Wild dwarf mongooses produce general alert and predator-specific alarm calls

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Short title: Dwarf mongoose alarm calls

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Dwarf mongooses, the smallest species in the mongoose family, produce a number of diverse alarm-call types, with several being general and two indicating predator type. Furthermore, the specificity of their alarm-call types appears higher for aerial than terrestrial threats and, unlike other mongoose species, they seem to use the same alarm-call type for both physically present terrestrial predators and secondary cues of their presence.

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ABSTRACT

Many species produce alarm calls in response to predator threats. Whilst these can be general alert calls, some are urgency-based, indicating perceived threat level, some are predator-specific, indicating the predator type present, and some encode information about both urgency level and predator type. Predator-specific calls given to a narrow range of stimuli and which elicit a specific, adaptive, response from the receiver are termed functionally referential. Differing escape strategies, habitat structural complexity and sociality may favor the evolution of functionally referential calls. A study of one captive group of dwarf mongooses (*Helogale parvula*) suggested their alarm calls could transmit information about species, distance and elevation of predators. Using recordings of natural predator encounters, predator presentations and audio playbacks, we investigated the alarm-call system in seven wild dwarf mongoose groups. We recorded 11 different alarm-call types given to nine stimulus categories. Of the five commonly emitted alarm-call types, three appeared to be non-specific and two predator-specific, given to aerial and terrestrial predators respectively. The remaining six call types were rarely produced. Furthermore, aerial alarms were given to a narrower range of stimuli than their terrestrial alarm calls, which were given to both visible terrestrial predators and secondary cues of predators. Unlike other mongoose species, dwarf mongoose seem to use the same alarm-call type for both physically present terrestrial predators and secondary cues of their presence. We argue that detailed knowledge of species' alarm-call systems under natural conditions can shed light on the evolutionary emergence of different types of alarm calls.

Key-words: Alarm calls – Functional reference – *Herpestidae* – Predator-specific – Sociality – Vocal communication

INTRODUCTION

Many animal species produce vocalizations when detecting predators (Zuberbühler 2006). A key function of such alarm calls is to alert group members to a threat and therefore increase their chances of survival (Marler 1967; Sherman 1977; Stankowich 2010). Whilst some alarm calls function as general alert calls (Zuberbühler et al. 1997), others have been shown to be urgency-based and to refer to the level of danger a predator represents, as seen in species such as alpine marmots (*Marmota marmota*; Blumstein and Arnold 1995), yellow-bellied marmots (*Marmota flaviventris*: Blumstein and Armitage 1997a), white-browed scrubwrens (*Sericornis frontalis*: Leavesley and Magrath 2005) and banded mongooses (*Mungos mungo*: Furrer & Manser, 2009a). Alarm calls can also be highly predator-specific, given only to a certain category of predator. If predator-specific alarm calls elicit qualitatively distinct behaviors from the receiver, that mirror responses shown when encountering different predator types, they are termed functionally referential (Macedonia and Evans 1993). The most often documented functionally referential alarm calls are those given to aerial and terrestrial predators, as seen in various primate species (vervet monkeys, *Chlorocebus aethiops*: Struhsaker 1967; Seyfarth et al. 1980; ringtailed lemurs, *Lemur catta*: Macedonia 1990; Diana monkeys, *Cercopithecus diana*: Zuberbühler et al. 1997; Campbell monkeys, *Cercopithecus campbelli*: Zuberbühler 2002; black-fronted titi monkeys, *Callicebus nigrifrons*: Cäsar, Byrne, Hoppitt et al. 2012). Functionally referential alarm calls can also potentially encode specific features of a predator, including its behavior (Siberian jays, *Perisoreus infaustus*: Griesser 2008; meerkats, *Suricata suricatta*: Manser et al. 2014), color (Gunnison's prairie dog, *Cynomys gunnisoni*: Slobodchikoff et al. 2009) and size (Gunnison's prairie dog: Ackers and Slobodchikoff 1999; black-capped chickadee, *Poecile atricapilla*: Templeton et al. 2005). Finally, a single alarm-call type can refer to both the level of urgency and predator type, as shown in meerkats (Manser 2001; Manser et al. 2002).

The need for qualitatively different, incompatible escape strategies for different predator classes has been suggested as one important factor promoting the production of predator-specific alarm-call types (Macedonia 1990). Macedonia and Evans (1993) proposed that habitat, and in particular its structural complexity, may also play a role in favoring such distinct responses and therefore functionally referential alarm calls. For example, ringtailed lemurs, that move both horizontally along the ground and vertically up and down trees, produce distinct functionally referential alarm calls to aerial and mammalian predators, whereas black and white ruffed lemurs (*Varecia variegata*), that remain primarily in the tree canopy, emit less specific alarm calls (Macedonia and Evans 1993). However, species living in less complex, more homogenous habitats, such as meerkats and Gunnison’s prairie dogs, also produce functionally referential alarm calls (Manser 2001; Manser et al. 2001; Slobodchikoff et al. 2009). On the other hand, Cape ground squirrels (*Xerus inauris*), sympatric with meerkats, produce urgency related alarm calls. This suggests that habitat complexity alone is an insufficient explanation for the evolution of different alarm-call types (Furrer and Manser 2009b).

