

Morphologically structured vocalisations in female Diana monkeys

Camille Coye^{1,2,3}, Klaus Zuberbühler^{2,3,4}, Alban Lemasson¹

¹ Université de Rennes 1, Ethologie animale et humaine - EthoS, U.M.R 6552-C.N.R.S, Station Biologique, 35380 Paimpont, France; ² University of St Andrews, School of Psychology and Neuroscience, St Andrews, Fife KY16 9AJ, UK; ³ Centre Suisse de Recherches Scientifiques, Tai Monkey Project, Adiopodoumé, Abidjan Ivory Coast; ⁴ Université de Neuchâtel, Institut de Biologie, rue Emile Argand 11, 2000 Neuchâtel, Switzerland

Corresponding author: E-mail: camille.coye@univ-rennes1.fr; Phone : 00332.99.61.81.55
Postal address: Station Biologique de Paimpont, 35380 Paimpont

Social complexity is often thought of as a driving force in the evolution of communication and cognition, but this is at odds with the fact that non-human primates generally display only very limited flexibility in vocal production. Some primates partially overcome their limited vocal flexibility by combining two or more acoustically inflexible calls into complex sequences. Equally relevant is that some primate calls consist of separable morphological elements whose combinations create different meanings. Here, we focus on the vocal system of wild female Diana monkeys (*Cercopithecus diana diana*), who produce three call units (R, L, A) either singly or merged as RA or LA call combinations. Previous work has shown that R and L convey information about external events, while A conveys information about caller identity. We tested this hypothesis experimentally, by broadcasting artificially combined utterances to eight adult females. To test the significance of the R and L ‘event’ units, we merged them with the A ‘identity’ unit of a group member. To test the significance of the ‘identity’ unit, we merged an R ‘event’ unit with an ‘identity’ unit from a group member or a neighbouring individual. Subjects responded in ways that suggested that both event and identity units were relevant, suggesting that Diana monkeys’ social calls possess morpho-semantic features. We discuss this finding in relation to the co-evolution of communication and social complexity in primates.

Keywords: acoustic playback, call combination, field experiment, guenons, morphology, social communication

32 INTRODUCTION

33 The evolution of vocal complexity in animals appears to be largely driven by social complexity
34 as well as by visually difficult and ecologically challenging habitats (Bouchet, Blois-Heulin, &
35 Lemasson, 2013; Dunbar, 1993; Dunbar, 1998; Marler, 1967; McComb & Semple, 2005).
36 Many vertebrates and most primates live in social groups with complex and dynamic social
37 networks and long-term bonds (de Waal, 1987; Lehmann, Korstjens, & Dunbar, 2007;
38 Wrangham, 1987). As a result, primates are constantly challenged to maintain cohesion during
39 travel and other activities to optimise foraging, to compete with neighbouring groups and to
40 protect themselves against predators (Dunbar & Shultz, 2007; Lehmann et al., 2007; van
41 Schaik, 1983; van Schaik & van Hooff, 1983). To this end, many species evolved specific
42 vocalisations to maintain cohesion and synchronise within-group activities (Gautier & Gautier,
43 1977; Oda, 1996; Uster & Zuberbühler, 2001). Calls are often individually distinct and function
44 to advertise individual identity or membership to specific social units (Bouchet, Pellier, Blois-
45 Heulin, & Lemasson, 2010; Crockford, Herbinger, Vigilant, & Boesch, 2004; Dunbar, 2003;
46 Neumann, Assahad, Hammerschmidt, Perwitasari-Farajallah, & Engelhardt, 2010; Rendall,
47 Rodman, & Emond, 1996).

48

49 In light of this, it is surprising that non-human primates are thought to have relatively limited,
50 species-specific vocal repertoires with a fixed set of call types that remain largely unchanged
51 throughout adult life (review by Bouchet et al., 2013) and little signs of flexibility or voluntary
52 control in call production (Hammerschmidt & Fischer, 2008). However, a more recent line of
53 research has continued to demonstrate a previously under-described source of communicative
54 complexity, namely the ability of individuals to assemble fixed acoustic units of their repertoire
55 into more complex utterances. There is now good evidence that several non-human primate
56 species produce calls in non-random sequences, with the information changing depending on

57 the order or temporal structure of call sequences (vervet monkeys *Chlorocebus aethiops*:
58 Seyfarth, Cheney, & Marler, 1980; Campbell's monkeys *Cercopithecus Campbelli*: Lemasson,
59 Ouattara, Bouchet, & Zuberbühler, 2010; Ouattara, Lemasson, & Zuberbühler, 2009a;
60 Zuberbühler, 2001; white-handed gibbons *Hylobates lar*: Clarke, Reichard, & Zuberbühler,
61 2006; bonobos *Pan paniscus* and chimpanzees *Pan troglodytes*: Clay & Zuberbühler, 2011;
62 Slocombe & Zuberbühler, 2005; Diana monkeys *Cercopithecus diana diana*: Zuberbühler,
63 2000). One argument has been that these combinatorial capacities evolved in primates to enable
64 more complex communication (Zuberbühler & Lemasson, 2014).

65

66 So far, however, most examples of call combinations are from studies on male primate alarm
67 calls, which is surprising because social events may be at least as complex as dealing with
68 predator encounters. Hence, if complex vocal abilities have evolved to deal with social
69 complexity, we should find combinatorial phenomena in vocal behaviour during social
70 interactions and also in females, the social core of primates species (Buzzard & Eckardt, 2007;
71 Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987).

72

73 One particularly promising candidate is the contact call of some forest living female guenons.
74 In Campbell's monkeys, for instance, adult females produce a short, low-pitched contact call,
75 either as a single unit or merged with a second long, arched, and frequency-modulated unit to
76 form multi-unit utterances (Lemasson & Hausberger, 2011). The acoustic structure of the first
77 unit varies depending on the degree of arousal experienced by the caller (Lemasson, Remeuf,
78 Rossard, & Zimmermann, 2012) and contains fewer identity cues than the second, arched unit,
79 which strongly relates to the caller's identity (Lemasson & Hausberger, 2011; Lemasson,
80 Hausberger, & Zuberbühler, 2005; Lemasson, Ouattara, Petit, & Zuberbühler, 2011). The

81 second unit is never uttered alone but functions as an affixation to the first unit, which can also
82 be uttered alone.

83 A second relevant example is the contact calls of female Diana monkeys, an arboreal forest-
84 dwelling primate living in groups of one adult male and seven to thirteen adult females with
85 their offspring (McGraw, Zuberbühler, & Noë, 2007). As in most primates, the females are the
86 philopatric sex and constitute the social core of the group (Candiotti et al., 2015). They produce,
87 amongst others, three acoustically distinct social calls (L, R and A) depending on context
88 (Candiotti, Zuberbühler, & Lemasson, 2012a, 2012b; Uster & Zuberbühler, 2001): L calls are
89 mostly given in socio-positive and neutral events (e.g., foraging, affiliative interactions). R calls
90 are mostly given in socio-negative events and mild danger (e.g., conflict within or between
91 groups, walking on the ground), suggesting that these calls relate to the external events or
92 emotional valences experienced by the caller. A calls, finally, are produced in unspecific ways
93 to a large variety of events, but here the acoustic structure varies substantially between
94 individuals, suggesting they function to signal the caller's identity, similar to what has been
95 found in Campbell's monkeys. The three call types can be emitted alone (A, L, R) or merged
96 as two combined utterances, either LA, or RA. Combined structures thus contain information
97 about the external event (L or R) and the caller's identity (Candiotti et al., 2012a, 2012b), with
98 some interesting parallels to the function of morphemes in human speech (Collier, Bickel,
99 Schaik, Manser, & Townsend, 2014; Hurford, 2008; Tellier, 2008; Veselinovic, Candiotti, &
100 Lemasson, 2014).

101

102 Here, we tested experimentally whether the information conveyed by complex calls of Diana
103 monkeys is compositional, i.e., whether the combined calls relate linearly to the information
104 conveyed by the units given singly, as suggested by Candiotti et al.'s (2012a) observational
105 data. To this end, we broadcast artificially combined calls to different subjects, eight female

106 Diana monkeys belonging to a study group habituated to human presence. We created
107 experimental stimuli by manipulating either the initial or final call unit using recordings from
108 group members, neighbours and completely unfamiliar individuals. Our goal was to test the
109 significance of the L and R ‘event’ and A ‘identity’ units. To this end, we merged L and R units
110 with A ‘identity’ units from familiar group members or neighbouring individuals. We predicted
111 that, if combinations of call units were meaningful to receivers, L and R units should cause
112 significant behavioural differences, particularly in terms of vocal responses, vigilance and
113 exploratory behaviours. Because Diana monkeys are highly territorial, we also predicted
114 different behavioural responses to identity-encoding A units, depending on whether they
115 originated from a group member or neighbour.

