



## The information banded mongooses extract from heterospecific alarms

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Predation is a powerful selective force shaping the behaviour of prey animals. As a consequence, a variety of birds and mammals have developed referential and/or urgency-based alarm call systems. Since antipredator behaviour is likely to be costly, it should pay to attend to warning signals given by other species. Evidence that animals respond to heterospecific alarm calls is abundant. However, studies showing whether animals extract information on predator types or urgency levels from heterospecific alarms are rare. Using playback experiments, we investigated whether banded mongooses, *Mungos mungo*, respond to alarm calls of several sympatric plover species, *Vanellus* spp. and how mongooses respond to plover alarms that differ in their level of urgency. Banded mongooses responded to alarm calls of the three plover species tested. Even though the response intensity varied over a large scale, the responses to plover alarms did not differ between calls representing high and low urgency. Our results indicate that banded mongooses use heterospecific alarms for predator avoidance but do not use additional information provided in these signals. How commonly animals attend to and why in some cases animals do not attend to additional information provided by heterospecific alarms remains an open question and deserves further investigation.

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Predation pressure is a powerful selective force shaping morphology and behaviour of prey animals (Lima & Dill 1990; Zuberbühler 2000a). A widely studied consequence is the sophisticated alarm call systems in birds and mammals (reviewed in Macedonia & Evans 1993; Bradbury & Vehrencamp 1998; Searcy & Nowicki 2005). Many species communicate not only the presence of predators with their alarm calls, the calls also include information about urgency, predator type and/or predator size (Macedonia & Evans 1993; Manser et al. 2001; Templeton et al. 2005). Since antipredator behaviour is likely to be costly (Pulliam 1973; Dimond & Lazarus 1974; Sherman 1977, 1985), it should pay animals that share common predators to exploit the vigilance of sympatric species and respond to their alarm calls. This may increase the probability of escaping a predator (Morse 1977) and may allow the reduction of vigilance in favour of other activities.

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Responses to heterospecific alarm calls occur in a variety of species, in particular birds, rodents and primates (reviewed in Fichtel 2004; Randler 2006). However, little is known about how attentive animals are to categorical and continuous information encoded in heterospecific alarms, such as predator types or urgency. A few studies have shown that animals can extract information on predator types and predator size from heterospecific alarms (Seyfarth & Cheney 1990; Zuberbühler 2000a; Fichtel 2004; Rainey et al. 2004; Templeton & Greene 2007). It can thus be predicted that animals also respond appropriately to the urgency level of heterospecific alarm calls, particularly because urgency level is more likely encoded in a consistent way across species than referential information (Morton 1977; Fichtel et al. 2001; Manser et al. 2001; Fichtel & Hammerschmidt 2002).

We studied responses to heterospecific alarms in banded mongooses, *Mungos mungo*, small (<2 kg) group-living carnivores. In the study area, banded mongoose groups share their home ranges with several plover species, *Vanellus* spp., but mongooses and plovers do not aggregate. Even though direct predation was not observed, mongooses

and plovers are likely to share predators, in particular large raptors such as martial eagles, *Polemaetus bellicosus* (Boshoff et al. 1990). These eagles are known to target banded mongooses (Rood 1983; Bell 2006) and both mongooses and plovers give alarms in response to them and other large raptors (personal observation). Natural observations suggest that banded mongooses respond to crowned plover, *Vanellus coronatus*, alarm calls and that these calls vary with level of urgency (personal observation).

We investigated whether banded mongooses respond to alarm calls of plovers and whether responses differ depending on urgency levels encoded in the plovers' alarms. We recorded alarm calls of crowned plovers given to humans at different distances and determined whether call rate and call duration change with distance to perceived threat, which was taken as a correlate of urgency. We also recorded alarm calls of the banded mongooses to test whether their calls change in a similar way with urgency. Additionally, we recorded alarm calls of two other plover species, spur-winged plovers, *Vanellus spinosus*, and wattled plovers, *Vanellus senegallus*. We then played back the alarm calls of the three plover species (for spectrograms see Fig. 1a–d) to banded mongoose groups and predicted that they would respond with antipredator behaviour. Finally, we conducted playback experiments varying two features of high- and low-urgency alarm calls of crowned plovers, call rate and call duration. We predicted that the mongooses would react more intensely to the high-urgency playbacks than to the low-urgency playbacks.

## METHODS

We studied a wild population of individually marked banded mongooses on and around Mweya Peninsular (8 km<sup>2</sup>) in Queen Elizabeth National Park, Uganda (0°12'S, 29°54'E; for details on the study site see Cant 2000) between August 2004 and September 2005. The study population consisted of 251 individuals in eight groups. Group size ranged from 8 to 60 individuals. Animals were classified as adults (>12 months), subadults (6–12 months) and infants (<6 months). Groups were habituated to close observation and all animals were trapped on a regular basis to refresh individual marks (colour-coded plastic collars or small shaves on the rump), detect pregnancies, take morphometric measures and estimate ectoparasite load. Procedures followed the guidelines of the Association for the Study of Animal Behaviour and are described in detail elsewhere (Cant 2000).

