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A simple test of vocal individual recognition in wild meerkats

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16 **ABSTRACT**

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19 Individual recognition is thought to be a crucial ability facilitating the evolution of animal  
20 societies. Given its central importance, much research has addressed the extent of this  
21 capacity across the animal kingdom. Recognition of individuals vocally has received  
22 particular attention due, in part, to the insights it provides regarding the cognitive processes  
23 that underlie this skill. Whilst much work has focused on vocal individual recognition in  
24 primates, there is currently very little data showing comparable skills in non-primate  
25 mammals under natural conditions. This may be because non-primate mammal societies do  
26 not provide obvious contexts in which vocal individual recognition can be rigorously tested.  
27 We addressed this gap in understanding by designing an experimental paradigm to test for  
28 individual recognition in meerkats (*Suricata suricatta*) without having to rely on naturally  
29 occurring social contexts. Results suggest that when confronted with a physically impossible  
30 scenario – the presence of the same conspecific meerkat in two different places – subjects  
31 responded more strongly than during the control, physically possible setup. We argue that  
32 this provides the first clear evidence for vocal individual recognition in wild non-primate  
33 mammals and hope that this novel experimental design will allow more systematic cross-  
34 species comparisons of individual recognition under natural settings.

35

36 **1. INTRODUCTION**

37

38 Individual recognition of conspecifics is considered to be crucial to the evolution of animal  
39 sociality [1, 2]. Given its central importance, much research has addressed the competence of  
40 numerous animal species in this behavioural and cognitive domain [3]. Due to their rich and  
41 multifaceted social lives, primates have received particular attention, with numerous studies  
42 demonstrating individual recognition through the playback of vocalizations [see 4]. Evidence  
43 for equivalent abilities in wild non-primates is much less clear for two reasons: (1) it has  
44 proven difficult to find socially meaningful contexts where individual vocal identification  
45 would be more advantageous than class-level vocal recognition, other than mother-infant  
46 interactions [5, 6], and (2) social and ecological differences make it hard to find a good  
47 experimental framework for cross-species comparisons [7]. We addressed these issues by  
48 devising a novel violation-of-expectation paradigm favouring individual recognition in  
49 meerkats (*Suricata suricatta*), but which does not depend on naturally occurring social  
50 interactions.

51

52 Meerkats, like primates, rely heavily on vocal communication to coordinate their activities  
53 according to their surrounding ecological situation, such as the risk of predation [8].  
54 However, exactly how important vocalizations are for tracking changes in their social  
55 environment is currently not clear [9]. During social foraging, meerkats frequently emit  
56 stereotyped, individually distinctive, ‘close calls’, which most likely function in maintaining  
57 group cohesion [10]. Using a dual-speaker setup we simulated two physical scenarios: 1)  
58 incongruent (test) condition: the same subordinate meerkat foraging on one side of the subject  
59 and then within a few seconds (physically impossible) appearing on the geometrically  
60 opposite side; and 2) congruent (control) condition: two subordinates foraging independently

61 on either side of the subject. If meerkats use vocalizations to recognize and track conspecific  
62 group members individually, we predicted they should respond more during the incongruent,  
63 physically impossible condition, in terms of vigilance behaviour and looking in the direction  
64 of the expectancy violation (loudspeaker from which the 2<sup>nd</sup> playback was broadcast), than  
65 during the socially and physically congruent condition.

66

## 67 **2. METHODS**

### 68 *Study site and subjects*

69 Recordings and playback experiments were conducted on wild but habituated meerkats at the Kalahari Meerkat  
70 Project (KMP), South Africa [8], between October-December, 2010 (see ESM).

71

### 72 *Call recording and playback construction*

73 We recorded close calls from male subordinate meerkats (>12 months) belonging to the same group as playback  
74 subjects at a distance of approximately 1-2m, using a Sennheiser directional microphone (ME66/K6) connected  
75 to a Marantz PMD-670 solid-state recorder. In one group subordinate females were recorded and used as  
76 playback stimuli, as no males in this group were habituated to a sufficient level to allow good quality call  
77 collection. Calls were transferred digitally onto a PC using Cool Edit Pro 2000. Up to six foraging close calls  
78 with a high signal-to-noise ratio were selected randomly from sound files and used to construct playbacks. In the  
79 test and control conditions two independent playbacks of 4.5secs consisting of between 2-3 close calls were  
80 created (see ESM). In the test (incongruent) condition, the two playback files consisted of different close calls  
81 recorded from the same individual. In the control (congruent) condition one playback file consisted of close calls  
82 from the same subordinate group member as used in the test condition and in the second playback file, close  
83 calls from a different subordinate meerkat.