116

117 MATERIAL AND METHODS

118 *Study site and subjects*

119 Field experiments were conducted between June and September 2014 in Taï National Park,
120 Ivory Coast (5°50’N, 7°21’W). The experimenter (CC) and two field assistants (FB and FG)
121 conducted playback experiments in a free-ranging group of Diana monkeys (*Cercopithecus*
122 *diana diana*) with individually known subjects habituated to human presence for more than
123 twenty years. At the time of the experiments, the group consisted of one adult male and eight
124 adult females with their offspring. The experiment involved all the adult females of the
125 habituated group.

126 *Playback stimuli*

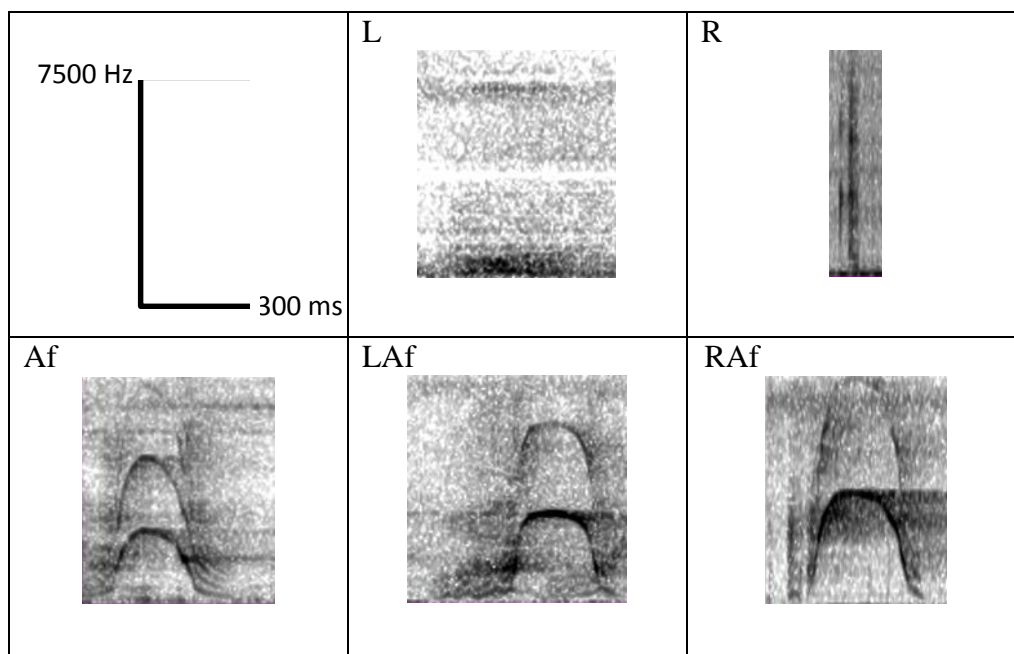
127 All calls (stimuli and subject’s reaction to the playbacks) were recorded using a Sennheiser
128 K6/ME66 directional microphone connected to a Marantz PMD660 recorder (sampling rate
129 44.1 kHz, resolution 16 bits, WAV sound format) in Taï National Park. Calls from group

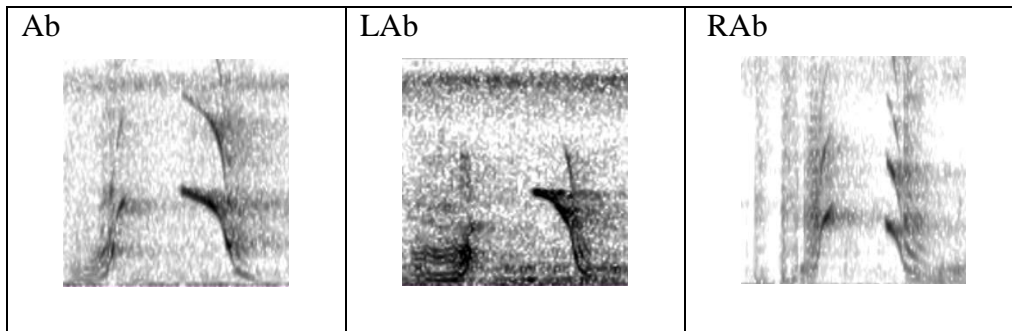
130 members were recorded in May 2014; calls from unfamiliar and neighbouring Diana monkeys
 131 were recorded in June-July 2013 and February-June 2010. All calls were recorded under similar
 132 environmental conditions and distances to ensure high quality, low background noise, and no
 133 overlap with any other sound.

134

135 When creating the playback stimuli, we followed Candiotti et al., (2012a) classification (Fig.
 136 1), who define L call units as continuous low-pitched trills with a general ascending frequency
 137 modulation (duration \pm SD: 409 \pm 106 ms, Minimum fundamental frequency \pm SD: 247 \pm 84 Hz,
 138 Maximum fundamental frequency \pm SD: 654 \pm 354 Hz), R call units as rapid repetitions of one to
 139 four short atonal units separated by brief periods of silence (duration \pm SD: 82 \pm 29 ms, Minimum
 140 fundamental frequency \pm SD: 331 \pm 170 Hz, Maximum fundamental frequency \pm SD: 429 \pm 199 Hz,
 141 First unit duration \pm SD: 28 \pm 11 ms, First inter-unit silence \pm SD: 46 \pm 18 ms) and A call units as
 142 tonal, arch-shaped frequency modulations (duration \pm SD: 298 \pm 105 ms, Minimum fundamental
 143 frequency \pm SD: 324 \pm 233 Hz, Maximum fundamental frequency \pm SD: 3090 \pm 696 Hz).

144



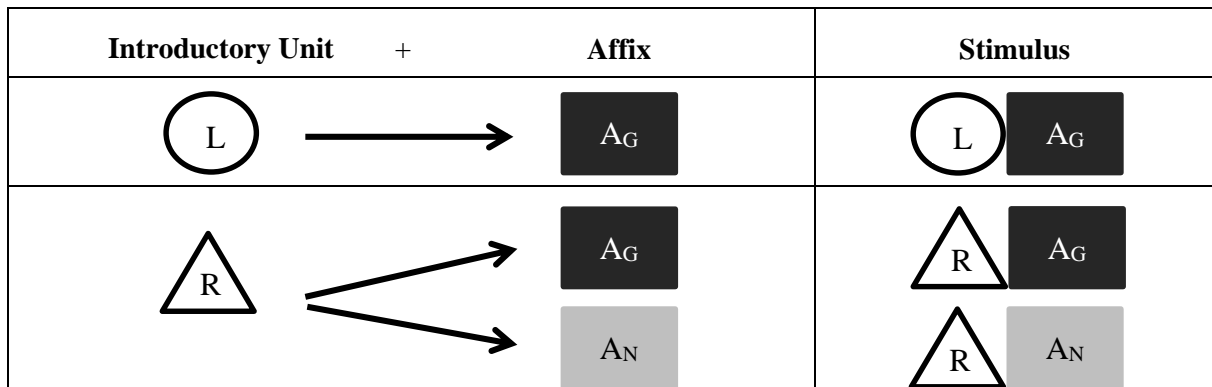


145 Figure 1: A, L and R call exemplars from female Diana monkeys emitted alone or merged into combined
 146 calls LA and RA (Ab and Af being two sub-types of A call).

147

148 We created twenty-four different playback stimuli to generate the following three categories
 149 (Fig. 2): LA_G : combination of an unfamiliar individual's L merged with an A from an adult
 150 female group member ($N=8$); RA_G : combination of an unfamiliar individual's R merged with
 151 an A from an adult female group member ($N=8$); RA_N : combination of an unfamiliar
 152 individual's R merged with an A from an adult female from a neighbouring group ($N=8$).

153



154 Figure 2: Stimulus creation. The geometric shapes indicate the valence of the call. Circle and triangle
 155 represent context-dependent units, respectively L (associated with positive and neutral events) and R
 156 (associated with negative events). Rectangles represent identity-dependent units A. The shading
 157 indicates the origin of the call recorded: white: unfamiliar individuals; black: group-members; grey:
 158 neighbouring individuals.