### Audio Recordings

We recorded 33 alarms of crowned plovers and 21 alarms of banded mongooses given in response to a moving human. The use of alarms elicited in such an artificial way has two advantages over naturally occurring alarms: the stimulus is kept constant and the alarm urgency is not confounded with possible referential information included in the alarms. This method has been successfully applied in a variety of species that, like banded mongooses and plovers, consistently respond with alarms to humans and, therefore, appear to consider them a potential threat

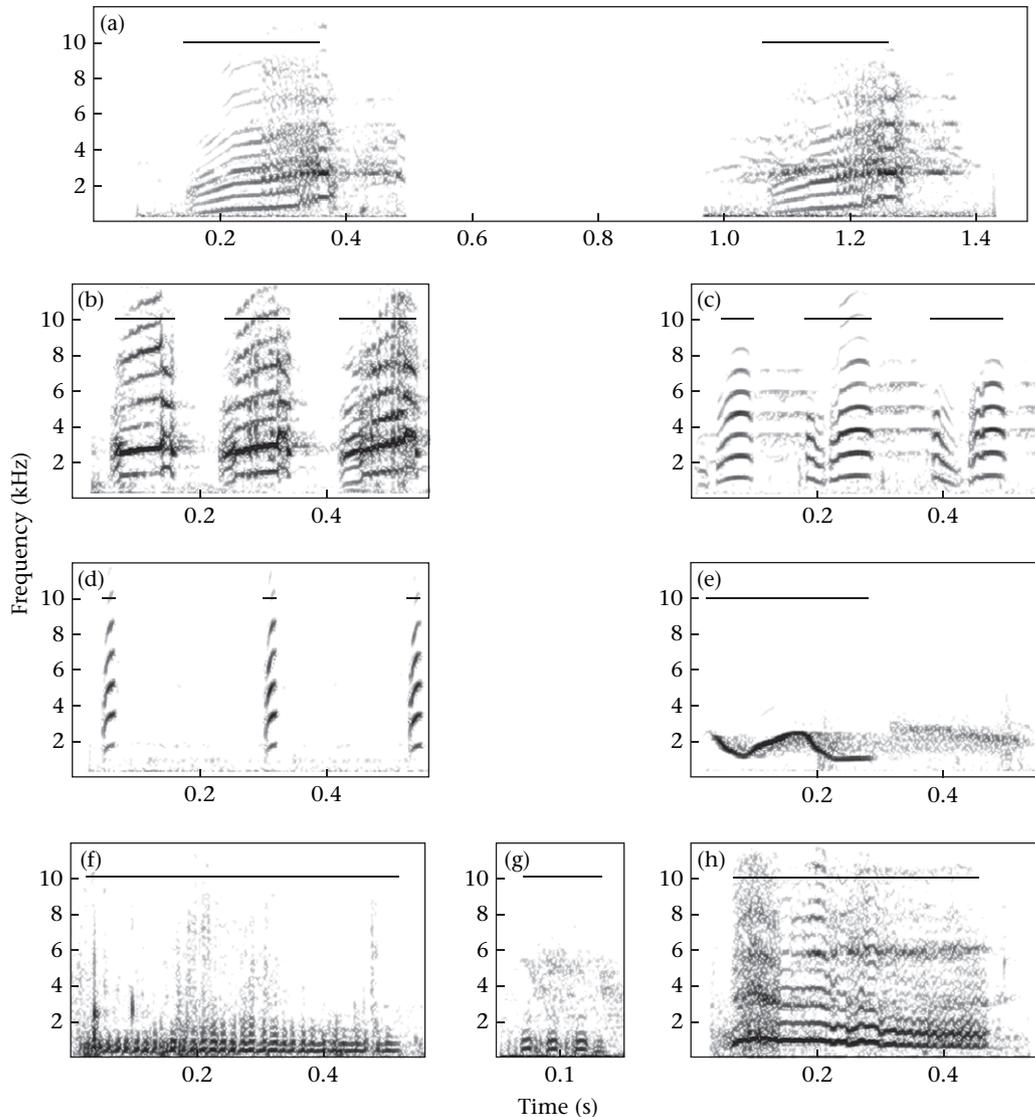
(e.g. Shriner 1998; Perla & Slobodchikoff 2002; Randall & Rogovin 2002). All recordings were sampled at 48 kHz and 16 bit. In 2004 we used a Sennheiser ME 66/K6 directional microphone (Sennheiser Electronic Corp., Old Lyme, CT, U.S.A.) connected to a Sony digital audiotape recorder (TCD-D100; Sony Corp., Tokyo, Japan) and transferred the recordings onto a personal computer using an ESI Waveterminal U24 (Ego Systems Inc., Seoul, Korea). In 2005 we used a Marantz PMD670 audio recorder (D&M Professional, Kanagawa, Japan).

Plover alarms were given to a person stepping out from behind a large bush at varying distances (10–57 m) and were recorded by the person representing the threat stimulus. The same procedure was used to obtain banded mongoose alarms, except that these alarms were recorded by a sitting observer (2–10 m from the alarming individual) and a second person represented the stimulus (distance 6–37 m). This difference in the procedure was necessary because plovers were not habituated to close observers and mongoose alarms were too soft to be recorded from a large distance. Distance between the threat and the alarming individual was determined using a Leica range-finder (LRF 800; Leica Camera AG, Solms, Germany). The stimulus was presented equally often at short, medium and long distances for both species. For the mongooses, distance was also balanced within groups.