Sociality is an additional factor that has been suggested to promote functionally referential alarm-call systems. Blumstein and Armitage (1997b) have highlighted that more socially complex groups (i.e. those with more complex, kin-structured social systems) could give rise to larger alarm-call repertoires and consequently to situationally specific (i.e. both urgency-based and functionally referential) signaling. Whilst it is suggested that social and vocal complexity are likely associated (Freeberg et al. 2012), evidence from the marmot studies that social complexity influences the production of functionally referential alarm calls (Blumstein 2007) is lacking. Yet the comparison between meerkats and Cape ground squirrels suggests that the need to coordinate group movement, representing a social constraint, may be an additional factor implicated in triggering the evolution of predator-specific alarm calls (Furrer and Manser 2009b).

Ultimately, comparative data are necessary if we are to shed light on the factors promoting the emergence of functionally referential alarm-call systems. The *Herpestidae* family represents an appropriate taxon for such research. These species vary in social systems, ranging from solitary to group-living species with varying social structures, as well as occupying various types of habitats (Manser et al. 2014). As some of these species have overlapping distributions but differing social structures, whilst other species with a similar social structure live in different habitats (Manser et al. 2014), the roles of habitat and social factors can begin to be disentangled. However, while the alarm-call system of one mongoose species in particular, the meerkat, has been well documented, less is known about the alarm-call systems of other mongoose species.

Dwarf mongooses (*Helogale parvula*) are social mongooses with a despotic social structure (Rasa 1987; Keane et al. 1994) comparable to that of meerkats (Clutton-Brock et al. 2001). They live in groups of up to 30 individuals (Rasa 1977) with reproduction generally limited to the dominant pair; related and unrelated subordinate group members cooperatively help to rear the young (Keane et al. 1994). Dwarf mongooses live in woodlands or wooded savannas (Sharpe et al. 2015) where visibility is often reduced, making predator detection more difficult, whilst their small size makes them vulnerable to a wide range of predators, both aerial and terrestrial (Rasa 1986; Kern and Radford 2014). A past study on dwarf mongooses suggests that they may have an even more sophisticated alarm-call system than meerkats, with alarm calls encoding predator species and urgency level, specifically distance and elevation (Beynon and Rasa 1989). However, this study was carried out on a single group of captive mongooses and the information receivers extract from these calls remains to be experimentally tested. We followed up these preliminary observations and investigated how dwarf mongooses both use and perceive warning signals, with the aim of providing a detailed description of their alarm-call system in the wild and providing further data for cross-species comparisons.

We first documented the different alarm-call types produced by dwarf mongooses in the wild. We then determined the usage of the most commonly produced calls according to their context of production. In particular, we predicted that callers would produce structurally distinct alarm-call types to aerial and terrestrial predators. We further examined responses to the call types that data on natural occurring predator encounters and experimental predator presentations identified as most likely to be aerial and terrestrial alarm calls and substantiated them using playback experiments. In line with behavioral responses observed in meerkats (Manser et al. 2001), we expected receivers to run for shelter and look at the sky in response to an aerial alarm, and to gather together and scan the area horizontally when hearing a terrestrial alarm call.

METHODS

Study Site and Species

The study was carried out on Sorabi Rock Lodge Reserve, a 4 km^2 private game reserve in Limpopo Province, South Africa (24°11'S, 30°46'E). For more detailed information about this study site, see Kern and Radford (2013). All data were collected between November 2014 and June 2015 and in January–February 2016 from adult (>1 year of age) wild dwarf mongooses belonging to seven different groups (mean group size: 11; range: 6–15). All mongooses were habituated to close observation on foot (<5 m) and individually identifiable by distinctive hair-dye marks (Wella UK Ltd., UK) or scars.

Alarm-Call Production

Dwarf mongoose groups were followed for approximately 3 h in the morning after they left the sleeping burrow and another 2–3 h in the evening until they returned to a sleeping burrow for the night. All vocalizations were recorded *ad libitum* (Altmann 1974). They were saved onto a PNY SD card (PNY, Parssipany, NJ, U.S.A.) using a Marantz PMD661 MKII solid-state recorder (D&M Holding, Inc., Kanagawa, Japan; sampling rate 44.1; 24 bit accuracy) attached to a Sennheiser ME66/K6 directional microphone (Sennheiser Electronic Corp., Old Lyme, CT, U.S.A.) with a windshield (Rycote Microphone Windshields, Stroud, Gloucestershire, U.K.). Whenever an alarm call was produced, it was marked on the audio file. Where possible, the external stimulus that elicited the alarm call, the mongooses' response, and the caller's identity were spoken into a microphone (TG V30d s, Beyerdynamic, Heilbronn, Germany) linked to a second channel.

To obtain additional recordings of alarms calls, especially those given in response to terrestrial predators for which, unlike aerial predators, we observed no natural encounters, simulated predator presentations were conducted. Given that preliminary experiments showed dwarf mongooses did not respond to taxidermy models of animals (unpub. data), we used a live domestic dog (*Canis lupus familiaris*) to simulate a terrestrial predator. The dog was walked slowly on a lead towards the mongoose group, stopped between 15 and 30 m away from the group once the mongooses reacted, and then walked slowly away until it was out of sight again around 50 m from the group. As terrain constraints prevented the use of kites, we used a large helium balloon (88 x 22 x 10 cm) in the shape of the number 6 or 8 to simulate aerial predator encounters. The experimenter holding the balloon remained hidden 20–40 m from the group behind bushes or small trees, and released the balloon until it was visible to the mongooses above the vegetation. We recorded all alarm calls produced by the dwarf mongooses in response to the experimental presentations (using the equipment described above) and filmed their responses on a Canon Legria HF R506 handheld camcorder (Cannon Inc., Tokyo, Japan). We considered data collected during observational and experimental studies separately.

