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The Evolution of Vocal Communication: Inertia and Divergence in Two Closely Related Primates

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1 **The evolution of vocal communication -**

2 **Inertia and divergence in two closely related primates**

3

4 ABSTRACT

5 Primate vocal repertoires change slowly over evolutionary time, making them good
6 indicators of phylogenetic relatedness. Occasionally, however, socio-ecological pressures
7 cause rapid divergence, even in closely related species, but overall it remains unclear how
8 inertia and divergence interact to evolve species-specific vocal repertoires. We addressed
9 this topic with a study of two closely related sympatric guenons, Diana monkeys
10 (*Cercopithecus diana*) and Campbell's monkeys (*C. campbelli*). We compiled published,
11 long-term data to compare repertoire size, call morphology and combinations in these
12 species, and complemented these data with new, machine-learning based acoustic analyses
13 of calls made by three individuals of each species to assess the degree of individual
14 differences in call types. In line with the phylogenetic inertia hypothesis, we found
15 similarities in the overall call repertoires, with six of eight vocal units shared between the
16 two species. The non-shared units all functioned in the predation context, suggesting that
17 alarm calls are especially susceptible to evolutionary change. In addition, Campbell's
18 monkeys (the species more exposed to predation) produced more inconspicuous calls
19 throughout their repertoire than Diana monkeys, suggesting that predation has a
20 generalised impact on vocal structure. Finally, although both species combined calls flexibly,
21 this feature was more prominent in Diana monkeys that live in larger groups and are less

1

22 exposed to ground predators. This suggests that, although predation appears to favour the
23 diversification of alarm call repertoires, it also inhibits the emergence of vocal combinations
24 in social communication. We conclude that interspecies competition, and the niche
25 specialisation this creates, is a key evolutionary driver of primate vocal behaviour. These
26 conclusions are preliminary since they are based on comparing only two species but open
27 a promising avenue for broader-scale comparisons.

28

29 Keywords: *Cercopithecus*, caller identity, call use, vocal evolution, predation, combinatoriality

30

31 **INTRODUCTION**

32

33 Vocal signals play a key role in most biological functions, including reproduction (Catchpole and
34 Slater 2003; Delgado 2006), predation avoidance (Macedonia and Evans 1993; Scheumann et al.
35 2007; Zuberbühler 2009), sociality (Radford and Ridley 2008; Waser 1975) and intergroup
36 competition (Byrne and da Cunha 2006; de Kort et al. 2009; Ramanankirahina et al. 2016, 2016).
37 Although the selective advantage of these signals is usually evident, it is often unclear why some
38 species have evolved larger repertoires for the same functions than others and why some
39 acoustic structures prevail over others (Endler 1992; Leighton and Birmingham 2020; Wilkins et
40 al. 2013).

41

42 Three factors seem to play a key role in the evolution of animal vocal signals: habitat structure,
43 predation and sociality (Catchpole and Slater 1995; Freeberg et al. 2012; Waser and Brown 1986;
44 Zuberbühler and Jenny 2002). First, habitat can influence the structure and use of vocal signals.
45 For example, visually dense habitats generally favour acoustic communication (Marler 1967),
46 with propagation properties and local 'soundscapes' having a direct impact on signal evolution
47 (Brown and Waser 1988; Marler 1967; Marten and Marler 1977; Waser and Brown 1986).
48 Depending on the proximity of the targeted recipient (close, long-distance), different signal
49 structures are favoured to maximise the transmission efficacy and minimise the costs imposed
50 by unintended overhearers (Dabelsteen et al. 1998; Ruxton 2009; Waser and Waser 1977).

51

52 Second, predation is generally thought to enhance signal diversification, both to inform
53 conspecifics (Blumstein 1999a, 1999b; Furrer and Manser 2009; Macedonia and Evans 1993) and
54 to affect predators (Shelley and Blumstein 2005; Zuberbühler et al. 1997). An important factor
55 here is whether signallers can actively interfere with a predator's hunting technique, either by
56 communicating or by minimising detection. This can be either in terms of behavioural
57 adaptations (e.g., altering or inhibiting signal production) or by evolving signal structures that are
58 difficult to detect (e.g., 'seeet' alarms of passerines, Jones and Hill 2001; McGraw et al. 2007;
59 Morisaka and Connor 2007; Ruxton 2009; Wilson and Hare 2004). The same predator fauna can
60 sometimes lead to different evolutionary outcomes, even in closely related prey species. For
61 instance, predation by coyotes (*Canis latrans*) has impacted differently on two closely related
62 deer species, due to basic differences in anti-predator behaviour (Lingle 2001). Although of
63 similar size, white-tailed deer (*Odocoileus virginianus*) flee from coyotes while mule deer (*O.*
64 *Hemionus*) fight back. As a result, natural selection appears to have favoured larger, more
65 cohesive groups in mule than white-tailed deer (Lingle 2001), with further evolutionary
66 consequences for their communication behaviour.

67

68 Finally, sociality favours signal evolution with increasing types and numbers of social interactions
69 (Freeberg et al. 2012; Houdelier et al. 2012; McComb and Semple 2005). Species living in complex
70 societies (e.g., multi-male, multi-female groups) are likely to encounter a more diverse range of
71 social problems than species living in simple societies (e.g., solitary species), and this again is
72 thought to impact on signal evolution (Bouchet et al. 2013; Kroodsma 1977; Manser et al. 2014;

73 McComb and Semple 2005; Rebout et al. 2020). In the social domain, one source of diversification
74 is whether it is advantageous for a signaller to encode individual identity. There is a wealth of
75 evidence that animals from various taxa can recognise each other by their calls (Aubin and
76 Jouventin 2002; Briseño-Jaramillo et al. 2014; Kondo and Watanabe 2009; Müller and Manser
77 2008; Rendall et al. 1996). Generally speaking, calls given in social interactions convey identity
78 better than calls that require urgent actions, such as alarm calls (Bouchet et al. 2013; Hasiniaina
79 et al. 2020; Leliveld et al. 2011). Call types often vary across the repertoire in terms of their
80 potential for identity coding (PIC). For example, in female Campbell's monkeys (*Cercopithecus*
81 *campbelli*) short repetitive alarm and threat calls had the lowest PIC, trilled social calls had
82 intermediate PIC and combined contact calls had the highest PIC (Lemasson and Hausberger
83 2011), which reflected their primary need in conveying information about caller's identity (Coye
84 et al. 2018).