We further recorded alarms of spur-winged plovers and wattled plovers following the same procedure (only for short distances to the threat; eight recordings of each species). These calls were used for playbacks but not related to urgency. The same applies to eight other crowned plover alarms obtained at long distances (30–50 m) but with distance estimated only by eye. Additionally, we recorded duet calls of 15 black-headed gonoleks, *Laniarius erythrogaster*, for use in control playbacks (for spectrogram see Fig. 1e). Gonolek calls were chosen because they are conspicuous but nonthreatening stimuli, which are similar to plover alarm calls in call length and in low between-call variation in acoustic structure.

Alarm calls of crowned plovers and banded mongooses were analysed for urgency-related differences. Only initial alarms (the first alarm given by any group member) were used in the analysis. Plover alarms consisted of repeated calls (see Fig. 1a, b) of which the average duration and average call rate over the first five calls was used in the analysis. Mongoose alarms were single calls (see Fig. 1f, g). Duration and rate of alarm calls were measured to the nearest millisecond in CoolEdit 2000 (Syntrillium Software Corp., Scottsdale, AZ, U.S.A.) from spectrograms with FFT length 512, frequency resolution 47 Hz and time resolution 0.67 ms. We did not analyse other acoustic parameters because the recordings of mongoose alarms were of rather poor quality and because the plover alarms were recorded from different distances, which potentially confounds these measures. Call rate and call duration in contrast are little affected by recording distance.

Since plovers were not individually recognizable and the identity of the alarming mongooses could not be determined on all occasions, it cannot be ruled out that some individuals contributed more than one alarm to the data set. Recordings of the same bird species were separated spatially by at least



**Figure 1.** Spectrograms of alarm calls (FFT length: 512, frequency resolution: 47 Hz, time resolution: 1.33 ms) created in Avisoft SASLab Pro 4.38 (R. Specht, Berlin, Germany). Horizontal bars denote single calls detected with a threshold of  $-15$  dB to the maximum amplitude and a hold time of 20 ms. (a) Crowned plover (low-urgency) alarm calls. (b) Crowned plover (high-urgency) alarm calls. (c) Wattled plover alarm calls. (d) Spurwinged plover alarm calls. (e) Black-headed gonolek duet call (used for control playbacks). (f) Banded mongoose low-urgency alarm call. (g) Banded mongoose high-urgency alarm call. (h) Banded mongoose panic call.

100 m. This reduced the likelihood that individual plovers were recorded repeatedly since all three plover species were breeding in the study area and individuals spent most of the time in limited areas close to the nest (personal observation). It is unlikely that individual mongooses contributed more than one alarm to the data set because initial alarm calls were typically given by the first individual to spot the danger and no particular individuals were much more likely to alarm than others (personal observation). We thus treated separate recordings as independent.

### Editing of Playbacks

The amplitude of plover alarm calls was standardized in CoolEdit and playbacks with a standardized call rate (high call rate: 120 calls/min, low call rate: 20 calls/min) were

compiled. Each playback consisted of 10 calls and included three to five calls played in a loop, resulting in a playback duration of 5 s for high-call-rate playbacks and 30 s for low-call-rate playbacks. This corresponds to alarm durations within the range of naturally occurring alarms. The set of calls was obtained from a different recording for each playback. Crowned plover alarms were categorized as low urgency if given to a threat (human observer) at more than 30 m distance without flying off and as high urgency if given to a threat at less than 20 m distance while flying off. The signal-to-noise ratio of the calls used for the playbacks (calculated according to Dabelsteen et al. 1993) did not differ between the two categories (averages over calls per playback: low-urgency calls:  $\bar{X} \pm SE = 21.8 \pm 1.5$  dB; high-urgency calls:  $\bar{X} \pm SE = 20.8 \pm 1.4$  dB;  $t$  test:  $t_{14} = 0.48$ ,  $P = 0.64$ ). Differences between high-urgency and low-urgency calls may communicate distance to threat. Alternatively, the

differences between these calls may be related to the act of flying off (Trillmich et al. 2004). In both cases, information about urgency is available to receivers due to consistent differences in the calls between the two contexts.

For each of the three plover species, eight playback sequences with high-urgency calls at the high call rate were prepared. For crowned plovers, we additionally prepared playbacks with high-urgency calls at the low call rate and playbacks of low-urgency calls at both call rates, resulting in six different plover playbacks per group (Table 1). Control playbacks (gonolek calls) matched experimental playbacks in duration, volume and call rate.

