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## Social factors drive vocal exchanges in red-capped mangabeys (*Cercocebus torquatus*)

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20 **ABSTRACT:**

21 Of all the calls made by non-human primates, the function of short-distance contact calls has  
22 largely remained to be determined. These calls are the most frequent in the repertoire and  
23 are most often exchanged between individuals in a non-random way. To our knowledge, no  
24 study has ever examined how vocal exchanges are structured in red-capped mangabeys  
25 (*Cercocebus torquatus*), a semi-terrestrial monkey living in the African forest with a complex  
26 semi-tolerant/semi-despotic social system. Our goal was to assess the organization of contact  
27 call exchanges in this species and their relationship with individual and social factors such as  
28 age, affinity, and hierarchy. Therefore, we observed several captive groups of red-capped  
29 mangabeys and collected data on vocal behavior, as well as grooming, agonistic behavior and  
30 spatial proximity. We defined a vocal exchange in this species as a series of contact calls made  
31 by two or more individuals within a maximum inter-caller interval of two seconds. At the  
32 individual level, the higher the individual's hierarchical rank, the less they initiated exchanges.  
33 Furthermore, the most socially integrated individuals had a longer average response time than  
34 the less integrated ones. At the dyadic level, preferred exchange partners were individuals  
35 often observed near one other or individuals most distant in age. Also, the further apart two  
36 individuals were in the dominance hierarchy, the shorter the response time. Our results  
37 support both the social bonding hypothesis and a modulating key role of the dominance  
38 hierarchy on the social use of contact calls, which is in line with the social style of this species.

39

40 **Keywords:** turn-taking, vocal response, social bonding, hierarchy, Old World Monkeys

41

42

**43 INTRODUCTION:**

44 Vocal communication in many animal species is achieved through several species-specific  
45 calls. Most of these calls are emitted in specific contexts, and the study of their function is  
46 therefore facilitated: anti-predation alarm calls (Macedonia and Evans, 1993), distress calls  
47 (Gouzoules et al., 1984), food calls (Slocombe and Zuberbühler, 2006), and copulation calls  
48 (Maestriperi and Roney, 2005; Zanolli et al., 2021). However, the function of so-called contact  
49 calls, emitted in a broad range of contexts (traveling, feeding, resting, grooming...), has long  
50 been a source of debate. The diversity of hypotheses is partially due to the "contact call"  
51 category covering a great diversity of calls ranging from loud long-distance calls to soft short-  
52 distance calls and the flexible use of contact calls depending logically on the social needs of  
53 the species. Several functions, all related to socio-spatial coordination within a group and not  
54 mutually exclusive, have been proposed. For some authors, these calls would have a  
55 determinant role in the initiation and/or regulation of group movements (Neumann and  
56 Zuberbühler, 2016; Sperber et al., 2017), in the coordination of subgroup fusions (Briseño-  
57 Jaramillo et al., 2022), or would allow for maintained contact between isolated or distant  
58 individuals by giving spatial indications (Digweed et al., 2007; Snowdon and Hodun, 1981).  
59 Therefore, a proposed key function of all contact calls is to inform about individual identity  
60 (reviewed in Kondo and Watanabe, 2009). Indeed, contact calls are typically individually  
61 variable (Bouchet et al., 2013), and the degree of acoustic identity coded varies according to  
62 the context: calls diverge more acoustically between callers when they move in visually closed  
63 areas, probably to highlight identity (Candiotti et al., 2012). This may allow receivers to  
64 anticipate a social encounter and to adapt their behaviors accordingly (Ramos-Fernández,  
65 2005; Rendall and Owren, 2002).

66 However, in most species, contact calls are also frequently emitted during the day in the wild  
67 and captivity, even when individuals are not separated. Thus, this also occurs in contexts  
68 where there is no need to coordinate group movements or a lesser need to identify oneself  
69 since individuals can see each other (Bouchet et al., 2010; Ramos-Fernández, 2005; Range and  
70 Fischer, 2004; Byrne and Teixidor, 1999; Kudo, 1987). A growing number of studies propose  
71 an additional function for contact calls: social bonding. Beyond identity coding, contact calls  
72 are sometimes described as social badges advertising affinities through shared acoustic  
73 patterns (i.e. individuals with a particular social bond produce similar acoustic structures;  
74 Levréro et al., 2019; Lemasson and Hausberger, 2004; Snowdon and Elowson, 1999). These  
75 calls could consequently be used to create new social bonds within a group and maintain  
76 existing bonds (Lemasson et al., 2011). This hypothesis is notably based on the fact that: (1)  
77 these calls are more often uttered within vocal interactions than in isolation and are, in fact,  
78 the most frequently exchanged call types in the vocal repertoire; (2) the temporal structure  
79 of the vocal exchanges is better explained by the nature of the social bond between  
80 interlocutors than by the inter-individual distances (Pougnault et al., 2020a). Parallels  
81 between contact call exchanges in nonhuman primates and human conversations have even  
82 been made (Pougnault et al., 2020a). These exchanges often occur in relaxed and peaceful  
83 contexts with visible partners in nonhuman primates. Moreover, exchange partners are not  
84 randomly chosen also in nonhuman primates. In several species, the social affinity between  
85 individuals within a group (i.e. inter-individual affiliative relationships are based on repeated  
86 positive and neutral interactions) is related to the frequency of exchanges between them  
87 (Arlet et al., 2015; Briseno-Jaramillo et al., 2018; Kulahci et al., 2015; Levréro et al., 2019). In  
88 some species, the age of the caller is related to the response rates, with, for example, older  
89 Campbell's monkey females being the most popular interlocutors (Lemasson et al., 2010a). In

90 other species, the caller's hierarchical status matters more, such as in western lowland  
91 gorillas, where higher-ranked group members exchange the most contact calls (Lemasson et  
92 al., 2018). These results are consistent with Dunbar's (1998) hypothesis that vocal exchanges  
93 fulfil the same bonding function as physical grooming, with the advantage that they can be  
94 performed at a distance, more frequently and with a greater number of partners.