Acoustic Analysis

Spectrograms of the alarm calls were generated using Praat version 5.3.85 (www.praat.org). We first divided the alarm calls into different classes by ear and visual inspection of the spectrograms, as in Candiotti et al. (2012). We excluded recruitment calls, given when the mongooses encounter a snake, as they are described elsewhere (Kern and Radford 2016); these recruitment calls provoke a mobbing response. We labelled each alarm-call type with a number reflecting the order in which the call types were identified. Due to the rare occurrence of some of the dwarf mongoose alarm calls, we focused our acoustic analyses on the five most commonly produced types (see Results). We selected calls with a good signal-to-noise ratio and, using the bioacoustics software Luscinia (Lachlan 2007), we extracted a number of temporal and spectral parameters: call length (ms); overall and mean peak frequency (Hz); maximum and minimum peak frequency (Hz); mean, maximum and minimum fundamental frequency (Hz); mean change in peak and fundamental frequency expressed on an arctan scale (0 means decreasing infinitely quickly, 1 increasing infinitely quickly and 0.5 indicates no change); mean Wiener entropy, mean frequency bandwidth (Hz); number of elements; and within-syllable gap (ms) (for definitions see table 1). Three exemplars per group of each of the five main alarm-call types, recorded from individuals belonging to four different groups (total= 60 calls), were used for analysis.

Alarm-Call Responses

When assessing the alarm-call responses during naturally occurring predator encounters, we only considered the reaction to the first call in a bout, with a bout being defined as a series of calls separated by <10 s from each other. The reaction to the first call in a bout was nearly always the strongest response and, furthermore, any reaction to the subsequent calls seemed to be influenced by the reaction to the first call (pers. obs.). Mongooses' responses were classed as either no reaction (when there was no visible change in behavior), vigilant (when the mongoose paused foraging and scanned the area horizontally), moved (when the mongoose took a few steps forwards but stopped short of cover), or ran for cover (when the mongoose moved quickly to the nearest bush or rocks). We excluded from analysis instances in which mongooses were already under cover, as in such cases individuals were constrained in expressing all of the response behaviors listed above.

To test whether dwarf mongooses responded differently to alarm calls given to aerial and terrestrial predators in particular (see Results), we carried out playback experiments using the call types that most frequently accompanied aerial and terrestrial encounters respectively (alarm-call types 1 and 4, see figure 1). To generate the playback stimuli, we only used alarm calls with a good signal-to-noise ratio, resulting in 15 exemplars of alarm-call type 1, and 12 of alarm-call type 4, obtained from adult individuals belonging to four and five different groups respectively. We only used alarm calls recorded from a different group to that of the subject to ensure that the latter did not hear its own calls during the experiment. The amplitude of the playback was set by ear to be equivalent to that of a naturally produced alarm call of around 55 dB sound pressure level A at 2 m (Kern et al. 2017).

Each alarm-call type was played back to a subset of 17 focal adult mongooses, belonging to seven different groups, drawn from a total of 23 individuals. For each stimulus, one individual was opportunistically tested twice, once in each field season (playbacks separated by 9 months), giving a total of 18 playbacks for each alarm-call type. All alarm-call exemplars were first used once, with several randomly selected exemplars used a second time for the remaining trials. Alarm calls were played back from a height of around 1 m, simulating an alarm call from a mongoose acting as a sentinel; an individual adopting a raised position to scan for danger (Kern and Radford 2013). Playbacks were started when the test subject was foraging in the open and its response was filmed with a handheld camcorder (as above). In line with previous work, we scored the response strength of the focal mongoose reaction as: 1=no reaction; 2=vigilant; 3=moved; or 4=ran for cover (Blumstein and Armitage 1997a; Fischer and Hammerschmidt 2001; Suzuki 2015). We also measured the focal individual's latency to relax following its initial reaction; that is, time to resume foraging or start grooming, in seconds. Additionally, we noted other behaviors potentially associated with predator encounters that occurred within 1 min of the playback. These included looking at the sky, which may allow the mongooses to detect aerial threats, and becoming a sentinel, which may improve the detection of any kind of predator. Playbacks were only performed if no alarm calls (conspecific or heterospecific) had been heard for at least 10 min, and no playbacks were carried out if the mongooses were showing signs of alarm or arousal from previous events such as predator encounters or intergroup interactions. To minimize the likelihood of habituation, playbacks within a given group were separated by at least 1 h. We carried out a maximum of three playbacks a day to a given group, over one or two sessions (morning and afternoon), but on one occasion we conducted four playbacks in a day over two sessions. This was well below the average of 18 alarm calls (or eight bouts) recorded per hour during observations (unpub. data).

Statistical Analysis

a) Alarm-call production

To determine whether the proportion of alarm-call types differed significantly in response to the different experimental predator presentations, we performed Generalized Linear Mixed Models (GLMMs) with a binomial family and a logit link function. We conducted a GLMM for each of the two main alarm-call types produced in response to aerial and terrestrial predators respectively (alarm-call types 1 and 4; see results). Predator type was fitted as fixed effect and group and date were fitted as random effects. We calculated p-values using likelihood ratio tests that compare full models, including all the explanatory variables, to reduced models that include the same explanatory variables with the exception of the variable of interest.

