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1
2 **Social-bond strength influences**
3 **vocally-mediated recruitment to mobbing**

4
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8
9 **Strong social bonds form between individuals in many group-living species, and these**
10 **relationships can have important fitness benefits. When responding to vocalisations**
11 **produced by groupmates, receivers are expected to adjust their behaviour depending on**
12 **the nature of the bond they share with the signaller. Here we investigate whether the**
13 **strength of the signaller–receiver social bond affects response to calls that attract others**
14 **to help mob a predator. Using field-based playback experiments on a habituated**
15 **population of wild dwarf mongooses (*Helogale parvula*), we first demonstrate that a**
16 **particular vocalisation given on detecting predatory snakes does act as a recruitment call;**
17 **receivers were more likely to look, approach and engage in mobbing behaviour than in**
18 **response to control close calls. We then show that individuals respond more strongly to**
19 **these recruitment calls if they are from groupmates with whom they are more strongly**
20 **bonded (those with whom they preferentially groom and forage). Our study therefore**
21 **provides novel evidence about the anti-predator benefits of close bonds within social**
22 **groups.**

23
24 **Introduction**

25 A common feature of stable social groups is the presence of close bonds, or friendships',
26 between individuals [1,2]. While there are many different ways to quantify the strength of such
27 relationships [3], it is recognised that 'strong' bonds with groupmates can provide considerable
28 long-term health and fitness benefits [1,2]. However, less is known about potential short-term
29 survival benefits [1,4]. Reduction of predation risk is facilitated in many species by a range of
30 different acoustic signals that can induce fleeing, increase vigilance and coordinate defensive
31 actions [5,6]. Recent work on chimpanzees (*Pan troglodytes*) and yellow-bellied marmots
32 (*Marmota flaviventris*) has shown that the propensity of individuals to give flee alarm calls can

33 depend on the presence of close affiliates and their own position in a social network [7,8].
34 Behavioural adjustments in *response* to at least some anti-predator vocalisations (e.g. those that
35 coordinate defence) might also be expected depending on the level of affiliation with the caller,
36 but little attention has been paid to receivers in this regard (see [4] for an exception).

37
38 In many taxa, certain vocalisations serve to attract others to the caller. These ‘recruitment’ calls
39 often advertise the location of a food source [9], but are also given when individuals encounter
40 specific predators [10]. Predator-related recruitment calls can engage both conspecifics and
41 heterospecifics in collective mobbing behaviour, with responders purposely approaching and
42 harassing the threat [10–12]. Mobbing is costly in terms of potential injury or death, lost
43 foraging time, and the risk of attracting further predators [13–15]. Like many other
44 vocalisations, predator-related recruitment calls can convey information about the caller’s
45 identity [4,16]. However, only one empirical study has considered how within-group signaller–
46 receiver bond strength might influence call responses: crested macaques (*Macaca nigra*)
47 oriented for longer towards a loudspeaker playing recruitment calls of close affiliates compared
48 to those of weak affiliates [4].

49
50 Here we use field playback experiments to examine whether caller identity influences receiver
51 responses to the calls given by dwarf mongooses (*Helogale parvula*) on encountering predatory
52 snakes. Having first demonstrated that these calls do indeed function to recruit group members,
53 we investigate the role of social-bond strength between callers and responders. Specifically,
54 we test whether individuals show greater responses to the recruitment calls of individuals to
55 which they are more strongly bonded.

56

57 **2. Material and Methods**

58 **(a) Study site and population**

59 Data were collected on Sorabi Rock Lodge Reserve, South Africa from nine wild dwarf
60 mongoose groups habituated to close observation [17,18]; full methodology in
61 Supplementary Material (SM); datasets available in [19]. Data on natural mobbing events –
62 approaching, cooperative harassing and attacking of a predator – were collected using all-
63 occurrence sampling between January 2014 and March 2016.

64

65

66 **(b) Playback experiment 1**

67 To test whether the calls given by dwarf mongooses when they detect a predator to be mobbed
68 (see Results) function to recruit others, we compared responses to playback of these calls and
69 control close calls given while foraging (Fig. SM1). Putative ‘recruitment’ calls were recorded
70 during natural snake-mobbing events and rubber-snake presentations. Close calls were
71 recorded opportunistically during foraging bouts. Nine randomly selected subordinate
72 individuals received separate 10-min playbacks of the two call types at natural rates and
73 amplitudes. Playbacks to the same focal individual were of calls from the same adult
74 subordinate group member and were separated by 1 h; the presentation order of the two
75 playback types was alternated to different focal individuals. Focal individuals were filmed
76 during playback, and data on looking, approaching and mobbing behaviour subsequently
77 extracted.

