



## Calling for help: dwarf mongoose recruitment calls inform receivers about context and elicit disparate responses



Janneke Rubow, Michael I. Cherry\*, Lynda L. Sharpe

Department of Botany and Zoology, Stellenbosch University, Matieland, South Africa

### ARTICLE INFO

#### Article history:

Received 7 September 2016

Initial acceptance 18 October 2016

Final acceptance 31 January 2017

MS. number: 16-00790R

#### Keywords:

acoustic analysis

context-specific

dwarf mongoose

functionally referential

*Helogale parvula*

mobbing

recruitment calls

Social complexity and communicative complexity appear to have coevolved in terrestrial vertebrates. Understanding the information conveyed within the social signals of group-living taxa can illuminate the selection pressures impacting on a species and help to identify the factors promoting sociality. Within vocal communication, recruitment calls are of great importance to many social species, helping to maintain group cohesion and facilitating cooperative behaviour. Yet recruitment vocalizations have received limited scientific attention and it is not clear whether they convey context-specific information to receivers. We investigated the recruitment calls of wild dwarf mongooses, *Helogale parvula*, to ascertain whether they showed context-specific acoustic differences and whether receivers displayed context-specific responses to recruitment calls in the absence of external cues. We recorded recruitment calls (from four wild groups of dwarf mongooses) from two contexts: when an individual became separated from its group and when an individual encountered a snake. Acoustic analysis revealed that calls from the two contexts differed in acoustic structure and were distinguishable with a discriminant function analysis. Playbacks of calls from both contexts successfully recruited target mongooses, but snake calls elicited a stronger reaction (with mongooses vigilant for longer and approaching the speaker more closely). More importantly, target mongooses also displayed behaviours that were unique to call context, exhibiting head bobbing, creeping and searching of the vegetation during snake call playbacks but never during isolation call playbacks. We conclude that dwarf mongoose recruitment calls refer to context and are perceived as functionally referential by receivers.

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In birds and mammals, there appears to be a close tie between social complexity and communicative complexity (Freeberg, Dunbar, & Ord, 2012; Manser et al., 2014; Pollard & Blumstein, 2012). As societies become more complex, group members need to communicate more information to regulate their interactions and relationships. This promotes the evolution of sophisticated signalling systems which, in turn, allow the development of more complicated social relationships (Pollard & Blumstein, 2012). However, it appears that the development of different aspects of sociality are associated with the development of different aspects of a species' signalling repertoire. For example, in social sciurid rodents the demographic complexity of the social group predicts alarm call repertoire size while social group size predicts vocal individuality (Pollard & Blumstein, 2012). In herpestids, social group size seems to influence the number of discrete vocal signals

employed, but other aspects of ecology and social complexity also play a role (Manser et al., 2014).

Within the context of vocal communication, one very important social signal is the aggregation or recruitment call. This vocalization is used by social birds and mammals to reunite separated group members (Miller, Scarl, & Hauser, 2004) and/or gather individuals for cooperative defence (Furrer & Manser, 2009b) or group movement (Gruber & Zuberbühler, 2013). Separation or isolation recruitment calls are of considerable importance in fission–fusion societies where group members often disperse widely (e.g. spotted hyaenas, *Crocuta crocuta*: Gersick, Cheney, Schneider, Seyfarth, & Holekamp, 2015) or after accidental separation within more cohesive societies (e.g. white-faced capuchins, *Cebus capucinus*: Digweed, Fedigan, & Rendall, 2007). Calls to recruit group members for cooperative defence may be given in response to predators (Manser, 2001) or competitors, including intragroup (Slocombe & Zuberbühler, 2007), intergroup (Furrer & Manser, 2009b) or inter-specific rivals (Gersick et al., 2015). Despite the critical role that recruitment calls play in maintaining group integrity and

\* Correspondence: M. I. Cherry, Department of Botany and Zoology, Stellenbosch University, Private Bag XI, Matieland, 7602, South Africa.

E-mail address: [mic@sun.ac.za](mailto:mic@sun.ac.za) (M. I. Cherry).

facilitating cooperation in many social vertebrates, the acoustic structure of these vocalizations has received limited scientific attention.

The recruitment function of recruitment calls has been demonstrated experimentally in a number of studies (Evans & Evans, 1999; Furrer & Manser, 2009b; Gruber & Zuberbühler, 2013; Kennedy, Evans, & McDonald, 2009; Kern & Radford, 2016; Manser, Seyfarth, & Cheney, 2001; Radford & Ridley, 2006; Suzuki, 2012; Welbergen & Davies, 2008). Nevertheless, the level of responsiveness shown by individual group members often varies (Digweed et al., 2007; Gersick et al., 2015; Rubow, 2017), presumably because individuals differ in the costs and benefits they accrue from responding. For group members to accurately evaluate these potential risks and benefits, they need to obtain information about context. This may be derived directly from external cues (Wheeler & Fischer, 2012) or from acoustic cues within the recruitment call (Furrer & Manser, 2009b).