159

160 Each of the eight subjects received its own set of LA_G , RA_G and RA_N call combinations. Within
 161 a given set, we systematically used the same R call unit and the same A call unit to create paired
 162 stimuli (i.e., LA_G - RA_G and RA_G - RA_N) to allow the comparison of the changes in subject's
 163 reaction due to changes in only one part of the call. L and R call units were systematically

164 extracted from naturally produced LA and RA call unit combinations. We further made sure
165 that all unfamiliar L and R call units came from different individuals by using recordings from
166 a different group. Only R calls composed of double units were used. ‘A’ call units were from
167 identified and habituated adult females of the focal group (A_G) or the neighbouring group (A_N).
168 For each focal female, group or neighbour identities were pseudo-randomly attributed. This
169 was done to avoid complete pair-matching between group members: if the call from female A
170 was used as a stimulus for female B, then the call from female B was not selected to serve as
171 stimulus for female A, to prevent any particular social relationship between two individuals to
172 be over-represented. ‘A’ call units can be subdivided into full arches (Af subtype) or broken
173 arches (Ab subtype) (Fig. 1). Females differ in how they make use of this feature, with some
174 females mainly using ‘Af’ or ‘Ab’ subtypes (Candiotti et al., 2012a). When editing playback
175 stimuli, we used a group-member’s most typical A subtype which was then matched with the
176 corresponding subtype for the neighbouring female stimulus.

177

178 Playback stimuli were created using Raven Pro 1.4 Software. Call exemplars were selected
179 based on recording quality and call duration (in seconds: mean \pm SE: L = 0.170 ± 0.012 s, R =
180 0.108 ± 0.002 s, A = 0.293 ± 0.014 s). We amplified stimuli when necessary to obtain a
181 naturalistic intensity. Final tests of broadcast intensity were made in the Taï National Park to
182 make sure that stimuli’s intensity was homogeneous and appropriate according to the natural
183 background noise.

184

185 *Experimental protocol*

186 Three observers followed the study group from 9:00 to 17:00 local time. Before the first
187 experiment, we ran a habituation phase on several consecutive days during which the equipment
188 was installed underneath the middle of the group in an open area so that it was fully visible to

189 the subjects. We repeated this until the subjects stopped giving alert calls and lost interest in the
190 equipment. Before starting an experimental trial, we ensured that the group was not travelling
191 or foraging 30 m or higher, that no neighbours were in the vicinity and that no male loud calls
192 had been produced for at least 15 min. The experimenters then selected the subject and
193 positioned the playback equipment at an elevation of 4 to 6 m above ground using a telescopic
194 perch, either in periphery of the group (stimuli made from neighbouring female calls) or within
195 the group. For within group trials, we kept the speaker about 5 m to 10 m away from the A call
196 unit providing female. We did not wait for the subject to move to a specific position within the
197 group and tested her where she was. Hence, playbacks of intra-group calls have been given
198 from varied positions (more or less peripheral) in the group, without any obvious consequence.
199 For each playback, CC continuously observed the subject, while FB and FG followed the call
200 provider (in-group trials) and handled the equipment, respectively. Before initiating a trial, we
201 ensured that (1) the subject was fully visible, (2) the call provider was 5 to 10 m away from the
202 speaker, and (3) no call was given by any group member for at least 8 s.

203

204 Playback stimuli were broadcast from a Marantz PMD660 solid-state recorder connected to a
205 Nagra DSM speaker/amplifier and a Bose 151 Environmental speaker that had been mounted
206 to a telescopic perch. We recorded the behaviour of the subject for 30 s and the group's vocal
207 behaviour for 60 s following each trial.

208

209 We never performed more than two trials per day and never for more than two days in a row.
210 We ensured that we never broadcast two combined calls of the same category within the same
211 day and we did not test the same individual in two consecutive experiments. Each day, we
212 performed one to three "mock" experiments (even on days when no experiment was scheduled)

213 by executing the full experimental protocol, but no sound diffusion, to prevent subjects from
214 anticipating a trial.

215

216 *Dependent variables*

217 During the 30 s post-playback period, we described the behaviour of the subject as the total
218 duration (s) and frequency (i.e., the number of times a behaviour was observed) of its posture
219 (i.e., sitting, standing or in vigilance posture), locomotion (i.e., immobile, walking, running or
220 jumping) and direction of gaze (i.e., looks at the speaker, above, under, at a conspecific, at the
221 observer and scans the environment). We also scored the latency in seconds for four behaviours:
222 adopting a vigilance posture, sitting, walking and looking at the speaker. Overall, this resulted
223 in 32 variables to describe each subject's behavioural response.

224

225 During the 1 min post-playback period, we also quantified the group's vocal activity using the
226 following variables: the latency to give first call (any call type), the number of social calls
227 (Coye, Ouattara, Zuberbühler, & Lemasson, 2015), the number of alert calls (Coye et al., 2015),
228 the number of calls given during vocal exchanges (a sequence of any calls separated by less
229 than 3 s of silence), the number of isolated calls (any call given more than 3 s before or after
230 another call), as well as the number of vocal exchanges (involving any call type) and the average
231 number of calls involved in a vocal exchange.

232

233 *Statistical analysis*

234 We expected the subjects' responses to differ in several subtle behavioural indicators
235 simultaneously (notably locomotion, vocalizations and direction of gaze), suggesting that
236 multivariate testing was most appropriate to deal with the potential co-variation of the variables.
237 Any pair of variables with an R Pearson's correlation coefficient above 0.7 was considered

238 colinear in case of which we systematically deleted one member of the colinear pair (Dormann
239 et al., 2013; Katz, 2011). Then, we used a Linear Discriminant Analysis as a preliminary guide
240 for variables selection but did not use this method for further statistical analysis due to repeated
241 measures present in our data (see Mundry & Sommer (2007) for details on LDA and discussion
242 of the case of repeated measures). This first, exploratory, step led to the selection of a subset of
243 seven biologically relevant variables susceptible to represent subjects' reaction (group's vocal
244 behaviour, subject locomotion and gaze direction) across the experimental conditions. We used
245 five quantitative variables: Number of isolated calls (given more than 3 seconds before or after
246 another call), Latency to give first call (s), Time spent walking (s), Latency before locomotion
247 (s), Duration of first look to the speaker (s), and two binary variables: Presence/absence of Look
248 towards the observer, and Presence/absence of Visual scanning of the environment (Fig. 3).

249

250 We calculated Gower's dissimilarity index between samples in the dataset (`daisy{cluster}`, R
251 statistical software, Maechler et al., 2015). This index "summarises" the difference between
252 two samples into a measure of distance, based on the samples' values for each variable included
253 in the analysis. Gower's distance is a common method which allows the use of various types of
254 variables (binary, ordinal, nominal and quantitative variables) (Gower, 1971; Oksanen et al.,
255 2007; Podani, 1999). The two binary variables were treated as symmetric variables and no
256 standardisation of variables was applied.

257

258 To study the impact of the introductory unit (L or R units) and the impact of the affix (A units
259 from a group-member or a neighbour), we performed two separate non-parametric MANOVAs
260 (`Adonis{vegan}`, R statistical software, Oksanen et al., 2007) on the matrixes of Gower's
261 dissimilarity index, giving the distance between trials in LA_G-RA_G and RA_G-RA_N conditions
262 respectively. Both NPMANOVAs were two-tailed, included the type of stimulus and the

263 identity of the subject as factors and were conducted using free permutation of the distance
264 matrixes, as suggested by Anderson (2001) and Gonzalez and Manly (1998) for small datasets.

265

266 NPMANOVA is a non-parametric multivariate method involving the calculation of an F-ratio
267 on an index of distances between samples. The computation of a p-value, like any other
268 permutational test, involves a comparison of the test value (i.e., the F-ratio) obtained on the
269 original dataset (i.e., the distance matrix) with test values computed on random permutations of
270 the same dataset. See Anderson (2001) for detailed explanation of the method and equations,
271 as well as Adams and Anthony (1996) for a discussion of the use of permutational tests on
272 behavioural data.

