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1 **Element repetition rates encode functionally distinct information in pied babbler**
2 **‘clucks’ and ‘purrs’**

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35 the University of Cape Town and the Northern Cape Conservation Authority, South Africa.

36 **Data accessibility.** The supporting dataset has been uploaded as part of the supplementary
37 material.

38 **Abstract**

39 Human language is a recombinant system that achieves its productivity through the
40 combination of a limited set of sounds. Research investigating the evolutionary origin of this
41 generative capacity has generally focused on the capacity of non-human animals to combine
42 different types of discrete sounds to encode new meaning, with less emphasis on meaning-
43 differentiating mechanisms achieved through potentially simpler temporal modifications
44 within a sequence of repeated sounds. Here we show that pied babblers (*Turdoides bicolor*)
45 generate two functionally distinct vocalisations composed of the same sound type, which can
46 only be distinguished by the number of repeated elements. Specifically, babblers produce
47 extended ‘purrs’, composed of, on average, around 17 element repetitions when drawing
48 young offspring to a food source, and truncated ‘clucks’ composed of a fixed number of 2-3
49 elements when collectively mediating imminent changes in foraging site. We propose that
50 meaning-differentiating temporal structuring might be a much more widespread
51 combinatorial mechanism than currently recognised, and is likely of particular value for
52 species with limited vocal repertoires in order to increase their communicative output.

53

54 **Introduction**

55 Animals employ various mechanisms to communicate and transfer information (Marler
56 1977). Combinatorial operations, whereby animals combine discrete sounds together into
57 larger meaningful structures, have received particular recent interest in part due to their
58 similarities to the combinatorial layers, phonology and syntax, in language (Collier et al.
59 2014). Animals, including birds and mammals, further encode information through
60 modifying the temporal arrangement of repeated elements within a sequence (Kershenbaum
61 et al. 2014). Such temporal structuring has been shown to convey information on motivation
62 or threat-levels experienced by an individual during aggressive or predatory encounters

63 (DuBois et al. 2009; Rek and Osiejuk 2012; Kershenbaum et al. 2014; Wheatcroft 2015)
64 (though see also Antunes et al. (2011)). Yellow-bellied marmots (*Marmota flaviventris*), for
65 example, decrease the inter-call interval between alarm calls with increasing proximity to a
66 threat (Blumstein 2007). Accordingly, temporal modifications generally constitute a graded
67 system correlating with a signaller's arousal level, and typically take the form of changes in
68 the number/rate of repeated elements or in inter-element intervals (DuBois et al. 2009; Rek
69 and Osiejuk 2012; Kershenbaum et al. 2014; Wheatcroft 2015). However, work on the alarm
70 calls of colobus monkeys (*Colobus guereza* & *polykomos*) and the social vocalisations of
71 Mexican free-tailed bats (*Tadarida brasiliensis*) have shown temporal changes can also
72 encode both discrete predator-specific (i.e. aerial versus terrestrial predator) and behaviour-
73 specific information (Bohn et al. 2008; Schel et al. 2009; Schel et al. 2010). These results
74 suggest that, besides transferring graded information, temporal modifications can encode
75 more discrete, categorical information; a feature more commonly associated with the
76 combination of different sound types (Zuberbühler 2015).

77 Here we investigate whether similar temporally induced meaning-differentiation also
78 exists outside of mammals, in the discrete vocal system of the pied babbler (*Turdoides*
79 *bicolor*). Babblers are social passerines, which live in stable, territorial groups of up to 15
80 individuals (Radford and Ridley 2006). They are weak flyers and spend most of their time on
81 the ground searching for invertebrate prey by probing the substrate and excavating the soil
82 using their bill (Radford and Ridley 2006). Given their limited visual contact with
83 conspecifics, babblers rely on vocal signals to keep track of changes in their social and
84 ecological environment (Radford and Ridley 2007; Hollén et al. 2008; Radford and Ridley
85 2008; Bell et al. 2009; Engesser et al. 2016). During the day, group members forage closely
86 together (~2m) and move cohesively between foraging sites (Thompson 2012). Babblers
87 typically forage below and around vegetation as well as in open areas (Ridley et al. 2014).

88 Foraging sites are therefore abundant and distributed unevenly throughout a group's territory
89 (average territory size 0.75km² (Humphries 2012)). Overnight, group members roost huddled
90 together in the same tree with an average of 53 roost trees (range 34-76) being used across a
91 group's territory (Raihani and Ridley 2007b; Golabek 2010).

