



Dwarf mongooses use sex and identity cues in isolation calls to discriminate between callers



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The information transmitted by acoustic signals has attracted much scientific interest in recent years. However, isolation calls, which are long-distance vocalizations used by lost group members to reunite with their social group, have been surprisingly neglected. These calls assist in maintaining group cohesion and are thus particularly important in species that depend on the group for survival or reproduction such as cooperative breeders. Our study therefore examined the information transmitted by the isolation vocalization in a wild cooperatively breeding carnivore: the dwarf mongoose, *Helogale parvula*. We ran an acoustic analysis for informative cues within isolation calls, and conducted a series of playback experiments to identify whether mongooses could discriminate between callers based on these cues. The acoustic structure of dwarf mongoose isolation vocalizations contained information concerning the caller's identity, sex and potentially also group membership. Target mongooses discriminated between callers of their own and other groups and biased their response based on the sex of the caller. They responded more quickly and for longer, and approached more closely, for calls of foreign females than calls of female group mates. This is the first time that sex specificity has been demonstrated in the vocalization of an herpestid, and we suggest that dwarf mongooses eavesdrop on the calls of isolated foreigners and may use isolation calls to attract and identify potential mates.

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Over the past few years, studies on animal vocalizations have burgeoned, and the information transmitted by acoustic signals is more widely understood (Taylor & Reby, 2010). There are, however, still many areas of acoustic communication that are poorly studied. One such vocalization is the isolation call which is found in many mammalian species. These calls (also called lost, separation or distress calls) are characterized by their high frequency and pure tone traits. Such traits transmit well in 'noisy' and densely vegetated environments and appear to be perceived as more 'fearful' and less aggressive than harsher tones (Manser et al., 2014; Morton, 1977; Scheumann, Zimmermann, & Deichsel, 2007). The isolation call is a long-distance recruitment call that facilitates a lost group member to reunite with its group. It is thus fundamentally important in maintaining group cohesion in social species (Digweed, Fedigan, & Rendall, 2007).

It is important for long-distance calls, in particular, to contain discernible information about context or identity, so that receivers are able to perform the appropriate response rapidly, in the absence of additional cues (Gersick, Cheney, Schneider, Seyfarth, &

Holekamp, 2015). Despite this importance, the majority of studies focus on only the calls of isolated infants (Balcombe, 1990; Bohn, Wilkinson, & Moss, 2007; Brudzynski, Kehoe, & Callahan, 1999; Gelfand & McCracken, 1986; Knörnschild, Nagy, Metz, Mayer, & von Helversen, 2012; Knörnschild, von Helversen, & Mayer, 2007; Monticelli, Tokumaru, & Ades, 2004; Scherrer & Wilkinson, 1993; Schneider & Fritzsche, 2011; Scheumann et al., 2012, 2007; Weary, Lawson, & Thompson, 1996). Studies on isolation calls in adult mammals, on the other hand, are rare, concentrating almost exclusively on primates. These primate calls commonly inform audience members about the individuality, sex, age, group or family membership and context of the call. For example, the isolation call (or combination long call) of cottontop tamarins, *Saguinus oedipus*, is specific to the sex of the caller and individuals respond favourably to the parameter traits of calls of the opposite sex (Miller, Scarf, & Hauser, 2004). The calls of white-faced capuchins, *Cebus capucinus*, differ between individuals, with group members responding most commonly to individuals of the highest rank (Digweed et al., 2007). Squirrel monkey, *Saimiri sciureus*, calls are individually distinct across all ages (Lieblich, Symmes, Newman, & Shapiro, 1980) and in chacma baboons, *Papio cynocephalus ursinus*, calls not only differ between individuals, but also provide an indication of the context in

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which they are produced (Fischer, Hammerschmidt, Cheney, & Seyfarth, 2001, 2002). In the latter two species, however, studies did not explore whether individuals are capable of recognizing and responding to these acoustic cues.

Little is known about nonprimate adult isolation vocalizations and the information they transmit. One study on Amazonian manatees, *Trichechus inunguis*, found individual, sex and age differences, although the recognition of individuals by manatees was tested only with preliminary playback analyses (Sousa-Lima, Paglia, & Fonseca, 2002). In other mammals, such as giant otters, *Pteronura brasiliensis* (Mumm & Knörnschild, 2014), isolation vocalizations have only been recorded and/or described but not examined for the information they convey to conspecifics.

Our study examined the information transmitted by the isolation calls of a wild cooperatively breeding mammal: the dwarf mongoose, *Helogale parvula*. Isolation calls are of special significance to cooperative species because individuals generally cannot survive or breed except within a group, and large group size is associated with many benefits. In dwarf mongooses and meerkats, *Suricata suricatta*, both juvenile and adult survival increase with group size. This is because larger packs are more able to defend themselves against predation and territorial incursions, and can raise more pups due to the higher number of helpers contributing to babysitting, feeding and protecting the young (Clutton-Brock et al., 1999; Rood, 1986). Separation from the group is costly and exposes individuals to high levels of predation and stress (e.g. Young & Monfort, 2009). Surprisingly though, only one study, that of cottontop tamarins (Miller et al., 2004), has investigated isolation calls in cooperative mammals.

