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Banded mongoose recruitment calls convey information about risk and not stimulus type

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Many species use specific vocalizations that attract conspecifics to food sources or that recruit other group members to inspect secondary predator cues or to mob predators. However, little is known regarding the variation in the acoustic structure of such calls and the associated meaning. In the cooperatively breeding banded mongoose, *Mungos mungo*, we investigated calls produced in the context of group recruitment to three different stimulus types: (1) secondary predator cues; (2) snakes; and (3) members of rival groups. Calls produced in response to predator faeces differed from the harsher variants elicited by snakes and rival groups, but the latter two elicited similar calls. Only a few calls of intermediate acoustic structure were produced in response to the different stimulus categories. Playbacks of calls elicited by the different stimuli caused individuals to approach the speaker in the same way. However, calls elicited specifically by snakes and rival mongooses resulted in a higher proportion of receivers responding and a faster receiver response than calls elicited by faeces. This suggests a graded rather than a discrete recruitment call system. Thus, despite obvious differences in stimulus type and the purpose of recruitment, the acoustic structure of calls conveys information about the risk of the encountered stimulus and not the stimulus type itself, allowing receivers to adjust their response according to the urgency. Since calling continued for prolonged periods after all group members had gathered around the callers, these calls may also function to deter rivals and to coordinate the subsequent group response.

Birds and mammals use specific calls that attract conspecifics to approach the location of the caller (Hauser 1996). These calls lead conspecifics to food sources, which may facilitate access to them (Marzluff & Heinrich 1991), increase the signaller's chances of attracting a potential mate (Collias & Joos 1953; Stokes 1971; Marler et al. 1986a, b) or reduce predation risk (Elgar 1986). In altricial pied babblers, *Turdoides bicolor*, breeders and helpers attract nutritionally independent but inexperienced young foragers to good feeding sites by giving 'recruitment calls' (Radford & Ridley 2006). Moreover, specific recruitment calls are also produced when social animals face potentially dangerous situations. Cooperatively breeding meerkats, *Suricata suricatta*, produce such calls when encountering secondary predator cues or snakes, and receivers respond by joining the caller either to inspect the cue or to mob the snake (Manser 2001; Manser et al. 2001). Furthermore, recent studies on vocalizations in the context of recruiting behaviour showed that mobbing calls in black-capped chickadees, *Poecile atricapillus*, vary with the size of the predator (Templeton et al. 2005), while in reed warblers, *Acrocephalus arundinaceus*, such calls vary systematically with the distance to the threat (Welbergen & Davies 2008). Although the recruitment function of calls produced in these different contexts has been tested experimentally (Evans & Evans 1999; Manser et al. 2001; Di Bitetti 2003; Gros-Louis 2004; Templeton et al. 2005; Radford & Ridley 2006; Welbergen & Davies 2008), little is known about how differences in the context of production affect the calls' acoustic structure.

The acoustic structure of alarm calls inducing vigilance or flight responses often varies with the context in which these calls are produced (Marler 1955; Sherman 1977). Alarm calls may encode information about the level of urgency to respond (Robinson 1981; Blumstein & Armitage 1997; Leavesley & Magrath 2005), denote the class of predators (Seyfarth et al. 1980; Gyger et al. 1987) or both (Manser 2001). Alarm calls signalling urgency appear to contain information about the risk the caller is facing (Robinson 1981) in a similar way as described for mobbing calls. On the other hand, functionally referential alarm calls denote the approaching predator type and contain information about specific objects or events in the external environment (reviewed in Macedonia & Evans 1993; Searcy & Nowicki 2005). The evolution of calls that are specific to

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predator type has been shown to relate to (1) differences in escape behaviours (Macedonia & Evans 1993), even if these are small (Manser 2001; Furrer & Manser 2009), or (2) an ability to locate the predator more quickly (Kirchhof & Hammerschmidt 2006). In line with these results, the analysis of the structural variation of recruitment calls may reveal graded differences according to the level of urgency or categorical differences in acoustic structure depending on stimulus type.