273

274 We completed the analysis with graphic representation of the results to describe the nature of
275 the behavioural changes (Fig. 3). We computed effect size for each variable included in the
276 multivariate testing. We used Cliff's delta for the quantitative (i.e., count and continuous)
277 variables (`cliff.delta{effsize}`), R statistical software, (Torchiano, 2015) using the original
278 formula proposed by (Cliff, 2014). And we used risk difference (`riskdifference{fmsb}`), R
279 statistical software (Nakazawa, 2015) with a 95% confidence interval for the binary variables.

280

281 *Ethical note*

282 Ethics approval was given by the St Andrews' University Ethics Boards; the research protocol
283 was authorised in Côte d'Ivoire, by the Minister of Scientific Research and the 'Office Ivoirien
284 des Parcs et Réserves' (OIPR). This study does not raise major issues regarding animal welfare.
285 Study groups have been habituated to human presence and followed on a regular basis since
286 1990 while the continued presence of researchers and field assistants has had a significant
287 impact on decreasing firearms-based poaching activities in the area. The habituation to the

288 playback equipment was conducted smoothly. Moreover, the call types broadcast during the
289 playbacks are naturally given at relatively high frequency: LA calls: 19.8 calls per hour, RA
290 calls: 2.7 calls per hour (Candiotti et al. 2012a). Intergroup encounters, as simulated by
291 playbacks of RA_N combinations (involving A calls from a neighbour), occur on average once
292 every three days (McGraw et al., 2007 p59). No playback enhanced male alarm calling
293 behaviour or triggered any sign of group panic or other abnormal behaviour.

294

295 RESULTS

296 *Impact of the Introductory Unit on subjects' reaction:*

297 When analysing the impact of the introductory unit, the NPMANOVA showed a significant
298 impact of the type of stimulus ($F_{1,7}= 3.37, P=0.043$) and no significant effect of the subject's
299 identity ($F_{7,7}= 1.71, P=0.142$). Graphic representation of the variables measured, combined
300 with measures of effect size, show that test subjects expressed distinct behavioural patterns in
301 the different experimental conditions (Fig. 3). Playbacks of LA_G ('positive' introduction, A
302 from a group member) and RA_G ('negative' introduction, A from a group member) stimuli
303 caused differences in locomotion, vocal behaviour and gaze direction (Fig. 3). Latency before
304 locomotion appears shorter after playbacks of RA_G than LA_G (medium effect size: $N= 16, Cliff's$
305 $delta= -0.47$), although we found no clear difference in the time spent walking (negligible effect
306 size: $N= 16, Cliff's delta= -0.125$). The group gave more isolated calls (i.e., calls not part of a
307 vocal exchange) in the RA_G than in the LA_G condition, with a medium effect size ($N= 16, Cliff's$
308 $delta= -0.47$). The latency to give a first call was shorter and much less variable in the RA_G than
309 in the LA_G condition although only a negligible effect was detected ($N= 16, Cliff's delta=$
310 0.125). Finally, the duration of the first look towards the speaker ($N= 16, Cliff's delta= -0.031,$
311 negligible effect) and the presence of looks towards the observer ($N= 16, RD= -0.125, P= 0.285$)

312 did not change between LA_G and RA_G conditions (0% of the LA_G trials, 12.5% of the RA_G
 313 trials), but subjects scanned the environment more after the playback of the negative (i.e., RA_G)
 314 stimulus (37.5% of the trials) than after playbacks of LA_G (0% of the trials; $N=16$, $RD=0.375$,
 315 $P=0.028$).

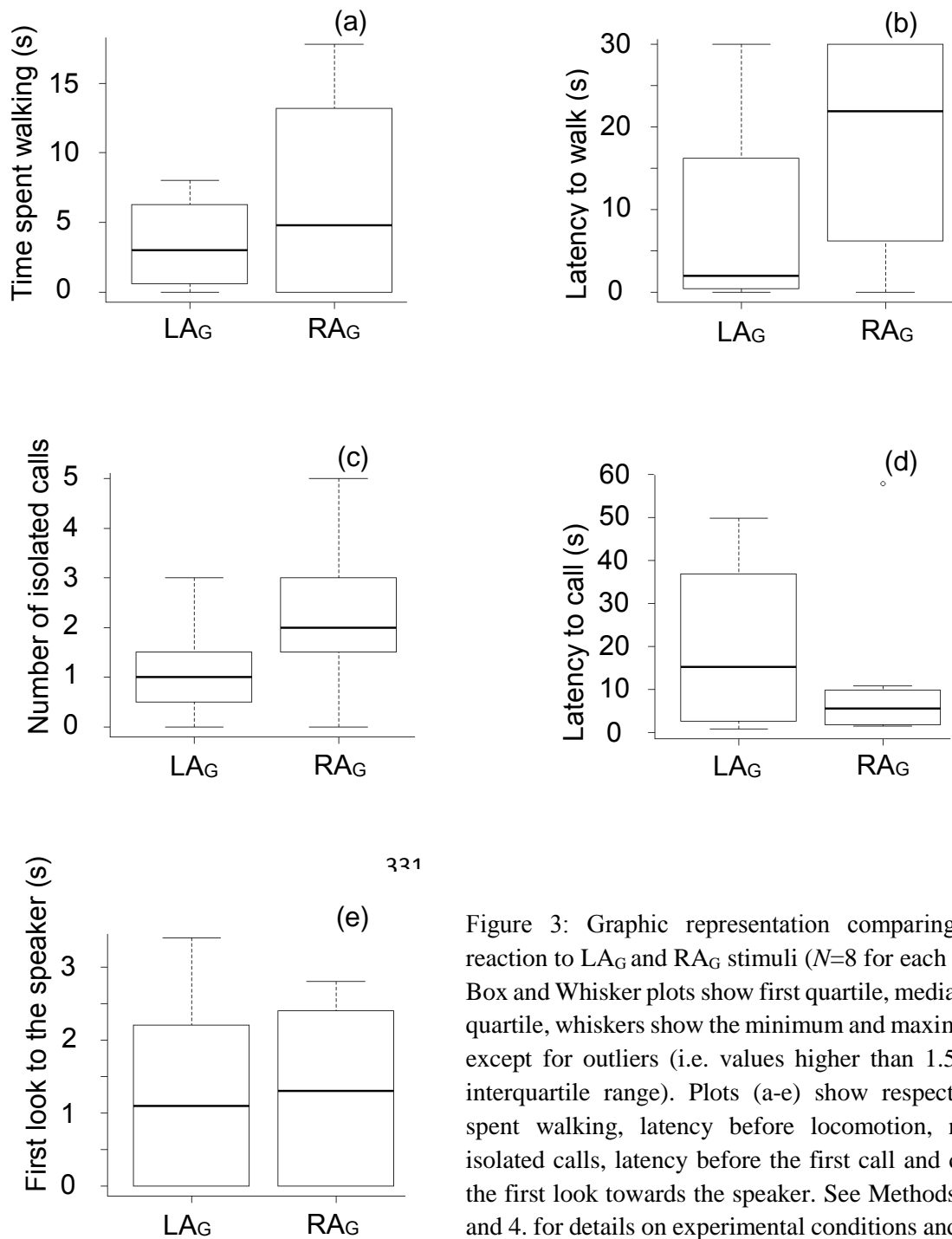


Figure 3: Graphic representation comparing subjects' reaction to LA_G and RA_G stimuli ($N=8$ for each condition). Box and Whisker plots show first quartile, median and third quartile, whiskers show the minimum and maximum values except for outliers (i.e. values higher than 1.5 times the interquartile range). Plots (a-e) show respectively time spent walking, latency before locomotion, number of isolated calls, latency before the first call and duration of the first look towards the speaker. See Methods section 2. and 4. for details on experimental conditions and variables.