85

86 Zimmermann and colleagues have argued that, to understand the evolution of vocal behaviour,
87 it is essential to take into account the separate impact of a species' phylogenetic history, its local
88 ecology and its current social system (Hasiniaina et al. 2018, 2020). With a research programme
89 based on broad-scale species comparisons, they showed the complex interplay between ecology,
90 predation and phylogeny in the evolution of vocal behaviour in Malagasy mouse lemurs
91 (Hasiniaina et al. 2018). This and other studies on primates confirmed that, across species, vocal
92 repertoires consist of limited collections of acoustically fixed signals, with closely related species
93 having more similar repertoires than more distantly related species, both in terms of calls

94 structure and function (Gautier 1988; Geissmann 1984; Hasiniaina et al. 2020; Ord and Garcia-
95 Porta 2012). However, the picture may not be that clear-cut and exploring the repertoire of
96 closely related species remains a useful endeavour, for several reasons. Firstly, there can
97 sometimes be surprising levels of variation within closely related taxa. For instance, the
98 repertoire sizes of lemuriforms varies from 5 to 22 calls, with no clear phylogenetic patterns
99 (Zimmermann 2017). Secondly, primate communication can sometimes be remarkably flexible
100 within species, such that closely related species differ considerably due to species differences in
101 flexible rather than basic repertoire size (Bouchet et al. 2013; Coye et al. 2017; Gustison et al.
102 2012; Ouattara, Lemasson, et al. 2009a).

103

104 While the evolution of the vocal behaviour of adult males has already been investigated in
105 guenons (e.g. (Arnold and Zuberbühler 2006; Keenan et al. 2013; Ouattara, Lemasson, et al.
106 2009a; Zuberbühler 2000a, 2004) relatively less is known about communication of females and
107 their offspring. However, female repertoires are usually larger and contain calls with more
108 diverse functions than those of males (Candiotti et al. 2012a; Coye et al. 2018; Lemasson and
109 Hausberger 2011; Ouattara, Lemasson, et al. 2009a, 2009b; Zuberbühler et al. 1997). Among
110 existing studies, data are available for adult females of two closely-related guenon species,
111 Campbell's and Diana monkeys (*Cercopithecus diana*) (Candiotti et al. 2012a, 2012b; Lemasson
112 and Hausberger 2011; Ouattara, Lemasson, et al. 2009b; Zuberbühler et al. 1997). These two
113 species are part of a rich primate fauna of the Upper Guinean forests, including six other species
114 (lesser spot-nosed monkeys, *Cercopithecus petaurista*, putty-nosed monkeys *C. nictitans*, olive

115 colobus *Procolobus verus*, red colobus *P. badius*, black-and-white colobus *Colobus polykomos* and
116 sooty mangabeys *Cercocebus atys*). The region has experienced drastic climate-related changes
117 over the past millennia, with a major dry period and substantially reduced and fragmented
118 forests some 18,000 years ago (Hamilton and Taylor 1991), which has led to a complex migration
119 history. As a result, the current primate species occupy distinct niches within the same habitat,
120 presumably to minimise feeding competition, but frequently form poly-specific associations to
121 maximise anti-predator benefits (Buzzard 2006a; McGraw and Zuberbühler 2008; Noë and
122 Bshary 1997).

123

124 Campbell's and Diana monkeys are similar in many ways (Table 1). They share the same habitat
125 and the same predators (crowned eagles *Stephanoaetus coronatus*, leopards *Panthera pardus*,
126 chimpanzees *Pan troglodytes*, *Homo sapiens* humans and large vipers) and both forage for fruits,
127 flowers and insects (although in differing proportions). The species have similar home range sizes
128 and group densities, with sometimes overlapping territories (Buzzard and Eckardt 2007). They
129 often form poly-specific groups (Buzzard 2006a; Buzzard 2006b) and have the same group
130 composition (Candiotti et al. 2015), i.e., single-male, multi-female groups with several females
131 and their offspring. Males of each group are spatially and socially peripheral but highly active in
132 anti-predator behaviour, while the females are the philopatric sex and form the social core of the
133 groups. The males also have a vocal repertoire distinct from that of females, mainly consisting of
134 a few alarm calls (Gautier 1988; McGraw et al. 2007; Ouattara, Lemasson, et al. 2009b;
135 Zuberbühler 2000b, 2000a). Finally, both Campbell's and Diana monkey females recognise each

7

136 other through their contact calls (Coye et al. 2016; Lemasson et al. 2005), suggesting that calls
137 convey identity markers. So far, PIC analyses have only been conducted with Campbell's monkeys
138 (Lemasson and Hausberger 2011), showing that the arched component (i.e. tonal, frequency-
139 modulated vocal unit with an ascending phase and a descending phase, Fig.1), of the vocal
140 combinations functions to convey identity to varying degrees.

141

142 Although Diana and Campbell's monkeys resemble each other in many features, with a shared
143 common ancestor some 6 million years ago (Perelman et al. 2011), they differ in many key
144 aspects. First, Campbell's monkeys live in smaller (mean=9.3 individuals) and more cohesive
145 groups (<25 m group spread) than Diana monkeys (23.5 individuals, which often spread over 25
146 to 50 m) (Buzzard and Eckardt 2007, data for two groups of each species). Second, inter-group
147 encounters are 10 times more frequent in Diana than in Campbell's monkeys although group
148 densities are similar for the two species (Table 1). Intra-group social interactions are also more
149 frequent in Diana monkeys, in which female maintain strong bonds and often form coalitions (as
150 opposed to the moderately strong bonds formed by female Campbell's monkeys; Buzzard 2004).
151 Third, Diana monkeys are conspicuous in their visual appearance and acoustic behaviour, larger
152 than Campbell's monkeys and boisterous in their locomotion with frequent running and leaping
153 (McGraw 1998) while Campbell's monkeys are much harder to find due to their cryptic
154 colouration and quiet locomotion (McGraw et al., 2007; McGraw, 2007). Fourth, Campbell's
155 monkeys are among the smallest diurnal primates in West African forests and are often displaced
156 by other species when foraging (Buzzard, 2006a; McGraw et al. 2007). In contrast, Diana monkeys