We investigated recruitment calls in banded mongooses, *Mungos mungo*, a small (less than 2 kg), cooperatively breeding, diurnal herpestid living in mixed-sex groups of 5–44 individuals (Cant 2000). They are preyed on by mammalian predators, reptiles such as the African rock python, *Python sabae*, and large raptors such as martial eagles, *Polemaetus bellicosus*, which were seen to target them at the study site (Rood 1983; Otali & Gilchrist 2004; Bell 2006). For banded mongooses group life provides individual protection, as group members gather to inspect secondary predator cues (Müller & Manser 2007) and bunch together to attack predators and competitors (Rood 1975). When inspecting secondary cues, such as faeces or urine of predators, individuals produce shrill calls that seem to recruit other group members (R. Furrer, personal observation). Similarly sounding vocalizations are produced while mobbing reptiles, chasing mammalian predators, such as rusty-spotted genets, *Genetta maculata* (Banded Mongoose Project, unpublished data), and attacking raptors (Rood 1983). Rival banded mongooses from foreign social groups are fiercely attacked during intergroup interactions, which can be fatal (Rood 1975; Cant et al. 2002; Gilchrist & Otali 2002). At least two adult individuals of the study population died in agonistic interactions during the period of this study (Banded Mongoose Project, unpublished data). During such encounters individuals produce ‘screeching calls’ (Cant et al. 2002), also named ‘war cries’ (Müller & Manser 2007), and these calls seem to alert the rest of the group, recruiting individuals of each group to bunch together and approach the other group en masse (for details on intergroup encounters see Cant et al. 2002).

We examined the acoustic structure of calls produced during encounters with different stimulus types that recruited other group members. In particular we investigated the vocalizations given when: (1) inspecting predator faeces; (2) mobbing African rock pythons; and (3) facing rival groups. We then systematically tested whether the information content of calls produced in each context was meaningful to recipients with playback experiments. We expected little overlap of call structure between the different stimulus types and appropriate, potentially different response strategies if calls were functionally referential. Alternatively, if the calls relate to the urgency to respond we expected their acoustic structure to grade along a continuum according to the risk of the context and predicted only urgency-based differences within a single response strategy. Thereby, we assumed that predator faeces posed a lower risk to banded mongooses than snakes or rival mongooses. Although it is more difficult to give an a priori assumption about the risks snakes and rival banded mongooses pose, it is likely that, once detected, snakes might pose a slightly lower immediate risk for the caller than rival mongooses. This is because the caller could easily avoid a detected snake by moving away, whereas this is less possible for a caller attacked by rival mongooses.

METHODS

Study Site and Animals

Data were collected from July to December 2006 and from May to December 2007 on a wild population of banded mongooses living on and around Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12′S; 29°54′E; for details of the study area see Cant 1998; Gilchrist 2001). The study population consisted of six groups of habituated banded mongooses totalling 150 adult individuals that allowed close-range observations. Animals were classified as adults (>12 months), subadults (6–12 months), juveniles (<6 months) and pups (<3 months). For individual identification, adults were fitted with colour-coded plastic collars. We marked subadults and infants by shaving a small area of fur on the rump, and pups by dyeing small areas of fur with blonde hair dye (see Cant 2000 for descriptions of trapping and marking techniques). All procedures were approved by the Uganda Wildlife Authority and Uganda National Council of Science and Technology.