## Playback Experiments

Each of the eight banded mongoose groups (mean size excluding infants = 22.5) was exposed to the six plover playbacks, which were conducted using the Marantz recorder and portable speakers (Creative Travelsound; Creative Technology Ltd., Singapore). Plover playbacks to the same mongoose group were spaced at least 7 days apart. We set playback amplitude to 65–70 dB at 50 cm from the speakers using a Voltcraft 329 sound level meter (Conrad Electronic, Hirschau, Germany). This matched the amplitude of naturally occurring alarms perceived by ear. The speakers were placed on the ground, 8–12 m from the nearest individual. Playbacks only were started when more than half the group had been foraging for at least 15 min and no alarm had occurred during this period. Since banded mongooses often foraged in thick bush, a handful of bait (20–50 g of a mix of rice and gravy) was used to persuade them to forage on open ground, which allowed direct observation of the responses. This amount of food was generally consumed within 1–2 min and playbacks were started after this period, when the mongooses had resumed normal foraging behaviour. Clumped food sources like this also occur naturally, for example in the form of piles of elephant dung abounding with insect larvae. Experiments were conducted between 0800 and 1100 hours and between 1630 and 1830 hours. Each playback of plover alarms was preceded (mean 7 min, range 5–20 min before) by a playback of gonolek calls. This allowed controlling for baseline vigilance, which may vary depending on presence of pups or recent exposure to predators. Since we had obtained only 15

recordings of gonoleks, we randomly chose one of these recordings for use as a control in each of the 48 experiments (each recording two to five times).

The response of individuals foraging within 20 m of the speakers was recorded using a digital video camera (Panasonic NV-GX7; Matsushita Electronic Industrial Co. Ltd., Osaka, Japan). Antipredator behaviour during the playbacks was determined for every individual visible on the tape (mean 11.5, range 4–23 individuals). We recorded look up rate, look up duration (determined frame by frame in Windows Movie Maker; Microsoft Corp., U.S.A.; 1 frame = 0.08 s) and moving towards cover. Look ups were defined as interrupting an activity and raising the head abruptly above shoulder level. Since the mongooses resumed normal foraging immediately after the end of the playbacks, we analysed the behaviour only until 3 s after the last played plover call. Infants rarely responded to the playbacks and were not included in the analyses. In each experiment, a different subsample of the group (mean 58%, range 10–100% of all individuals) was visible on the videotape. Thus, most individuals contributed to the measured response during several experiments, but some did not. Since we videotaped the responses using a wide angle to include a large number of individuals, we could not read the individual identities reliably. We therefore analysed the response to the playbacks at group level, assuming that the individuals visible on the videotape were a representative sample of the group.

## Statistical Analyses

Call rate and call duration of crowned plover alarms were analysed in an analysis of variance, treating every recording as an independent data point. Duration of banded mongoose alarm calls and antipredator behaviour of mongoose groups during the playbacks were analysed using linear mixed models (LMMs) with the residual maximum likelihood method and group identity included as a random factor. The occurrence of alert behaviour (rise on hind legs and/or move to cover) was analysed in a generalized linear mixed model (GLMM) with binomial error structure and a logit link function.

Since playback duration varied, we scored response intensity of the mongoose groups to the playbacks as the proportion of time rather than the absolute amount of

**Table 1.** Treatments of alarm call playbacks

	Urgency			
	High	Medium	Medium	Low
Call rate	High	High	Low	Low
Call duration	Short	Long	Short	Long
CR	<i>N</i> =8 (11.8, 5–18)	<i>N</i> =8 (10.9, 5–20)	<i>N</i> =8 (13.9, 6–19)	<i>N</i> =8 (10.6, 5–21)
WA	<i>N</i> =8 (9.5, 4–14)	—	—	—
SP	<i>N</i> =8 (12.0, 8–17)	—	—	—

CR: crowned plover, WA: wattled plover, SP: spurwinged plover. Each treatment was preceded by a control playback of gonolek calls with the matching call rate. *N* gives the number of mongoose groups tested. Numbers in parentheses give mean and range of the number of animals that were visible on the videotapes. For the control playbacks, the mean was 11.6 individuals with a range of 4–23 individuals.

time that individuals engaged in antipredator behaviour (look up and/or move to cover) during the playbacks. The proportion of antipredator behaviour was determined for every individual visible on the videotape and then averaged over all visible individuals for each experiment. Response intensity thus increased when more individuals responded and/or when individuals showed antipredator behaviour for a longer time. Proportions were arcsine-transformed to attain normality and analysed in a LMM, controlling for the presence of pups (present during 21 of the 48 experiments). To account for the widespread group-size effect on antipredator vigilance (Lima & Dill 1990), the number of individuals visible on the videotape was taken as a measure of how many individuals were nearby. This slightly underestimates the relevant measure of foraging aggregation size (Blumstein 1996), but it is more accurate than social group size since banded mongooses may spread out considerably during foraging and spend much time invisible to each other in thick bush (personal observation). Social group size did not influence the responses to the playbacks ( $P$  values for the main effect and all interactions were larger than 0.1) and was dropped from the models. Responses to plover playbacks were additionally controlled for the proportion of time spent vigilant during the control playbacks. Data analysis was carried out in R 2.2.1 (R Development Core Team 2005) using the packages nlme (Pinheiro et al. 2006) and MASS (Venables & Ripley 2002).