157 occupy a central place in the Tai primate community with several other primate species actively
158 seeking associations with them and following them through their home range (e.g. red colobus:
159 *Ptilocolobus badius*; Noë and Bshary 1997). Fifth, Diana monkeys are sometimes considered as
160 forest ‘sentinels’ because they detect danger faster and from greater distances than the other
161 species (McGraw and Zuberbühler 2008; Noë and Bshary 1997; Wolters and Zuberbühler 2003).
162 Sixth, the two species differ in their anti-predator strategies: Diana monkeys follow a strategy of
163 active signalling when they detect leopards or eagles (Uster and Zuberbühler 2001; Zuberbühler
164 et al. 1997), while Campbell’s monkeys seek to avoid detection (McGraw et al. 2007). Finally,
165 while Diana monkeys forage mostly in the top canopy layers (>20 m), Campbell’s monkeys spend
166 up to 50% of their time in the lowest forest canopy layers (*i.e.* 0-5 m) (Buzzard (2006b; McGraw,
167 2007) and where they are much more exposed to predators. In particular, forest leopards and
168 chimpanzees are highly specialised in hunting primates and both predators exert considerable
169 pressure on the monkeys (Bshary 2007; Jenny and Zuberbühler 2005; McGraw et al. 2007;
170 Zuberbühler et al. 1999; Zuberbühler and Jenny 2002). In addition, the crowned eagles of Tai
171 Forest pursue a sit-and-wait strategy when hunting monkeys, anticipating the travelling path of
172 a group and attacking them from within the forest canopy (Shultz 2007). Overall, this suggests
173 that foraging in the lower forest strata is more dangerous than foraging in the open upper forest
174 strata, which are less accessible to all primate predators.

175

176 In this study, we were interested in the relative importance of general phylogenetic and specific
177 socio-ecological factors in the evolution of primate vocal behaviour. We combined published data

178 on the vocal repertoires of the two species with new data to compare their acoustic diversity,
179 use of single and combined calls and their potential to convey identity. In line with the
180 phylogenetic inertia hypothesis and given the phylogenetic relatedness between the two species,
181 we predicted similarities in vocal repertoires, specifically in terms of identity coding (conveyed
182 by the arched element of contact calls: Candiotti et al. 2012a). Specifically, we predicted that
183 contact call structure (i.e., the arched-shaped, frequency-modulated part of the call) and function
184 (maintaining contact, signalling identity) is conserved in these two species. However, given their
185 opposite ecological niches, we also predicted differences in call use, call combinations, call rates
186 and call functions. Specifically, we predicted that Diana monkeys make more use of call
187 combinations (due to their larger groups) and produce more frequent and more conspicuous calls
188 than Campbell's monkeys due to differences in relative predation pressure.

189

190 **METHODS**

191 **Shared and idiosyncratic vocal units, call function, vocal combinations, and call rates**

192 To compare the vocal behaviour of the two species we reviewed published data on vocal
193 combinations, contextual use and call rates (Table 2). Most of the published data were collected
194 in Taï National Park, Côte d'Ivoire, but one study included data from Tiwai island, Sierra Leone
195 (Oates et al., 1990) and one included data from a captive group in France (Lemasson et al, 2006).
196 Some studies involved an experimental paradigm (Coye et al. 2015, 2016; Lemasson et al. 2005;
197 Zuberbühler 2000a, 2000b), but most studies relied on observational data. Data collection
198 protocols varied between studies and included regular scan sampling (Buzzard 2006b, McGraw

10

199 1998, Wolters and Zuberbühler 2003, Buzzard and Eckardt 2007), transects (Oates et al., 1990),
200 all-day group follows (Buzzard, 2006a) and focal sampling of individually known subjects
201 (Candiotti et al., 2015, Lemasson et al., 2006, Ouattara et al., 2009, Candiotti et al., 2012a, b).

202

203 We report the numbers of shared vocal units, and the number which occur in only one species
204 (idiosyncratic vocal units), call function, vocal combinations and call rates.

205

206 **New data collection**

207 We collected new data in Taï National Park, a tropical evergreen lowland forest in the South-
208 West part of Côte d'Ivoire (5° 20' –6° 10' N; 6° 50' –7° 25' W). Taï Forest is one of the largest
209 relatively intact segments of the ancestral Upper Guinean Forest belt. It has an estimated surface
210 of over 5,300 km² (Office Ivoirien des Parcs et Réserves 2006) and consists of dense ombrophilous
211 vegetation with a continuous 40-60 m high canopy and emergent trees (Kolongo et al. 2006;
212 Riezebos et al. 1994). The climate is characterised by stable temperatures over the year and an
213 alternation of dry and wet seasons (Korstjens 2001).

214

215 We recorded habituated females using focal sampling between 8 am and 5 pm, several days per
216 week. We conducted recordings between January 2013 and September 2014, using a Sennheiser
217 K6/ME66 directional microphone and a Marantz PMD660 solid-state recorder (sampling rate,
218 44.1 kHz; resolution, 16 bits) for Diana monkeys and between August 2006 and February 2007

219 using a Sony TCD D100 stereo cassette recorder and a Sennheiser ME88 microphone for the
220 Campbell's monkeys.