Recording Methods

To determine whether the acoustic structure of calls varies between different contexts, we focused on calls elicited by predator faeces, African rock pythons and rival conspecifics. Calls were recorded within 3 m of the caller using a Marantz PMD670 solid state recorder (.wav format, sampling frequency of 44.1 kHz, resolution 16 bit) and a Sennheiser ME 66/K6 directional microphone. We recorded calls produced in response to secondary predator cues by putting fresh faeces deposited by the predator during the previous night on the predicted foraging route. As stimuli we used faeces deposited by leopards, *Panthera pardus*, and lions, *Panthera leo*, which are both common predators at the study site. We conducted 15 presentations with lion faeces and 12 with leopard faeces in six groups. The two predator species may represent different threat levels to banded mongooses as leopards are known to prey on mongooses (Hayward et al. 2006), whereas banded mongooses do not appear on the lion’s prey species list (Hayward & Kerley 2005). Faeces from adult lions exceed 35 mm in diameter and were therefore clearly identifiable (Bodendorfer et al. 2006). Since faeces deposited by leopards could be confused with faeces of immature lions we were advised on species identification by specialists of the Uganda Large Predator Program. We recorded calls produced in response to natural encounters with African rock pythons and rival banded mongooses. In both cases we quickly moved to the place where either the snake was confronted or the rival banded mongooses were sighted and recorded the calls. In the latter case we recorded calls that were produced during the first stage of encounters between two groups of banded mongooses when members of the two different packs sighted each other, stood erect and started calling. After group members bunched up to confront the snake or the rival banded mongooses, we stopped recording calls as they often overlapped and could not be assigned to a particular individual. Because calls elicited by African rock pythons and rival mongooses were recorded during natural encounters, there was a delay in recording of 5–15 s after the first call had been given. We recorded calls produced during seven encounters with African rock pythons in five groups and calls elicited by conspecifics from 14 intergroup encounters involving each of the six groups. We used calls from one or several callers per presentation or encounter and analysed the first call produced by an adult individual that had good signal to noise ratio.

Acoustic Analyses

To generate spectrograms of calls we carried out 1024-point fast Fourier transformation (Hamming window; overlap: 93.75%; time resolution: 1.45 ms; frequency resolution: 43 Hz) of all calls using Avisoft-SASLab pro 4.38 (R. Specht, Berlin, Germany). We measured 18 acoustic parameters from the spectrograms (see Table 1 for parameters used in the different analyses). Including many acoustic parameters enables an analysis of complex patterns without

Table 1
Acoustic parameters used in the analyses

Acoustic parameter	Parameter category	Analysis
Entropy (centre)	Entropy	1
Entropy (mean)	Entropy	1, 2
Frequency bandwidth (mean)	Frequency distribution	1, 2
Maximum frequency (centre)	Frequency	1
Maximum frequency (mean)	Frequency	1
Maximum frequency of quartile 25 (mean)	Frequency distribution	2
Maximum frequency of quartile 50 (mean)	Frequency distribution	1
Maximum frequency of quartile 75 (centre)	Frequency distribution	1
Number of peaks (mean)	Frequency distribution	2
Peak frequency (mean)	Frequency	2

The acoustic parameters shown were used in (1) discriminant function analyses of calls elicited by lion and leopard faeces, and (2) tests of classification probabilities comparing calls produced in response to predator faeces, African rock pythons and rival mongooses. All correlation parameters with $r_S > 0.8$ were excluded from the parameter set. Either the location of the measurement of the acoustic parameter was in the centre of the call (centre) or a mean value of the acoustic parameter was calculated over the whole call (mean).

a priori assumptions of the importance of specific parameters (Schrader & Hammerschmidt 1997). Analyses included parameters describing temporal and frequency dynamics and entropy of calls. For frequency- and entropy-related parameters we chose the mean spectrum of the entire element and the centre of the element as temporal locations of the measurements.

Playback Experiments

Selection and amplitude of calls

To test whether receivers extract specific information from calls produced in different contexts, we carried out playback experiments. We selected calls with the typical acoustic structure of the context and a good signal to noise ratio. We avoided pseudoreplication by creating for each playback a unique file lasting 30 s. To test specifically the influence of the acoustic structure, we standardized the number of calls used in all playbacks. Each file contained 12 calls produced by two to four individuals of the same group during the same event. The amplitude of the calls used in the playbacks was adjusted to the observed amplitude of calls when subjects encountered the stimuli and was measured with a digital sound level meter Voltcraft SL-100 (sound level range: 30–130 dB; frequency range: 31.5 Hz–8 kHz; response time: 100–125 ms; resolution 0.1 dB; Conrad Electronic, Hirschau, Germany).