92 During nestling provisioning and when attracting fledglings towards food sources,
93 babblers produce soft 'purr' vocalisations, composed of an extended number of up to ~40
94 repetitions of the same acoustic element. They are generally produced by a single individual
95 providing a food item or foraging at a sharable food patch, and are directed to dependent or
96 inexperienced offspring resulting in only the offspring approaching the caller, with adults not
97 responding (Radford and Ridley 2006; Raihani and Ridley 2007a, 2008). Purrs are typically
98 emitted until the caller is approached by the recipient, resulting in purrs of varying length.
99 Preliminary work indicated that babblers also produce truncated variants of purrs with a
100 considerably reduced, finite number of 2-3 elements, named here as 'clucks' (Fig. 1). Initial
101 observations indicated that, in contrast to purrs, clucks are jointly produced by multiple group
102 members (usually over several minutes) before groups cohesively move to the first foraging
103 site in the morning, or generally before switching between foraging sites. Crucially, the
104 number of clucking individuals seems to impact a group's decision to move between foraging
105 sites, with the number of callers appearing to correlate with the distance a group eventually
106 moves to a new site. Accordingly, clucks may represent an egalitarian decision-making
107 mechanism, linking individual preferences to group travel processes.

108 In order to investigate the temporal features of clucks and purrs, we used acoustic
109 analyses to examine whether the same element is used within and across the two call types,
110 and whether their temporal distinctiveness is determined by the number of repeated elements.
111 To support previous work indicating purrs function to recruit offspring to a food source, and
112 to verify the functional specificity of clucks, behavioural observations were conducted where

113 the context in which both calls were produced, and responses of receivers were recorded.
114 Specifically, in line with earlier findings, we expected purrs to only be produced by a single
115 individual and lead to a single recipient approaching the caller with the remaining group
116 members not moving, while for clucks we expected the number of individuals calling prior to
117 movement to impact the subsequent distance moved by the whole group.

118

119 **Methods**

120 **Study site and species**

121 The study was conducted on a population of free-living, habituated pied babblers at the
122 Kuruman River Reserve, South Africa (26°58'S, 21°49'E) (for details on the habitat see
123 (Raihani and Ridley 2007a; Hollén et al. 2011)). All birds in the study population are
124 individually recognisable through the combination of three coloured rings and one numbered
125 metal leg ring (Radford and Ridley 2008). During the data collection period, mean group size
126 ranged between 2 and 7 individuals (mean±SD=5±1, Fig. 2).

127

128 **Acoustic analyses**

129 Data for acoustic analyses were collected between January and May 2013, 2014 and 2015. To
130 verify the acoustic similarity among cluck and purr elements we acoustically analysed at least
131 one purr and one cluck vocalisation of a given individual in 16 different groups, and recorded
132 the number of element repetitions constituting the call. For each call, the first element and a
133 further randomly chosen element (determined using a random number generator (R-Core-
134 Team 2014)) were acoustically analysed resulting in the following 4 element categories: 1st
135 cluck element, nth cluck element, 1st purr element, nth purr element. Only vocalisations of one
136 individual per group were chosen to avoid including calls of genetically related individuals
137 (i.e. group members) and to ensure assumptions regarding independence of the data were

138 upheld (Sharp et al. 2005). While audio recordings were conducted during the breeding
139 seasons of 3 consecutive years, in order to avoid age-related variations (Humphries et al.
140 2016), we only considered cluck-purr pairs of an individual recorded in the same season.
141 This, in addition to the low amplitude nature of the vocalisations, making high signal-to-noise
142 ratio calls difficult to obtain, reduced our dataset to comprise only 7 individuals with more
143 than one example per specific element category (see supplementary dataset).

144 All vocalisations were recorded using a Rode NTG-2 directional microphone coupled
145 with a Rode Blimp Suspension Windshield (Rode microphones) and a Roland R-26 portable
146 recorder (Roland Corporation) (sampling frequency 48kHz, 24-bit accuracy). During vocal
147 recordings, the identity of the caller was noted. The extracted elements for the acoustic
148 analyses were analysed using Praat (v. 5.3.55). Since the elements comprising clucks and
149 purrs are often characterised by atonal, noisy structures, where a clear fundamental frequency
150 (F0) cannot be resolved, we only extracted non-F0 related spectral parameters including:
151 element duration, frequency value at the maximum amplitude, time-percentage to maximum
152 amplitude, amplitude variation, as well as the frequency values at the first, second and third
153 energy quartiles.