95 Parallels between contact call exchanges and human conversations rely on the temporal rules  
96 structuring these interactions. For example, speech overlap avoidance and turn-taking are  
97 universal temporal rules in humans (Stivers et al., 2009). Pioneering studies on new world  
98 monkeys have shown that monkeys also take turns and that the individual's social status  
99 determines the order of vocalizations within a vocal exchange (Snowdon and Cleveland, 1984).  
100 In marmosets, turn-taking respects the characteristics of coupled oscillators found in human  
101 conversations (Takahashi et al., 2013). To avoid call overlaps, individuals respect a species-  
102 specific response time, but it can also vary according to social factors. In squirrel monkeys,  
103 response times are shorter between individuals with high affinity than between individuals  
104 with low affinity (Masataka and Biben, 1987). In Japanese macaques, response times vary with  
105 the physical distance between exchange partners (Sugiura, 2007) and between populations,  
106 suggesting a cultural transmission (Sugiura and Masataka, 1995) as found in humans (Stivers  
107 et al., 2009). As these examples show, vocal turn-taking is present in many animal species  
108 (reviewed in Pika et al., 2018).

109 While turn-taking skills may have an evolutionary inheritance component (turn-taking being  
110 widely distributed in primates), the importance of this coordinated behavior in daily life varies  
111 greatly between species. Turn-taking and call overlap are vocal interacting patterns found in  
112 nonhuman primates, and they can be used strategically by each species. In howler monkeys,

113 while males take turns, females prefer to call simultaneously, likely compensating for their  
114 less intense voice (Briseño-Jaramillo et al., 2021). In apes, vocal interactions are more frequent  
115 in social species than in more solitary ones (i.e. orangutans), and turn-taking is more frequent  
116 in tolerant societies (i.e. bonobos and gorillas). In contrast, overlap occurs more often in  
117 despotic ones (i.e. chimpanzees) (Pougnault et al., 2022). Also, even in species using turn-  
118 taking regularly, some individuals fail to respect this rule more often than others (juveniles in  
119 Campbell's monkeys: Lemasson et al., 2011; subordinate males in Japanese macaques:  
120 Lemasson et al., 2013). Using playback experiments of vocal exchanges violating the rule or  
121 respecting the overlap avoidance (Gorillas: Pougnault et al., 2020b) and the alternation  
122 between interlocutors (Campbell's monkeys: Lemasson et al., 2011), authors confirmed the  
123 relevance of turn-taking for animals by their different reactions to the stimuli presented (head  
124 orientation, gazes towards the loudspeaker).

125 The studies mentioned above on vocal turn-taking in nonhuman primates and the possible  
126 social factors responsible for the observed diversity of use encourage researchers to carry out  
127 more comparative studies on the subject, focusing on a broader range of species. Here, we  
128 conducted a study on several captive groups of red-capped mangabeys (*Cercocebus*  
129 *torquatus*). To our knowledge, no study has ever investigated the structure and potential  
130 function of the vocal exchanges of this species. We wanted to assess how temporally  
131 structured vocal exchanges may reflect an individual's social position in the group. Red-capped  
132 mangabeys are interesting models for this topic for several reasons. First, they live in the wild  
133 in forested areas making vocal communication important for the species. Second, although  
134 they show a noticeable sexual dimorphism and sex differences in social and vocal behaviors,  
135 both males and females produce contact calls (Bouchet et al., 2010). In the wild, red-capped  
136 mangabeys are often seen in multi-male, multi-female groups with seasonal fission-fusion

137 dynamics (Dolado et al., 2016), making the species socially flexible. Third, they have a semi-  
138 despotic/semi-tolerant social organization with both some of the characteristics of despotic  
139 societies (i.e. steep gradient of hierarchy, unidirectionality of aggression) and tolerant  
140 societies (i.e. high proximity between individuals, reciprocal grooming behavior and dominant  
141 individuals occupying peripheral positions) (Dolado and Beltran, 2012). Fourth, turn-taking-  
142 based contact call exchanges were found in closely related species (guenons, macaques, and  
143 baboons). Our first objective was to confirm the existence of turn-taking-based vocal  
144 exchanges in red-capped mangabeys and that it principally or exclusively concerns the contact  
145 call type. Investigations on more socially varied species are needed to better understand the  
146 evolution of “conversational rules” in the primate lineage. Our second objective was to test  
147 which, if any, age-related, affinity-related, and hierarchy-related parameters best shape these  
148 exchanges in that species and thus to understand more about their function.

149

## 150 **METHODS:**

### 151 **Ethical note**

152 This purely observational study was conducted without modifying the living conditions of the  
153 captive mangabeys housed at the Station Biologique de Paimpont (University Rennes 1,  
154 France), where animal facilities and animal care procedures are regularly monitored by the  
155 responsible local authorities (Housing agreement for research D35-211-18, delivered by the  
156 “Direction Départementale de la Cohésion Sociale et de la Protection des Populations”  
157 (DDCSPP). This research protocol has been approved by the CREEA Ethic committee (“Comité  
158 Rennais d’Ethique en matière d’expérimentation animale”) under the reference APAFIS#  
159 2021081711259974.