Experimental design

Calls used in playbacks were elicited by leopard and lion faeces, African rock pythons and rival banded mongooses. We conducted 43 playbacks in six groups in a randomized order. Prior to the playback experiments, we verified the presence of all individuals of the focal group. We then placed the loudspeaker (JBL on Tour, Harman Multimedia, Northridge, CA, U.S.A.; frequency range: 100 Hz–20 kHz; power consumption: 6 W maximum) on the ground along the predicted foraging route, so that it was covered by vegetation, and connected it to a Marantz PMD670. Afterwards we defined a location where we intended to gather the focal group prior to the playback as the ‘start location’. This spot was situated in an open area at a previously measured distance 20 m from the speaker. When the focal group came close we attracted the individuals to the start location by distributing a small quantity of bait (approximately 20 g of a mix of rice and gravy) on the ground within a circle of 1 m diameter. As soon as individuals finished searching for bait and began to move away again, the playback was started. To collect data on the subjects’ responses one person observed their behaviour at the start location while another watched from a distance of 5 m from the speaker, to make detailed observation of the area close to the speaker. We observed the subjects’ responses to playback, measured the time until the first subject arrived within 1 m of the speaker using a stopwatch (M-Quartz alarm chronograph, Mondaine Watch Ltd, Zurich, Switzerland) and counted out of the total number of group members present the number of subjects arriving within 1 m of the speaker. As a control treatment, we recorded calls of the yellow-fronted tinkerbird, *Pogoniulus chrysoconus*, and conducted six control playbacks with the same design. Yellow-fronted tinkerbird calls were chosen as control stimuli because these nonthreatening, conspicuous calls are produced over prolonged periods. We only performed playbacks if the focal group had not encountered predator faeces, snakes or rival conspecifics during the previous 30 min. To avoid habituation, only one playback was conducted per group per day followed by a period of at least 7 days without the same or a similar type of playback.

Statistical Analyses

Acoustic analyses

Statistical analyses were conducted using SPSS 13.0 (SPSS Inc., Chicago, IL, U.S.A.). To exclude acoustic parameters that correlated highly with others we conducted Spearman correlations (exclusion criteria: $r_S > 0.8$). The remaining parameters were entered into a discriminant function analysis (DFA) to determine classification probabilities of calls produced. DFA identifies linear combinations of predictor variables that best characterize the differences between groups and assigns each call to its appropriate group (correct assignment) or to another group (incorrect assignment). For external validation, we used a leave-one-out cross-validation procedure and to test the significance of the classification level achieved, two-tailed binomial tests were performed. To fulfil the requirements of independence in DFA (Mundry & Sommer 2007) parameters of only one randomly chosen call per individual were entered into the DFA. For each stimulus category, calls recorded from individuals of both sexes and from all groups available were entered into the DFA. As the entered number of calls from each sex and group was not fully balanced overall, we conducted post hoc DFAs to control for possible sex- or group-specific call characteristics.

Playback experiments

Statistical tests were performed using R 2.4.1 (R Development Core Team 2006). To analyse the influence of the stimuli eliciting the calls used in the playbacks on the time to approach the speaker and the percentage of group members approaching, we carried out linear mixed-effects models (LMMs). In these analyses we controlled for the repeated sampling in the same group with ‘group’ fitted as a random factor (Crawley 2002) by conducting random intercepts models using the packages nlme (Pinheiro et al. 2006) and MASS (Venables & Ripley 2002). Since the order of playbacks was randomized in each group and the identity of the first individual approaching the speaker varied greatly, we omitted these factors from the statistical models. To fulfil the requirements of normally distributed data we used logarithmic and arcsine-transformed data (Sokal & Rohlf 1995).

