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

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ABSTRACT:

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

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

INTRODUCTION:

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

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

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

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

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

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

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

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

METHODS:

Ethical note

This purely observational study was conducted without modifying the living conditions of the captive mangabeys housed at the Station Biologique de Paimpont (University Rennes 1, France), where animal facilities and animal care procedures are regularly monitored by the responsible local authorities (Housing agreement for research D35-211-18, delivered by the “Direction Départementale de la Cohésion Sociale et de la Protection des Populations” (DDCSPP). This research protocol has been approved by the CREEA Ethic committee (“Comité Rennais d’Ethique en matière d’expérimentation animale”) under the reference APAFIS# 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 27m²) and an outdoor portion (from 15 to 37m²), 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.

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

Vocal data collection and processing

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

Social data collection and processing

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

Four indices were calculated at the individual level to study whether the exchange pattern varied with the social status of individuals. We calculated a dominance index for each individual following the method initially proposed by Zumpe and Michael (1986) and used by Aychet et al. (2022) in red-capped mangabeys. To calculate the dominance index of individual A according to this method: 1) we reported aggressive behaviors given by individual A to individual B as a proportion of all the aggressive behaviors sampled in the dyad AB, and we did the same for submissive behaviors received by individual A from individual B; 2) We then 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 scores of all within-group dyads involving A (e.g. AB, AC, AD...).

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

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

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

Data analysis

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

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

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

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

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

RESULTS:

Temporal calling patterns and definition of a vocal exchange

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

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

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

Influence of the caller's characteristics on exchange rate, exchange position and response delay

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

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

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

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

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

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

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

DISCUSSION:

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

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

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

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

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

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

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

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

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

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

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

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Declarations

The authors declare no competing interests.

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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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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

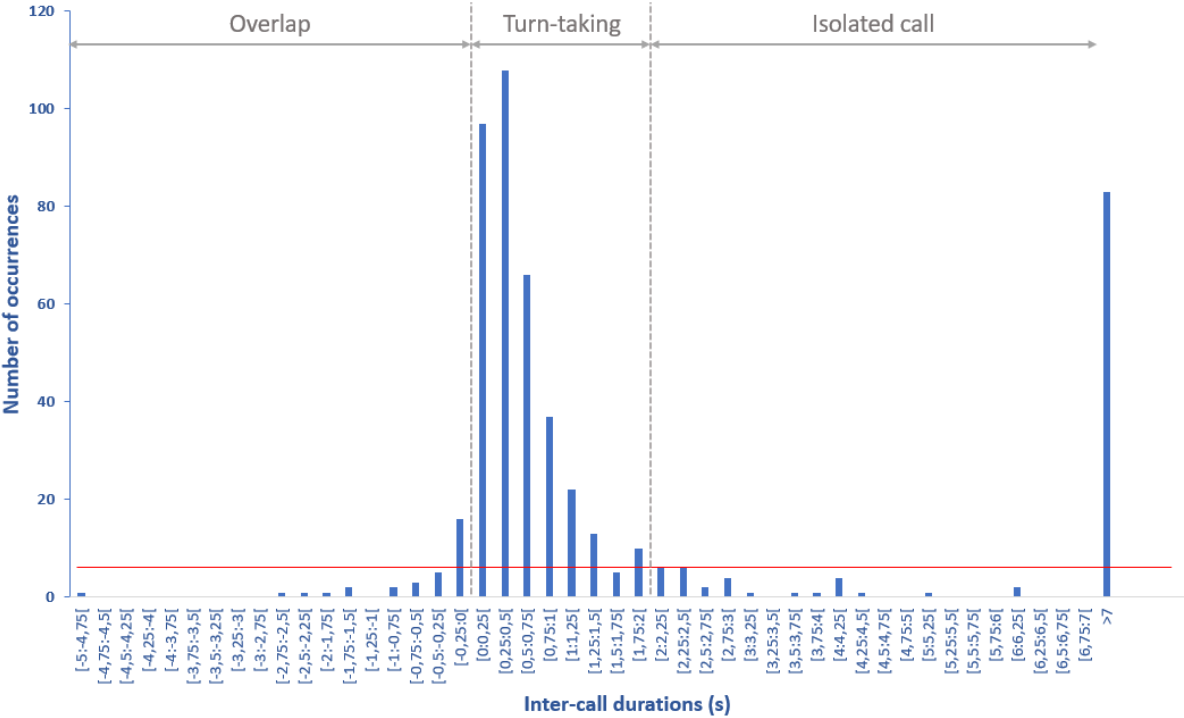


Fig. 1 Distribution of inter-call intervals. The red line shows the baseline when two calls are emitted independently from one another. The dotted lines mark the three temporal patterns.