154 Statistical analyses were performed in R (v. 3.2.3) (R-Core-Team 2014). Model
155 assumptions were inspected visually, and potential multicollinearity among predictor
156 variables was controlled by removing variables with variance inflation factors (VIF) > 10
157 (Filzmoser et al. 2005; Fox and Weisberg 2011; Frank 2011). Due to a high VIF, the
158 frequency measurements at the second energy quartile were excluded from the acoustic
159 analyses. To verify the acoustic similarity among the elements within, as well as across
160 clucks and purrs, a permuted Discriminant Function Analysis (pDFA) with 1000
161 permutations was conducted (script provided by R. Mundry). The pDFA tested the
162 classification probability of element to element category, while at the same time controlling

163 for repeated measurements from the same individuals (Venables and Ripley 2002; Mundry
164 and Sommer 2007).

165 Lastly, a two-tailed, paired Wilcoxon signed-rank test was conducted to investigate
166 whether clucks and purrs differed in the number of element repetitions (Venables and Ripley
167 2002). For instances where more than one cluck or purr call were obtained for one individual,
168 the average was used.

169

170 **Natural calling observations**

171 *Purrs*

172 To support previous research on purrs functioning to recruit offspring to a food source,
173 observations on purring events in 11 groups from 2015 were analysed. We recorded the
174 number of callers during a purring event, the context of calling, the recipient's behaviour and
175 its status (fledgling, yearling, adult), as well as whether a group movement ensued.

176

177 *Clucks*

178 To investigate whether and how clucks influence movement between foraging sites, we
179 collected two sets of observational data on 14 babbler groups in 2015. The first set included
180 natural observations conducted at dawn at a group's roost, before the birds started to forage.
181 We recorded the number of individuals producing clucks (including cases when no clucks
182 were produced), and the distance the group subsequently moved to their first foraging site.
183 Additionally, we documented a group's overall clucking duration to rule out the possibility
184 that longer calling durations might result in more calling individuals, in addition to the
185 group's size to investigate whether the distance travelled is mediated by the absolute or
186 relative number of clucking individuals. Foraging sites were classified as locations where at
187 least half of the group collected to forage. Distances were measured using a handheld GPS

188 data logger (eTrex 10, Garmin).

189 The second set of observations were conducted later in the morning or in the early
190 evening when groups were continuously foraging. We collected the same behavioural data as
191 for the first set of observations, but only considered events when clucks were produced.
192 While data on foraging site-switches which have not been preceded by clucking would have
193 been feasible to collect, similar data on non-clucking events that did not result in a site-
194 switch cannot be determined and thus could not be collected. Such non-clucking/non-
195 movement events could only be detected in the roosting context due to clear change in the
196 group's behaviour from roosting to initiating foraging. Finally, since group movements are
197 often lead by the dominant male (Engesser et al. in prep), we additionally investigated
198 whether the dominant male's call contribution influenced the distance travelled by the group.
199 Because individual ring combinations enabling dominant male identification were not visible
200 at the roost tree, these data could only be collected during daylight hours.

201 Linear mixed models were fitted in R and model selection based on Akaike's
202 information criterion corrected for small sample sizes (AICc) were applied to investigate the
203 effect of the predictor variables on the distance a group moved (i) from the roost to the first
204 foraging site, and (ii) between two foraging sites (Barto'n 2014; Bates et al. 2014). Response
205 variables were transformed when necessary. Since multiple observations per group were
206 used, group identity was fitted as random term. The best model was selected based on the
207 Akaike's information criterion corrected for small sample sizes (AICc), with a threshold
208 difference (ΔAIC) of one (Burnham and Anderson 2002). Parametric bootstrapping was
209 applied to assess the significance of the fixed effects (pbkrtest using 10000 iterations which
210 provides *PBtest* as test statistic (Halekoh and Højsgaard 2014)).

211

212 **Results**

213 **Acoustic analyses**

214 The results of the pDFA revealed that cluck and purr elements could not be discriminated
215 based on their spectral features (correctly cross-classified elements=5.37 (=35.80%),
216 expected number correctly cross-classified elements=4.29 (=28.62%), $P=0.228$, $N=79$
217 elements of 16 individuals; Fig. 3). However, both call types could clearly be distinguished
218 by the number of element repetitions (paired, two-tailed Wilcoxon signed rank test: $V=136$,
219 $P<0.001$, $N=16$). Specifically, clucks were composed of 2-3 repeated elements (mean \pm SD
220 =2.3 \pm 0.4), and purrs of 5-38 (mean \pm SD =17.4 \pm 9.7).

