WARWICK
THE UNIVERSITY OF WARWICK

Original citation:
Engesser, Sabrina, Ridley, Amanda R. and Townsend, Simon. (2017) Element repetition rates encode functionally distinct information in pied babbler 'clucks' and 'purrs'. Animal Cognition.

Permanent WRAP URL:
http://wrap.warwick.ac.uk/89798

Publisher's statement:
"The final publication is available at Springer via http://doi.org/10.1007/s10071-017-1114-6

warwick.ac.uk/lib-publications

1   **Element repetition rates encode functionally distinct information in pied babbler**
2   **'clucks' and 'purrs'**
3   Sabrina Engesser [a,b,1], Amanda R. Ridley [b,c,d], Simon W. Townsend [a,b,e,f]

4

5   [a] Animal Behaviour, Department of Evolutionary Biology and Environmental Studies,
6   University of Zurich, 8057 Zurich, Switzerland

7   [b] Pied Babbler Research Project, Kuruman River Reserve, Northern Cape 8467, South Africa

8   [c] Centre for Evolutionary Biology, School of Animal Biology, The University of Western
9   Australia, Crawley WA 6009, Australia

10 [d] Percy FitzPatrick Institute, University of Cape Town, Rondebosch 7701, South Africa

11 [e] Department of Psychology, University of Warwick, Coventry CV4 7AL, United Kingdom

12 [f] Department of Comparative Linguistics, University of Zurich, 8032 Zurich, Switzerland

13

14 [1] Corresponding author:

15 Department of Comparative Linguistics, University of Zurich, 8032 Zurich, Switzerland;
16 email: sabrina.engesser@outlook.com; tel. office.: +41 (0) 634 0223; ORCID-ID: 0000-
17 0003-0425-2179
18

19

20

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 0.75km^2 (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, n^{th} cluck element, 1st purr element, n^{th} 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 permutated 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±SD

220 =2.3±0.4), and purrs of 5-38 (mean±SD =17.4±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

322   **References**

323   Antunes R, Schulz T, Gero S, Whitehead H, Gordon J, Rendell L (2011) Individually
324   distinctive acoustic features in sperm whale codas. Anim Behav 81:723-730.
325   doi:10.1016/j.anbehav.2010.12.019

326   Barto'n K (2014) MuMIn: multi-model inference. R package version 1.10.5. http://cran.r-
327   project.org/package=MuMIn. Accessed 29 Apr 2016

328   Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using
329   lme4. J Stat Softw 67:1-48. doi:10.18637/jss.v067.i01

330   Bell MBV, Radford AN, Rose R, Wade HM, Ridley AR (2009) The value of constant
331   surveillance in a risky environment. Proc R Soc B 276:2997-3005.
332   doi:10.1098/rspb.2009.0276

333   Blumstein DT (2007) The Evolution, Function, and Meaning of Marmot Alarm
334   Communication. Adv Stud Behav 37:371-401. doi:10.1016/s0065-3454(07)37008-3

335   Bohn KM, Schmidt-French B, Ma ST, Pollak GD (2008) Syllable acoustics, temporal
336   patterns, and call composition vary with behavioral context in Mexican free-tailed bats. J
337   Acoust Soc Am 124:1838-1848. doi:10.1121/1.2953314

338   Bousquet CA, Sumpter DJ, Manser MB (2011) Moving calls: a vocal mechanism underlying
339   quorum decisions in cohesive groups. Proc R Soc B 278:1482-1488.
340   doi:10.1098/rspb.2010.1739

341   Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical
342   information-theoretic approach. 2nd edn. Springer, New York

343 Collier K, Bickel B, van Schaik CP, Manser MB, Townsend SW (2014) Language evolution:
344   syntax before phonology? Proc R Soc B 281:20140263. doi:10.1098/rspb.2014.0263

345 DuBois AL, Nowicki S, Searcy WA (2009) Swamp sparrows modulate vocal performance in
346   an aggressive context. Biol Lett 5:163-165. doi:10.1098/rsbl.2008.0626

347 Engesser S, Ridley AR, Townsend SW (2016) Meaningful call combinations and
348   compositional processing in the southern pied babbler. Proc Natl Acad Sci USA 113:5976-
349   5981. doi:10.1073/pnas.1600970113

350 Filzmoser P, Garrett RG, Reimann C (2005) Multivariate outlier detection in exploration
351   geochemistry. Comput Geosci 31:579-587. doi:10.1016/j.cageo.2004.11.013

352 Fox J, Weisberg W (2011) An {R} Companion to Applied Regression. 2nd edn. Sage,
353   Thousand Oaks CA

354 Frank AF (2011) R-hacks/mer-utils.R. https://github.com/aufrank/R-hacks/blob/master/mer-
355   utils.R. Accessed 29 Apr 2016

356 Golabek KA (2010) Vocal communication and the facilitation of social behaviour in the
357   southern pied babbler (*Turdoides bicolor*). Dissertation, University of Bristol

358 Halekoh U, Højsgaard S (2014) A Kenward-Roger Approximation and Parametric Bootstrap
359   Methods for Tests in Linear Mixed Models - TheRPackagepbkrtest. J Stat Softw 59:1-32.
360   doi:10.18637/jss.v059.i09