221

222 **Comparing identity markers between species**

223 To compare the potential to convey identity in Campbell's and Diana monkey full-arched calls
224 (CHf and LAf respectively, i.e., contact calls with a full arch, as opposed to 'broken arches', in
225 which the 'top of the arch' is not uttered by the individuals, Figure 1), we used an automated
226 classification using artificial neural networks (ANNs), based on a supervised machine learning
227 procedure developed for guenon calls (Mielke and Zuberbühler 2013). For each caller, we trained
228 the ANN using a set of call exemplars before testing classification performance on new calls from
229 the same caller. We ran the analyses separately for both species to compare results with chance
230 levels and with each other. We used a set of high-quality recordings from three females from
231 each species. Training sets consisted of 19-28 calls per individual (mean \pm SE: 23.0 ± 1.6 calls)
232 selected for their quality (low background noise and no overlap with other calls or human
233 speech). We applied a low-pass filter at 12,000 Hz to eliminate high-frequency sounds,
234 particularly from cicadas. We extracted the Mel-Frequency Cepstral Coefficients (MFCCs) from
235 each call (Mielke and Zuberbühler 2013). The general principle of MFCC extraction is to slice the
236 power spectrum in sections (i.e. frames) small enough to be statistically stationary. Each frame
237 is then multiplied with a Hamming window and the Fast Fourier Transform (FFT) is computed.
238 The frames are subsequently mel-scaled (the spectrum's frequency axis is transformed from
239 Hertz scale into mel scale using filter banks) and the MFCCs are calculated by applying a discrete

240 cosine transform to the energy from the frequency band filters (Logan 2000). We then used the
241 MFCC extracted to train 15 identical ANNs per species. We built ANNs using the cascade forward
242 architecture (cascadeforwardnet) neural network in Matlab software. The ANNs consisted of an
243 input layer of 448 neurons (= number of MFCCs extracted per call), a hidden layer with only two
244 neurons (to prevent overfitting) and an output layer whose size corresponded to the distinct
245 classification outputs possible (i.e., 3 corresponding to the 3 individuals per species). We used
246 the 'trainbr' training function of Matlab (Bayesian regularization backpropagation training
247 function), with a maximum of 1000 epochs (i.e. training iterations). We also used two
248 complementary Input-Output processing functions: 'mapminmax' (which normalizes inputs and
249 targets between -1 and +1) and 'mapstd' (which standardizes inputs and targets to have zero
250 mean and unity variance). To determine when to stop the training, we measured network
251 performance using the mean squared errors ('mse' performance function in Matlab[®]), with
252 normalization set to its standard value (i.e., normalizing errors between -2 and +2). Following
253 training, we tested the ANN's performance using 24 calls that were not in the training set (4 calls
254 from each subject, in each species). To maximize classification efficiency, we repeated the
255 training and testing procedures on 15 identical ANNs (for each species) whose results we then
256 averaged to obtain the final classification result.

257

258 **RESULTS**

259 **Shared and idiosyncratic vocal units and call function**

260 Females of both species produced eight distinct acoustic units, six of which were shared between
261 species. The shared units consisted of two repetitive structures given during threats (Campbell's:
262 RRC; Diana: Brrr) and mild alert (Campbell's: RRA1; Diana: R), two trill-based structures given in
263 relaxed social contexts (Campbell's: ST/SH; Diana H/L) and two arch-shaped combined calls to
264 remain in contact (Campbell's: CHf/CHb; Diana: Af/Ab) (Fig. 1).

265

266 The remaining four acoustic units were only present in one species. These idiosyncratic units
267 consisted of variations of shared call types, two for each species (Fig. 1, Table 2). Interestingly,
268 although all idiosyncratic calls functioned as alarm calls, the respective source calls were different
269 between species. While in Campbell's monkeys they resembled the short repetitive units
270 (notably RRA1), in Diana monkeys they resembled the tonal arched units (Af, Ab). In Campbell's
271 monkey, the idiosyncratic units were given to eagles and leopards (RRA3 and RRA4 respectively).
272 They were used in addition to the general alert (RRA1) and were distinguishable by the number
273 and structure of repetitive units (Ouattara, Zuberbühler, et al. 2009), Fig. 1). We found no
274 counterpart of RRA3 and RRA4 in the female Diana monkey vocal repertoire.

275

276 In Diana monkeys, the idiosyncratic units (Alk, W) also served as alarm calls, but these calls
277 originated from the arched contact calls (Af; Fig. 1; Coye et al. 2015; Zuberbühler et al. 1997) with
278 no structural equivalent in the Campbell's monkey repertoire. Alk resembled an arched call
279 whose lower frequencies were truncated and whose top was sharper, and W was composed of a

280 short, high-pitched and arched-shaped note preceding an Alk-like truncated arch (Fig. 1, Candiotti
281 2012; Coye et al. 2015; Zuberbühler et al. 1997).

282

283 **Vocal combinations**

284 Females of both species combined vocal units in similar ways, by assembling non-arched units
285 with full or broken arches (Figure 2). While both species used their arched units to cast
286 combinations, Diana monkeys produced four arched structures (two shared: Af, Ab; two
287 idiosyncratic: Alk, W) and Campbell's monkeys produced two (CHb, CHf) (Table 2). In addition,
288 Diana monkeys used their four arched units both singly and in combination with high- and low-
289 pitched trills (L and H) or repetitive alarm calls (R) in both social and alarm contexts (Fig. 3).

290

291 As a result of their higher propensity to combine calls, the female Diana monkey repertoire
292 consisted of sixteen calls, i.e., eight non-combined calls (Brrr, R, L, H, Af, Ab, Alk and W) and eight
293 combined calls (L-Af, L-Ab, H-Af, H-Ab, R-Af, R-Ab, R-Alk and R-W), while the Campbell's monkey
294 repertoire consisted of only eight calls. This is because, in Campbell's monkeys, arched units were
295 always produced in combination, never as single calls, and only with low-pitched trills (SH),
296 resulting in only two combined calls (CHb and Chf), which serve as contact calls, and six non-
297 combined calls (RRC, RRA1, RRA3, RRA4, SH, ST, Table 2).

298

299 **Call rates**

300 Diana monkeys were 4.5 times more vocal than Campbell's monkeys in terms of contact call rates
301 (Table 2). Rates of both single and combined contact calls were higher in Diana than Campbell's
302 monkeys (Fig. 3). However, Campbell's monkeys emitted two call types at higher rates: cryptic
303 SH calls (homologous to the Diana L call; Fig. 1, Table 2) and alarm calls (RRA / R). In addition,
304 while Campbell's monkeys mainly produced broken arches (79% CHb calls), Diana monkeys
305 produced mainly full arches (72% LAf calls, homologous to Campbell's CHf calls; Fig. 3).