343 *Impact of the affix on subjects' reaction:*

344 When analysing the impact of the affix, the NPMANOVA showed a significant impact of the
345 type of stimulus involved ($F_{1,7} = 4.29$, $P = 0.02$) and no significant role of subject's identity
346 ($F_{7,7} = 1.66$, $P = 0.155$). Graphic representation of the variables, combined with measures of
347 effect size, show that test subjects expressed distinct behavioural patterns in the experimental
348 conditions (Fig. 4): Comparison between responses to RA_G ('negative' introduction, A from
349 group member) and RA_N ('negative' introduction, A from a neighbour) stimuli highlighted
350 differences in locomotion, vocal behaviour and gaze direction but with a different pattern from
351 the one found for the impact of the introductory unit (Fig. 4). Subjects spent less time walking
352 ($N = 16$, *Cliff's delta* = 0.31, small effect size) and had a greater latency before locomotion ($N =$
353 16 , *Cliff's delta* = -0.38, medium effect size) after playback of RA_N than RA_G stimuli. The
354 results also suggest slight differences in group's vocal behaviour: groups gave fewer isolated
355 calls ($N = 16$, *Cliff's delta* = 0.33) and displayed slightly greater and more variable latencies
356 when giving the first calls ($N = 16$, *Cliff's delta* = -0.23) after playbacks of RA_N than RA_G
357 stimuli. Finally, the pattern of gaze direction differed strongly between RA_G and RA_N stimuli:
358 after playbacks of RA_N stimuli, subjects' first looks to the speaker were longer ($N = 16$, *Cliff's*
359 *delta* = -0.73) with a large effect size. Subjects looked more at the observer ($N = 16$, *RD* = -0.375,
360 $P = 0.077$) in the RA_N condition (50% of the RA_N trials vs 12.5% of the RA_G trials) but visual
361 scanning of the environment did not seem to differ strongly between the playback of RA_G
362 (37.5% of the trials) and RA_N (12.5% of the trials) stimuli ($N = 16$, *RD* = 0.25, $P = 0.23$).

363

364
365
366
367
368
369
370
371
372
373
374
375
376
377
378
379
380
381
382
383
384
385
386
387
388
389
390
391
392
393
394

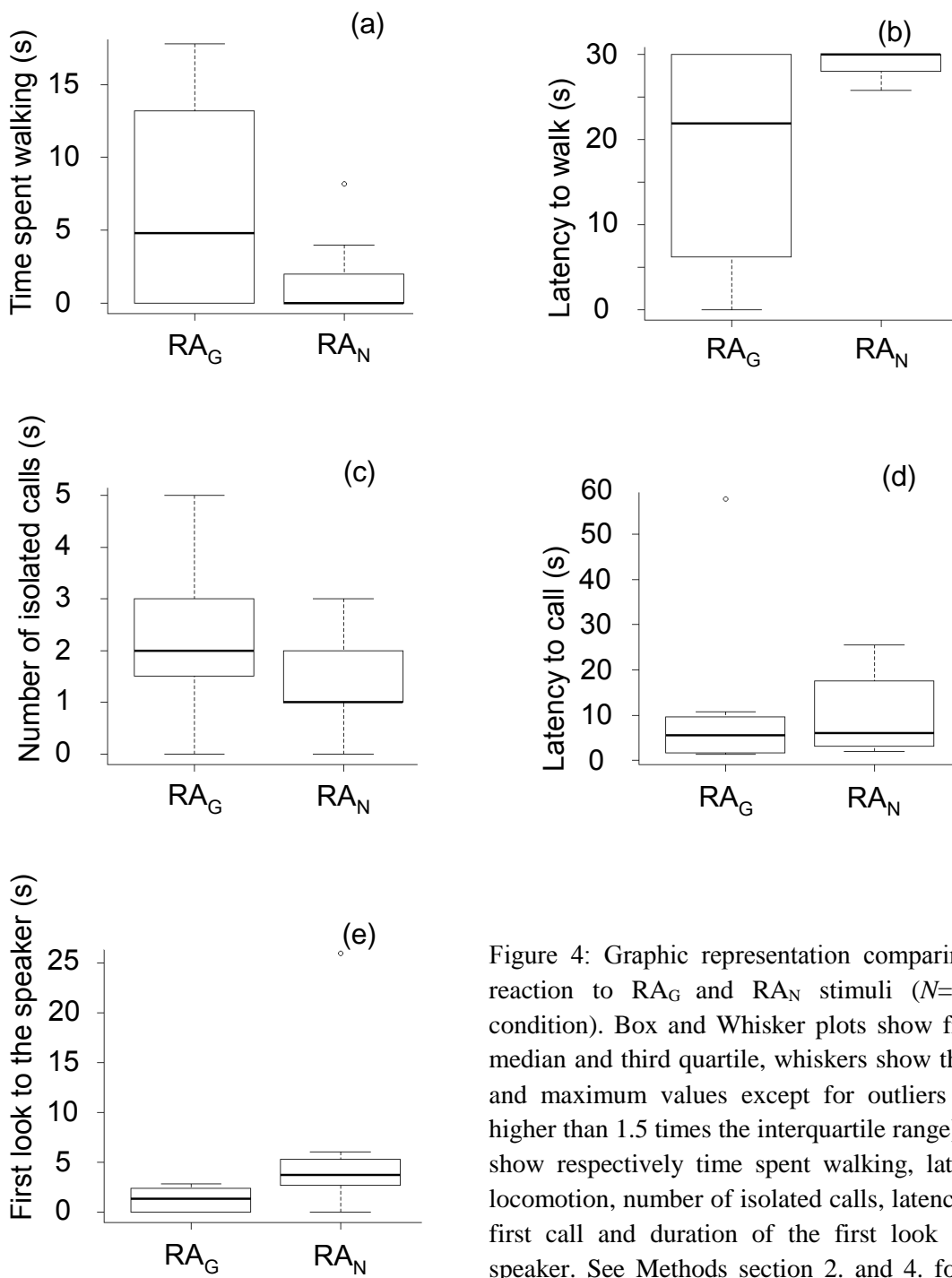


Figure 4: Graphic representation comparing subjects' reaction to RA_G and RA_N stimuli ($N=8$ for each condition). Box and Whisker plots show first quartile, median and third quartile, whiskers show the minimum and maximum values except for outliers (i.e. values higher than 1.5 times the interquartile range). Plots (a-e) show respectively time spent walking, latency before locomotion, number of isolated calls, latency before the first call and duration of the first look towards the speaker. See Methods section 2. and 4. for details on experimental conditions and variables.

395 DISCUSSION

396 In this study, we demonstrated experimentally that Diana monkeys responded differently to
397 social calls composed of different morphological units in ways that suggested that at least two
398 levels of information were conveyed. Morphological compounds consisted of L or R units,
399 which related to different external events experienced by the caller (Candiotti et al., 2012a),
400 and of A units, which related to caller identity. Response pattern suggested that recipients
401 attended to these different levels of information conveyed by the call compounds. Specifically,
402 our findings supported the idea that the initial morphemic unit of a combined call (L or R)
403 encodes information about the social context experienced by the caller. R call units are typically
404 associated with negative events, such as the detection of mild danger. Here, subjects responded
405 with isolated social calls, prolonged latency before locomotion and scanning of the environment
406 compared to L call units (typically associated with neutral and positive events) Overall, these
407 results suggest that recipients associated the R and L call units with distinct socio-
408 environmental contexts and adapted their behaviour accordingly.

409
410 The ability to reveal one's motivational states is a well-known function of animal
411 communication (Briefer, 2012; Lemasson et al., 2012; Schehka & Zimmermann, 2009; Taylor
412 & Reby, 2010), although it is often difficult to make a compelling argument about the exact
413 nature of the underlying inner processes. Interestingly, the acoustically homologous call of
414 Diana's monkey L unit in Campbell's monkeys increases in duration and frequency according
415 to presumed differences in arousal (Lemasson et al., 2012). Here, we confirm the importance
416 of this acoustic component to convey information about the emotional context, but we also
417 show a different use in Diana monkey, whose social calls (L vs R) relate to the general valence
418 of the external world as perceived by the caller. Importantly, L and R call units can be emitted
419 singly or, more often, combined with A units into a compound call. More detailed contextual

420 analyses are required to determine which social situations are associated with single or
421 combined calls. For example, it is possible that the distance between the caller and the receiver
422 determines whether an A unit is affixed. Another possible explanation lies in variations in the
423 degree of visibility in the habitat (Candiotti et al., 2012a, 2012b).

424

425 Call compounds that contained A units from a neighbouring individual ('RA_N') triggered a high
426 decrease of locomotion, a slight decrease of vocal activity and an increased visual scanning
427 towards the presumed caller compared to call compounds that contained A units from a group-
428 member ('RA_G'). This pattern is similar to what has been observed in other primates reacting
429 to unexpected stimuli (Bergman, Beehner, Cheney, & Seyfarth, 2003; Briseño-Jaramillo,
430 Estrada, & Lemasson, 2014; Zuberbühler & Wittig, 2011). These behavioural patterns suggest
431 that both RA stimuli were perceived as urgent but that subjects based decisions on differences
432 in the Affix.