361 Hollén LI, Bell MBV, Radford AN (2008) Cooperative Sentinel Calling? Foragers Gain
362   Increased Biomass Intake. Curr Biol 18:576-579. doi:10.1016/j.cub.2008.02.078

363 Hollén LI, Bell MBV, Russell A, Niven F, Ridley AR, Radford AN (2011) Calling by
364   Concluding Sentinels: Coordinating Cooperation or Revealing Risk? PLoS ONE
365   6:e25010. doi:0.1371/journal.pone.0025010

366 Humphries D (2012) The mechanisms and function of social recognition in the cooperatively
367   breeding Southern pied babbler, *Turdoides bicolor*. Dissertation, Macquarie University

368 Humphries D, Finch FM, Bell MB, Ridley AR (2016) Vocal Cues to Identity: Pied Babblers
369   Produce Individually Distinct But Not Stable Loud Calls. Ethology 122:609-619.
370   doi:10.1111/eth.12 508

371 Janik V, Slater P (1997) Vocal Learning in Mammals. Adv Stud Behav 26:59-99.
372   doi:10.1016/s0065-3454(08)60377-0

373 Kershenbaum A, Blumstein DT, Roch MA et al. (2014) Acoustic sequences in non-human
374   animals: a tutorial review and prospectus. Biol Rev Camb Philos Soc 91:13-52.
375   doi:10.1111/brv.12160

376 Marler P (1977) The structure of animal communication sounds. Recognition of complex
377   acoustic signals: report of Dahlem workshop. Abakon Verlagsgesellschaft, Berlin

378 Mundry R, Sommer C (2007) Discriminant function analysis with nonindependent data:
379 consequences and an alternative. Anim Behav 74:965-976.
380 doi:10.1016/j.anbehav.2006.12.028

381 R-Core-Team (2014) R: A language and environment for statistical computing. R Foundation
382 for Statistical Computing, Vienna, Austria

383 Radford AN, Ridley AR (2006) Recruitment Calling: A Novel Form of Extended Parental
384 Care in an Altricial Species. Curr Biol 16:1700-1704. doi:10.1016/j.cub.2006.06.053

385 Radford AN, Ridley AR (2007) Individuals in foraging groups may use vocal cues when
386 assessing their need for anti-predator vigilance. Biol Lett 3:249-252.
387 doi:10.1098/rsbl.2007.0110

388 Radford AN, Ridley AR (2008) Close calling regulates spacing between foraging competitors
389 in the group-living pied babbler. Anim Behav 75:519-527.
390 doi:10.1016/j.anbehav.2007.05.016

391 Raihani NJ, Ridley AR (2007a) Adult vocalizations during provisioning: offspring response
392 and postfledging benefits in wild pied babblers. Anim Behav 74:1303-1309.
393 doi:10.1016/j.anbehav.2007.02.025

394 Raihani NJ, Ridley AR (2007b) Variable fledging age according to group size: trade-offs in a
395 cooperatively breeding bird. Biol Lett 3:624-627. doi:10.1098/rsbl.2007.0435

396 Raihani NJ, Ridley AR (2008) Experimental evidence for teaching in wild pied babblers.
397 Anim Behav 75:3-11. doi:10.1016/j.anbehav.2007.07.024

398 Rek P, Osiejuk TS (2012) Temporal patterns of broadcast calls in the corncrake encode
399 information arbitrarily. Behav Ecol 24:547-552. doi:10.1093/beheco/ars196

400 Ridley AR, Wiley EM, Thompson AM (2014) The ecological benefits of interceptive
401 eavesdropping. Funct Ecol 28:197-205. doi:10.1111/1365-2435.12153

402 Schel AM, Candiotti A, Zuberbühler K (2010) Predator-deterring alarm call sequences in
403 Guereza colobus monkeys are meaningful to conspecifics. Anim Behav 80:799-808.
404 doi:10.1016/j.anbehav.2010.07.012

405 Schel AM, Tranquilli S, Zuberbühler K (2009) The alarm call system of two species of black-
406 and-white colobus monkeys (*Colobus polykomos* and *Colobus guereza*). J Comp Psychol
407 123:136-150. doi:10.1037/a0014280

408 Sharp SP, McGowan A, Wood MJ, Hatchwell BJ (2005) Learned kin recognition cues in a
409 social bird. Nature 434:1127-1130. doi:10.1038/nature03522

410 Sueur C, Deneubourg JL (2011) Self-Organization in Primates: Understanding the Rules
411 Underlying Collective Movements. Int J Primatol 32:1413-1432. doi:10.1007/s10764-011-
412 9520-0

413 Thompson A (2012) Post-fledging begging and development in Southern Pied Babblers
414 (*Turdoides bicolor*). Dissertation, University of Cape Town

415   Venables WN, Ripley BD (2002) Modern Applied Statistics with S. 4th edn. Springer, New
416   York

417   Wheatcroft D (2015) Repetition rate of calls used in multiple contexts communicates
418   presence of predators to nestlings and adult birds. Anim Behav 103:35-44.
419   doi:10.1016/j.anbehav.2015.02.009

420   Zuberbühler K (2015) Linguistic capacity of non-human animals. WIREs Cogn Sci 6:313-
421   321. doi:10.1002/wcs.1338
422

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 n^{th}

434 cluck element=20, N 1st purr element=19, N n^{th} 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.