RESULTS

Acoustic Structure of Recruitment Calls

The three different stimuli elicited calls with two acoustically distinct structures which graded into each other. Individuals produced calls with a comparatively small frequency bandwidth when detecting predator faeces (Fig. 1a) and calls with a large frequency bandwidth when encountering snakes or rival banded mongooses (Fig. 1b). Calls showing intermediate characteristics were elicited by all stimuli (Fig. 1c). The classification probabilities of calls elicited by leopard faeces ($N = 16$) versus lion faeces ($N = 16$) showed that the first discriminant function explained 100% of the total variance. The first function of the DFA showed 56.3% correct cross-validated assignment to the appropriate context (Wilk's $\lambda = 0.79$, $\chi^2_7 = 6.25$, $P = 0.51$) a level not substantially higher than expected by chance (50%; binomial tests: leopard faeces: $N = 16$, $P = 0.8$; lion faeces: $N = 16$, $P = 0.8$). We therefore randomly selected nine calls elicited by leopard and lion faeces, respectively, and pooled them as calls elicited by predator faeces. Then, we tested the classification probabilities of calls produced in response to predator faeces ($N = 18$), African rock pythons ($N = 14$) and rival mongooses ($N = 16$). The prior probabilities for calls entered into the DFA elicited in the three contexts were: predator faeces: 0.375; African rock pythons: 0.292; rival mongooses: 0.333. The first discriminant function explained 98.3% of the total variance. The DFA yielded an overall cross-validated correct assignment of 52.1% (Wilk's $\lambda = 0.246$, $\chi^2_{10} = 60.31$, $P < 0.0001$; Fig. 2) compared to 33.33% expected by chance (binomial tests: predator faeces: $N = 18$, $P = 0.001$; African rock pythons: $N = 14$, $P = 0.424$; rival mongooses: $N = 16$, $P = 0.077$). The acoustic structure of calls produced in response to African rock pythons and rival banded mongooses did not differ (post hoc DFA: Wilk's $\lambda = 0.924$, $\chi^2_5 = 2.03$, $P = 0.845$). Calls elicited by predator faeces yielded a high percentage of cross-validated correct assignment to the appropriate context whereas calls produced in response to African rock pythons and rival mongooses yielded only a low percentage of correct assignment, respectively, and were often misclassified to the other context in which noisier calls were produced (Table 2). There were neither sex-specific call characteristics (post hoc DFA, sex-specificity, first function: Wilk's $\lambda = 0.964$, $\chi^2_5 = 1.61$, $P = 0.9$; binomial test: $N = 48$, $P = 0.88$) nor group-specific call characteristics (post hoc DFA, group-specificity, first function: Wilk's $\lambda = 0.483$, $\chi^2_{25} = 30.1$, $P = 0.22$; binomial test: $N = 48$, $P = 0.32$). Furthermore, in 22 of 27 presentations of predator faeces at least one of the individuals arriving in the last quarter of all group members was calling. In all encounters with pythons and in all intergroup interactions group members continued to call after gathering together.

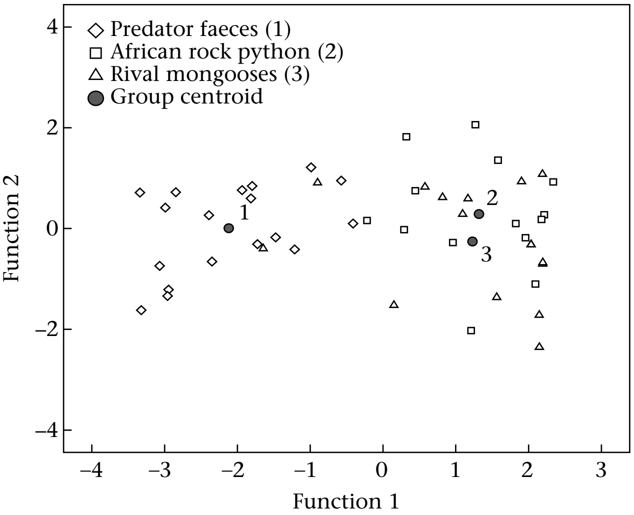

Figure 2. Discriminant function scores and group centroids of calls elicited by predator faeces, African rock pythons and rival mongooses.