84

### 85 *Playback protocol*

86 Playback experiments were conducted on 8 male subordinate meerkats belonging to 8 different groups. All  
87 subjects were followed whilst foraging for a minimum of 30 minutes (range 0.5-2.5 hours) prior to playback.  
88 While the subject was foraging, both experimenters attached a loudspeaker (model: JBL on tour) to their legs at  
89 a height similar to that of another foraging meerkat and positioned themselves at geometrically opposite sides of

90 the subject. Experimenter one was approximately 2m from the subject to allow accurate filming of subjects at a  
91 close distance, whilst experimenter two was approximately 5m from subject and 7m from experimenter 1 (Fig  
92 1). The experimental setup was kept exactly the same in both test and control conditions so as to rule out any  
93 distance-based effects due to asymmetrical speaker placement, that might otherwise explain subjects' response.  
94 Keeping track of the spatial position of the two subordinates used as stimuli (to ensure spatial congruency), we  
95 then played back from an iPod touch either different calls from the same individual from both sides (test  
96 condition), or calls from two different individuals from both sides (control condition), with an approximately 4  
97 second interval between stimuli. In the test condition, we therefore simulated an incongruent situation; that a  
98 subordinate individual was relaxed and foraging on one side of the subject and then a few seconds later appears  
99 on the opposite side 7m from its original position, again in a relaxed social foraging state. By presenting subjects  
100 with different calls from the same individual, we ensure that any violation of expectation response in the  
101 incongruent condition would be based on the listener's recognition that the calls came from the same individual,  
102 not that they constituted the exact same stimulus. In the control condition, we simulated a congruent scenario:  
103 the presence of two relaxed independently foraging meerkats on opposite sides of the subject. Subjects were  
104 filmed by the observer closer to the subject for 30s prior to the beginning of the first playback and one minute  
105 after the end of the second playback. To avoid order effects, we randomized the order in which subjects heard  
106 test and control conditions.

107

### 108 *Behavioural responses*

109 We analysed videos frame-by-frame using iMovie (MAC OS, 2010). Because we were playing back close calls,  
110 a frequently produced, low-arousal state vocalization, and because the situation we were simulating was not  
111 socially significant in comparison to previous vocal individual recognition studies [11], we did not expect overt  
112 behavioural responses to the violation-of-expectation setup. We therefore primarily focused on the employment  
113 of vigilance behaviour, a common alert-related behaviour which meerkats are known to demonstrate during  
114 socially or ecologically important events [10], for the duration of the second playback plus a 5 second time  
115 window following the final call played back. This time window was specifically chosen to compensate for  
116 possible responses to the final call played back and because all subjects had already returned to relaxed foraging  
117 by this time. The first playbacks in both the test and control conditions were used to assess baseline vigilance  
118 behaviour (see ESM). We noted: 1) each time the subject was observed to scan the surrounding terrestrial area;  
119 2) the duration of each vigilance bout, defined as the frame at which the meerkat began vigilance after having

120 previously held its head in a different position to the frame at which the meerkat returned its head to a foraging  
121 posture; and 3) if vigilance performed was in the direction of the speaker from which the second playback was  
122 broadcast. To ensure accurate coding of videotapes a second observer blind-coded 50% of trials (8 videos, see  
123 ESM).

124

125 *Statistical analysis*

126 Due to the non-normal nature of the data and the small sample size, we employed exact non-parametric tests [12,  
127 see ESM].