78

79 **(c) Playback experiment 2**

80 To assess how the response to recruitment calls is influenced by signaller–receiver social-bond
81 strength, we conducted a second playback experiment. Eight individuals from four groups
82 (those with sufficient subordinate group members to enable comparison of a stronger and
83 weaker social bond) each received two 10-min playbacks of recruitment calls, one from a
84 subordinate groupmate with whom they shared a relatively strong bond and one with whom
85 they shared a relatively weak bond. Social-bond strengths were determined from composite
86 sociality indexes (CSI) [4,20] based on grooming and nearest-neighbour foraging distances.
87 The use of multiple behavioural indices strengthens the assessment of bond strength, and
88 previous research has established that grooming and foraging associations are strongly
89 correlated within dwarf mongoose groups (full details in SM). Experimental signaller–receiver
90 dyads were selected to maximise the difference in CSI scores for a given focal individual.
91 Playbacks to the same focal individual were separated by 7.5 ± 2.3 days (mean \pm SE; range: 2–
92 15); group size was the same for both trials to the same individual. Variation in the time
93 between trials to the same focal individual did not significantly affect either the absolute
94 response shown in the second trial (Jonckheere-Terpstra test, duration of looking: $T_{JT}=17$,
95 $N=8$, $P=0.24$; duration of physical response: $T_{JT}=11$, $N=8$, $P=0.61$) or the difference in
96 response between the two trials (duration of looking: $T_{JT}=12$, $N=8$, $P=0.90$; duration of
97 physical response: $T_{JT}=15$, $N=8$, $P=0.43$). The presentation order of the two playbacks was

98 alternated to different focal individuals. Focal individuals were filmed, and data extracted, as
99 in Experiment 1.

100 **(d) Statistical analysis**

101 The response of focal foragers to the two types of call (Experiment 1) were analysed using two
102 McNemar related-samples tests (for tendencies to look at and to approach the speaker) and two
103 Wilcoxon signed-rank tests (for durations of looking and physical responses; the latter defined
104 as the time spent approaching and mobbing). Data from Experiment 2 were analysed using
105 linear mixed models (LMMs) and generalized linear mixed models (GLMMs), to account for
106 data collection from more than one focal individual per group. For all models, the fixed effects
107 of social-bond strength (strong, weak), group size and trial order (1, 2) were fitted, and focal
108 individual nested in group was included as a random term.

109

110 **3. Results**

111 Sixty-one natural mobbing events were observed in response to snakes (puff adders (*Bitis*
112 *arietans*), Mozambique spitting cobras (*Naja mossambica*), black mambas (*Dendroaspis*
113 *polylepis*), African rock pythons (*Python sebae*)). In all cases, the first individual to locate the
114 threat gave a particular vocalisation (Fig. SM1a); this was the vocalisation tested in the
115 playback experiments. Other group members approached the caller, searched for the threat and
116 then surrounded the predator, displaying typical mobbing behaviours such as head bobbing and
117 weaving, striking at the predator, and threat scratching. Mobbing events lasted for 697 ± 148 s
118 (mean \pm SE) and involved $62\% \pm 4\%$ of the group.

119

120 Compared to close-call playback, playback of calls given on detecting snakes (see above)
121 resulted in focal foragers being more likely to look at the speaker (McNemar's test: $N=9$ paired
122 playbacks, $P=0.013$), looking for longer (Wilcoxon signed-rank test: $Z=0$, $N=9$, $P=0.004$),
123 being more likely to approach the speaker (McNemar's test: $N=9$ paired playbacks, $P=0.041$)
124 and responding physically for longer (Wilcoxon signed-rank test: $Z=0$, $N=9$, $P=0.014$).

125

126 Controlling for a significant negative effect of trial order in several cases (Table SM1), focal
127 foragers were more likely to look at the speaker (GLMM: $\chi^2=4.56$, $df=1$, $P=0.033$; Fig. 1a),
128 looked for longer (LMM: $\chi^2=11.06$, $df=1$, $P=0.001$; Fig. 1b), were more likely to approach the
129 speaker (GLMM: $\chi^2=10.62$, $df=1$, $P=0.001$; Fig. 1c), and responded physically for longer
130 (LMM: $\chi^2=854.95$, $df=1$, $P<0.001$; Fig. 1d) when played recruitment calls from individuals to

131 which they were strongly bonded compared to those from groupmates to which they were more
132 weakly bonded.

