Owings and Owings 1979; Tamura 1989). Group size increased far more when the group approached the predator than if members simply stared.

Gazelle group size and predator inspection

The results of this study showed that for individual gazelles the costs and benefts of approaching varied with group size, but was complicated by the fact that these costs and benefits are dependent on the behaviour of other group members. The probability that at least one gazelle approached the cheetah was higher in large groups than in small ones. Since a gazelle initiating predator inspection from a larger group will be joined by more gazelles than a gazelle initiating from a smaller group, one explanation is that the risks of approaching were lower for individuals from large groups as a result of the dilution effect. However, it is also probable that larger groups were more likely to contain a gazelle for which the benefits of inspecting a predator were high, and therefore was more likely to initiate predator inspection.

In groups where at least one group member approached, the percentage of group members approaching decreased with increasing group size. Consequently, it seemed that a higher proportion of gazelles in larger groups were deciding that, as long as some group members approached, it was not worthwhile for them to approach since they could forego the costs of predator inspection without foregoing all the benefits. As long as sufficient gazelles approached to cause the predator to move on, gazelles staying behind would still benefit.

The costs and benefits of approaching, therefore, vary with group size, not only because the risks are lower in larger groups but also because the effectiveness of predator inspection does not increase linearly with the number of inspectors. As a result, the benefits to be gained from participating in predator inspection, compared to remaining behind and benefiting from others approaching the predator (defecting), will decrease as group size increases. If the benefits of predator inspection are shared between individuals which inspect and those that defect, the evolution of predator inspection would appear to rely on cooperation, with individuals that consistently approach the predator considered to be cooperators, and those that consistently remain behind considered defectors (Dugatkin 1990). The sharing of benefits could result from the transfer of information between inspectors and non-inspectors (e.g. in fish, Magurran and Higham 1988) or because predator inspection reduces the risk for all prey in the local area, for example by causing the predator to move away. In Thomson's gazelles, however, some gazelles are likely to benefit from actually participating in predator inspection more than others (for example younger animals learning about predators). Consequently, an individual's decision to inspect will depend on the relative benefits of actually participating in predator inspection versus benefits that can be derived from other gazelles inspecting the predator (such as moving the predator on).

In larger groups, the number of gazelles for which the benefits of participating in inspection behaviour are sufficient for them to approach, irrespective of whether other group members approach or not, will be greater. Consequently, gazelles for which the benefits derived from actually participating in predator inspection are low will be unlikely to approach, since they will still benefit from the predator being moved on. In contrast, in smaller groups, if any group member stays behind, the number of gazelles participating in predator inspection may not be sufficient to move the cheetah on. In this case, it might be worthwhile for all group members to participate in predator inspection, irrespective of whether they benefit from experiencing the predator at close quarters. As a result, a higher percentage of group members will participate in predator inspection in small groups than in large. The fact that it is not possible for gazelles to share all the benefits of predator inspection with non-participating group members may explain why a relatively high proportion of group members approach the predator, while in minnows, where inspectors transmit the information they collect, either passively or actively, to non-inspectors (Magurran and Higham 1988), only a few individuals from each group usually approach (Magurran and Pitcher 1987).

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References

Albon SD, Mitchell B, Huby BJ, Brown D (1986) Fertility in female red deer *Cervus elaphus*: the effects of body composition. J Zool London 209:447–460

Altmann SA (1956) Avian mobbing behaviour and predator recognition. Condor 58:241–253

Andersson M, Wiklund CG, Rundgren H (1980) Parental defence of offspring: a model and an example. Anim Behav 28:536–542

Bartecki U, Heymann EW (1987) Field observations of snake-mobbing in a group of saddle-back tamarins, *Saguinus fuscicollis nigrifrons*. Folia Primatol 48:199–202

Berger J (1979) "Predator harassment" as a defensive strategy in ungulates. Am Midland Nat 102:197–199

Bildstein KL (1982) Responses of northern harriers to mobbing passerines. J Field Ornithol 53:7–14

Buitron D (1983) Variability in the responses of black-billed magpies to natural predators. Behaviour 87:209–236

Campbell KLI, Kajuni AR, Huish SA, Mng'ong'o GB (1990) Serengeti ecological monitoring programme (Biennial report, 1988–1989). Serengeti Wildlife Research Centre

Caro TM (1993) Cheetahs of the Serengeti plains: grouping in an asocial species. University of Chicago Press, Chicago (in press)

Clutton-Brock TH, Price OF, Albon SD, Jewell PA (1992) Early development and population fluctuations in Soay sheep. J Anim Ecol 61:381–396

Cox DR (1970) The analysis of binary data. Methuen, London

Csányi V (1985) Ethological analysis of predator avoidance by the paradise fish (*Macropodus opercularis* L.). I. Recognition and learning of predators. Behaviour 92:227–240

Curio E (1978) The adaptive significance of avian mobbing. I. Teleonomic hypotheses and predictions. Z Tierpsychol 48:175–183

Curio E, Regelmann K (1985) The behavioural dynamics of great tits (*Parus major*) approaching a predator. Z Tierpsychol 69: 3–18

Curio E, Regelmann K (1986) Predator harassment implies a deadly risk: a reply to Hennessy. Ethology 72:75–78

Curio E, Ernst U, Vieth W (1978a) Cultural transmission of enemy recognition: one function of mobbing. Science 202:899–901

Curio E, Ernst U, Vieth W (1978b) The adaptive significance of avian mobbing. II. Cultural transmission of enemy recognition in blackbirds: effectiveness and some constraints. Z Tierpsychol 48:185–20

Curio E, Klump G, Regelmann K (1983) An antipredator response in the great tit (*Parus major*): is it tuned to predator risk? Oecologia 60:83–88

Curio E, Regelmann K, Zimmermann U (1985) Brood defence in the great tit (*Parus major*): the influence of life-history and habitat. Behav Ecol Sociobiol 16:273–28

Dugatkin LA (1990) N-person games and the evolution of co-operation: a model based on predator inspection in fish. J Theor Biol 142:123–135.