Dwarf mongooses are an ideal study species in which to investigate isolation calls. They live in stable social groups of up to 30 individuals of which females are the philopatric sex. They can be found in wooded savannah regions of Africa, taking refuge in termite mounds by night and foraging as a dispersed group by day (Manser et al., 2014; Rood, 1990; Sharpe, Joustra, & Cherry, 2010). Foraging group members maintain contact using individually recognizable contact calls (Sharpe, Hill, & Cherry, 2013) but when an individual becomes inadvertently separated from the group it produces monosyllabic, high-pitched isolation calls to facilitate its reunion. We undertook acoustic analysis and playback experiments to determine what information, such as identity, sex and group membership, is contained within dwarf mongoose isolation calls and whether individuals were capable of recognizing and responding to these acoustic cues.

METHODS

Sound Recording

We recorded the isolation recruitment calls of dwarf mongooses that had become separated naturally from their group, between March 2015 and March 2016. Calls were collected from 40 mongooses across four wild groups (mean group size 16) at Phuzi Moya Private Game Reserve (coordinates: 24°16'10"S, 30°47'46"E), in Limpopo, South Africa. See Sharpe et al. (2010) for details on climate and vegetation. Each individual in the study population was marked for recognition using small spots of blonde hair dye, applied with a long-handled paintbrush while the animal was sunning. Mongooses less than 9 months old were excluded from the study. This population has been studied since 2006 and the mongooses were habituated to close observation, allowing us to record calls within 3 m. Vocalizations were captured using a Marantz PMD-670 solid state recorder and a Roland R26 portable recorder, both attached to Sennheiser directional microphones (model ME66/K6) with windshields. We recorded calls opportunistically during the

mongooses' morning foraging period by following the mongoose group on foot and finding the separated caller when isolation calls were heard. The close proximity to the study subject allowed for positive identification of both the caller and the context. However, since the distance from the callers was not constant and background noises could not be controlled, the amplitude (volume) of individual recordings and isolation calls varied. We terminated recordings if wind speeds were greater than 11 km/h or if cicadas began calling, as their call frequency overlapped with that of the mongoose isolation calls (Fig. 1d). We performed spot checks using a Velleman sound level meter (model DVM805; range 30–100 dB; 1.5 dB accuracy) to obtain calling amplitudes for playback and standardization purposes.

We digitized (wav format, 48 kHz, 16 bit) and edited recordings for playback and analysis using Adobe Audition 2.0 (Adobe Systems Inc., San Jose, CA, U.S.A.). Of the 1407 calls isolated from recordings, 875 were from known callers and were of sufficient quality to be used in analysis, resulting in a sample of 40 mongooses. Owing to the rarity of these calls, and therefore small sample size per individual, all available calls of sufficient quality were analysed. We deemed calls to be of high quality if they had a high signal to noise ratio, did not overlap, had little background interference (such as wind, cicadas, birds or flies) and at least the first formant above the fundamental frequency band was clearly visible (Fig. 1). The calls of younger mongooses were often too high for the second formant to be within recorded frequencies. Therefore, only the fundamental and first formant frequency bands were considered. We constructed spectrograms for visualization of vocalizations in Raven Lite 1.0 (50% brightness, 60% contrast and spectrogram sharpness 512 pts; www.birds.cornell.edu/brp/raven/ravenversions.html).

Sound Analysis

Methods

To examine isolation calls for potential informative characteristics, we used Luscinia bioacoustics software (RF Lachlan version 2.0, <http://rflachlan.github.io/Luscinia/>) and analysed all possible acoustic parameters of 875 calls, for both formants (F0 and F1), by fast Fourier transformation (1024 points, Hamming window, time step 0.36 ms, frame length 23.22 ms, spectral overlap 98.45%). One advantage of this software is that for each individual call, the frequency bands of interest must be highlighted manually, increasing accuracy of measurements particularly as background noise can confuse automated measures (Baker & Logue, 2003). We analysed temporal and spectral parameters with all frequency-related variables being measured at the mean, median, maximum, minimum, time of maximum, time of minimum, start and end of each call. We chose 20 of the most commonly used parameters for statistical analysis of isolation calls. For both the fundamental (F0) and first formant (F1) frequency bands, the following parameters were measured: overall peak, minimum and maximum frequency; peak frequency (at mean); and mean frequency (at mean and maximum). In addition, we measured the duration, power spectrum quartiles, Wiener entropy, bandwidth (at mean and maximum) and range of the fundamental frequency. Finally, we calculated the gap, or formant dispersion, between the two frequency bands (mean F1–F0).

Although parameters were measured for all calls of sufficient quality, only calls from those individuals with more than six exemplars were used for statistical analysis ($N = 784$ calls from 28 individuals, mean 28 and range 6–115 calls per individual). Furthermore, one mongoose female was excluded from the statistical analysis because her calls were on average 2249 Hz lower than those of the other mongooses (Fig. 2).

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