b) Acoustic analysis

We calculated the variance inflation factors (VIF) of the measured acoustic parameters to determine which were collinear. We removed the parameter with the highest VIF and repeated the procedure until all the remaining acoustic parameters had a VIF inferior to 6 and hence collinearity should be minimized (Belsley et al. 2005). We then entered the remaining parameters into a discriminant function analysis (DFA). However, as we had repeated measures, with multiple recordings from the same group, which can lead to inflated significance in conventional DFAs (Mundry and Sommer 2007), we conducted a crossed permutated discriminant function analysis (pDFA) using a function provided by R. Mundry (Cäsar, Byrne, Young et al. 2012; Clay et al. 2015). Permutated DFAs allow for repeated measures linked to multiple recordings from the same individual or group and avoid inflation or over-estimation of p-values. All statistics were carried out using R version 3.2.1 (R Core Team 2015) with the packages usdm (Naimi 2013) and MASS (Venables and Ripley 2002).

c) Alarm-call responses

To investigate the strength of response in relation to stimuli type, we carried out Cumulative Link Mixed Models (CLMMs) using the ordinal package in R (Christensen 2015). For latencies to relax, we performed Linear Mixed Models (LMMs), using R package lme4 (Bates et al. 2015). Diagnostic tests indicated there were no violations of the assumptions of linearity, homoscedasticity and normality of the residuals. Finally, given the binomial nature of the looking behavior (looked up or not) and sentinel behavior (sentinel or not) we used GLMMs with a binomial family and a logit link function to test whether these variables differed across playback types. As some individual mongooses were used as subjects more than once and multiple individuals from the same group were tested, we nested individual within group and fitted this as random effect whilst the stimulus type (alarm-call type 1 or 4) was fitted as a fixed effect. We used likelihood ratio tests to calculate p-values.

Ethical Note

Our work was carried out under permission from the Limpopo Department of Economic Development, Environment and Tourism (permit number: 001-CPM403-00013) and the Ethical Committee of Pretoria University, South Africa (permit number: EC049-16).

RESULTS

Dwarf Mongoose Alarm-Call Repertoire

We obtained over 150 h (range: 12–43 h per group) of recordings with a total of 2684 alarm calls (1214 bouts) from seven mongoose groups, comprising a total of 76 adult individuals (36 females; 40 male) over the two field seasons. From these recordings, we collected 900 alarm calls (402 bouts), produced by adult dwarf mongooses, that were given to an identifiable external stimulus other than the observer. Nineteen of the callers (nine female, 10 male), producing 142 alarm calls (47 bouts), could be individually identified with identification of the remaining callers being limited to age group. We also extracted 588 alarm calls (349 bouts) that were given to the observer by adult individuals, of which 29 mongooses (14 female, 15 male) producing 148 calls (96 bouts) could be identified. The remaining 1196 alarm calls (463 bouts) were given to unidentified stimuli and so are not discussed further here. Visual inspection of the spectrograms suggested these alarm calls could be divided into 11 different types, some of which seemed to resemble combinations of two other alarm-call types (figure 1). Five of the alarm-call types were more commonly produced (recorded 97 times or more), with the remaining six alarm-call types each recorded 41 times or less over the study period. Statistical analysis confirmed that the five most-produced alarm-call types could also be distinguished by their acoustic parameters alone, with significantly more calls being correctly cross-classified in the respective groups than expected by chance (pDFA, percentage correctly classified = 89%, p=0.001) (figure 2).

Alarm-Call Production

During natural observations, dwarf mongooses gave alarm calls to various external stimuli that included physically present animals of both predatory and non-predatory species, and scents which can be secondary cues of predators or competing mongoose groups. These stimuli could be divided into nine different categories (for details see table 2). The same alarm-call type could be given to several types of stimuli (figure 3), however there were differences in the production of alarm-call types in response to the diverse stimuli. Seventy-three percent of the 374 "type 1" alarm calls recorded were given to aerial stimuli. "Type 2" alarm calls were mostly produced in response to the observer (69% of 169 calls recorded). Of the 304 "type 3" alarm calls recorded, 48% were produced in response to the observer and 41% in response to aerial stimuli. Fifty-two percent of the 454 "type 4" alarm calls recorded were given to scents and 44% to the observer. Of the 97 "type 5" alarm calls recorded, 32% were given to aerial stimuli, 21% to the observer and 19% in response to heterospecific alarm calls.

The alarm-call types produced in response to predator presentations differed according to stimulus type. Mongooses produced a higher proportion of type 4 alarm calls in response to dog than helium-balloon presentations (GLMM, $\chi^2=27$, N=19, df=1, $p<0.001$). Conversely, a higher proportion of type 1 alarm calls was emitted in response to helium-balloon than dog presentations (GLMM, $\chi^2=21$, N=19, df=1, $p<0.001$). Although the mongooses produced eight different types of alarm calls when presented with the dog, 69% of the 280 calls recorded were type 4 alarm calls and 17% of them were type 3 alarm calls. The other alarm-call types were each recorded 13 times or less. The dwarf mongooses produced seven different alarm-call types in response to the helium balloon presentation of which 45% of the 478 calls recorded were type 3, 41% type 1 and 10% type 2 alarm calls. All the other alarm-call types were produced seven times or less (table 3).

Responses to Alarm Calls Emitted During Naturally Occurring Predator Encounters

There appeared to be a predictable relation between each alarm-call type and the responses it elicited during naturally occurring predator encounters. For the 51 cases for which a response was reported in reaction to a naturally produced type 1 alarm call, mongooses ran for cover in 47% of the events or became vigilant in 39% of the cases. The rest of the time, the mongooses showed no reaction or moved slightly without reaching cover. In 77% of the 13 occurrences of hearing a type 2 alarm call, the mongooses ran for cover. When hearing a type 3 alarm, subjects became vigilant in 94% of the 17 events. Out of 180 occurrences, mongooses became vigilant 93% of the time after hearing a type 4 alarm call. Finally, they either became vigilant for 65%, ran for cover for 20% or moved for 10% of the 20 cases in which they heard a type 5 alarm call (table 4).