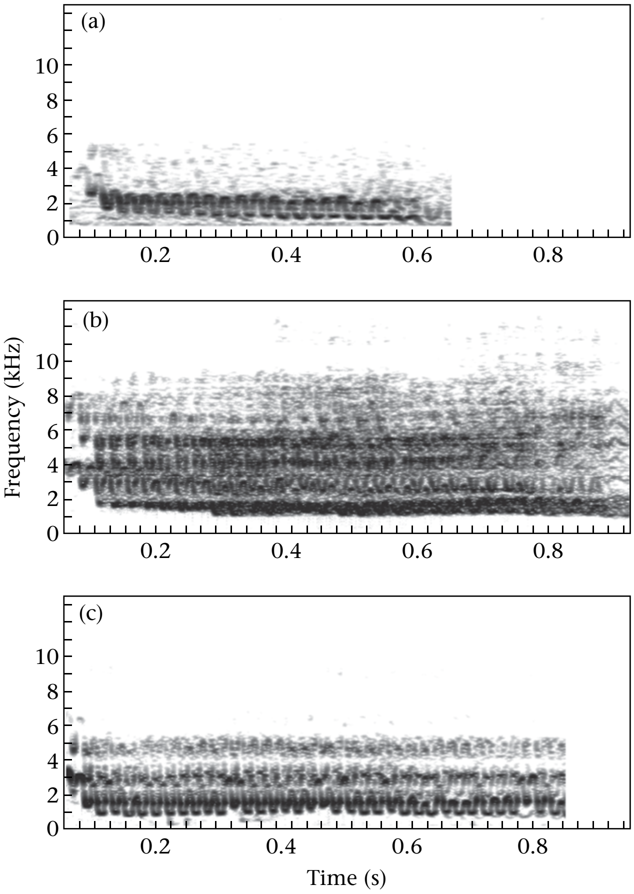

Figure 1. Spectrograms of calls produced in the context of recruitment: (a) when encountering predator faeces (here lion faeces); (b) at the beginning of an intergroup encounter with rival banded mongooses; and (c) at the beginning of an intergroup encounter with rival banded mongooses showing intermediate acoustic structure.

Responses to Playbacks

Subjects responded to playbacks of calls elicited during the encounter of all three different stimulus types. Typically, subjects responded by looking towards the speaker, and then approaching it as a cohesive group. The time to approach the speaker for the first individual of the group did not vary between calls elicited by the two different secondary predator cues (leopard: 51.72 (untransformed mean), $N = 11$; lion: 54.91 s, $N = 12$; $F_{1,17} = 0.13$, $P = 0.72$). Therefore, we pooled the responses to calls elicited by leopard and lion faeces by randomly selecting six playbacks each. We conducted the randomization five times, and used the one with the median mean time to approach the speaker. The time to approach the speaker for the first individual of the group varied significantly

Table 2
Cross-validated percentages of assignment of analysed calls to the three given contexts

Context	Predicted group membership			Total
	1	2	3	
1	88.9	5.6	5.6	100
2	0	35.7	64.3	100
3	12.5	62.5	25.0	100

Context 1: predator faeces; context 2: African rock pythons; context 3: rival banded mongooses.

between playbacks of calls elicited by predator faeces (52.83 s (untransformed mean), $N = 12$), African rock pythons (38.8 s, $N = 10$) and rival mongooses (36.6 s, $N = 10$; $F_{1,26} = 8.358$, $P = 0.008$; Fig. 3). The percentage of individuals approaching the speaker varied between calls elicited by the different stimulus types (predator faeces: 53% (untransformed mean), $N = 12$; African rock pythons: 71%, $N = 10$; rival mongooses: 76.3 %, $N = 10$; $F_{1,26} = 4.768$, $P = 0.038$; Fig. 4). None of the individuals approached the speaker in any of the six control playbacks using calls of the yellow-fronted tinkerbird as stimuli.

DISCUSSION

In banded mongooses, recruitment calls did not convey stimulus-specific information, but appeared to vary with the degree of risk faced by the caller. The acoustic structure of the calls graded from more tonal variants in less risky encounters of secondary predator cues, to calls with a harsher, noisier acoustic structure produced during high-risk confrontations with snakes or rival conspecifics. The possibly higher threat level represented by leopards than lions was reflected neither in the acoustic structure of calls elicited in response to their faeces, nor in the response time to playbacks of these calls. The acoustic structure of calls produced in response to African rock pythons and rival banded mongooses did not differ. A higher proportion of tested subjects approached the speaker playing calls elicited by snakes and rival mongooses and they also did this faster in comparison to playbacks of calls produced in response to predator faeces.