160

**161 Subjects and housing conditions**

162 Twenty captive adult red-capped mangabeys (*Cercocebus torquatus*) were observed (N=13  
163 males, N = 7 females, Table 1). These individuals, all born in captivity, were housed at the  
164 Station Biologique de Paimpont. Individuals were divided into four groups (i.e., three only-  
165 male groups and one one-male multi-female group, Table 1), group compositions have been  
166 stable for several months or years. The enclosures for each group included an indoor portion  
167 (from 8 to 27m<sup>2</sup>) and an outdoor portion (from 15 to 37m<sup>2</sup>), with a height ranging from 2.5 to  
168 4m. Individuals were free to come and go between different sections via tunnels, except  
169 during our observations when the monkeys were kept outside. The indoor enclosure  
170 temperature was maintained at 22°C, and the floor was covered with straw and wood shavings,  
171 while the outdoor floor was made of cement or covered with bark. All spaces were enriched  
172 with wood and metal perches. The mangabeys were fed twice daily, with fresh fruits and  
173 vegetables in the morning and monkey chows in the afternoon. Water was available *ad*  
174 *libitum*.

175

**176 Data collection**

177 A.G. observed groups II, III and IV between September and October 2015, and B.M. observed  
178 group I between February and April 2021. As the data collections were made six years apart,  
179 it was impossible to calculate inter-observer agreement. Therefore, we decided to sample only  
180 non-confusing vocal and non-vocal behaviors in the same way. We applied a 15 min - focal  
181 sampling method (Altmann, 1974), with 10 (Groups II, III, IV) or 15 (Group I) sessions per  
182 individual for a total of 60 hours of observation. Observations were done between 9h and 17h.

183 Mangabeys were observed in a pseudo-randomized order so that each individual was  
184 observed at different times of the day.

### 185 **Vocal data collection and processing**

186 We recorded vocalizations using a Sony ECM-672 semi-directional microphone connected to  
187 a Marantz PMD660 digital stereo recorder (sampling rate: 44.1kHz, amplitude resolution: 16  
188 bits, WAV format). To compare the temporal emission pattern of contact calls with those of  
189 other call types (described below), we sampled all vocalizations emitted by the focal individual  
190 and vocalizations from others emitted in the same sequence. We defined a sequence as a  
191 series of vocalizations preceded and followed by a silence of at least 7 seconds. This choice of  
192 a long delay was a precaution to be sure to collect all the potential vocal exchanges of interest  
193 for our study, knowing that all the studies carried out previously on exchanges of contact calls  
194 in primates defined a response delay threshold between 1 and 3 seconds (Levréro et al., 2019;  
195 Briseno-Jaramillo et al., 2018; Candiotti et al., 2012; Lemasson et al., 2018, 2010a; Sugiura,  
196 1993; Masataka and Biben, 1987). For each sequence, we noted all inter-call durations (time  
197 between the end of one call and the beginning of the following call), caller identities and call  
198 types. A negative duration signals an overlap of calls. Call types were determined using the  
199 red-capped mangabey's vocal repertoire published by Bouchet et al. (2010): *Oe+* (female  
200 sexual call), *Wi* (female distress call), *Ti+(Uh)* (female food excitement call), *A+(Uh)* (male food  
201 competition call), *Un+(Uh)* (female and male threat call), *Ro+(Uh)* (female and male contact  
202 call), *WaHoo* (female and male alert call), and *Whoop-Gobble* (loud male call). The  
203 identification of callers was relatively simple as: i) there were few individuals per group  
204 (maximum 8); ii) red-capped mangabeys open their mouths when they produce a call; and iii)  
205 their vocal repertoire is relatively discrete, with no ambiguity between call types.

**206 Social data collection and processing**

207 We reported the duration (in seconds) of grooming received or emitted, the duration (in  
208 seconds) other individuals spent within arm's length, and the number of agonistic interactions  
209 received or emitted (in occurrences) for each focal individual. This latter included aggressive  
210 (e.g. grab the tail roughly, chase, hit, push, supplant) and submissive (e.g. flee, withdraw)  
211 behaviors.

212 Four indices were calculated at the individual level to study whether the exchange pattern  
213 varied with the social status of individuals. We calculated a dominance index for each  
214 individual following the method initially proposed by Zumpe and Michael (1986) and used by  
215 Aychet et al. (2022) in red-capped mangabeys. To calculate the dominance index of individual  
216 A according to this method: 1) we reported aggressive behaviors given by individual A to  
217 individual B as a proportion of all the aggressive behaviors sampled in the dyad AB, and we  
218 did the same for submissive behaviors received by individual A from individual B; 2) We then  
219 averaged these two measures (i.e. for dyad AB:  $(\% \text{ aggressive behaviors given by A} + \% \text{ submissive behaviors received by A})/2$ ); 3) A dominance index was obtained by averaging the  
220 scores of all within-group dyads involving A (e.g. AB, AC, AD...).

222 We also calculated an individual index of spatial integration (cumulative time during which  
223 individual A had a conspecific within arm's reach), as well as an individual index of social  
224 integration (cumulative time individual A was grooming or being groomed by a conspecific).  
225 All durations were weighted to consider differences in the total observation time per subject.  
226 We also reported the age of each subject in months.

227 Because the inherent nature of vocal exchanges is dyadic, we also calculated these four indices  
228 at the dyadic level to study if there are any variations in the exchanges based on the partners

229 involved. For each possible within-group dyad (e.g. AB), we calculated the following: the  
230 hierarchical difference (difference between the dominance indices of individuals A and B,  
231 bidirectional index:  $A \leftrightarrow B$ ), the spatial proximity (cumulative duration of observations when  
232 A and B were within each other's arm's reach, bidirectional index), the social grooming  
233 (cumulative time within A and B observations when A groomed B, unidirectional index:  $A \rightarrow B$ ),  
234 and the age difference (in months, bidirectional index). We always subtracted the lowest score  
235 from the highest for bidirectional indices to maintain positive values.

236

### 237 **Data analysis**

238 Statistics analyses were conducted using R software version 4.1.2 (R Core Team, 2021) with a  
239 significance threshold set at 0.05.