Responses to Call Playbacks

In response to playback experiments testing whether the two types of alarm calls that most frequently accompanied aerial and terrestrial encounters elicited distinct responses, the subjects showed a difference in their reaction. Specifically, subjects reacted differently and more strongly in response to a type 1 than a type 4 alarm call (CLMM: χ^2=7.01, N=36, df=1, p=0.008; figure 4). In response to a type 1 alarm call, most mongooses ran for cover (12/18), whereas in response to a type 4 alarm-call, most of them became vigilant, looking out horizontally (12/18). Mongooses only looked at the sky in response to a type 1 alarm call and never in response to a type 4 alarm call (respectively 5/18 and 0/18 times; GLMM: χ^2=7.39, N=36, df=1, p=0.007). However, they showed no significant difference in latency to relax (LMM: χ^2=1.05, N=36, df=1, p=0.31) or likelihood to become a sentinel (GLMM: χ^2=0.21, N=36, df=1, p=0.65) in response to alarm-call types 1 and 4.

DISCUSSION

Dwarf Mongoose Alarm Calls

Overall, we found that adult dwarf mongooses produced 11 distinct types of alarm calls, of which only five were commonly produced. The alarm calls we recorded were given to nine different types of stimuli that included both potential predators, such as raptors and dogs, and, contrary to previous studies (Rasa 1983), non-predators including antelope, small terrestrial animals and non-predatory birds such as vultures and low-flying hornbills, especially if they appeared suddenly. This difference with previous research is most likely due to differing observation methods as our recordings were carried out from within the group rather than at a distance, increasing our chances of detecting the majority of alarm calls.

Non Predator-Specific Alarm Calls

Based on the responses they elicited and the multiple stimuli the different alarm-call types were given to, types 2, 3 and 5 did not appear to be predator-specific. Type 2 alarm calls seemed to provoke a stronger response than any other alarm-call type, resulting in subjects running for cover 77% of the time, indicating that these alarm calls may be high urgency calls, though this remains to be tested. Alarm-call types 3 and 5 were produced non-specifically in response to a variety of stimuli, suggesting they may be general alarm calls. The predominant natural response to both of these alarm-call types, to become vigilant, was not as strong as to a type 2 alarm call, implying that these calls may be produced in lower urgency situations.

Predator-Specific Alarm Calls

Alarm-call types 1 and 4 appeared to be associated with specific types of threat. The majority of these calls recorded during natural encounters with predators were given respectively to aerial stimuli and to scents. Dwarf mongooses can react to scents or secondary cues left by predators (Morris-Drake et al. 2016) or conspecifics from another group (Christensen et al. 2016), both of which can represent a threat. Hence, we considered scents to be potential indirect secondary cues of terrestrial threats. Additionally, predator presentations showed that alarm-call type 1 is one of the principal calls given to helium-balloons (in the air) and alarm-call type 4 is the primary call given to terrestrial predators. Furthermore, test subjects reacted differently to the playbacks of these two call types. In line with other studies (Manser et al. 2002; Cäsar, Byrne, Hoppitt, et al. 2012), this difference in reaction allows us to exclude the possibility that subjects are simply reacting to any broadcast noise as, in that case, we would not expect to see differentiated behaviors when responding to different sounds. Subjects showed reactions consistent with avoiding an imminent attack from above when hearing call type 1: running for cover and looking at the sky. Subjects did not react as strongly to type 4 alarm calls, primarily becoming vigilant, looking out horizontally. Terrestrial predators can attack from any direction on the ground, therefore scanning the environment to detect the location of the danger before reacting could potentially improve the receiver's chances of survival.

Since alarm-call types 1 and 4 are given to specific predator classes and they elicit adaptive responses from receivers even in the absence of external stimuli, we suggest they fit the definition of functionally referential alarm calls (Macedonia and Evans 1993). Previous work has demonstrated that predator-specific alarm calls can also carry information about perceived urgency (Manser et al. 2001, 2002). Further research taking into account, for example, predator distance, would allow us to determine if this is also the case for dwarf mongoose aerial and terrestrial alarm calls.

Dwarf mongoose aerial alarm calls seem to show more production specificity than their terrestrial alarm calls. Aerial alarm calls were only given to visible aerial threats, whereas terrestrial alarm calls were given to both visible terrestrial predators and secondary cues, namely scents. A similar pattern is seen in several primate species, with the terrestrial alarm call being less specific than the aerial alarm, to the point where it is not considered referential (red-fronted lemurs, *Eulemur fulvus rufus* and Verreaux sifakas, *Propithecus verreauxi*: Fichtel and Kappeler 2002; tufted capuchins, *Cebus apella nigritus*: Wheeler 2010).

Production specificity of a functionally referential alarm call may be linked to the response specificity of the receiver, with the categories to which alarm calls are given being defined by the categories to which receivers show distinct responses. For example, dwarf mongooses show the same response, specifically vigilance, whether an alarm call is elicited by a potential terrestrial predator (e.g. dog) or by a secondary cue, and thereby may not necessitate differentiated alarm calls. Alternatively, production specificity of functionally referential calls may be a function of urgency to respond to a certain category of predator. Producing an alarm to a narrower predator category could allow the receiver to react appropriately and rapidly to the situation, which may be crucial to its survival if this predator presents an immediate, high threat. However, if an instant response is not critical to survival, a less specific call may be sufficient as the receiver would have time to integrate contextual cues before responding appropriately (Manser 2009; Wheeler and Fischer 2012; Price et al. 2015).