The acoustic structure of the recruitment calls produced during encounters of the three different stimuli varied greatly between secondary predator cues and snakes and rival groups. Although only very few calls of intermediate acoustic structure were elicited by all the different stimulus categories, the acoustic structure of calls elicited by predator faeces graded towards the acoustic structure elicited by the other two contexts (and vice versa), indicating a risk-based system. However, while calls elicited by snakes and rival groups greatly overlapped, there was little overlap between these calls and those elicited by predator faeces (only two calls elicited by foreign mongooses were similar in acoustic structure to those elicited by predator faeces). The lack of differences in call structure and response time suggests that banded mongooses cannot discriminate between lion and leopard faeces and respond to them acoustically in the same way. It may also be that they actually can discriminate between them, but that the level of arousal caused by lion and leopard faeces is similarly low in comparison to that elicited by snakes and rival groups. These findings may suggest that banded mongooses distinguish between discrete threat categories, specifically secondary cues and live animals. However, playbacks showed that the same response type always occurs (with differences in the speed of the response and the number of group members responding, according to the level of urgency), which suggests a graded rather than a discrete call system in the context of recruitment. Since the perceived risk for the caller might decrease with time, calls occurring later in the bout could reflect decreased urgency. This could be a confounding factor in our study as calls produced in response to predator faeces were recorded from the very beginning of the calling bout during presentations, while calls elicited by African rock pythons and rival conspecifics were recorded with a delay of 5–15 s on occurrence. However, this potential methodological restriction is not likely to affect the validity of our results since calls produced in response to African rock pythons and rival mongooses indicate higher urgency, even though recording started with a short delay in time in these two contexts.

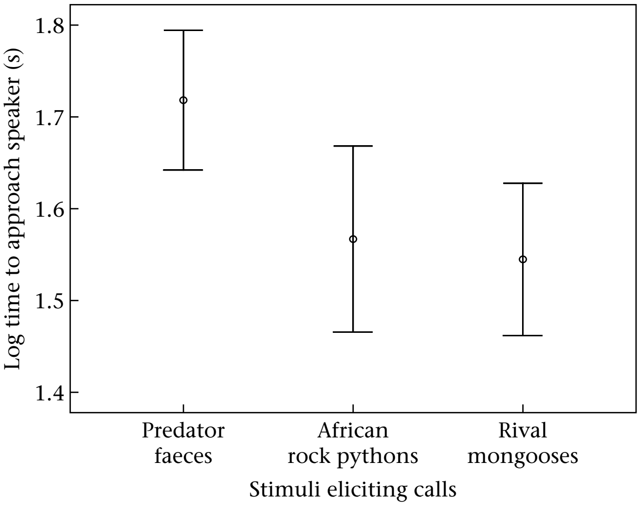

Figure 3. The time taken by the first individual to approach the speaker during playback of calls elicited when exposed to three different stimuli. Means±SD are shown.

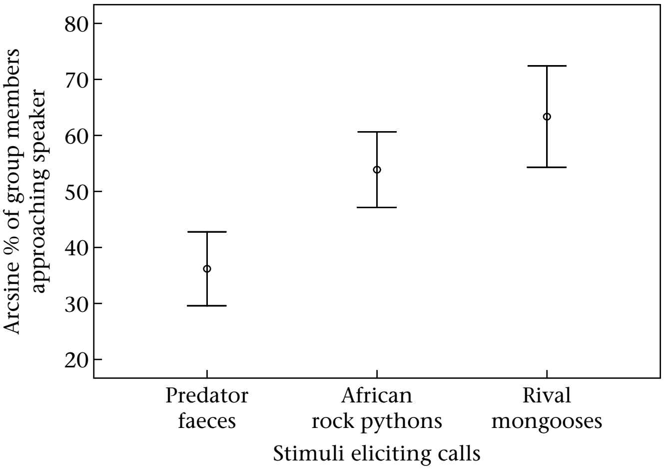

Figure 4. The arcsine-transformed percentage of individuals approaching the speaker during playbacks of calls elicited when exposed to three different stimuli. Means±SE are shown.