221

222 **Natural calling observations**

223 *Purrs*

224 From a total of 40 purring events from 20 individuals of 11 groups, purrs were only ever
225 produced by one adult individual. In 39 occasions (97.5%) the recipient approached the
226 stationary caller, while the remaining group members did not approach or move. We only
227 observed one instance where the caller moved 30m to a new foraging site while purring and
228 was followed by its group members (2.5%). Of the 39 cases where the birds approached the
229 caller, the recipient had either been recruited to a sharable food source (17 cases, 44%), was
230 provided with a prey item (20 cases, 51%), or was recruited without providing food (2
231 instances, 5%). Moreover, of these 39 recruitment events, in 32 cases fledglings were
232 approaching (82%, in 3 cases a pair of fledglings and in the remaining a single fledgling), in
233 1 case, a yearling (3%), and in 6 cases, adults (15%, in 1 case a pair of adults in the
234 remaining a single adult).

235

236 *Clucks*

237 Behavioural observations on clucking events revealed groups travelled a greater distance to
238 the first foraging site in the morning, and between foraging sites during the day when more
239 individuals were clucking prior to movement (roosting: PBtest=21.61, $P < 0.001$, $N = 36$
240 observations from 13 groups; foraging: PBtest=6.79, $P = 0.01$, $N = 89$ observations from 11
241 groups; Fig. 4). Moreover, in the foraging context the distance a group moved was lower
242 when the dominant male did not participate in clucking (PBtest=10.33, $P < 0.01$ $N = 89$
243 observations on 11 groups; Fig. 4). Group size and the overall clucking duration of a group
244 did not affect subsequent movements in either of the two models (Table 1).

245

246 **Discussion**

247 Acoustic analyses confirmed that babbler clucks and purrs are composed of the same acoustic
248 elements, with only the number of element repetitions distinguishing the two calls. Our
249 behavioural observations suggest, however, that, although composed of identical elements,
250 clucks and purrs are produced in different contexts. In line with previous work, our findings
251 on purrs demonstrate that purrs serve to primarily attract dependent or inexperienced
252 offspring towards a food source, with one individual purring and the recipient approaching,
253 while the rest of the group remains unresponsive (Radford and Ridley 2006; Raihani and
254 Ridley 2007a, 2008). When clucks were produced at the roost tree in the morning, babblers
255 flew further to a foraging site when more group members were clucking. In contrast, when no
256 babblers were clucking, groups generally started to forage in the immediate vicinity of the
257 roost tree. This result was supported by observations conducted during foraging, showing
258 when more individuals were clucking prior to switching foraging sites, the distance moved
259 between the two sites was larger. Besides the number of clucking individuals, the dominant
260 male's clucking behaviour also appeared to impact a group's decision to move, with groups

261 moving shorter distances if the dominant male did not participate in clucking. Since
262 individual clucking contribution at dawn when groups left their night roost could not be
263 determined, this effect could only be investigated specifically in the foraging context.
264 Nevertheless, the result supports similar findings in babblers indicating dominant males play
265 a central role in leading the group through their territory (Engesser et al. in prep).

266 Our work suggests that clucks might function to mediate imminent movements.
267 However, the factors that drive their production need further investigation. Clucks are
268 potentially produced to initiate movement when individual foraging patches are depleted, or
269 when the location of the roost tree is sub-optimal as a suitable foraging site. A similar
270 mechanism is implemented by the socially foraging meerkat (*Suricata suricatta*), where
271 ‘move’ calls produced by multiple individuals may indicate a depletion of the foraging site,
272 and induce group movement (Bousquet et al. 2011). In line with this, babbler clucks might
273 function as a vocal tool to gather information on individual preferences or assessments of the
274 group’s current location (Bousquet et al. 2011). Specifically, cluck production might reflect
275 the caller’s independent assessment of the (decreasing) quality of the current foraging area.
276 Therefore, an increasing number of clucking individuals might indicate a greater proportion
277 of the group is motivated to switch foraging sites, with groups subsequently moving further
278 when more individuals have signalled the motivation to switch sites. The more individuals
279 exhibiting a particular preference, the greater the magnitude of the particular behaviour.
280 However, the magnitude might also be context specific, diminishing or changing under
281 certain circumstances (Sueur and Deneubourg 2011). During foraging post-roosting, for
282 example, babblers might have stronger tendencies to stay, or indeed switch sites, since
283 individual foraging patches and needs might vary more in comparison to directly after
284 roosting, where all group members are equally motivated to feed. Alternatively, decreased
285 visibility at dawn (compared to in daylight) might require a tighter vocal coordination,

