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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.

Keywords: antipredator behaviour; banded mongoose; Herpestidae; heterospecific alarming; *Mungos mungo*; playback; urgency level; vigilance

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

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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, spurwinged 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^2) 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 rangefinder (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 spurwinged 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