In addition to variation in the acoustic structure of calls, variation in call rate may also influence the receiver's responses (Blumstein & Armitage 1997; Warkentin et al. 2001). As several banded mongooses often called almost at the same time, we cannot provide a detailed analysis of the number of calls produced in the different contexts per individual. We can generally say that when encountering predator faeces, each calling individual produced only few calls (range 1–3; R. Furrer, personal observation) and call duration by the whole group lasted from less than 1 min to up to 5 min whereas when encountering African rock pythons or rival banded mongooses individuals typically produced many calls (up to 20 or even more calls depending on the severity of the encounter; R. Furrer, personal observation) and group calling could last for 15 min or more.

The acoustic variation of banded mongoose recruitment calls was not stimulus specific and therefore the calls are not functionally referential. This suggests that, in the banded mongoose, information on risk is more important than specific information regarding the external stimulus type, as the general response in the different contexts did not differ, and only the urgency level appeared relevant. The acoustic structure of recruitment calls may express the caller's emotional state at the moment of calling, with noisier call variants produced during high arousal situations (Morton 1977; Marler et al. 1992). Receivers seemed to extract specific information on the level of urgency from the acoustic structure of calls, and adjusted their speed of response accordingly. A previous study on banded mongooses indicated that receivers do not extract information on urgency levels from heterospecific alarm calls of plover species (Müller & Manser 2008). However, this may be explained by perception differences of urgency levels between mongooses and plovers or indeed by the costs of wrong responses to heterospecific alarms (Müller & Manser 2008). Although banded mongoose alarm calls given to aerial and terrestrial predators (causing receivers to become vigilant or to escape to shelter) are acoustically distinct from the recruitment calls (R. Furrer, personal observations), it is currently unknown whether they are functionally referential and refer to specific predator types. It may therefore be that alarm calls in this species are, in general, based on risk or urgency level rather than denoting an external stimulus, in a functionally referential way. It would be interesting to see whether species with confirmed predator-specific aerial and terrestrial calls, such as meerkats, have also evolved stimulus-specific recruitment calls.

Receivers responded to all noncontrol playback stimuli by approaching the speaker, confirming that these calls function to recruit other group members. However, since later arriving mongooses continued to call while inspecting the predator faeces and group members called for prolonged periods while mobbing a snake or facing a rival banded mongoose group, additional adaptive functions should be considered (see also Welbergen & Davies 2008). In banded mongooses it remains to be tested whether, besides physical harassment during the mobbing (Curio et al. 1978; Owings & Owings 1979; Dugatkin & Godin 1992; Graw & Manser 2007), continued calling itself could deter encountered predators and rivals. When sighting rival mongooses, individuals started calling, which recruited other group members. The bunched group continued calling, similar to territorial vocal rallying in birds (Radford 2003; Radford & Du Plessis 2004). However, in banded mongooses calling can go beyond a form of group display, continuing during one-to-one fights and chases (Cant et al. 2002). Therefore, it may not only deter bunched rival mongooses but also discourage opponents during agonistic encounters on the individual level. Furthermore, the continued calling when encountering secondary predator cues and snakes suggests these calls may also play a role in group decision making to coordinate the response of group members. Whether these calls function imperatively (as an 'order' to approach given by the caller; Evans 1997) or are just expressions of the caller's arousal, still has to be tested. For example, this could be done in the context where a solitary mongoose encounters a secondary predator cue or predator, while separated from its group members and therefore unable to recruit them. One would predict that if calls functioned imperatively the solitary individual would not call, whereas if calls were just an expression of the caller's arousal solitary mongooses would still be likely to call.

In conclusion, the acoustic structure of recruitment calls was not stimulus specific, but appeared to vary according to the risk of the situation. This is equivalent to mobbing calls described for birds, where calls towards different stimuli vary acoustically, in a graded manner according to size or distance of the predator (Templeton et al. 2005; Welbergen & Davies 2008). Despite different stimulus types eliciting the calls and different purposes for recruitment, a graded call system in banded mongooses seems sufficient for receivers to respond appropriately. Playbacks showed that these calls function to recruit other group members. However, since calling continues even after most or all group members are gathered, calls may also function to deter or chase off predators or rival conspecifics, or play a role in group decision making to coordinate the response of all individuals.

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