Dwarf mongooses predominantly produced terrestrial (type 4) alarm calls in response to human observers, suggesting that they principally classified observers as terrestrial. However, subjects also occasionally produced aerial (type 1) alarm calls in response to researchers, implying that this stimulus could sometimes be perceived as aerial. Such classification could be the result of the close proximity of human observers to the group and hence presenting a greater saliency in the vertical rather than the horizontal plane. Additionally, a large number of type 3 alarm calls were produced in response to the observer. As type 3 appears to be a general alarm call, as opposed to a predator-specific alarm, this further points towards the observer as a potentially ambiguous stimulus.

Comparison with other Mongoose Species

The dwarf mongoose alarm-call system is similar in size and content to the repertoire of meerkats (12 alarm-call types, including both functionally referential and urgency-related alarm calls; Manser 2001), despite differences in habitat between the two species. However, the dwarf mongoose's alarm-call repertoire is larger than those documented in other closely related mongoose species exposed to similar predators, including social species (banded mongoose; four alarm-call types) and more solitary species (yellow mongoose, *Cynictis penicillata*: four alarm-call types; slender mongoose, *Galerella sanguinea*: two alarm-call types; Manser et al. 2014). The social complexity hypothesis posits that species that form larger social groups will also possess a larger vocal repertoire (Freeberg et al. 2012), which may explain the discrepancy in repertoire size between dwarf mongooses and more solitary related species. Furthermore, in some taxa, including mongooses, repertoire size does not co-vary with group size, but instead with other social factors such as social structure (Manser et al. 2014), potentially explaining the difference in repertoire size between dwarf and banded mongooses. Social structure may also explain variation in alarm-call repertoire content, as, to our knowledge, functionally referential alarm calls are only produced by social mongoose species. However, as not all social mongoose species produce functionally referential alarm calls, it would seem that a complex social structure may be essential but not sufficient for the production of such alarm calls. Other factors such as differing escape strategies or the need to coordinate group movement during escape may be necessary, in addition to sociality, in order for functionally referential alarm calls to emerge.

Conclusion

Wild dwarf mongooses have a large repertoire of alarm calls, comparable in size and function to that of the closely related meerkats. Dwarf mongooses produce both functionally referential and less specific alarm calls. Unlike other mongoose species, they seem to use the same alarm-call type for both physically present terrestrial predators and secondary cues of their presence. Further work is needed to investigate the function of the rarer alarm calls and to determine if other forms of information, such as distance and elevation of the predator, are also transmitted in wild dwarf mongoose alarm calls. Finally, additional comparative research may help identify the factors responsible for differences in alarm calling behavior across closely related species.

FUNDING

This work was supported by a collaborative University of Zurich Research Priority Program grant (University Research Priority Programs: Evolution in Action), grant number URPP U-702-06. ANR was funded by the University of Bristol, SWT by the University of Zurich and the University of Warwick, and MM by the University of Zurich.

ACKNOWLEDGEMENTS

We would like to thank H. Yeates for allowing us to work on Sorabi Rock Lodge, and C. Esterhuizen for logistical support in the field. We are indebted to J. Kern for creating and running the Dwarf Mongoose Project, as well as for all her help. We also thank L. Sharpe for lending us Magic, the dog. We are grateful to the research assistants who helped with data collection and habituation of the groups: E. Ackerley, A. Bracken, F. Carr, C. Christensen, B. Davison, S. Edwards, H. McElliott, A. Morris-Drake, K. Rogerson. We also thank B. Wong, R. Seyfarth and one anonymous reviewer for comments and input on previous versions of the manuscript.

DATA ACCESSIBILTY

Analyses reported in this article can be reproduced using the data provided by Collier et al. (2017).

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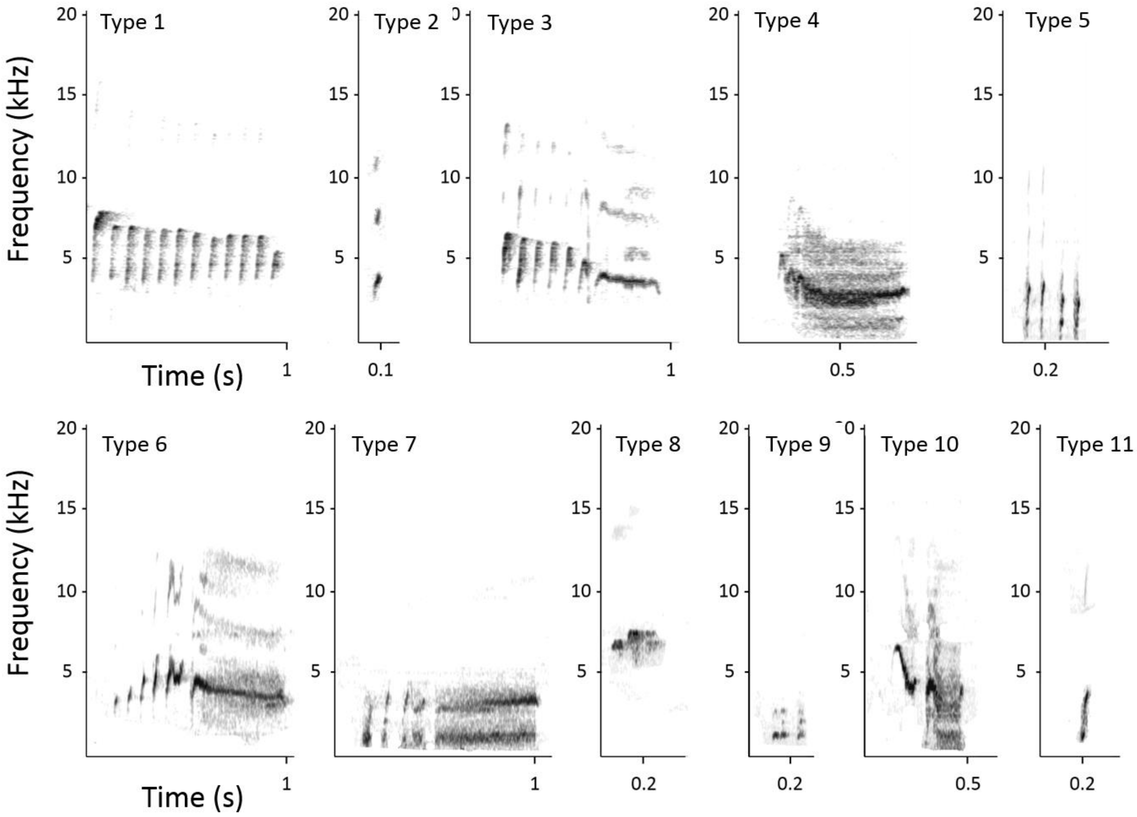