433

434 Individual acoustic variations and auditory discrimination by receivers have been reported in
435 many primate species (putty-nosed monkeys *Cercopithecus nictitans*: Price, Arnold,
436 Zuberbühler, & Semple, 2009; marmosets *Callithrix jacchus*: Miller & Thomas, 2012; Olive
437 baboons *Papio hamadryas anubis*: Lemasson, Palombit, & Jubin, 2008; Japanese macaques
438 *Macaca fuscata*: Ceugniet & Izumi, 2003; squirrel monkey *Saimiri sciureus*: Kaplan, Winship-
439 Ball, & Sim, 1978), suggesting that providing identity cues in primate calls is of considerable
440 biological importance (Blumstein, Verneyre, & Daniel, 2004; Lemasson et al., 2007; Seyfarth
441 et al., 2010; Seyfarth & Cheney, 2010).

442 This is likely so in this species in which vocal exchanges play an important role to ensure social
443 cohesion and in which females differ in their vocal activity depending on their social integration
444 within the group (Candiotti et al., 2015). In line with this, a previous study on Campbell's

445 monkeys found that familiar calls (using homologous calls of Diana monkeys' LA) elicited
446 more affiliative calling and vocal responses than unfamiliar calls (Lemasson et al., 2005). Taken
447 together, the responses given by the subjects to the different types of stimuli suggest that the
448 first unit (i.e., L or R) allows the receiver to get information about the direct social and physical
449 environment –probably by associative learning- while the identity conveyed by the second unit
450 (A) may influence receiver's decision regarding the behaviour to adopt in line with their
451 respective positions in the social network. For example, receivers may have different reactions
452 depending on the identity of the caller when hearing an RA call which signals that a given
453 individual has spotted something disturbing. But it seems premature to draw stronger
454 conclusions about the relative importance of both types of information conveyed as here no
455 playback of LA_N call was done. In future experiments, it would therefore be necessary to test
456 subjects' reaction to L call units combined with A call units from neighbours as well as L call
457 units combined with A calls from immature or more or less affiliated group members.

458

459 Our study has high external validity because the data are from spontaneous reactions of
460 untrained and free-ranging animals living in their natural habitat. The results obtained here
461 suggest that the main social calls given by the adult females are linear combinations of different
462 morphological units that convey information about the social context and the identity of the
463 caller. In a related study based on analysis tools from formal linguistics (Veselinovic et al.,
464 2014), call sequences of wild adult females Diana monkeys were analysed which revealed non-
465 random patterns in terms of the order and type of calls units that were merged. The authors
466 concluded that calls consisting of combinations of call units functioned as single calls rather
467 than rapid sequences of independent units (Veselinovic et al., 2014).

468

469 Nevertheless, this study remains only a first step towards understanding the use of complex
470 calls and combinatorial abilities. Several technical and conceptual limitations must be
471 acknowledged. Firstly each combined stimulus was created from call units taken from two
472 distinct individuals and we do not know if the same reactions would be observed if we combined
473 calls from the same caller. This choice was based on evidence in Campbell's monkey, a closely
474 related species, that calls homologous to L and R calls in Diana monkeys (i.e., SH and RRC
475 calls) relate to a much lesser extent to caller's identity than the arched structure homologous to
476 Diana monkeys' A calls (i.e., CH) (Lemasson and Hausberger, 2011). Hence, if those data
477 suggest that receivers discriminate caller's identity mostly from the arched part of the call, its
478 actual importance in L and R calls remains to be tested in Diana monkeys. However, the fact
479 that LA_G did not trigger any reaction showing that subjects were disturbed supports our
480 hypothesis.

481

482 Moreover, in our experimental design, the L and R units of stimuli were taken from combined
483 calls but A units were taken from calls emitted alone (i.e., not combined to another unit). The
484 question remains whether the acoustic structure of A calls (when combined or not) differs
485 slightly. But again, the fact that LA_G (socio-positive calls) did not trigger disturbed reactions in
486 subjects suggests that this question may remain peripheral for the results obtained here. Testing
487 this question could generate an interesting comparison with males Campbell's monkeys in
488 which previous work found similar responses to natural Krak calls and artificial Krak calls
489 created from Krak-oo calls (Coye et al., 2015).

490 An alternative solution to determine both the potential of the first unit (i.e., L or R) to signal
491 caller's identity, and the influence of a possible variation in the structure of A calls' between
492 combined and single calls would be to develop a playback experiment comparing sets of
493 artificial stimuli. Notably a set of artificially combined calls created from single calls (i.e., L, R

494 and A calls combined in LA and RA complex calls) and a set of artificial ‘single calls’ taken
495 from complex calls (i.e., breaking down LA and RA calls into L, R and A units), using either
496 calls from a group-member or calls from a neighbour.

497

498 Interestingly, combinatorial abilities have been found in several animal species both at the call
499 level and at the sequence level, in both males and females, and notably in species where males
500 are more integrated socially (Bouchet et al., 2013; Bouchet, Laporte, Candiotti, & Lemasson,
501 2014; Bouchet et al., 2010; Coye et al., 2015; Lemasson, 2011; Ouattara, Lemasson, &
502 Zuberbühler, 2009b). Although most studies based their conclusions on contextual and acoustic
503 (non-experimental) analyses, they all suggest that combinatorial phenomena are an
504 evolutionary adaptive response to an increased need for complex communication, which may
505 be more widespread than initially thought. Whether the combinatorial abilities of non-human
506 and human primates originated in an ancestral capacity or result from convergent evolution
507 remains unclear and will require further comparative studies, notably to investigate
508 phylogenetic and cognitive aspects of the evolution of combinatorial phenomena.

509

510 **Acknowledgements**

511 Research has been funded by the French Ministry of Research, Institut Universitaire de France,
512 ANR ‘Orilang’ and the European Union's Seventh Framework Programme (FP7/2007-2013) /
513 ERC grant agreement n° 283871. The Ethics approval was given by the St Andrews’ University
514 Ethics Boards (UK). In Côte d’Ivoire, we thank the Minister of Scientific Research and the
515 ‘Office Ivoirien des Parcs et Réserves’ (OIPR) for permission to conduct research in Taï
516 National Park. We thank A. Bitty, the Centre Suisse de Recherches Scientifiques and B. Diero
517 for logistic support, our field assistants F. Bélé and F. Gnepa for their invaluable help with data
518 collection, the Taï Chimpanzee Project (TCP) and the ‘Centre de Recherche en Ecologie’ (CRE)

519 for their support in the field. We thank Brandon Wheeler and an anonymous referee for very
520 relevant comments which greatly improved this article. We are very grateful for comments and
521 fruitful discussions from C. Neumann and C. Rochais.

522

523

524 REFERENCES

525 Adams, D. C., & Anthony, C. D. (1996). Using randomization techniques to analyse behavioural data.

526 *Animal Behaviour*, 51(4), 733–738.

527 Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral*

528 *Ecology*, 26(1), 32–46.

529 Bergman, T. J., Beehner, J. C., Cheney, D. L., & Seyfarth, R. M. (2003). Hierarchical Classification by

530 Rank and Kinship in Baboons. *Science*, 302(5648), 1234–1236. Retrieved from:

531 <http://doi.org/10.1126/science.1087513>

532 Blumstein, D. T., Verneyre, L., & Daniel, J. C. (2004). Reliability and the adaptive utility of

533 discrimination among alarm callers. *Proceedings of the Royal Society of London. Series B:*

534 *Biological Sciences*, 271(1550), 1851–1857. Retrieved from:

535 <http://doi.org/10.1098/rspb.2004.2808>

536 Bouchet, H., Blois-Heulin, C., & Lemasson, A. (2013). Social complexity parallels vocal complexity: a

537 comparison of three non-human primate species. *Frontiers in Psychology*, 4. Retrieved from:

538 <http://doi.org/10.3389/fpsyg.2013.00390>

539 Bouchet, H., Laporte, M., Candiotti, A., & Lemasson, A. (2014). Flexibilité vocale sous influences

540 sociales chez les primates non-humains. *Revue de primatologie*, (5). Retrieved from

541 <http://primatologie.revues.org/1794>

542 Bouchet, H., Pellier, A.-S., Blois-Heulin, C., & Lemasson, A. (2010). Sex differences in the vocal

543 repertoire of adult red-capped mangabeys (*Cercocebus torquatus*): a multi-level acoustic analysis.