240 First, we defined vocal interactions for mangabeys. Therefore, we plotted a frequency  
241 distribution graph with all occurrences of time intervals between two calls (i.e. two  
242 consecutive calls emitted by two different individuals) within sequences and between the last  
243 and the first calls of two consecutive sequences. We then graphically determined (by visual  
244 inspection of the graph) the vocal response threshold time characterizing a call interaction  
245 and defined three vocal patterns: isolated calling, vocal interactions with call overlap, and  
246 vocal interactions based on turn-taking, i.e. without call overlap (methods notably previously  
247 used by Briseno-Jaramillo et al., 2018; Lemasson et al., 2018; Masataka and Biben, 1987). We  
248 then statistically tested whether the contact calls were principally involved in these  
249 temporally-coordinated vocal interactions compared to others call types. To test for the  
250 homogeneity in call type contributing to calling patterns, we ran a generalized linear mixed  
251 model fit by maximum likelihood with a negative binomial distribution (model with Poisson

252 distribution was overdispersed) and a log link function using `glmer.nb` function of “MASS”  
253 package version 7.3.54 (Venables and Ripley, 2002): call type and pattern as fixed effects,  
254 number of calls as the dependent variable, and caller identity as a random factor. We analyzed  
255 this by running a type II ANOVA with a Wald chi-square test (using the `Anova` function of  
256 “rstatix” package version 0.7.0; (Kassambara, 2021). We did post hoc tests with a contrast  
257 table to explore a few chosen comparisons - which will be detailed in the results section – with  
258 FDR adjustments for p-value using the `contrast` function of the “emmeans” package version  
259 1.7.2 (Lenth, 2022).

260 Second, once the vocal interaction was defined, we could extract all dyadic interactions of  
261 contact calls (named here vocal exchange). For example, a vocal exchange with three  
262 consecutive callers, A and B and then C, was broken down into two dyadic exchanges AB and  
263 BC. It is possible that C also responds to A in this case, but since it is difficult to know, we ruled  
264 out this possibility. However, a previous study showed that the results were quite similar when  
265 considering all possible dyads (AB, BC, and AC) than when focusing only on direct successions  
266 (only AB and BC) (Lemasson et al., 2018). These dyadic exchanges were used to assess the  
267 individual contributions to such vocal interactions (i.e. the number of dyadic exchanges to  
268 which a given individual appeared/contributed) and their positions in the interaction. For this  
269 latter measure, we counted the number of times that individual A was in first position (i.e. AB  
270 + AC + AD...) minus the number of times individual A was in second position (i.e. BA + CA +  
271 DA...) divided by the total number of dyadic exchanges involving A. This calculation gave an  
272 index that was negative when the individual was more likely to respond to a call and positive  
273 when he was more likely to trigger a response. Then, we measured the average response time  
274 to each one of the other group members for each individual.

275 Third, using correlation tests, we investigated the possible relationship between these three  
276 variables (i.e. contribution to exchanges, position in exchanging dyads and response time) and  
277 the aforementioned social individual and dyadic indices. To test for the influence of individual  
278 characteristics on vocal behavior, the number of calls emitted was divided by the number of  
279 focal sessions since sampling efforts differ between groups. Non-parametric tests were used  
280 when the conditions for using parametric ones were not met. Before that, we confirmed that  
281 individual indices were not correlated, and we did the same for dyadic indices.

282

## 283 **RESULTS:**

### 284 **Temporal calling patterns and definition of a vocal exchange**

285 The graphical analysis of the distribution of inter-individual inter-call delays allowed us to set  
286 a maximum response time threshold defining a vocal interaction at 2 seconds (Fig. 1). Beyond  
287 2 seconds, two consecutive calls could no longer be considered part of the same interaction.  
288 We could also distinguish interactions with call overlap (negative response time) and without  
289 call overlap ( $0 < \text{response time} < 2\text{s}$ ): the latter being an interaction based on the turn-taking  
290 principle. The contribution of the different call types to the three calling patterns was not  
291 random (Table 2). We tested the different contributions of four call types, Ro+(Uh), Ti+(Uh),  
292 Un+(Uh) and Wahoo (others being produced too infrequently for statistical analysis), to the  
293 different calling patterns. We found a significant interaction between the two factors (GLMM:  
294 call types\*calling pattern interaction,  $\chi^2=14.767$ ,  $p=0.02$ ). To test our prediction about contact  
295 calls being more frequently used in interactions, we focused on the Ro+(Uh) call type to do  
296 our post hoc comparisons using a contrast table. We showed that; i) there is no significant  
297 difference between the occurrence of Ro+(Uh) or other call types in interactions with overlap

298 (GLMM: estimate= -0.988, SE= 1.899, z-ratio=-0.520, p=0.6); ii) there is significantly more  
299 Ro+(Uh) than other call types in turn-taking based interactions (GLMM: estimate= 6.048, SE=  
300 1.284, z-ratio= 4.709, p<0.0001) and in isolated calls (GLMM: estimate= 3.925, SE= 1.648, z-  
301 ratio= 2.383, p=0.02), and iii) there are significantly more Ro+(Uh) in turn-taking based  
302 interactions than in other temporal patterns (GLMM: estimate= 6.803, SE= 0.991, z-ratio=  
303 3.864, p<0.0001). We thus defined a turn-taking-based vocal exchange as a sequence of  
304 Ro+(Uh) calls (i.e. contact calls) emitted by two or more individual callers within a 0-to-2-  
305 second inter-call interval.

306 According to this definition, we could identify 62 vocal exchanges. They most frequently  
307 involved only 2 individuals (only 5 exchanges involved more than 2 individuals, none involved  
308 more than 4 individuals) at a time. The number of calls in these exchanges ranged from 2 to  
309 16, with a median of 3 calls per exchange. These vocal sequences could then be broken down  
310 into 115 dyadic exchanges to examine the possible effect of social factors.