Figure 1: Spectrograms of the alarm calls present in the dwarf mongoose repertoire.

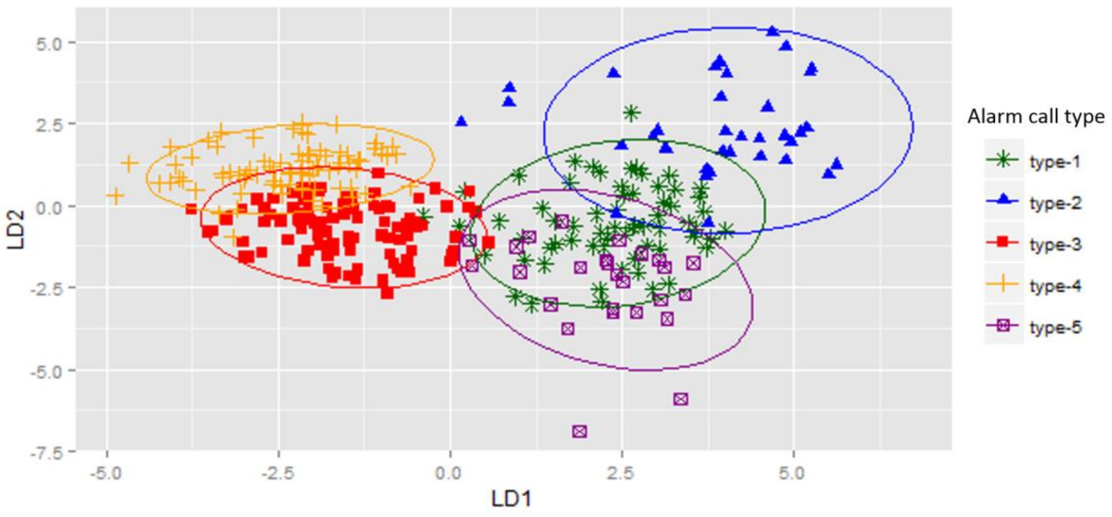

Figure 2: Output of the discriminant function analysis of alarm-call acoustic parameters showing the distribution of discriminant scores along the two principal discriminant functions. LD: linear discriminant function.

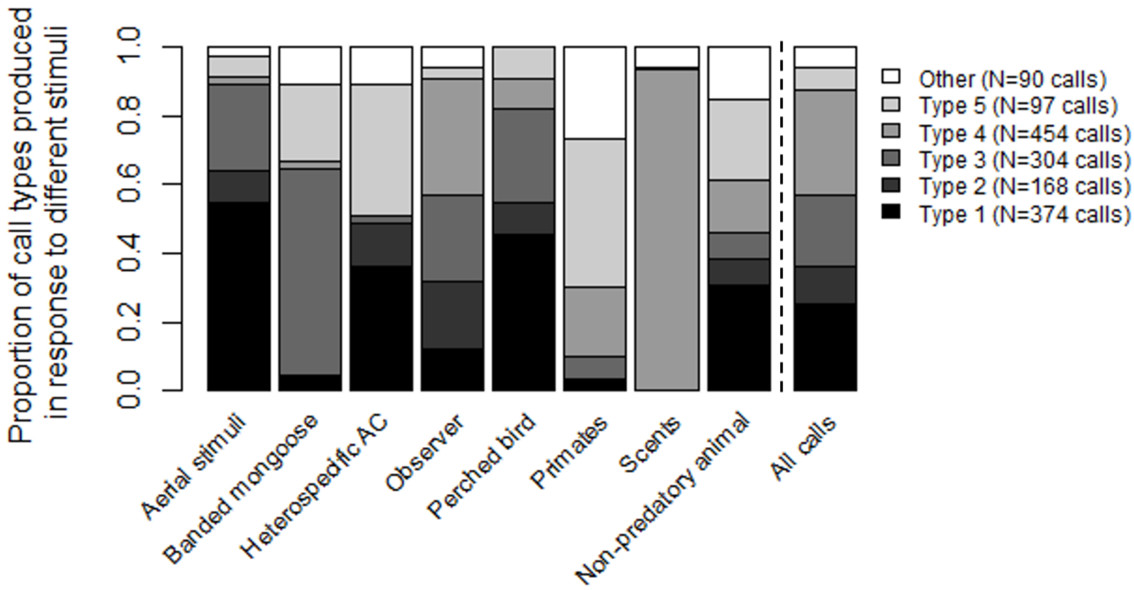

Figure 3: Proportion of alarm-call types produced by dwarf mongooses in response to various stimuli. AC: alarm call. ‘Other’ includes all the rarely produced alarm-call types 06 to 11.