544 *American Journal of Primatology*, 72(4), 360–375. Retrieved from:
545 <http://doi.org/10.1002/ajp.20791>

546 Briefer, E. F. (2012). Vocal expression of emotions in mammals: mechanisms of production and
547 evidence. *Journal of Zoology*, 288(1), 1–20. Retrieved from: <http://doi.org/10.1111/j.1469-7998.2012.00920.x>

548

549 Briseño-Jaramillo, M., Estrada, A., & Lemasson, A. (2014). Individual voice recognition and an
550 auditory map of neighbours in free-ranging black howler monkeys (*Alouatta pigra*). *Behavioral Ecology and Sociobiology*, 69(1), 13–25. Retrieved from: <http://doi.org/10.1007/s00265-014-1813-9>

551

552

553 Buzzard, P., & Eckardt, W. (2007). The social system of guenons. In S. W. McGraw, K. Zuberbühler, &
554 R. Noë (Eds.), *Monkeys of the Tai Forest: An African Primate Community* (pp. 51–71). Cambridge, U.K.: Cambridge University Press .

555

556 Candiotti, A., Coye, C., Ouattara, K., Petit, E. J., Vallet, D., Zuberbühler, K., & Lemasson, A. (2015).
557 Female Bonds and Kinship in Forest Guenons. *International Journal of Primatology*, 1–21.
558 Retrieved from: <http://doi.org/10.1007/s10764-015-9829-1>

559 Candiotti, A., Zuberbühler, K., & Lemasson, A. (2012a). Context-related call combinations in female
560 Diana monkeys. *Animal Cognition*, 15(3), 327–339. Retrieved from:
561 <http://doi.org/10.1007/s10071-011-0456-8>

562 Candiotti, A., Zuberbühler, K., & Lemasson, A. (2012b). Convergence and divergence in Diana monkey
563 vocalizations. *Biology Letters*, 8(3), 382–385. Retrieved from:
564 <http://doi.org/10.1098/rsbl.2011.1182>

565 Ceugniet, M., & Izumi, A. (2003). Vocal individual discrimination in Japanese monkeys. *Primates*,
566 45(2), 119–128. Retrieved from: <http://doi.org/10.1007/s10329-003-0067-3>

567 Clarke, E., Reichard, U. H., & Zuberbühler, K. (2006). The Syntax and Meaning of Wild Gibbon Songs.
568 *PLoS ONE*, 1(1), e73. Retrieved from: <http://doi.org/10.1371/journal.pone.0000073>

569 Clay, Z., & Zuberbühler, K. (2011). Bonobos Extract Meaning from Call Sequences. *PLoS ONE*, 6(4),
570 e18786. Retrieved from: <http://doi.org/10.1371/journal.pone.0018786>

571 Cliff, N. (2014). *Ordinal methods for behavioral data analysis*. Psychology Press.

572 Collier, K., Bickel, B., Schaik, C. P. van, Manser, M. B., & Townsend, S. W. (2014). Language evolution:
573 syntax before phonology? *Proceedings of the Royal Society B: Biological Sciences*, 281(1788),
574 20140263. Retrieved from: <http://doi.org/10.1098/rspb.2014.0263>

575 Coye, C., Ouattara, K., Zuberbühler, K., & Lemasson, A. (2015). Suffixation influences receivers'
576 behaviour in non-human primates. *Proceedings of the Royal Society of London B: Biological*
577 *Sciences*, 282(1807), 20150265. Retrieved from: <http://doi.org/10.1098/rspb.2015.0265>

578 Crockford, C., Herbinger, I., Vigilant, L., & Boesch, C. (2004). Wild Chimpanzees Produce Group-
579 Specific Calls: a Case for Vocal Learning? *Ethology*, 110(3), 221–243. Retrieved from:
580 <http://doi.org/10.1111/j.1439-0310.2004.00968.x>

581 de Waal, F. B. M. (1987). Dynamics of social relationships. In *Primate societies* (Vol. xi). Chicago, IL,
582 US: University of Chicago Press.

583 Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... Lautenbach, S. (2013).
584 Collinearity: a review of methods to deal with it and a simulation study evaluating their
585 performance. *Ecography*, 36(1), 27–46. Retrieved from: [http://doi.org/10.1111/j.1600-](http://doi.org/10.1111/j.1600-0587.2012.07348.x)
586 [0587.2012.07348.x](http://doi.org/10.1111/j.1600-0587.2012.07348.x)

587 Dunbar, R. I. M. (1993). Coevolution of neocortical size, group size and language in humans.
588 *Behavioral and Brain Sciences*, 16(04), 681–694. Retrieved from:
589 <http://doi.org/10.1017/S0140525X00032325>

590 Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and*
591 *Reviews*, 6(5), 178–190. Retrieved from: [http://doi.org/10.1002/\(SICI\)1520-](http://doi.org/10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8)
592 [6505\(1998\)6:5<178::AID-EVAN5>3.0.CO;2-8](http://doi.org/10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8)

593 Dunbar, R. I. M. (2003). The Social Brain: Mind, Language, and Society in Evolutionary Perspective.
594 *Annual Review of Anthropology*, 32, 163–181.

595 Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the Social Brain. *Science*, 317(5843), 1344–1347.
596 Retrieved from: <http://doi.org/10.1126/science.1145463>

597 Gautier, J. P., & Gautier, A. (1977). Communication in old world monkeys. In *How animals*
598 *communicate* Bloomington, IN, U.S.A: Indiana University Press (pp. 890–964)..

599 Gonzalez, L., & Manly, B. (1998). Analysis of variance by randomization with small data sets.
600 *Environmetrics*, 9(1), 53–65.

601 Gower, J. C. (1971). A general coefficient of similarity and some of its properties. *Biometrics*, 857–
602 871.

603 Hammerschmidt, K., & Fischer, J. (2008). Constraints in primate vocal production. In *Evolution of*
604 *communicative flexibility: complexity, creativity, and adaptability in human and animal*
605 *communication*. Cambridge, MA, U.S.A: The MIT Press (pp. 93–119). Eds: Oller D.K. & Griebel U.

606 Hurford, J. (2008). The evolution of human communication and language. In P. d’Etoire & D. P. Hughes
607 (Eds.), *Sociobiology of communication: an interdisciplinary perspective* (pp. 249–264). Oxford,
608 U.K.: Oxford University Press.

609 Kaplan, J. N., Winship-Ball, A., & Sim, L. (1978). Maternal discrimination of infant vocalizations in
610 squirrel monkeys. *Primates*, 19(1), 187–193. Retrieved from: <http://doi.org/10.1007/BF02373235>

611 Katz, M. H. (2011). *Multivariable Analysis: A Practical Guide for Clinicians and Public Health*
612 *Researchers*. Cambridge, U.K.: Cambridge University Press.

613 Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Group size, grooming and social cohesion in
614 primates. *Animal Behaviour*, 74(6), 1617–1629. Retrieved from:
615 <http://doi.org/10.1016/j.anbehav.2006.10.025>

616 Lemasson, A. (2011). What can forest guenons ‘tell’ us about the origin of language. *Primate*
617 *Communication and Human Language: Vocalisation, Gestures, Imitation and Deixis in Humans and*
618 *Non-Humans*. Amsterdam, The Netherlands: John Benjamins (pp. 39–70).

619 Lemasson, A., & Hausberger, M. (2011). Acoustic variability and social significance of calls in female
620 Campbell's monkeys (*Cercopithecus campbelli campbelli*). *The Journal of the Acoustical Society of*
621 *America*, 129(5), 3341–3352. Retrieved from: <http://doi.org/10.1121/1.3569704>

622 Lemasson, A., Hausberger, M., & Zuberbühler, K. (2005). Socially Meaningful Vocal Plasticity in Adult
623 Campbell's Monkeys (*Cercopithecus campbelli*). *Journal of Comparative Psychology*, 119(2), 220–
624 229. Retrieved from: <http://doi.org/10.1037/0735-7036.119.2.220>

625 Lemasson, A., Ouattara, K., Bouchet, H., & Zuberbühler, K. (2010). Speed of call delivery is related to
626 context and caller identity in Campbell's monkey males. *Naturwissenschaften*, 97(11), 1023–1027.
627 Retrieved from: <http://doi.org/10.1007/s00114-010-0715-6>

628 Lemasson, A., Ouattara, K., Petit, E. J., & Zuberbühler, K. (2011). Social learning of vocal structure in a
629 nonhuman primate? *BMC Evolutionary Biology*, 11(1), 362. Retrieved from:
630 <http://doi.org/10.1186/1471-2148-11-362>

631 Lemasson, A., Palombit, R. A., & Jubin, R. (2007). Friendships between males and lactating females in
632 a free-ranging group of olive baboons (*Papio hamadryas anubis*): evidence from playback
633 experiments. *Behavioral Ecology and Sociobiology*, 62(6), 1027–1035. Retrieved from:
634 <http://doi.org/10.1007/s00265-007-0530-z>

635 Lemasson, A., Remeuf, K., Rossard, A., & Zimmermann, E. (2012). Cross-Taxa Similarities in Affect-
636 Induced Changes of Vocal Behavior and Voice in Arboreal Monkeys. *PLoS ONE*, 7(9), e45106.
637 Retrieved from: <http://doi.org/10.1371/journal.pone.0045106>

638 Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., Studer, M., & Roudier, P. (2015).
639 Package 'cluster'.