311

### 312 **Influence of the caller's characteristics on exchange rate, exchange position and response** 313 **delay**

314 Individual characteristics did not clearly relate to their propensity to contribute to contact call  
315 exchanges. We did not find any correlation between the dominance, spatial integration or  
316 social integration status of individuals with the number of dyadic exchanges in which they  
317 were involved (dominance: spearman test,  $r_s=-0.05$ ,  $p=0.85$ ; spatial integration: spearman  
318 test,  $r_s=0.05$ ,  $p=0.85$ ; social integration: spearman test,  $r_s=0.32$ ,  $p=0.17$ ). We found a trend for  
319 age, with older individuals tending to exchange more (Spearman test,  $r_s=0.43$ ,  $p=0.06$ ).

320 However, when we considered individual's positions within exchanges rather than their  
321 general involvement, we found a clear link of dominance (spearman test,  $r_s=-0.52$ ,  $p=0.02$ ),  
322 with higher-ranked individuals being more frequently found in response positions (Fig. 2).  
323 There was no link of other positional characteristics of an individual to the exchanges (age:  
324 Pearson test,  $r_s=-0.26$ ,  $p=0.27$ ; spatial integration: Pearson test,  $r_s=0.01$ ,  $p=0.96$ ; social  
325 integration: Spearman test,  $r_s=-0.02$ ,  $p=0.93$ ).

326 Regarding the average response time of each individual, the more socially integrated an  
327 individual was, the slower its response (Spearman test,  $r_s=0.722$ ,  $p=0.001$ ; Fig. 2). Age,  
328 dominance, and spatial integration, however, did not influence this parameter (age: Pearson  
329 test,  $r_s=0.38$ ,  $p=0.13$ ; dominance: Pearson test,  $r_s=-0.11$ ,  $p=0.69$ ; spatial integration: Pearson  
330 test,  $r_s=0.16$ ,  $p=0.54$ ).

331

### 332 **Influence of the dyads' characteristics on exchange rate and response delay**

333 Age difference and spatial proximity were positively correlated with the number of exchanges  
334 between two individuals (age difference: spearman test,  $r_s=0.31$ ,  $p=0.003$ ; spatial proximity:  
335 spearman test,  $r_s=0.31$ ,  $p=0.003$ ). The greater the age difference between two individuals, or  
336 the more time they spent close to one another (Fig. 3), the more they vocally exchanged.  
337 However, there was no correlation between hierarchical difference or social affinity with the  
338 number of exchanges made between two group members (hierarchical difference: spearman  
339 test,  $r_s=-0.02$ ,  $p=0.84$ ; social affinity: spearman test,  $r_s=0.13$ ,  $p=0.21$ ).

340 The hierarchical difference was negatively correlated with response delays (spearman test,  
341  $r_s=-0.43$ ,  $p=0.003$ ). The further away a member was from another one in the group hierarchy,  
342 the shorter the response time (Fig. 3). However, there was no correlation between age



343 difference, spatial proximity and social affinity with the response delays (age difference:  
344 spearman test,  $r_s=0.11$ ,  $p=0.45$ ; spatial proximity: spearman test,  $r_s=-0.15$ ,  $p\text{-value}=0.34$ ;  
345 social affinity: spearman test,  $r_s=-0.006$ ,  $p=0.97$ ).

346

## 347 **DISCUSSION:**

348 Red-capped mangabeys, a semi-tolerant species, exchange, as predicted, turn-taking-based  
349 contact calls in a non-random and socially predictive way. Indeed, the red-capped mangabeys  
350 respond in a time window that does not exceed two seconds and seem to avoid overlapping  
351 as illustrated by the gap in the frequencies between inter-call interval  $[-0.25s;0s[$  (*i.e.*  
352 overlapping vocalizations) and inter-call interval  $[0s;0.25s[$  (*i.e.* turn-taking based vocalization)  
353 (Fig. 1). The social status of callers, consisting of parameters reflecting both affinity (cf.  
354 tolerant society) and hierarchy (cf. despotic society), affects the response rate, the position in  
355 the exchange (initiator or respondent) and the response delay.

356 In our study, individuals exchanged more with the close-proximity partners with whom they  
357 spent the most time rather than their preferred grooming partners. Although these two  
358 behaviors (*i.e.* spatial proximity and grooming) may both indicate an affiliative social  
359 relationship, they are not necessarily equivalent (Dunbar and Shultz, 2010; Silk et al., 2013).  
360 Indeed, in some studies, grooming behaviors are closely related to vocal exchanges (Arlet et  
361 al., 2015; Kulahci et al., 2015; Ramos-Fernández, 2005), while in other studies, spatial  
362 proximity is a better predictor of the exchange rate between two given individuals (Lemasson  
363 et al., 2018; Levréro et al., 2019). Rather than being due to a methodological issue, we believe  
364 that social grooming and spatial proximity have different affinity values according to the  
365 species. Even in studies where both proximity and grooming indices have been used, they

366 correlate to vocal exchange rates differently in different species (Arlet et al., 2015; Lemasson  
367 et al., 2018). In the same vein, several studies on other mammalian species highlighted no  
368 correlation between the networks of spatial proximity and socio-positive behaviors (e.g. pigs:  
369 Camerlink et al., 2022; horses: Wolter et al., 2018). Treves and Baguma (2002) showed that  
370 spatial proximity better predicted social organizations in several non-human primate species  
371 than social behaviors such as social grooming. Compared to many rarer but more visible  
372 behaviors, spatial proximity would thus be a subtle but more reliable behavioral measure of  
373 social bonding for many taxa because it is common and continuous (Dunbar and Shultz, 2010).  
374 Social grooming is, moreover, subject to ambiguity for several primate species. Indeed,  
375 Seyfarth (1977) proposed a model of social grooming in non-human female primates that was  
376 later confirmed by a meta-analysis (Schino, 2001); the “grooming up the hierarchy model” is  
377 based on the fact that there is competition between members of the same group for the  
378 grooming of higher ranked individuals, as well as a preference for grooming related  
379 individuals. Other authors report that social grooming can be exchanged as a commodity  
380 whose value depends on the local food context (whether there is competition or not), which  
381 they, therefore, compare to market prices (Barrett et al., 1999). This evidence shows that  
382 motivations other than affinity may underlie this behavior.