## RESULTS

### Alarm Calls and Urgency

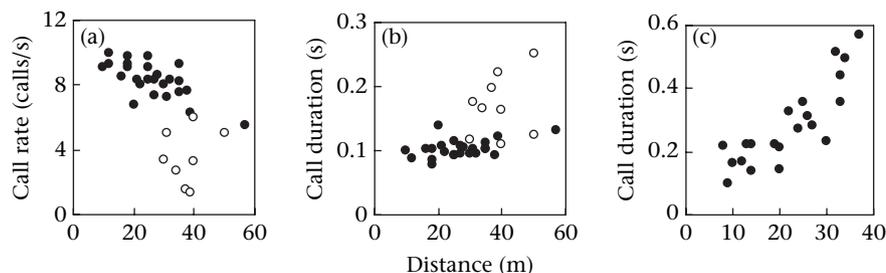
We obtained 33 alarm bouts of crowned plovers for which distance to threat was known. Plover behaviour and distance to threat explained a large proportion of the variance in call rate ( $r^2 = 0.79$ ) and average duration of calls ( $r^2 = 0.59$ ). Alarms of plovers flying off had a higher call rate (LMM:  $F_{1,30} = 107.6$ ,  $P < 0.0001$ ; Fig. 2a) and were shorter ( $F_{1,30} = 41.0$ ,  $P < 0.0001$ ; Fig. 2b) than alarms of plovers remaining sedentary. After controlling for this, call rate decreased with distance to threat ( $F_{1,30} = 8.57$ ,  $P = 0.006$ ), whereas the duration of calls did not increase significantly with distance to threat ( $F_{1,30} = 2.10$ ,  $P = 0.16$ ).

We recorded 21 alarm calls given by banded mongooses from six groups in response to approaching humans. The duration of these alarm calls was positively correlated with distance to threat (LMM:  $F_{1,14} = 106.9$ ,  $P < 0.0001$ ; Fig. 2c). At very close distances ( $< 8$  m), a structurally different call was given (panic call; Fig. 1h). Initial alarms were always single calls. Repeated calls were sometimes given after retreat from the threat.

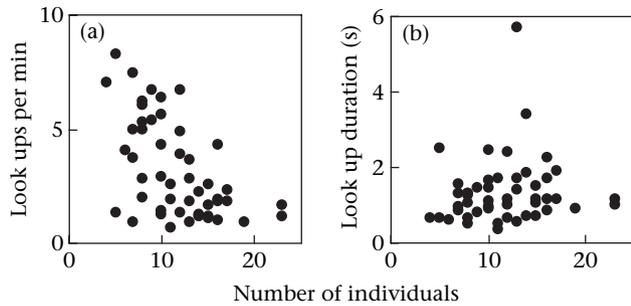
### Response to Calls of Different Species

During control playbacks (gonolek calls), mongooses spent on average 10.3% (SE = 1.4%,  $N = 48$  experiments) of the time displaying vigilance behaviour. The average look up rate per individual decreased with increasing number of individuals nearby (LMM:  $F_{1,37} = 6.53$ ,  $P = 0.015$ ; Fig. 3a), whereas average look up duration did not change (LMM on log transformed data:  $F_{1,37} = 0.05$ ,  $P = 0.83$ , Fig. 3b). The presence of pups influenced neither look up rate nor look up duration (look up rate:  $F_{1,37} = 0.003$ ,  $P = 0.96$ ; look up duration:  $F_{1,37} = 0.04$ ,  $P = 0.84$ ). Both measures also did not change with the rate at which gonolek calls were played back (look up rate:  $F_{1,37} = 0.78$ ,  $P = 0.38$ ; look up duration:  $F_{1,37} = 0.07$ ,  $P = 0.79$ ).

Mongoose groups responded to the high-urgency plover playbacks (cf. left column in Table 1) with increased vigilance compared to control playbacks and sometimes retreated towards cover (moving 2–10 m). Mongoose groups spent a larger proportion of the time displaying antipredator behaviour (look up and/or move to cover) during the playbacks of plover alarm calls compared to the gonolek playbacks (LMM:  $F_{1,34} = 36.5$ ,  $P < 0.0001$ ,  $N = 24$  plover + 24 gonolek playbacks; Fig. 4). This response was not dependent on which plover species was played back. However, the increase in antipredator behaviour was highest during spurwinged plover playbacks, intermediate during wattled plover playbacks and lowest during crowned plover playbacks (species  $\times$  treatment interaction:  $F_{2,34} = 3.00$ ,  $P = 0.06$ ). Neither the presence of pups ( $F_{1,34} = 0.15$ ,  $P = 0.70$ ) nor the number of individuals whose response was recorded ( $F_{1,34} = 0.09$ ,  $P = 0.77$ ) had an influence on the proportion of time spent displaying antipredator behaviour. Alert behaviour (rise on hind legs and/or move to cover) of at least one individual was observed during 11 of the 24 high-urgency playbacks, whereas during only one of the control playbacks did an



**Figure 2.** Temporal characteristics of alarm calls of crowned plovers ( $N = 33$ ) and banded mongooses ( $N = 21$ ) varied with distance to perceived threat. (a) Call rate of crowned plover alarms. (b) Duration of crowned plover alarm calls. (●): Plovers flying off while alarming. (○): Plovers remaining sedentary while alarming. (c) Duration of banded mongoose alarm calls.



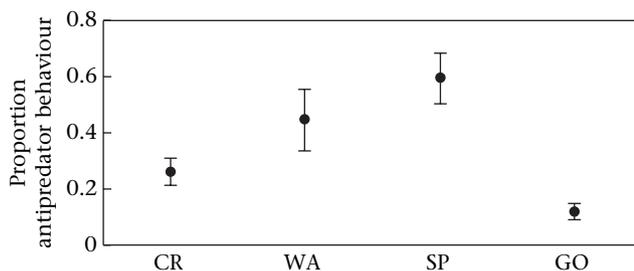
**Figure 3.** Vigilance behaviour of banded mongooses as a function of number of individuals nearby. (a) Look up rate per individual. (b) Average look up duration.  $N = 48$  experiments.

individual show alert behaviour (GLMM:  $F_{1,37} = 10.7$ ,  $P = 0.002$ ). Mongoose alarm calls were observed on one occasion, during a wattled plover playback.