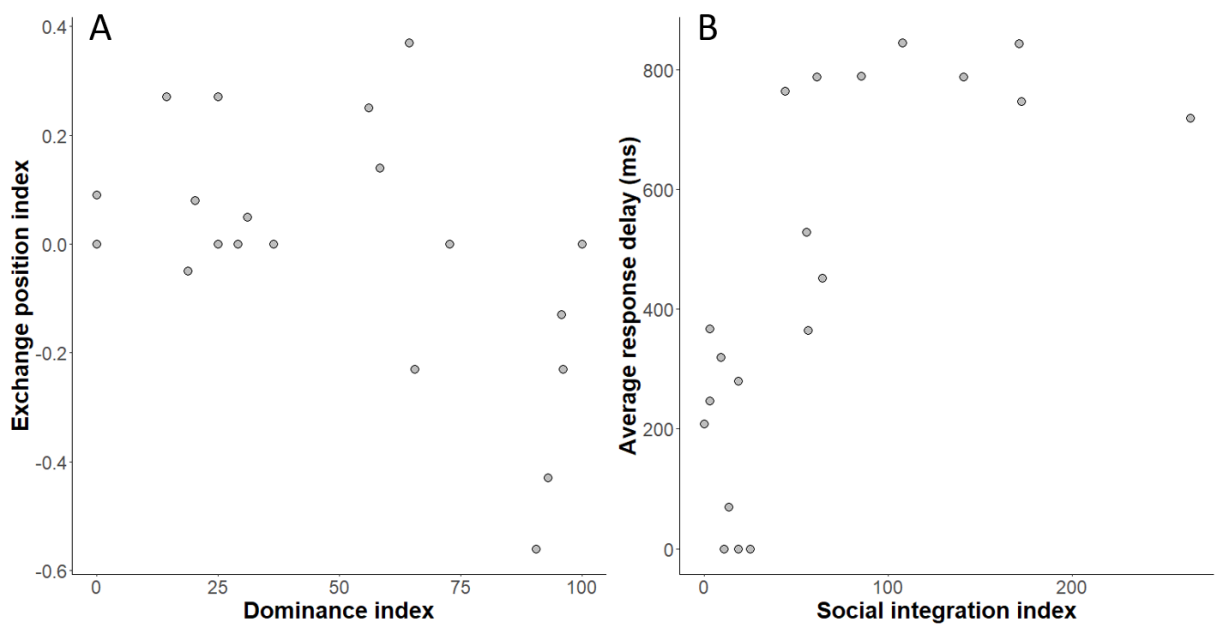


Fig. 2 Relationship between individual characteristics (dominance index or social integration index, A and B respectively) and its implication in exchanges (position index or response delay, A and B respectively). In A, when the index has a positive value, the individual was more often in the first position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

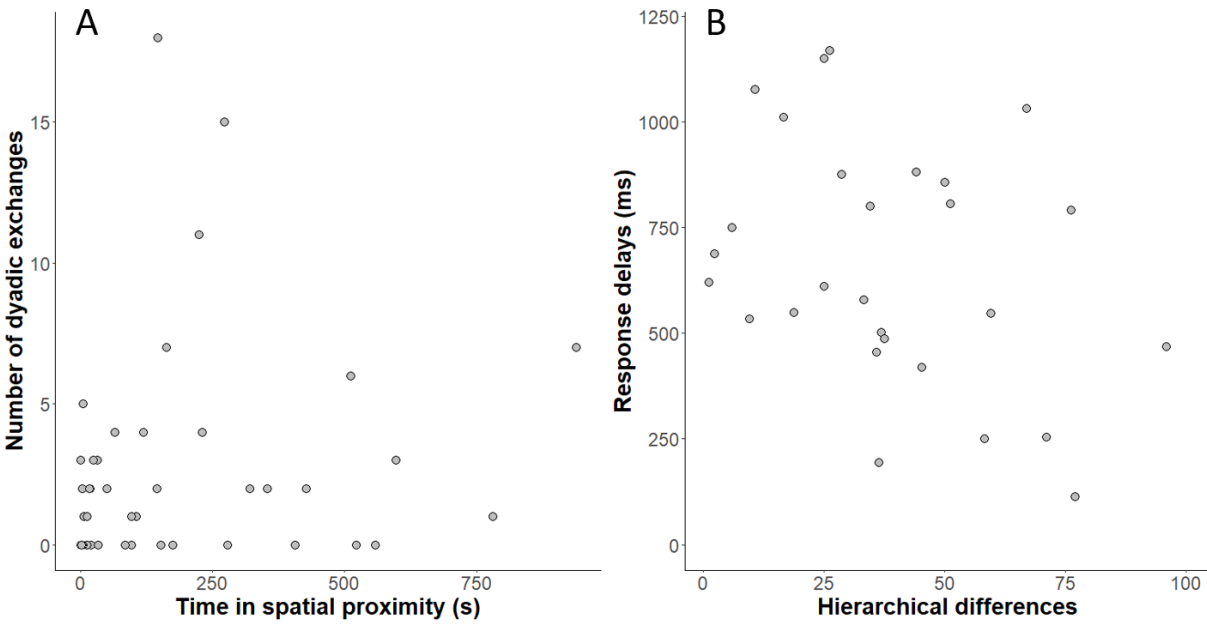


Fig. 3 Relationship between dyadic characteristics (spatial proximity or hierarchical differences, A and B respectively) and its implication in exchanges (number of exchanges or response delay, A and B respectively). Each dot represents a dyad