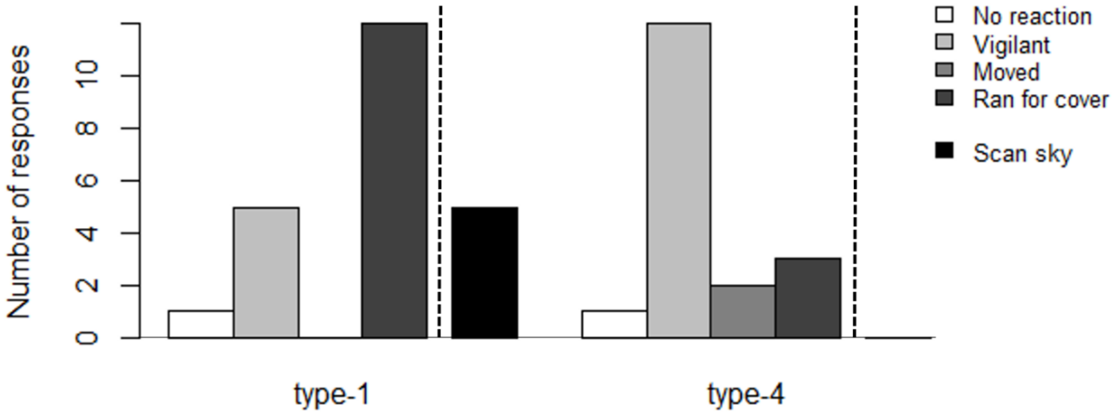

Figure 4: Dwarf mongooses' main mutually exclusive responses to the playbacks of type 1 and type 4 alarm calls and, to the right of the dashed line, an additional, non mutually-exclusive, behavior, scanning the sky. $N_{(type\ 1)}=18$, $N_{(type\ 4)}=18$.

Table 1: Description of the acoustic parameters measured for the alarm calls. The parameters in bold were entered into the permutated discriminant function analysis (pDFA).

Acoustic parameter	Description
Call length	Time elapsed between the beginning and the end of the call.
Overall peak frequency	Peak frequency is the frequency of maximum amplitude within one spectrum of the spectrogram. Overall peak frequency is the frequency of maximum amplitude within the call.
Mean peak frequency	Mean of all peak frequencies within the call.
Maximum peak frequency	Peak frequency of highest peak frequency within the call.
Minimum peak frequency	Peak frequency of the lowest peak frequency within the call.
Mean fundamental frequency	Average fundamental frequency across the whole call. Fundamental frequency is the lowest frequency of a periodic waveform.
Maximum fundamental frequency	Fundamental frequency of highest frequency within the call.
Minimum fundamental frequency	Fundamental frequency of lowest frequency within the call.
Mean change in peak frequency	Mean change in peak frequency over time.
Mean change in fundamental frequency	Mean change in fundamental frequency over time.
Mean Wiener entropy	A measure of noisiness: Ratio of the geometric mean to the arithmetic mean of the power spectrum.
Mean frequency bandwidth	Frequency difference between the first and final maximum intensity in the signal.
Number of elements	Number of continuous traces on the spectrogram that compose the call.

Within-syllable gap	Total duration of silence between the elements of a call.

Table 2: Different categories of external stimuli to which dwarf mongooses produced alarm calls.

Category	**Description**
Aerial stimuli	Includes flying birds of prey, flying non-predatory birds and aircraft such as planes or helicopters
Banded mongoose	Banded mongoose
Dog	Dog during predator presentations
Heterospecific alarm	Alarm calls given by non-predatory birds, tree squirrels and impala
Non-predatory animal	Includes antelope such as impala or duiker, hares, and tree squirrels moving on the ground
Observer	Human researcher or any part of her equipment (e.g. microphone)
Perched bird	Predatory and non-predatory birds perched in a tree
Primates	Includes vervet monkeys and baboons, both on the ground or in trees
Scent	Defined as when mongooses alarm called at a specific section of a rock or a tree in the absence of other visible potential stimuli; in cases with clearer visibility, sniffing behavior was observed; possible dwarf mongoose or predator latrines

Table 3: The number of alarm calls of each type produced in response to the different types of predator presentations (dog N=12; balloon N=7). ‘Other’ includes all the rarely produced alarm-call types 06 to 11.

	type-01	type-02	type-03	type-04	type-05	Other	**Total**
dog	2	3	48	194	13	20	**280**
helium balloon	197	49	216	0	7	9	**478**

Table 4: Dwarf mongoose responses to the first alarm call in a bout in relation to its type when hearing a naturally produced alarm call. ‘Other’ includes all the rarely produced alarm-call types 06 to 11.

	type-01	type-02	type-03	type-04	type-05	Other	**Total**
moved	5	2	0	1	2	2	**12**
no reaction	2	0	0	10	1	0	**13**
ran to cover	24	10	1	0	4	4	**43**
sniffing	0	0	0	2	0	1	**3**
vigilant	20	1	16	167	13	6	**223**
Total	**51**	**13**	**17**	**180**	**20**	**13**	**294**