383 We also found an influence of age in this study, with individuals exchanging more grunts with  
384 partners of different ages. Age is an important social marker in non-human primates, and  
385 many studies have shown its influence on vocal exchanges. For instance, in both Campbell's  
386 monkeys and common marmosets, older individuals elicit more vocal responses, showing that  
387 they are preferred exchange partners for the group as a whole (Chen et al., 2009; Lemasson  
388 et al., 2010a).

389 Our study also highlighted that the order of callers within the exchange was not random and  
390 was influenced by the hierarchical status of the individuals involved. A collaborative study  
391 using data on 26 non-human primate species showed that the influence of hierarchy on vocal  
392 behavior is well established. Dominant individuals who were tolerant with their subordinate  
393 partners vocalized at a higher rate than dominant despotic individuals, showing that more  
394 tolerant individuals have a greater need to communicate to manage their dominance in a  
395 group (Kavanagh et al., 2021). In our study, the higher an individual was in the hierarchy, the  
396 more he or she was in a position to respond rather than to initiate an exchange. This similar  
397 exchange pattern was found in western lowland gorillas (Lemasson et al., 2018). This similarity  
398 between mangabeys and gorillas is consistent with the results of the collaborative study  
399 mentioned above, which established an equivalent dominance index for these two species  
400 directly in the middle of the tolerant/despotic spectrum (see fig 4 in Kavanagh et al., 2021).  
401 Therefore, we can infer that this pattern is expected in species living in semi-tolerant/semi-  
402 despotic social systems.

403 Finally, our results reveal that the response delay was influenced by social factors at both the  
404 individual and dyadic levels. On the one hand, the more socially integrated an individual, the  
405 longer its average response time; conversely, the more significant the hierarchical gap  
406 between the two callers, the shorter the response time between their calls. This variation can  
407 be explained in several non-mutually exclusive ways, the first being stress. Indeed, stress is an  
408 internal factor strongly related to vocal production, as evidenced by the study of Lemasson et  
409 al. (2010b), which established that the more a primate is confronted with a stressful situation,  
410 the higher the number of calls in a sequence. In a society with despotic characteristics, such  
411 as the red-capped mangabeys, the least socially integrated individuals are those with a higher  
412 stress baseline (Brent et al., 2011; Crockford et al., 2008). A higher stress baseline may induce

413 a shorter reaction time to various contextual factors, including contact calls. This fact could  
414 better explain why they have a shorter response time on average and why the response time  
415 is shorter when a subordinate answers to a dominant. However, this does not explain why a  
416 dominant would answer more quickly to a subordinate than to another dominant. Another  
417 hypothesis to explain variations in response time is because responding quickly prevents  
418 another individual from responding. In songbirds, for instance, Henry et al. (2015) showed that  
419 individuals adjust the spacing between their consecutive songs to allow more or less room for  
420 others to take turns. In our study, a shorter response time for less socially integrated  
421 individuals and hierarchically distant callers could thus be viewed as individuals rushing to  
422 respond to a vocalization before someone else does in order to gain a social advantage in  
423 establishing, securing a relationship or to appease the partner before an interaction. A less  
424 integrated and subordinate individual could be highly motivated to answer quickly, in general,  
425 to jump at the chance to social bond with others, especially with highly dominant ones. From  
426 a dominant perspective, rushing to respond to a vocalization may be a way for the dominant  
427 respondent to monopolize the floor to prevent one individual from linking up with another  
428 and avoid long-term coalition building. A final explanation, especially for cases of response  
429 latency close to zero, can be that responding quickly may be an attempt to cut off the  
430 initiator's voice. Overlapping is associated with aggressiveness and strong personality in  
431 humans (ter Maat et al., 2010), as well as dominance in songbirds (Baker et al., 2012).  
432 Consequently, responding quickly to a subordinate when at the top of the hierarchy is a less  
433 costly way to demonstrate dominance than aggression or intimidation.

434 We acknowledge the somewhat exploratory nature of our study, and we are aware that the  
435 small size of groups in captivity, as well as the artificial composition (more or less recent) of  
436 groups, does not allow us to describe all the social uses of contact calls in a species.

437 Nevertheless, the significant number of individuals represented in our analysis, from which  
438 interesting correlations arise, opens doors to new research perspectives on the social function  
439 of vocal exchange in primates. Studies on free-ranging and large multi-male, multi-female  
440 groups are still necessary to confirm and extend these first findings. This would allow us to  
441 investigate potential sex-related roles during the exchange of contact calls. Further analyses  
442 for polyadic exchanges may also be interesting, but a larger sample size is needed. Finally,  
443 studies using playbacks of exchanges broadcast in captivity and/or in the wild are also crucial  
444 to better understand the extent to which red-capped mangabeys are aware of these exchange  
445 patterns and may use the potential information coded in these interactions in a strategic  
446 manner. Beyond these limitations, our study offers a valuable contribution to the literature,  
447 given the limited number of studies on primates' "proto-conversations" and the limited  
448 knowledge about vocal communication in mangabey species (Snowdon and Cleveland, 1984).