Dugatkin LA (1991) Dynamics of the TIT FOR TAT strategy during predator inspection in the guppy (*Poecilia reticulata*). Behav Ecol Sociobiol 29:127–132

Dugatkin LA (1992) Tendency to inspect predators predicts mortality risk in the guppy (*Poecilia reticulata*). Behav Ecol 3:124–127

Dugatkin LA, Godin J-GJ (1992) Prey approaching predators: a cost-benefit perspective. Ann Zool Fenn 29:233–252

Fanshawe JH, FitzGibbon CD (1993) Factors influencing the hunting success of a wild dog pack. Anim Behav 45:479–490

FitzGibbon CD (1989) A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. Anim Behav 37:508–510

FitzGibbon CD (1990) Antipredator strategies of immature Thomson's gazelles: hiding and the prone response. Anim Behav 40:846–855

FitzGibbon CD, Fanshawe JH (1988) Stotting in Thomson's gazelles: an honest signal of condition. Behav Ecol Sociobiol 23:69–74

Frame GW (1986) Carnivore competition and resource use in the Serengeti ecosystem of Tanzania. PhD thesis, Utah State University, Logan

Harvey PH, Greenwood PJ (1978) Anti-predator defence strategies: some evolutionary problems. In: Krebs JR, Davies NB (eds) Behavioural ecology. Blackwell Scientific, Oxford, pp 129–151

Hoogland JL, Sherman PW (1976) Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. Ecol Monogr 46:33–58

Ishihara M (1987) Effect of mobbing toward predators by the damselfish *Pomacentrus coelestis* (Pisces: Pomacentridae). J Ethol 5:43–52

Kruuk H (1972) The spotted hyena. Chicago University Press, Chicago

Kruuk H (1976) The biological function of gull's attraction towards predators. Anim Behav 24:146–153

Kruuk H, Turner M (1967) Comparative notes on predation by lion, leopard, cheetah and wild dog in the Serengeti area, East Africa. Mammalia 31:1–27

Licht T (1989) Discriminating between hungry and satiated predators: the responses of guppies (*Poecilia reticulata*) from high and low predation sites. Ethology 82:238–243

Lipetz VE, Bekoff M (1980) Possible functions of predator harassment in pronghorn antelopes. J Mammal 61:741–743

Magurran AE, Girling SL (1986) Predator model recognition and response habituation in shoaling minnows. Anim Behav 34:510–518

Magurran AE, Higham A (1988) Information transfer across fish shoals under predator threat. Ethology 78:153–158

Magurran AE, Pitcher TJ (1987) Provenance, shoal size and the sociobiology of predator-evasion behaviour in minnow shoals. Proc R Soc London B 229:439–465

Montgomerie RD, Weatherhead PJ (1988) Risks and rewards of nest defence by parental birds. Q Rev Biol 63:167–187

Owings DH, Coss RG (1977) Snake mobbing by California ground squirrels: adaptive variation and ontogeny. Behaviour 62:50–69

Owings DH, Owings SC (1979) Snake-directed behaviour by black-tailed prairie dogs (*Cynomys ludovicianus*). Z Tierpsychol 49:35–54

Pettifor RA (1990) The effects of avian mobbing on a potential predator, the European kestrel, *Falco tinnunculus*. Anim Behav 39:821–827

Pitcher TJ (1980) Some ecological consequences of fish school volumes. Freshwater Biol 10:539–544

Pitcher TJ (1986) Functions of shoaling behaviour in teleosts. In: Pitcher TJ (ed) The behaviour of teleost fishes. Croom Helm, Beckenham Kent, pp 294–337

Pitcher TJ, Green D, Magurran AE (1986) Dicing with death: predator inspection behaviour in minnow shoals. J Fish Biol 28:439–448

Poiani A, Yorke M (1989) Predator harassment: more evidence on the deadly risk. Ethology 83:167–169

Robinson, SR (1980) Antipredator behaviour and predator recognition in Belding's ground squirrels. Anim Behav 28:840–852

Rowe MP, Owings DH (1990) Probing, assessment, and management during interactions between ground squirrels and rattlesnakes. Part I. Risks related to rattlesnake size and body temperature. Ethology 86:237–249

Schaller GB (1972) The Serengeti lion: a study of predator-prey relationships. University of Chicago Press, Chicago

Shedd DH (1982) Seasonal variation and function of mobbing and related antipredator behaviors of the American robin (*Turdus migratorius*). Auk 99:342–346

Sordahl TA (1990) The risks of avian mobbing and distraction behaviour: an anecdotal review. Wilson Bull 102:349–352

Tamura N (1989) Snake-directed mobbing by the Formosan squirrel *Calliosciurus erythraeus thaiwensis*. Behav Ecol Sociobiol 24:175–180

Van Orsdal KG (1984) Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. Afr J Ecol 22:79–99

Walther FR (1969) Flight behaviour and avoidance of predators in Thomson's gazelle (*Gazella thomsoni* Guenther 1884). Behaviour 34:184–221

Walther FR (1973) On age class recognition and individual identification of Thomson's gazelle in the field. J S Afr Wildl Manage Assoc 2:9–15