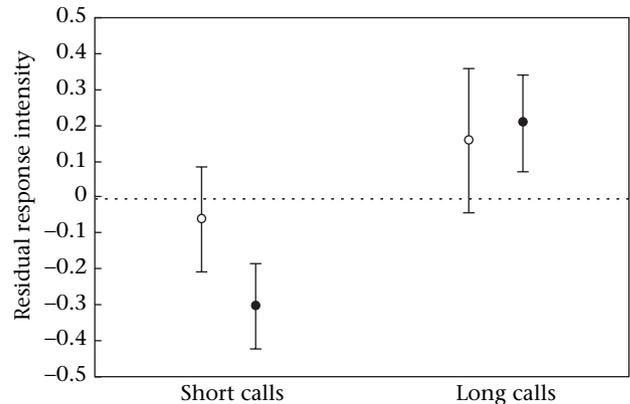
### Response Depending on Urgency

We tested whether the responses differed between playbacks of crowned plover alarms of varying urgency (cf. top row in Table 1). The calls used for the playbacks differed between treatments in call rate (high call rate: 120 calls/min; low call rate: 20 calls/min) and duration (averages over calls per playback: short calls:  $\bar{X} \pm SE = 90.6 \pm 3.0$  ms; long calls:  $\bar{X} \pm SE = 172.4 \pm 14.2$  ms;  $t$  test for unequal variances:  $t_{7,6} = 5.6$ ,  $P = 0.001$ ).

The response to the playbacks varied over a large scale (proportion of time spent displaying antipredator behaviour: 0.01–1.00) but was not influenced by the call rate at which crowned plover alarms were played back (LMM:  $F_{1,20} = 0.41$ ,  $P = 0.53$ ,  $N = 32$  experiments; Fig. 5). However, mongoose groups reacted more strongly to playbacks of long (low-urgency) alarm calls than to those of short (high-urgency) alarms (proportion antipredator behaviour: long calls:  $\bar{X} \pm SE = 0.357 \pm 0.108$ ; short calls  $\bar{X} \pm SE = 0.183 \pm 0.037$ ;  $F_{1,20} = 5.28$ ,  $P = 0.03$ ; Fig. 5). No interaction between call rate and call duration was detected ( $F_{1,20} = 0.63$ ,  $P = 0.44$ ). The response to the playbacks was not influenced by the presence of pups ( $F_{1,20} = 0.04$ ,  $P = 0.85$ ) or the number of individuals whose responses were recorded ( $F_{1,20} = 1.09$ ,  $P = 0.31$ ).



**Figure 4.** Proportion of time spent displaying antipredator behaviour during playbacks of plover alarm calls for eight banded mongoose groups. Shown are mean  $\pm$  SE of responses to alarm calls of crowned plovers (CR), wattled plovers (WA) and spurwinged plovers (SP) and to control playbacks of black-headed gonolek duet calls (GO).



**Figure 5.** Response intensity of eight banded mongoose groups to playbacks of short and long crowned plover alarm calls played at a low call rate (●) and at a high call rate (○). Shown are residuals of a LMM controlling for vigilance during the control playback and including group identity as a random factor. Mean  $\pm$  SE are given.

### DISCUSSION

Banded mongoose groups responded to playbacks of plover alarm calls with increased vigilance compared to playbacks of nonthreatening songbird calls and sometimes retreated to cover. This response is qualitatively equivalent to the mongooses' response to conspecific alarm calls observed in natural situations (personal observation). The mongooses responded to alarm calls of all three plover species, yet the response intensity tended to differ among the three plover species. This effect may be attributable to sensory biases which, for example, might make the detection of spurwinged plover calls more likely because of their steeper frequency modulation (Vallet & Kreutzer 1995). It remains to be shown whether banded mongooses decrease vigilance when foraging in the presence of plovers, analogous to the widely occurring group-size effect on vigilance within species (reviewed in Elgar 1989; Quenette 1990; Roberts 1996; Treves 2000) which we also found in our study. If confirmed, this would represent a direct benefit of attentiveness to heterospecific alarm calls, allowing for increased foraging efficiency (Pulliam 1973).