306

307 **Conveying individual identity**

308 The results of machine learning showed high levels of individual differences in Campbell's CHf
309 and Diana's LAf contact calls (91.7% accurate classification in both species; chance level: 33.3%),
310 suggesting equivalent power to convey identity.

311

312 **DISCUSSION**

313 We found that females in two closely related, sympatric forest primates, Diana and Campbell's
314 monkeys, produced eight basic vocal units, six of which shared and four idiosyncratic (two per
315 species), suggesting similar articulatory capacities caused by shared phylogeny. Both species
316 produced arched structures that functioned as contact calls and main carriers of identity. Our
317 machine learning based analyses suggested that this occurred to similar extents in both species,
318 although the results need to be considered with caution given small sample sizes. Finally, females

319 of both species produced combined calls consisting of one arched vocal unit that follows a non-
320 arched unit.

321

322 We also found a number of species differences, most likely caused by adaptations to their
323 respective niches, particularly differences in predation pressure. Campbell's monkeys are very
324 cryptic, both in terms of visual appearance as well as vocal and non-vocal behaviour, and live in
325 small, cohesive groups. Diana monkeys are different and live in large, spread out groups with
326 individuals relying on vocalisations to remain in contact and warn each other about danger (Uster
327 and Zuberbühler 2001; Zuberbühler et al. 1997). Both species produce two idiosyncratic alarm
328 calls whose structures differed strikingly. Although both species produced call combinations,
329 Diana monkeys used this feature more by producing twice as many combined call types
330 compared to Campbell's monkeys. Diana monkeys also used combined calls in a greater range of
331 contexts, including alarm and social contexts, whereas Campbell's monkeys combined calls
332 function only as contact calls. Finally, both species differed in the rate of call production across
333 call types. Campbell's monkeys were less vocal and favoured the quieter, broken arched calls
334 compared to Diana monkeys, who preferred the full arched calls and used them at high rates.

335

336 Overall, our results show that, even in species with limited articulatory capacities, primate vocal
337 behaviour can evolve rapidly in response to environmental pressures, partly due to flexible use
338 of existing vocal units. Predation appears to play a main role as both species possessed
339 idiosyncratic call units in this context, consistent with their respective anti-predator strategies.

340 The Diana monkeys' idiosyncratic calls (sharp arches – W and Alk) are amongst the most
341 conspicuous calls in the forest while the Campbell's monkeys' idiosyncratic calls were short
342 repetitive structures that (for humans) are difficult to detect (RRA1, RRA3 and RRA4). We found
343 no counterpart of RRA3 and RRA4 in the female Diana monkey vocal repertoire, which suggests
344 that these calls were either lost by Diana monkeys or emerged recently in Campbell's monkeys.
345 Interestingly, another call type with a similar structure (RRA2) was documented in the repertoire
346 of captive Campbell's monkeys and produced to signal the arrival of an unfamiliar human in the
347 facility (Ouattara, Zuberbühler, et al. 2009).

348

349 Another source of the flexibility that we identified concerned the ability to use distinct call types
350 flexibly and to combine existing vocal units. First, both species used the more detectable full-
351 arched calls depending on context. For instance, female Campbell's monkeys used a single unit
352 call (SH) and two combined units (CHb, CHf) to establish and maintain contact (Coye et al., 2018).
353 The single-unit call is the quietest and least perceptible, due to its low-pitched, quavered
354 structure. Females produced this call when predation risk was high and when they were not
355 associated with other primate species (Coye et al., 2018). The two combined units (CHb and CHf)
356 were more audible and given in non-predatory contexts to maintain contact, with the full-arched
357 call (CHf) mainly given during vocal exchanges (Coye et al. 2018). Female Diana monkeys followed
358 a similar pattern: calls with full arches were used in contexts in which signalling identity was
359 important, e.g., at territory borders where encounters with neighbours were likely (Candiotti et
360 al. 2012a). Second, although both species use combined calls, Diana monkeys do so to a much

361 greater extent and in a diverse range of contexts. In particular, female Diana monkeys not only
362 combined low-pitch trills (L) but also high-pitched trills (H) and repetitive alarm call (R) with full
363 and broken arches (Af, Ab). In previous work, we showed that the first unit (H, L or R) conveys
364 the caller's perceived valence of an event (positive, neutral, negative context) while the arch
365 contains the caller's identity (Candiotti et al. 2012a). In a playback study, changing the first unit
366 (e.g. L with R) or the arch (i.e. identity) were both perceived by listeners and caused differences
367 in reactions, suggesting that both units contributed to the overall meaning (Coye et al. 2016).
368 Interestingly, the Diana monkeys' two idiosyncratic arched units (Alk, W) were only seen in
369 combination with the repetitive alarm call (R), which generated a novel alarm call (Candiotti
370 2012; Coye et al. 2015). In Campbell's monkeys, combined calls functioned to convey individual
371 identity although this appeared to be in trade-off with minimising detection. In Diana monkeys,
372 pressure from ground predation is low due to their upper forest canopy niche, which may have
373 enabled them to exploit the potential for combinations to a fuller extent. Our findings align with
374 theoretical work predicting that vocal combinations may emerge as an alternative strategy to
375 acoustic diversification in species facing the need for a larger vocal repertoire (Nowak and
376 Komarova 2001).

377

378 There is consensus in the literature that social and vocal complexity coevolve (e.g. Aubin and
379 Jouventin 2002; Blumstein 1999b, 2003; Houdelier et al. 2012; Kroodsma 1977; Mathevon et al.
380 2003; Pollard and Blumstein 2012; Wilkinson 2003). This conclusion is based on comparative
381 studies of vocal repertoire sizes, although it is often unclear how to accurately determine

382 repertoire size. Our results show that, in both species, vocal units can be part of vocal
383 combinations, with sometimes distinct functions. These combinations can greatly increase the
384 repertoire size as is the case in Diana monkeys. Furthermore, we identified another source of
385 variation: the flexibility of call use, which further increases the effective repertoire size.