640 Marler, P. (1967). Animal communication systems. *Science*, (157), 769–774.

641 McComb, K., & Semple, S. (2005). Coevolution of vocal communication and sociality in primates.
642 *Biology Letters*, 1(4), 381–385. Retrieved from: <http://doi.org/10.1098/rsbl.2005.0366>

643 McGraw, W. S., Zuberbühler, K., & Noë, R. (2007). *Monkeys of the Tai Forest: An African Primate*
644 *Community*. Cambridge, U.K.: Cambridge University Press.

645 Miller, C. T., & Thomas, A. W. (2012). Individual recognition during bouts of antiphonal calling in
646 common marmosets. *Journal of Comparative Physiology A*, 198(5), 337–346. Retrieved from:
647 <http://doi.org/10.1007/s00359-012-0712-7>

648 Mundry, R., & Sommer, C. (2007). Discriminant function analysis with nonindependent data:
649 consequences and an alternative. *Animal Behaviour*, 74(4), 965–976.

650 Nakazawa, M. (2015). fmsb: Functions for Medical Statistics Book with some Demographic Data.
651 *CRAN- R Package Version 0.5.2*. Retrieved from: <http://CRAN.R-project.org/package=fmsb>

652 Neumann, C., Assahad, G., Hammerschmidt, K., Perwitasari-Farajallah, D., & Engelhardt, A. (2010).
653 Loud calls in male crested macaques, *Macaca nigra*: a signal of dominance in a tolerant species.
654 *Animal Behaviour*, 79(1), 187–193. Retrieved from:
655 <http://doi.org/10.1016/j.anbehav.2009.10.026>

656 Oda, R. (1996). Effects of contextual and social variables on contact call production in free-ranging
657 ringtailed lemurs (*Lemur catta*). *International Journal of Primatology*, 17(2), 191–205.

658 Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J., & Suggests, M.
659 (2007). The vegan package. *Community Ecology Package*, 631–637.

660 Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009a). Campbell's monkeys concatenate vocalizations
661 into context-specific call sequences. *Proceedings of the National Academy of Sciences*, 106(51),
662 22026–22031. Retrieved from: <http://doi.org/10.1073/pnas.0908118106>

663 Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009b). Campbell's monkeys use affixation to alter call
664 meaning. *PloS One*, 4(11), e7808–e7808.

665 Podani, J. (1999). Extending Gower's general coefficient of similarity to ordinal characters. *Taxon*,
666 331–340.

667 Price, T., Arnold, K., Zuberbühler, K., & Semple, S. (2009). Pyow but not hack calls of the male putty-
668 nosed monkey (*Cercopithecus nictitans*) convey information about caller identity. *Behaviour*,
669 146(7), 871–888. Retrieved from: <http://doi.org/10.1163/156853908X396610>

670 Rendall, D., Rodman, P. S., & Emond, R. E. (1996). Vocal recognition of individuals and kin in free-
671 ranging rhesus monkeys. *Animal Behaviour*, 51(5), 1007–1015. Retrieved from:
672 <http://doi.org/10.1006/anbe.1996.0103>

673 Schehka, S., & Zimmermann, E. (2009). Acoustic features to arousal and identity in disturbance calls
674 of tree shrews (*Tupaia belangeri*). *Behavioural Brain Research*, 203(2), 223–231. Retrieved from:
675 <http://doi.org/10.1016/j.bbr.2009.05.007>

676 Seyfarth, R. M., & Cheney, D. L. (2010). Production, usage, and comprehension in animal
677 vocalizations. *Brain and Language*, 115(1), 92–100. Retrieved from:
678 <http://doi.org/10.1016/j.bandl.2009.10.003>

679 Seyfarth, R. M., Cheney, D. L., Bergman, T., Fischer, J., Zuberbühler, K., & Hammerschmidt, K. (2010).
680 The central importance of information in studies of animal communication. *Animal Behaviour*,
681 80(1), 3–8. Retrieved from: <http://doi.org/10.1016/j.anbehav.2010.04.012>

682 Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: Semantic
683 communication in a free-ranging primate. *Animal Behaviour*, 28(4), 1070–1094. Retrieved from:
684 [http://doi.org/10.1016/S0003-3472\(80\)80097-2](http://doi.org/10.1016/S0003-3472(80)80097-2)

685 Slocombe, K. E., & Zuberbühler, K. (2005). Functionally Referential Communication in a Chimpanzee.
686 *Current Biology*, 15(19), 1779–1784. Retrieved from: <http://doi.org/10.1016/j.cub.2005.08.068>

687 Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., & Struhsaker, T. T. (1987). Appendix. In
688 *Primate societies* (Vol. xi, pp. 501–505). Chicago, IL, US: University of Chicago Press.

689 Taylor, A. M., & Reby, D. (2010). The contribution of source–filter theory to mammal vocal
690 communication research. *Journal of Zoology*, 280(3), 221–236. Retrieved from:
691 <http://doi.org/10.1111/j.1469-7998.2009.00661.x>

692 Tellier, I. (2008). Introduction au TALN et à l'ingénierie linguistique. Université de Lille 3.

693 Torchiano, M. (2015). effsize: Efficient Effect Size Computation. *CRAN - R Package Version 0.5.4*.
694 Retrieved from <http://CRAN.R-project.org/package=effsize>

695 Uster, D., & Zuberbühler, K. (2001). The functional significance of Diana monkey clear' calls.
696 *Behaviour*, 138, 741–756.

697 van Schaik, C. P. (1983). Why Are Diurnal Primates Living in Groups? *Behaviour*, 87(1), 120–144.
698 Retrieved from: <http://doi.org/10.1163/156853983X00147>

699 van Schaik, C. P., & van Hooff, J. A. R. A. M. (1983). On the Ultimate Causes of Primate Social Systems.
700 *Behaviour*, 85(1/2), 91–117.

701 Veselinovic, D., Candiotti, A., & Lemasson, A. (Under revision). Female Diana monkey (Cercopithecus
702 diana) have complex calls. *LI Squibs*.

703 Wrangham, R. W. (1987). Evolution of social structure. In *Primate societies* (Vol. xi, pp. 282–296).
704 Chicago, IL, US: University of Chicago Press.

705 Zuberbühler, K. (2000). Referential labelling in Diana monkeys. *Animal Behaviour*, 59(5), 917–927.
706 Retrieved from: <http://doi.org/10.1006/anbe.1999.1317>

707 Zuberbühler, K. (2001). Predator-specific alarm calls in Campbell's monkeys, *Cercopithecus campbelli*.
708 *Behavioral Ecology and Sociobiology*, 50(5), 414–422. Retrieved from:
709 <http://doi.org/10.1007/s002650100383>

710 Zuberbühler, K., & Lemasson, A. (2014). Primate Communication: Meaning from Strings of Calls. In F.
711 Lowenthal & L. Lefebvre (Eds.), *Language and Recursion* (pp. 115–125). New York City, NY, U.S.A.:
712 Springer New York. Retrieved from: [http://link.springer.com/chapter/10.1007/978-1-4614-9414-](http://link.springer.com/chapter/10.1007/978-1-4614-9414-0_9)
713 [0_9](http://link.springer.com/chapter/10.1007/978-1-4614-9414-0_9)

714 Zuberbühler, K., & Wittig, R. (2011). Field experiments with nonhuman primates: a tutorial. *Field and*
715 *Laboratory Methods in Primatology: A Practical Guide*. Cambridge, U.K.: Cambridge University
716 Press (pp. 207–224).

717