Even though response intensity varied over a large scale, banded mongoose groups did not respond to playbacks of crowned plover alarms according to urgency of the alarms. The consistent variation with distance to perceived threat in crowned plover alarms potentially allows other species to estimate the urgency level even if the crowned plovers do not use an urgency-based alarm call system. However, banded mongooses may not be attentive to changes in the call rate of heterospecific alarm calls because the mongooses do not give repeated calls for initial alarms. More surprising was our finding that the mongooses also did not respond to crowned plover alarm calls according to the urgency level encoded in the duration of the calls, even though the duration of banded mongoose alarms changed in a similar way with distance to threat. On the contrary, banded mongooses responded more intensely to longer crowned plover alarm calls (representing lower urgency), possibly because longer calls represented

stronger stimuli. This finding cannot be explained by a lower quality of recordings of the long alarm calls, which were recorded from a larger distance than the short alarm calls. First, the signal-to-noise ratio was not significantly lower for the playbacks with long calls than for those with short calls; second, a lower quality of the playbacks with long calls would predict a weaker rather than a stronger response to these playbacks compared to the playbacks of short calls. We do not know whether banded mongooses use urgency-related differences in their own alarm calls because, due to the poor recording quality, we were not able to do playback experiments with conspecific alarm calls. Also, we cannot exclude that banded mongooses use parameters other than call duration to encode urgency in their alarm calls (for example tonality) and, therefore, do not attend to urgency-related differences in either call rate or call duration of crowned plover alarms.

Recent studies have shown that animals may extract referential information from heterospecific alarms (Zuberbühler 2000a; Fichtel 2004; Rainey et al. 2004). That banded mongooses do not attend to urgency-based differences in plover alarm calls suggests that at least some species may respond to heterospecific alarms in a more crude way without using additional information encoded in these alarms. The lack of use of additional information in our study may be related to differences in the perception of urgency between plovers and mongooses, to the absence of complementary cues indicating urgency and/or to the costs of correct and wrong responses.

First, crowned plovers and banded mongooses may differ in their perception of urgency in a given situation. For instance, a situation representing high urgency for the plovers may still be perceived as only moderate urgency by the mongooses. In this case, the difference between low- and high-urgency plover alarms may be of minor relevance to the mongooses. Indeed, only three of the eight high-urgency crowned plover playbacks incited some mongooses to rise on their hind legs and no playbacks incited moving to cover, indicating that our playbacks did not include stimuli of utmost urgency even though we varied call rate by a factor of six and call duration by a factor of two.

Second, banded mongooses may categorize all plover alarms as only moderate-urgency alarms unless additional cues, such as plovers flying off, reinforce the stimulus. This argument is supported by the finding that playbacks of alarm calls may fail to elicit as strong a response as was observed when the calls were recorded, as shown for example in Barbary macaques (*Macaca sylvanus*; Fischer & Hammerschmidt 2001). This could explain our results if mongooses categorize alarms as high urgency only if they are accompanied by the additional visual cue.

Third, ignoring urgency-related information and responding to low-urgency alarms as if they were of higher urgency incurs the costs of the response only, and brief scanning and/or moving a short distance towards cover is probably comparatively cheap. Conversely, referential information in alarm calls usually elicits discreet responses (Seyfarth et al. 1980; Zuberbühler 2000b; Manser et al. 2001; but see Fischer & Hammerschmidt 2001) and ignoring this information in both conspecific and heterospecific

alarms may lead to an inappropriate reaction, increasing the vulnerability to the predator with possibly fatal consequences. Therefore selection pressure for the use of referential information may be higher than selection pressure for the use of urgency-related information. Animals may thus be more likely to pay attention to referential than to urgency-related information in heterospecific alarms.

In conclusion, we found that banded mongooses use heterospecific alarms for predator avoidance but do not attend to additional urgency-related information provided by these signals. This stands in contrast to other studies which found differentiated responses to heterospecific alarms. How commonly animals attend to and why in some cases animals do not attend to additional information provided by heterospecific alarms remains an open question and deserves further investigation.

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### References

- Bell, M. B. V. 2006. Communication, cooperation and conflict in banded mongooses. Ph.D. thesis, Cambridge University, U.K.
- Blumstein, D. T. 1996. How much does social group size influence golden marmot vigilance? *Behaviour*, **133**, 1133–1151.
- Boshoff, A. F., Palmer, N. G. & Avery, G. 1990. Regional variation in the diet of martial eagles in the Cape Province, South Africa. *South African Journal of Wildlife Research*, **20**, 57–68.
- Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer.
- Cant, M. A. 2000. Social control of reproduction in banded mongooses. *Animal Behaviour*, **59**, 147–158. doi:10.1006/anbe.1999.1279.
- Dabelsteen, T., Larsen, O. N. & Pedersen, S. B. 1993. Habitat-induced degradation of sound signals: quantifying the effects of communication sounds and bird location on blur ratio, excess attenuation, and signal-to-noise ratio in blackbird song. *Journal of the Acoustical Society of America*, **93**, 2206–2220. doi:10.1121/1.406682.
- Dimond, S. & Lazarus, J. 1974. The problem of vigilance in animal life. *Brain Behavior and Evolution*, **9**, 60–79.
- Elgar, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews*, **64**, 13–33.