386 Some studies have adopted an alternative approach to comparing the size of the repertoire,
387 instead assessing the complexity of repertoires using indicators such as the presence of identity-
388 rich structures (Bouchet et al. 2013), vocal combinations (Manser et al., 2014) or gradation
389 between call types (Rebout et al. 2020). Here again sociality appears to be a main evolutionary
390 driver. For example, across different mongoose species, repetition of vocal units was generally
391 present, but only obligate social species produced combinations of calls (Collier et al. 2020;
392 Manser et al. 2014). Similarly, across three species of primates (Campbell's monkeys, DeBrazza
393 monkeys (*C. neglectus*) and red-capped mangabeys, (*Cercocebus torquatus*) call rates and vocal
394 combinations increased with social complexity (single-male, single female with their offspring;
395 single-male, multifemale with their offspring; multi-male multi-females; Bouchet et al. 2013). In
396 line with these observations, Diana monkeys have higher rates of social interactions, more
397 differentiated intragroup social relations, more frequent intergroup encounters than Campbell's
398 monkeys (Table 1), and a correspondingly larger and more complex vocal repertoire.

399

400 In conclusion, we found that two closely related primate species, adapted to different ecological
401 niches within the same habitat, have correspondingly adapted vocal systems in call structure,

402 production patterns, total effective repertoire size (partly caused by vocal combinations) and
403 functional diversity of calls. We found several homologous vocal units due to phylogenetic inertia
404 but both predation and social complexity seem to play a major role in the evolutionary
405 divergence of vocal repertoires in these two species. Predation is particularly interesting as it can
406 both increase the repertoire size and, if pressure is too large, inhibit the evolution of vocal
407 combinations. Social complexity generally appears to favours diversification especially as
408 combinations of call units. Future research on other species and taxa are required to test these
409 conclusions at a larger scale than this comparison of two species.

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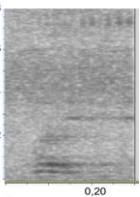
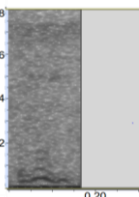
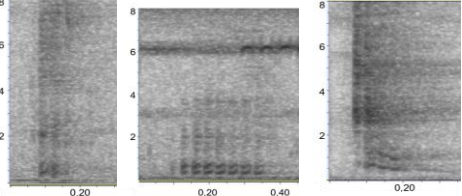
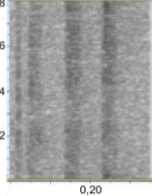
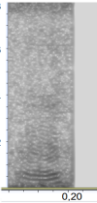
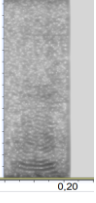
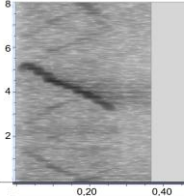
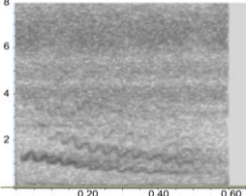
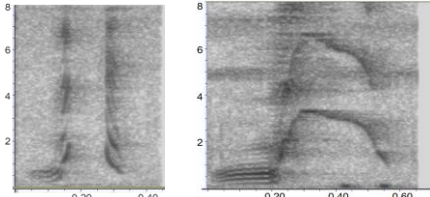
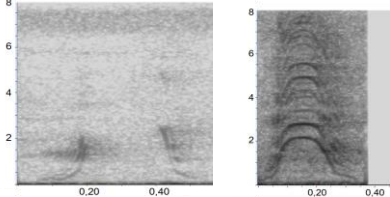
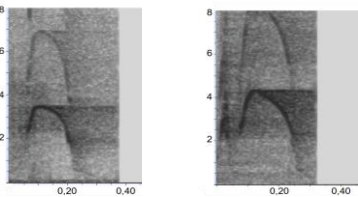
Figure captions

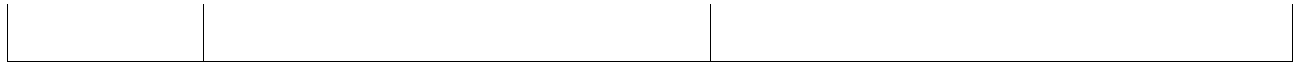
Figure 1: Distinct acoustic elements found in the vocal repertoire of female Campbell’s and Diana monkeys. Acoustic structures are listed regardless of their use in single-element or combined calls. In Campbell’s monkeys, arches homologous to Ab/Af calls of Diana monkeys are only found in calls composed of an SH unit with an arch (CHb, Chf). We produced spectrograms using Audacity 3.0.2, with default settings (Algorithm=Frequencies, window=Hann, window size =1024s; minimum frequency displayed 0kHz, maximum frequency displayed 8000kHz). Data for Campbell’s monkeys are taken from Lemasson and Hausberger (2011) collected on 6 captive adult females in Paimpont, France, in 2000. Data for