286 constraining behavioural flexibility. This may explain the less pronounced relationship
287 between clucking individuals and the distance moved during foraging compared to after
288 roosting. Lastly, the absence of an interaction effect between group size and the number of
289 clucking individuals on the distance a group subsequently moved suggests that babblers
290 attend to the absolute rather than to the relative number of clucking individuals when
291 mediating movements, though the small variation in observed group sizes might have
292 obscured the detection of a potential effect (Fig. 2). Further systematic studies are now
293 needed in order to determine how the production of clucks translates into the distance a group
294 moves. Considering the effect the dominant male appears to have on his group's movement
295 behaviour, investigating the contribution of individuals of different social or age categories to
296 clucking events, as well as determining who is initiating the clucking and who subsequently
297 takes the lead to a new site, is one important avenue of investigation. Furthermore, playback
298 experiments, where the number and indeed identity of individuals involved in clucking events
299 can be manipulated, will be important to experimentally verify our observational findings.
300 Central to this work is the demonstration that clucks and purrs convey sender specific
301 information to receivers and receivers discriminate this, though preliminary acoustic analyses
302 are indeed suggestive of this with clucks and purrs differing systematically between
303 individuals (see supplementary material).

304 While future work is needed to help clarify the mechanisms underlying cluck-
305 mediated group movements in pied babblers, our key advance is that we provide evidence
306 suggesting babblers modify element repetition rates to generate two functionally distinct
307 signals: the 'truncated' clucks and the 'extended' purrs. Recent work has begun to address
308 non-human animal vocal combinatorial abilities, but the main focus has been on the ability to
309 combine different sound types to encode new, discrete information (Marler 1977; Collier et
310 al. 2014; Zuberbühler 2015). Temporal mechanisms have largely been neglected, potentially

311 because they do not present an obvious analogue to language's combinatorial layers. In line
312 with previous work in both primates and bats (Bohn et al. 2008; Schel et al. 2009; Schel et al.
313 2010) we show that, rather than encoding quantitative information related to arousal levels,
314 modifications of temporal patterns can additionally transfer qualitatively different
315 information and we provide evidence for this capacity in an avian system. Although such
316 temporal modifications seem relatively simple and are likely less constrained by the vocal
317 apparatus when compared with changes in frequency-related parameters (Janik and Slater
318 1997), we propose that they may still play an important role in increasing a species' vocal
319 repertoire, and similarly to combinations of discrete sounds, temporal operations might be a
320 widespread mechanism applied by various animals to encode diverse information sets.

321

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422

423 **Figure legends**

424 **Fig. 1** Spectrograms of clucks (top row) and purrs (lower 2 rows) of different individuals.

425 Spectrograms were drawn in a Hamming window (Fast Fourier transformation length 512,

426 75% overlap).

427

428 **Fig. 2** Group size distribution during observational data collection on clucks. Roosting

429 context (grey): group size range=4-7, mean±SD=5±0.9. Foraging context (black): group size

430 range=2-7, mean±SD=5±1.0.

431

432 **Fig. 3** DFA output on cluck and purr elements. Circles represent clusters assuming a

433 multivariate normal distribution with a 95% confidence level. N 1st cluck element=21, N nth

434 cluck element=20, N 1st purr element=19, N nth purr element=19.

435

436 **Fig. 4** Distance a group moved to a foraging site as a function of the number of clucking

437 individuals, in the morning when leaving the roost and during foraging. Shaded areas

438 illustrate the 95% confidence intervals. Dots show the raw data with the size corresponding to

439 the frequency of occurrences. Within the foraging context specifically, the dominant male's

440 contribution to clucking was further investigated. Solid line and triangular dots represent

441 dominant male clucking events; dashed line and circular dots events when the dominant male

442 did not cluck. Roosting context: conditional $R^2=0.64$, N=36; Foraging context: conditional

443 $R^2=0.25$, N=89.