133

134 **4. Discussion**

135 Our study shows that, on detecting predatory snakes, dwarf mongooses produce specific
136 vocalisations that act as recruitment calls. These calls increase the likelihood of the caller being
137 joined by other group members in mobbing the threat, as is the case in various other species
138 [8,9]. We demonstrate experimentally that the response to these recruitment calls differs
139 depending on the social-bond strength shared by the signaller and receiver. Individuals showed
140 a greater response (in terms of looking, approaching and mobbing) when hearing recruitment
141 calls from groupmates to which they were strongly bonded compared to those with which they
142 shared a weaker bond. Although a previous study indicated that crested macaques orientated
143 more to (i.e. looked in the direction of) the recruitment calls of close affiliates than weak
144 affiliates, they found no difference in the tendency to approach or duration of response [3]. To
145 our knowledge, the current work is therefore the first to show greater active responses to the
146 recruitment calls of groupmates with whom receivers share stronger bonds (see [21] for an
147 example of how long-term familiarity increases the likelihood that neighbours assist one
148 another in nest defence).

149

150 Heightened responses to the recruitment calling of particular group members could
151 theoretically be a by-product of factors influencing the formation of social bonds. If individuals
152 were more likely to form strong bonds with groupmates of similar age and size, for example,
153 dyads with strong bonds would have similar risk profiles. Mobbing behaviour by one of these
154 other individuals would thus be a potentially good indication of a threat to self. Within dwarf
155 mongoose groups, however, there is much variation in social-bond strength between
156 individuals of the same age (JM Kern unpub. data). Indeed, in several cases, the strongly and
157 weakly bonded experimental individuals were littermates. Instead, the preferential response to
158 recruitment calls from strongly bonded groupmates may arise from a trade-off between the
159 benefits and costs, given that mobbing behaviour is costly [11–13]. There are a number of
160 potential such possibilities.

161

162 First, it has been suggested that mobbing may function as a costly signal, advertising individual
163 quality to conspecifics [17]. Individuals may invest more in signalling their quality to those

164 with which they share strong bonds to uphold their attractiveness as a close partner, though so
165 far support for this hypothesis is lacking [10,18]. Second, individuals may preferentially
166 associate with close affiliates in stressful situations. In pilot whales (*Globicephala melas*), for
167 example, closely affiliated dyads increase their synchronization when swimming in stressful
168 circumstances [19]. Third, there may be variation in the relative costs and benefits of
169 responding to callers with whom receivers have stronger or weaker bonds. The effectiveness
170 of mobbing increases with the number of participants [13], thus groupmates may directly
171 improve the survival chances of a caller when they respond to recruitment calls. Reciprocal
172 cooperation, often performed over long time periods, may also be more likely between strongly
173 bonded individuals [20]. Receivers who respond to close affiliates now may therefore stand to
174 gain future advantages, including likely assistance themselves in future mobbing events or
175 intra-group conflicts [21], in addition to the ongoing advantages of close friendships.

176

177 Recent experimental work using other call types has demonstrated an effect of social-bond
178 strength and other social attributes on caller behaviour [7, 8]. Here, we show an effect of social
179 bonds on receiver responses (see also [3]), enhancing our understanding of the role of social
180 bonds in intra-group interactions. While the long-term benefits of close social bonds are well
181 established, particularly in primates, the potential in other species and in the context of
182 predation has been little explored. In general, by adjusting their responses depending on caller
183 identity, receivers can facilitate more efficient and effective use of social information.

184

185 **Ethics** This study was conducted under all required ethical approvals.

186 **Data accessibility** All data for this paper will be archived in Dryad.

187 **Author contributions** J.M.K. & A.N.R. designed the study; J.M.K. collected the data; J.M.K.
188 analysed the data with advice from A.N.R.; J.M.K & A.N.R. interpreted the data and co-wrote
189 the paper.

190 **Competing interests** We have no competing interests.

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194

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261 **Figure Legends**

262 **Figure 1** Response of dwarf mongooses to the playback of recruitment calls given by
263 groupmates to which they are strongly or weakly bonded. (a) Proportion of trials eliciting
264 looking at speaker, (b) total duration looking at speaker, (c) proportion of trials eliciting
265 approach to speaker, and (d) total duration of physical response. For (a)–(c), N =eight
266 individuals, four groups; for (d), N =seven individuals, three groups. Shown for (b) and (d) are
267 results for each focal individual separately (lines) and the overall treatment mean (solid
268 squares) \pm SE.

Figure 1