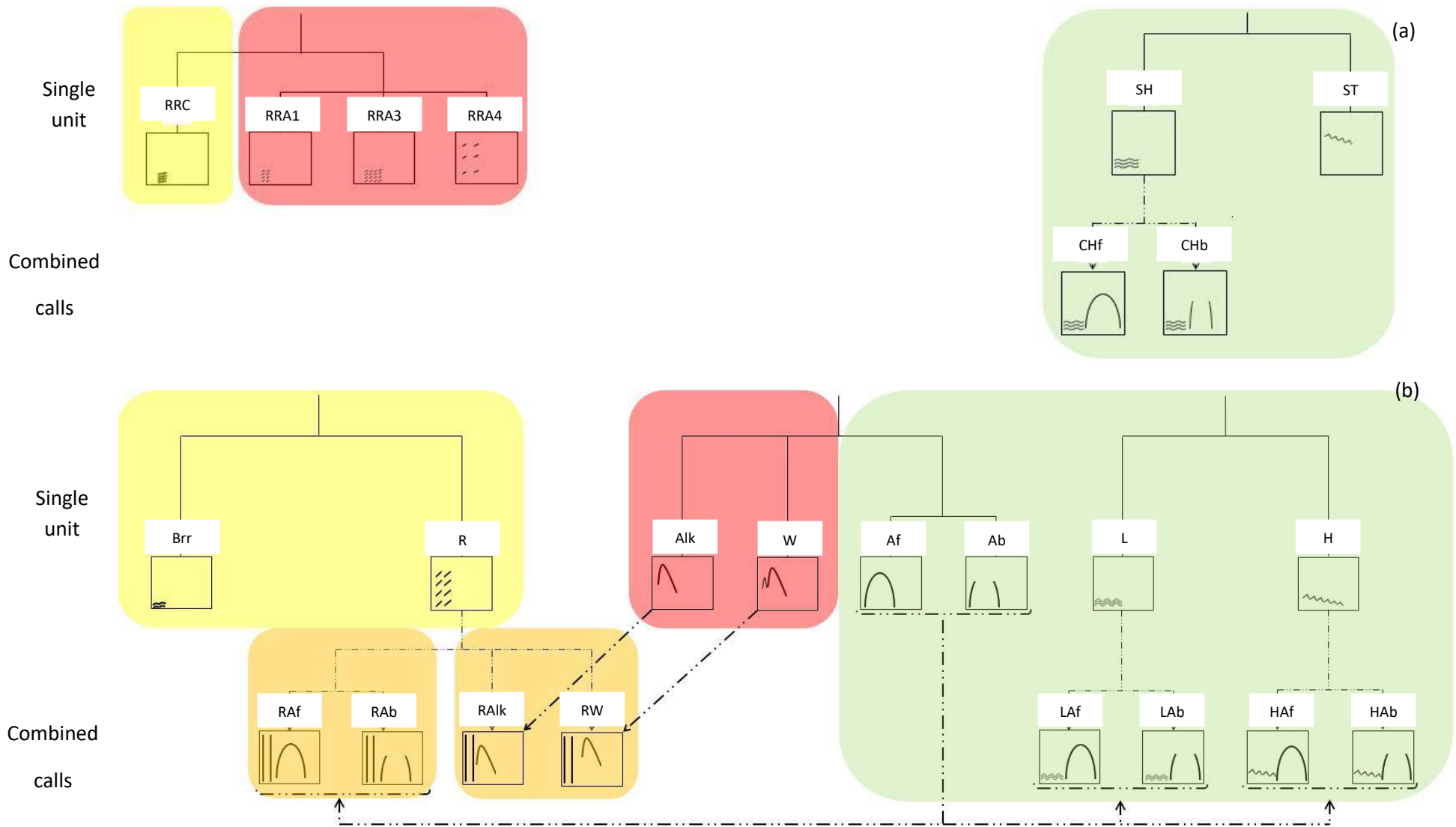
Diana monkeys are taken from Candiotti et al., 2012 collected on 19 wild adult females in Taï National Parc, Côte d'Ivoire, in 2009-2010.

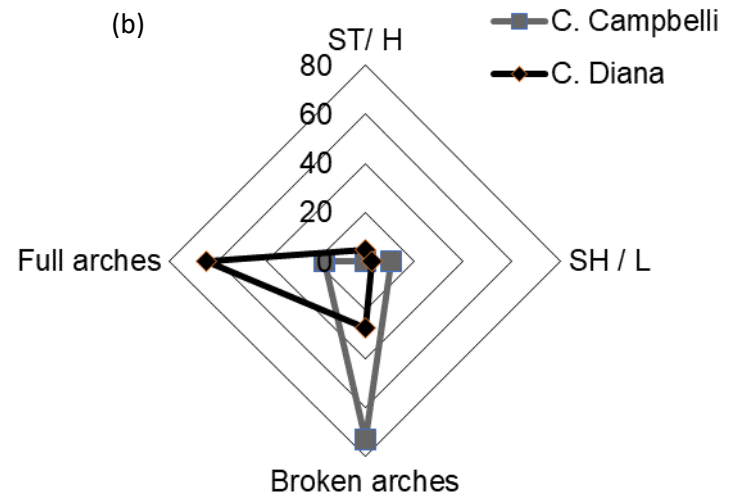
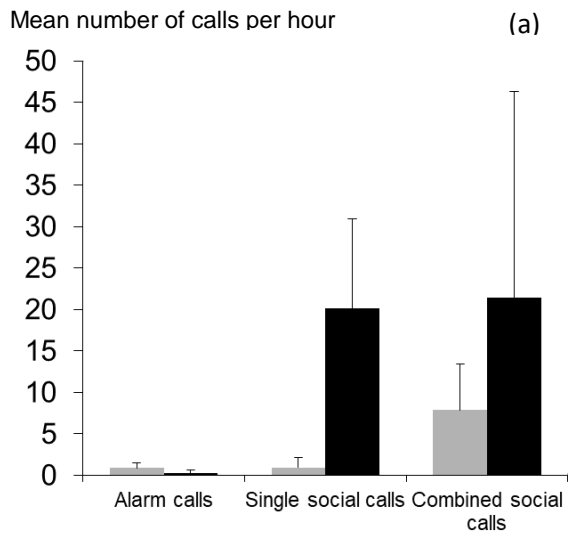
Figure 2: Schematic trees representing the vocal repertoires of (a) Campbell's and (b) Diana monkeys. On both plots, the line entitled "Single unit" shows calls consisting of one call unit only, the line entitled "Combined" shows combined calls, composed of two units. We plotted simple calls onto the same tree when presenting close acoustic structures. Vocal units composing combined calls are indicated by arrows with dashed lines. Shadings show the general function of calls, with green for socio-positive contact calls, yellow for socio-negative calls (threat, mild alarm) and red for alarm calls. Orange shows combination of calls from different functional categories (mixed calls).

Figure 3: (a) Mean call rate per hour for distinct call types in Campbell's (grey) and Diana monkeys (black). Error bars show standard deviation. (b) Radar representing the percentage of total calls given by Campbell's (grey) and Diana monkeys (black). Calls presented include: High-pitched trills (ST / H), Low-pitched trills (SH / L), broken arches (alone or combined: CHb/ Ab and any X-Ab combination in Diana monkeys) and full arches (alone or combined: CHf/Ab and any X-Af combination in Diana monkeys). Data for figure 3 are taken from Candiotti et al., 2012a on 19 wild Diana monkeys in Taï National Park, Côte d'Ivoire, collected in 2009 and 2010 and from Coye et al., 2018 on 10 wild adult female Campbell's monkeys in Taï National Park, Côte d'Ivoire, in 2006 and 2007.