Much of the research on recruitment vocalizations has focused on the information that these signals convey about the caller. The recruitment calls of certain species inform receivers of caller identity, status, sex, kinship or degree of arousal (Gouzoules & Gouzoules, 1990; Kennedy et al., 2009; Scheumann et al., 2012), all factors that may impact on a receiver's decision to respond. For example, the long-distance recruitment call of cottontop tamarins, *Saguinus oedipus*, informs receivers of caller sex and group members bias their response to the opposite sex (Miller et al., 2004). Both spotted hyaenas (Gersick et al., 2015) and white-faced capuchins (Digweed et al., 2007) can ascertain caller rank from recruitment calls and respond more readily to dominant individuals. Dwarf mongooses, *Helogale parvula* (Kern & Radford, 2016) and crested macaques, *Macaca nigra* (Micheletta et al., 2012) respond more strongly to the recruitment calls of group members with whom they share close bonds.

In addition to details about the caller, information about external context is likely to play a critical role when an individual is deciding whether to respond to a recruitment call. This is particularly so in taxa that use one recruitment call in a variety of situations. Spotted hyaenas, for example, use recruitment whoops to muster support during both intergroup and interspecific conflicts (Gersick et al., 2015), cottontop tamarins reunite lost group members and attract mates with their combination long call (Miller et al., 2004), and both meerkats, *Suricata suricatta*, and banded mongooses, *Mungos mungo*, use their recruitment call when mobbing snakes, investigating secondary predator cues and repelling conspecific intruders (Furrer & Manser, 2009b; Manser, Bell, & Fletcher, 2001). These contexts vary considerably in the degree of risk they impose, which could significantly impact on an individual's decision to participate in cooperative activities. Under such circumstances, we would expect selection to promote the evolution of recruitment calls that convey contextual information. Few studies, however, have examined whether the acoustic structure of recruitment calls is context specific. For a signal to be 'context specific' it should be structurally unique, referring only to a particular situation or stimulus (Scheumann, Zimmermann, & Deichsel, 2007). To be 'functionally referential', this information must also be perceivable by others, i.e. specific to both context and response type (Macedonia & Evans, 1993; Townsend & Manser, 2013).

Attempts to ascertain whether recruitment calls provide specific information about their external stimuli have largely been limited to studies of avian mobbing calls. Mobbing calls differ from alarm calls in that they recruit group members to a potential threat instead of causing them to flee a threat. Eight species of group-living bird are known to produce mobbing recruitment calls that convey contextual information (reviewed in Suzuki, 2016), but only

in two instances are these calls functionally referential. The mobbing calls of Siberian jays, *Perisoreus infaustus*, differ acoustically with predator behaviour (Griesser, 2009), and those of Australian magpies, *Gymnorhina tibicen*, differ with predator type (Kaplan & Rogers, 2013). In both species, receivers respond to these distinct mobbing calls with different behaviours. In the other six avian species, mobbing calls (and the receivers' response) differ in intensity only and reflect the arousal (or anxiety) of the caller (influenced by the type, size and proximity of the predator) rather than referring to the specific context (Suzuki, 2016). Meerkat recruitment calls, elicited by encounters with snakes and with predator faeces, also appear to signal urgency (or arousal of the caller) rather than stimulus type, even though this species employs functionally referential alarm calls (Manser, 2001; Manser, Bell, et al., 2001).

Only one study has compared recruitment vocalizations elicited by predator and nonpredator stimuli. Furrer and Manser (2009b) examined the acoustic structure of banded mongoose recruitment calls elicited by snakes, predator faeces and intergroup encounters. They found that, although calls differed acoustically between these three contexts, the differences were graded and appeared to be urgency or arousal based rather than context specific. Similarly, although group members responded more strongly to the playback of calls recorded in high-urgency contexts, their behavioural response (cautious investigation) did not differ between contexts, indicating that they were not functionally referential.

In this study, we examined whether the recruitment calls used by dwarf mongooses convey information about external context. Dwarf mongooses are small (200–300 g), social carnivores that live in cooperatively breeding groups of up to 30 individuals in the savannah woodlands of Africa (Sharpe, Joustra, & Cherry, 2010). Foraging with their groups in (relatively) dense vegetation, this species has a sophisticated system of vocal signals. These include 'close' contact calls to maintain group cohesion, twitters to indicate excitement (Beynon & Rasa, 1989), functionally referential alarm calls (Beynon & Rasa, 1989) and a high-pitched recruitment call to attract conspecifics (Kern & Radford, 2016).

The recruitment vocalization is used in five different contexts: to reunite lost group members, to coordinate group retreat during rival encounters, to attract potential mates, to muster group members for the cooperative mobbing of snakes and to recruit heterospecific foraging partners. The recruitment calls employed in these five contexts are identical to the human ear, yet receivers respond quickly and appropriately according to the context, suggesting that calls may transmit informative cues of context or urgency. We compared recruitment calls elicited in the two most commonly occurring contexts (snake encounter and isolated individual) to answer three questions. First, are there acoustic differences between recruitment call types (snake versus isolation) which may act as cues of context? Second, do dwarf mongooses respond appropriately to recruitment calls elicited in these two distinct contexts, in the absence of external cues? Third, are the recruitment calls functionally referential with regard to context, as opposed to being graded in response to urgency? We undertook both acoustic analyses and playback experiments to address these questions.

## METHODS

### Sound Recording

We recorded recruitment calls opportunistically from dwarf mongoose adults in four wild groups on Phuza Moya Private Game Reserve (24°16'10"S, 30°47'46"E) between March 2015 and 2016.

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