128

### 129 **3. RESULTS**

130

131 Meerkats were more vigilant and vigilant for longer during the incongruent condition than the  
132 congruent condition (vigilance frequency (mean  $\pm$  SD): incongruent = 2.12  $\pm$  1.5, congruent  
133 = 0.37  $\pm$  0.51, exact Wilcoxon test,  $Z = -2.38$ ,  $p = 0.016$  (figure 2); vigilance duration (s):  
134 incongruent = 2.17  $\pm$  2.21, congruent = 0.14  $\pm$  0.22, exact Wilcoxon test,  $Z = -2.41$ ,  $p = 0.016$   
135 (figure 2)). Subjects were also more likely to look towards the speaker during the incongruent  
136 condition than the congruent condition (Number of looks at speaker: incongruent = 0.875  $\pm$   
137 0.64, congruent: 0, Exact sign test:  $p = 0.031$ ). Baseline vigilance behaviour did not differ  
138 between conditions (vigilance frequency: incongruent = 0.12  $\pm$  0.35, congruent = 0.25  $\pm$  0.46,  
139 exact Wilcoxon test,  $Z = -0.57$ ,  $p = 1.0$ ) vigilance duration (s): incongruent = 0.25  $\pm$  0.7,  
140 congruent = 0.53  $\pm$  1.03, exact Wilcoxon test,  $Z = -1.28$ ,  $p = 0.375$ ).

141

### 142 **4. DISCUSSION**

143 Although vocal individual recognition is assumed to be widespread amongst non-primate  
144 animals, clear experimental evidence obtained under natural settings is surprisingly elusive.  
145 The lack of evidence is most likely due to the difficulty of empirically testing between  
146 individual recognition and categorization based on social status [3]. Our results suggest that

147 when confronted with an impossible socio-physical scenario – the presence of the same  
148 individual on two different sides - meerkats are more vigilant and more likely to look in the  
149 direction of the expectancy violation, than when the presence of two different individuals is  
150 simulated. In both conditions subordinates from within the same group were used as subjects  
151 and playback stimuli; this allows us to rebut the common argument that discrimination occurs  
152 only at the more rudimentary class or group level, leading us to conclude that meerkats  
153 distinguish between individuals.

154

155 Meerkats live in stable, cooperatively breeding social groups of up to 50 individuals [13].  
156 Individuals are continually exposed to a number of social challenges, including aggression,  
157 competition for dominance and coordination of cooperative behaviours [14]. Keeping track of  
158 conspecifics with whom individuals have differentiated competitive and cooperative relations  
159 is therefore a crucial requirement for the successful maintenance of meerkat social systems.  
160 Commonly emitted close calls, indicating the position and identity of the caller, may be one  
161 medium through which this occurs.

162

163 A recent study at the same site has shown that subordinate female meerkats can recognize the  
164 dominant female vocally [15]; however, given that there is only ever one dominant female in  
165 each group, that study could not logically show this goes beyond category-level recognition  
166 of dominant females. In the current study we have shown within-class discrimination of  
167 subordinate individuals who are tracked spatially. Hence we suggest that meerkats do indeed  
168 have a concept of conspecifics as “individuals” recognized perceptually. Exactly what  
169 cognitive mechanisms underlie this discrimination is not clear. For example, this experiment  
170 does not allow us to determine whether or not meerkats form a global representation of  
171 individuals by integrating identity cues from multiple modalities [16]. The absence of

172 experimental evidence for multiple modality integration does not necessarily negate the  
173 presence of individual recognition through auditory cues alone. Humans recognize the voices  
174 of radio personalities they have never seen, and recent work in auditory perception suggests  
175 that short-term memory in hearing is based on auditory objects that bind related elements of  
176 the auditory scene into a single representation [17].

177

178 Understanding how animals experience the individuals within their social worlds is key to  
179 deciphering the evolution of social and communicative capacities as sophisticated as those in  
180 humans [18]. Our results, indicating individual recognition in a non-primate mammal under  
181 natural conditions, highlight the possibility that the task of monitoring the location of group  
182 members based on their vocalizations may employ recognition mechanisms similar to those  
183 demonstrated in more complex social interactions, such as third-party relationships, or  
184 coalition formations. We hope our results will encourage others to employ similar violation-  
185 of-expectancy experimental paradigms when natural social contexts in which to test  
186 individual recognition are lacking. This may ultimately allow more systematic cross-species  
187 comparison of individual recognition.

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240 **Figures**

241

242 **Figure 1**

243 Schematic design outlining the playback protocol used in both the incongruent (test) and

244 congruent (control) conditions.

245

246

247 **Figure 2**

248

249 a) Frequency of vigilance and b) vigilance duration (mean $\pm$  1SE) during both the

250 incongruent (test) and congruent (control) experimental conditions.

251