449 Beyond the debate on the function of contact calls, the study of turn-taking exchanges allows  
450 us to understand the social strategies of non-human primates better. There is a theoretical  
451 convergence between the study of call exchanges in non-human primates and the  
452 Conversation Analysis conducted by sociologists. These two fields seek to explain how group-  
453 level communicative phenomena emerge from individual-level behavioral mechanisms (Logue  
454 and Stivers, 2012). Turn-taking exchanges are thus at the foundation of all human institutions  
455 (Goodwin and Heritage, 1990) since it forms the core of all human interactions, verbal or not.  
456 Language, however, offers unparalleled flexibility in transmitting information and especially  
457 intentions, making parallels between the functioning of human societies and societies of non-  
458 human primates difficult. Nevertheless, the latter is embedded in an interactive engine  
459 defined by several elements that are all present as primordia in non-human primates: (i) in  
460 the multimodality of signals (joint use of gestures, vocalizations, gazes, and facial displays), (ii)

461 in the control of timing (short delay of responses), (iii) in the contingencies between initiations  
462 and responses, and (iv) in the sharing of intentions via communicative acts (the theory of  
463 mind) (Levinson, 2022). The results of this study thus illustrate how animals without language  
464 can instead exploit a simple aspect of their communication to elicit a plurality of meanings  
465 and functions. They offer interesting insights into the ability of red-capped mangabeys to  
466 control the timing of a vocalization to manage their social position in their group.

467

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477

#### 478 **Declarations**

479 The authors declare no competing interests.

480

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- 684

685 **Table 1.** Characteristics of the studied red-capped mangabeys

Social group	Subject	Sex	Date of birth
I.	Chipie	Female	28/06/1992
	Bell	Female	31/03/2002
	Julie	Female	08/05/2004
	Kargi	Male	19/05/2005
	Chipse	Female	03/01/2006
	Many	Female	14/08/2008
	Maillette	Female	29/12/2009
	Triskelle	Female	21/04/2015
II.	Isba	Male	20/04/2004
	Marti	Male	16/10/1998
	Lenni	Male	07/10/2006
III.	Pirate	Male	17/10/1992
	Carillon	Male	02/04/2007
	Georges	Male	05/06/2006
	Elky	Male	06/11/2006
IV.	Lupa	Male	27/09/2006
	Kamel	Male	07/09/2010
	Roby	Male	18/11/2010
	Tips	Male	10/07/2011
	Coët	Male	31/08/2011

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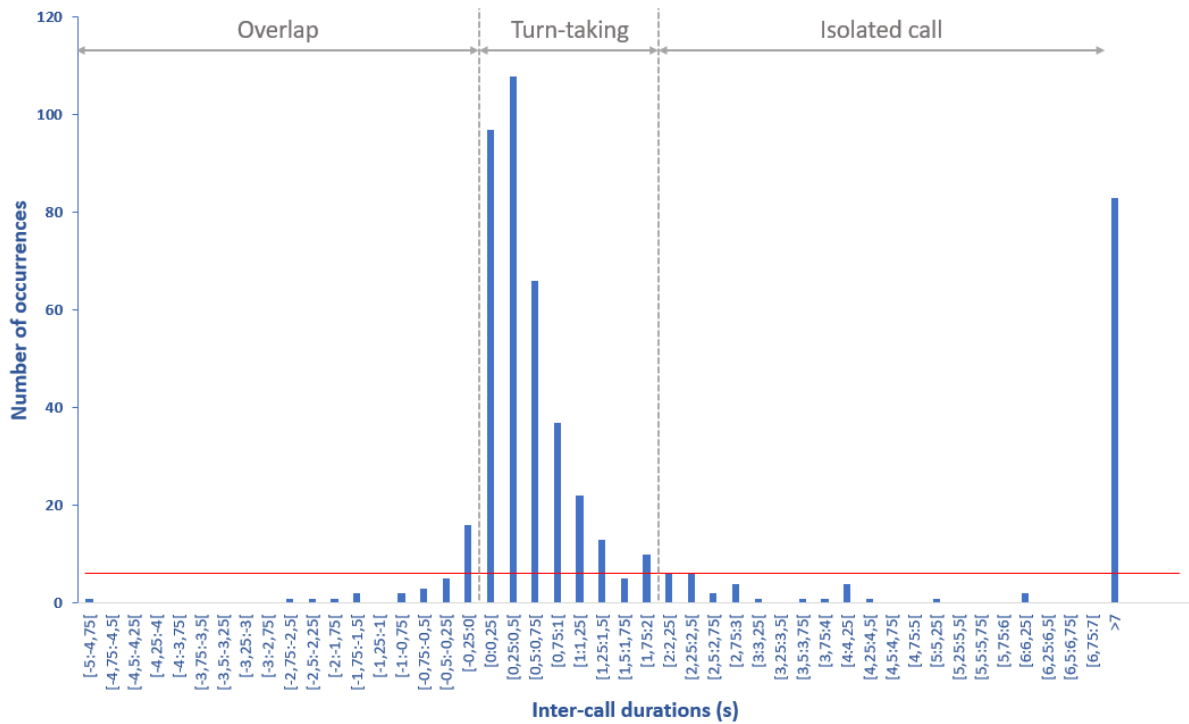
690 **Table 2.** Distribution of call types per calling pattern

Call type	Calling pattern		
	Overlapped calls	Turn-taking based interactions	Isolated calls
Ro+(Uh)	6	188	55
Ti+(Uh)	12	94	27
Un+(Uh)	9	54	10
WaHoo	4	19	11
A+(Uh)	0	1	1
Oe+	1	0	1
Whoop-Gobble	0	1	0
Wi	0	0	0