Description	Campbell's monkeys	Diana monkeys
Repetitive chevrons-shaped units Frequency (kHz)  Time (s)	 <p>RRC</p>	 <p>Brr</p>
Repetitive atonal units	 <p>RRA1 RRA3 RRA4</p>	 <p>R</p>
Low-pitched trills	 <p>SH</p>	 <p>L</p>
High-pitched trills	 <p>ST</p>	 <p>H</p>
Blunt arches (=social arches)	 <p>CHb CHf</p>	 <p>Ab Af</p>
Sharp arches (=alarm arches)	<p>X</p>	 <p>Alk W</p>







	Characteristic	Campbell's monkeys	Diana monkeys	Number of study subjects	Study site and dates	Reference
Morphology	Body mass (kg)	♂: 4.5 ♀: 2.7	♂: 5.2 ♀: 3.9	15 <i>C. diana</i> , 19 <i>C. Campbelli</i>	Tiwaï island, Sierra Leone, 1984	Oates et al. 1990
	Physical appearance	Grey and white, dull and poorly contrasted colours	Black, white and red; bright and highly contrasted colours	N/A N/A	N/A N/A	Kingdon 2015; McGraw et al. 2007 pp. 21–24
Ecology	Habitat	Dense tropical forest		N/A (analysis of vegetation)	1998-1999	Kolongo et al. 2006
	Predators	Leopard, crowned-hawk eagle, chimpanzee and human		N/A	N/A	Mcgraw and Zuberbühler 2008
	Diet	Fruit: 46% Prey: 33% Foliage: 8%	Fruit: 59% Prey: 16% Foliage: 16%	2 groups of each species	2000-2001	Buzzard 2006a
Locomotion and spatial distribution	Locomotor profile	Quadrupedal	Quadrupedal + leaping	1 group pf each species N/A	1993-1994 1993-1994, 1996, 1998, 2000	McGraw 1998 McGraw et al. 2007 pp. 223–250
	Cryptic locomotion during travel	Yes	No	N/A	1993-1994	McGraw et al. 2007 p. 21; p248
	Preferred strata	Ground and low (< 5m)	Medium and high (> 5m and above 20 m)	2 groups of each species	2000-2001	Buzzard 2006a, 2006b
	Mean group spread (m)	<25	< 50	2 groups of each species	2000	Wolters and Zuberbühler 2003
	Group density (groups/km ²)	2.5	2.6	2 groups of each species 26 groups of <i>C. diana</i> . 9 groups of <i>C. campbelli</i>	2000-2001 1976-1983	Buzzard and Eckardt 2007; Galat and Galat-Luong 1985
	Home range size (ha)	56	56.8	N/A	N/A	McGraw et al. 2007
	Population density (ind./km ²)	24	62	2 groups of each species	2000-2001	Buzzard and Eckardt 2007

Hetero-specific interactions	Percentage of time in polyspecific groups	76%	86%	26 groups of <i>C. diana</i> , 9 groups of <i>C. campbelli</i>	1976-1983	Galat and Galat-Luong 1985
	Rank in polyspecific associations	Subordinate	Dominant	2 groups of each species N/A	2000-2001 N/A	Buzzard 2006b; McGraw et al. 2007 p. 22
Intra-specific: Intergroup interactions	Frequency of intergroup encounters (N per day)	0.033	0.358	N/A	N/A	McGraw et al. 2007
	Aggressive intergroup encounters (%)	67	35	N/A	N/A	McGraw et al. 2007
Intra-specific: group organisation and intragroup interactions	Social structure	Single male, multi-female groups		2 groups of each species 2 groups of each species 2 groups of <i>C. Campbelli</i>	2000-2001 2009-2011 for <i>C. diana</i> 2006-2007 for <i>C. campbelli</i> 2006-2007	Buzzard and Eckardt 2007 Candiotti et al. 2015, 2015 Ouattara, Zuberbühler, et al. 2009
	Female philopatry	Yes		N/A	N/A	McGraw et al. 2007
	Position of male in the group	Socially peripheral		2 groups of each species 1 group of <i>C. campbelli</i>	2000-2001 1999-2001, captive group in Paimpont, France	Buzzard and Eckardt 2007 Lemasson et al. 2006
	Generation overlap	3 to 4 overlapping generations of offspring stay in the group before dispersion		2 groups of each species	2000-2001	Buzzard & Eckardt, 2007

Group size (number of adult females)	9.3 (5.3)	23.5 (11.5)	2 groups of each species 2 groups of <i>C. campbelli</i>	2000-2001 2006-2007	Buzzard and Eckardt 2007 Ouattara, Zuberbühler, et al. 2009
% time spent within one arm length	0.8	1.25	2 groups of <i>C. diana</i> ; 2 groups of <i>C. campbelli</i>	<i>C. diana</i> 2009-2011; <i>C. campbelli</i> 2006-2007	Candiotti et al. 2015
% time spent grooming	0.65	1.9	2 groups of each species	<i>C. diana</i> : 2009-2011; <i>C. Campbelli</i> : 2006-2007	Candiotti et al. 2015
Rate of agonistic interactions (/h)	0.001	0.0055	2 groups of each species	<i>C. diana</i> : 2009-2011; <i>C. Campbelli</i> : 2006-2007	Candiotti et al. 2015
Coalition between females	Rare	Fairly common	1 group of <i>C. Campbelli</i> 2 groups of each species, 2000-2001	1999-2001 - captive group in Paimpont, France 2000-2001	Lemasson et al. 2006; McGraw et al. 2007 p. 59, from Buzzard 2004
Bonds between females	Moderately differentiated	Strongly differentiated	2 groups of each species	<i>C. diana</i> : 2009-2011; <i>C. Campbelli</i> : 2006-2007	Candiotti et al. 2015

Table 1: Summary of socio-ecological characteristics of Campbell's and Diana monkeys. Study site is Tai National Park, Cote d'Ivoire, unless otherwise stated. N/A mentions in the table signal articles for which the information (number of study subjects or date of collection) was not available, with the exception of Kolongo et al., 2006, in which no data was collected on primates (analyses of vegetation).