- Fichtel, C. 2004. Reciprocal recognition of sifaka (*Propithecus verreauxi verreauxi*) and redfronted lemur (*Eulemur fulvus rufus*) alarm calls. *Animal Cognition*, **7**, 45–52. doi:10.1007/s10071-003-0180-0.
- Fichtel, C. & Hammerschmidt, K. 2002. Responses of redfronted lemurs to experimentally modified alarm calls: evidence for urgency-based changes in call structure. *Ethology*, **108**, 763–777. doi:10.1046/j.1439-0310.2002.00816.x.
- Fichtel, C., Hammerschmidt, K. & Jürgens, U. 2001. On the vocal expression of emotion: a multi-parametric analysis of different states of aversion in the squirrel monkey. *Behaviour*, **138**, 97–116. doi:10.1163/15685390151067094.
- Fischer, J. & Hammerschmidt, K. 2001. Functional referents and acoustic similarity revisited: the case of Barbary macaque alarm calls. *Animal Cognition*, **4**, 29–35. doi:10.1007/s100710100093.
- Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.
- Macedonia, J. M. & Evans, C. S. 1993. Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*, **93**, 177–197.
- Manser, M. B., Bell, M. B. & Fletcher, L. B. 2001. The information that receivers extract from alarm calls in suricates. *Proceedings of the Royal Society of London, Series B*, **268**, 2485–2491. doi:10.1098/rspb.2001.1772.
- Morse, D. H. 1977. Feeding behavior and predator avoidance in heterospecific groups. *Bioscience*, **27**, 332–339.
- Morton, E. S. 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist*, **111**, 855–869.
- Perla, B. S. & Slobodchikoff, C. N. 2002. Habitat structure and alarm call dialects in Gunnison's prairie dog (*Cynomys gunnisoni*). *Behavioral Ecology*, **13**, 844–850.
- Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. 2006. nlme: linear and nonlinear mixed effects models. R package version 3.1–68.1.
- Pulliam, H. R. 1973. On the advantages of flocking. *Journal of Theoretical Biology*, **38**, 419–422.
- Quenette, P. Y. 1990. Functions of vigilance behaviour in mammals: a review. *Acta Oecologica*, **11**, 801–818.
- R Development Core Team. 2005. *R: a Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org>.
- Rainey, H. J., Zuberbühler, K. & Slater, P. J. B. 2004. Hornbills can distinguish between primate alarm calls. *Proceedings of the Royal Society of London, Series B*, **271**, 755–759. doi:10.1098/rspb.2003.2619.
- Randall, J. A. & Rogovin, K. A. 2002. Variation in and meaning of alarm calls in a social desert rodent *Rhombomys opimus*. *Ethology*, **108**, 513–527.
- Randler, C. 2006. Red squirrels (*Sciurus vulgaris*) respond to alarm calls of Eurasian jays (*Garrulus glandarius*). *Ethology*, **112**, 411–416. doi:10.1111/j.1439-310.2006.01191.x.
- Roberts, G. 1996. Why individual vigilance declines as group size increases. *Animal Behaviour*, **51**, 1077–1086. doi:10.1006/anbe.1996.0109.
- Rood, J. P. 1983. Banded mongoose rescues pack member from eagle. *Animal Behaviour*, **31**, 1261–1262.
- Searcy, W. A. & Nowicki, S. 2005. *The Evolution of Animal Communication*. Princeton, New Jersey: Princeton University Press.
- Seyfarth, R. & Cheney, D. 1990. The assessment by vervet monkeys of their own and another species' alarm calls. *Animal Behaviour*, **40**, 754–764. doi:10.1016/S0003-3472(05)80704-3.
- Seyfarth, R. M., Cheney, D. L. & Marler, P. 1980. Monkey responses to 3 different alarm calls: evidence of predator classification and semantic communication. *Science*, **210**, 801–803.
- Sherman, P. W. 1977. Nepotism and the evolution of alarm calls. *Science*, **197**, 1246–1253.
- Sherman, P. W. 1985. Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation? *Behavioral Ecology and Sociobiology*, **17**, 313–323. doi:10.1007/BF00293209.
- Shriner, W. M. 1998. Yellow-bellied marmot and golden-mantled ground squirrel responses to heterospecific alarm calls. *Animal Behaviour*, **55**, 529–536. doi:10.1006/anbe.1997.0623.
- Templeton, C. N. & Greene, E. 2007. Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *Proceedings of the National Academy of Sciences, U.S.A.*, **104**, 5479–5482. doi:10.1073/pnas.0605183104.
- Templeton, C. N., Greene, E. & Davis, K. 2005. Allometry of alarm calls: black-capped chickadees encode information about predator size. *Science*, **308**, 1934–1937. doi:10.1126/science.1108841.
- Treves, A. 2000. Theory and method in studies of vigilance and aggregation. *Animal Behaviour*, **60**, 711–722. doi:10.1006/anbe.2000.1528.
- Trillmich, J., Fichtel, C. & Kappeler, P. M. 2004. Coordination of group movements in wild Verreaux's sifakas (*Propithecus verreauxi*). *Behaviour*, **141**, 1103–1120. doi:10.1163/1568539042664579.
- Vallet, E. & Kreutzer, M. 1995. Female canaries are sexually responsive to special song phrases. *Animal Behaviour*, **49**, 1603–1610. doi:10.1016/0003-3472(95)90082-9.
- Venables, W. M. & Ripley, B. D. 2002. *Modern Applied Statistics with S*. New York: Springer.
- Zuberbühler, K. 2000a. Interspecies semantic communication in two forest primates. *Proceedings of the Royal Society of London, Series B*, **267**, 713–718. doi:10.1098/rspb.2000.1061.
- Zuberbühler, K. 2000b. Causal knowledge of predators' behaviour in wild Diana monkeys. *Animal Behaviour*, **59**, 209–220. doi:10.1098/rspb.2000.1061.