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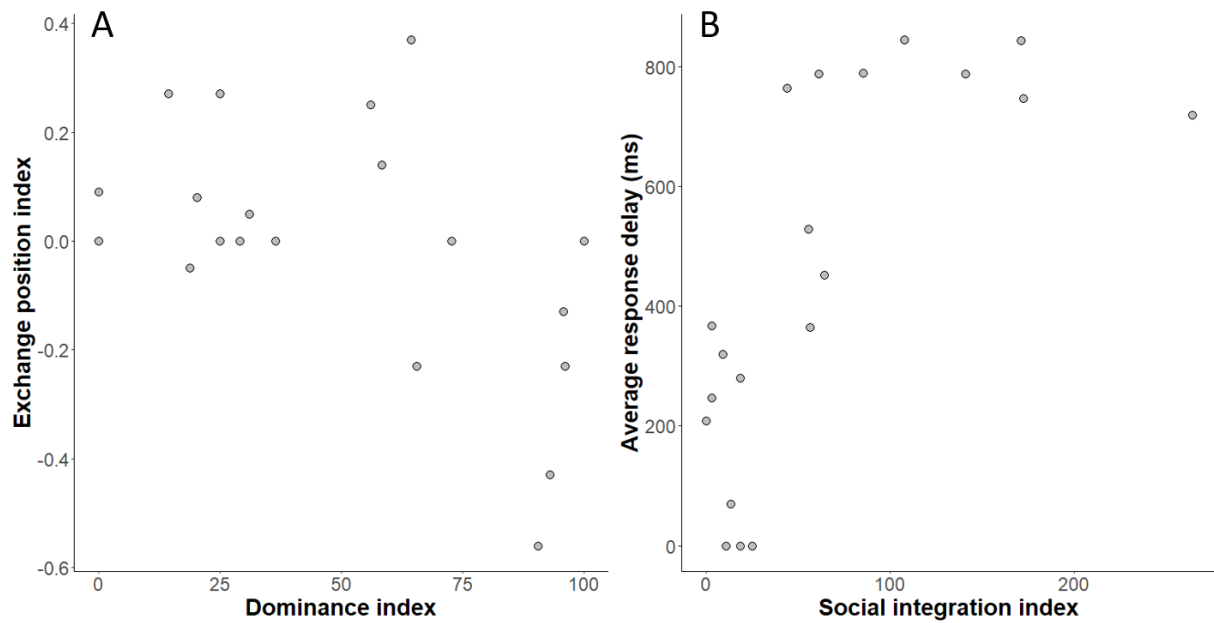
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695 **Fig. 1** Distribution of inter-call intervals. The red line shows the baseline when two calls are  
 696 emitted independently from one another. The dotted lines mark the three temporal  
 697 patterns.

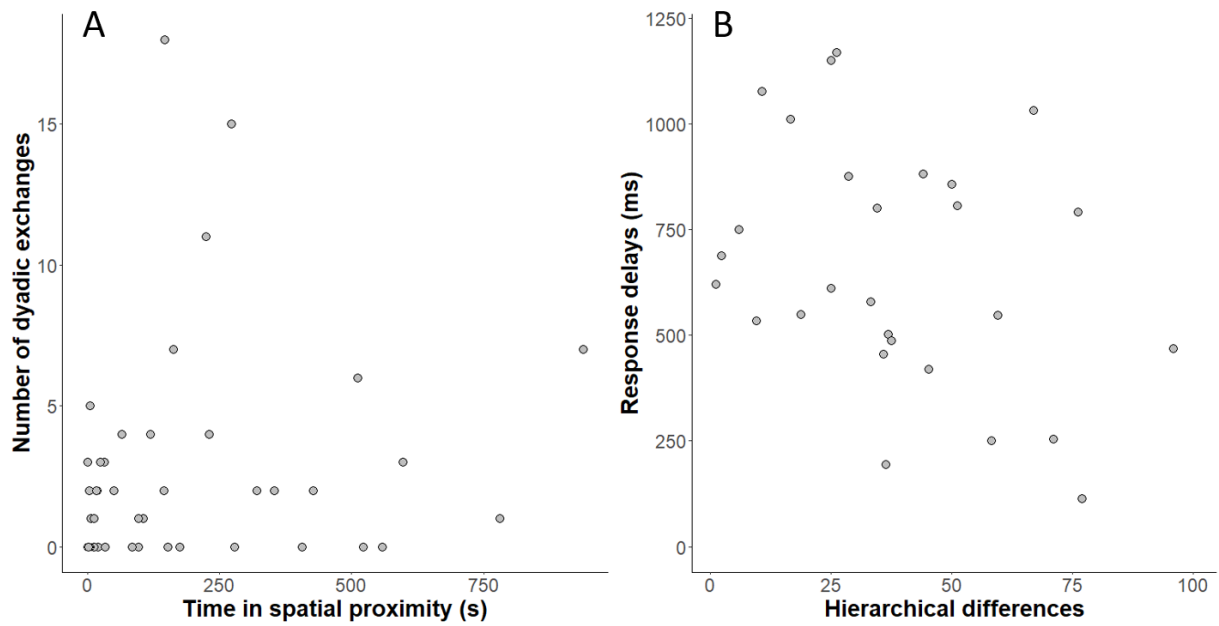
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700 **Fig. 2** Relationship between individual characteristics (dominance index or social integration  
 701 index, A and B respectively) and its implication in exchanges (position index or response delay,  
 702 A and B respectively). In A, when the index has a positive value, the individual was more often  
 703 in the first position within exchanges (i.e. initiated the exchange); when the index is negative,  
 704 the individual responded more often to a previous vocalization. Each dot represents an  
 705 individual.

706



707

708 **Fig. 3** Relationship between dyadic characteristics (spatial proximity or hierarchical  
709 differences, A and B respectively) and its implication in exchanges (number of exchanges or  
710 response delay, A and B respectively). Each dot represents a dyad

711