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ARTICLE FOR THE SPECIAL ISSUE ON PRIMATE COMMUNICATION

**A pilot study of calling patterns and vocal turn-taking in wild bonobos *Pan paniscus***

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Highlights :

- This pilot study shows that wild bonobos display the fundamental temporal rules of vocal turn-taking
- Occurrences of calling patterns are in line with the unique observation collected from a captive group
- Calling patterns do not differ significantly with age and sex
- Calling patterns appear context-dependent

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3 29 In several species of non-human primates, non-agonistic vocal exchanges can be seen as a  
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5 30 primitive form of conversation, as they respect basic temporal rules (i.e. turn-taking, overlap  
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7 31 avoidance), the same as those that guide human conversations. Conversational rules have  
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9 32 recently been suggested in captive great ape species, yet the only study investigating vocal turn-  
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11 33 taking in wild great apes did not find any evidence of such vocal roles. Whether the  
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13 34 environmental conditions (captive versus free ranging) or the social organization of a given  
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15 35 species shape temporally-ruled vocal exchanges remain open questions. Here, we investigated  
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17 36 general calling patterns of peaceful vocal exchanges in a wild bonobo community. This pilot  
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19 37 study revealed that wild bonobos respect the fundamental temporal rules of vocal turn-taking,  
20  
21 38 namely the avoidance of overlapping and the presence of short call-intervals between  
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23 39 interlocutors on the order of 2 sec, corroborating findings from captive bonobos. Despite the  
24  
25 40 limited sample size, our finding suggests that vocal exchanges appear context-dependent but  
26  
27 41 neither age nor sex seem to influence their occurrence. While further studies are needed to  
28  
29 42 confirm these observations, this study helps to fill a major gap in research on the vocal  
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31 43 communication of wild great apes, paving the way for more extensive comparative studies,  
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33 44 representing a further step toward a better understanding of how vocal turn-taking arose in  
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35 45 humans.

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44 47 KEY WORDS: wild bonobo, vocal communication, vocal behaviour, calling patterns, vocal turn-  
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46 48 taking.

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50 **Running head:** Vocal turn-taking evidence in wild bonobo

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## 52 INTRODUCTION

53 In human communication, conversational interactions between two or more people are  
54 highly codified and respect temporal ‘rules’ (e.g., Sacks et al. 1974; Levinson 2016). One key  
55 rule is the alternation of utterances between interlocutors wherein only one party is normally  
56 talking at a given time, followed by a rapid switching of turns between talkers. Another  
57 important rule is the avoidance of vocal overlap (but see Stivers et al. 2009 for evidence that  
58 overlap and alternation of utterances are not mutually exclusive in humans), which when  
59 violated, can appear as a conversation failure and can lead to the end of the exchange (Sacks et  
60 al. 1974; Holler et al. 2015). These vocal turn-taking and overlap avoidance rules, used to  
61 regulate human verbal exchanges, are observed universally across cultures and languages  
62 including sign languages (Stivers et al. 2009; Levinson 2016).

63 Although spoken language is uniquely human, rule-governed call exchanges can be seen as a  
64 primitive form of conversation in non-human primates (hereafter primates; reviewed in Pika et  
65 al. 2018; Pougnault et al. 2020a). Indeed, many primate species appear to respect the same basic  
66 temporal rules (i.e., turn-taking, overlap avoidance) as those that guide human conversations.  
67 Studies on vocal turn-taking behaviours across diverse taxa have revealed functional  
68 similarities, and suggest that conversational rules may be an essential prerequisite to maintain  
69 and reinforce social bonds or to facilitate socio-spatial cohesion between group members (e.g.,  
70 reviewed in Henry et al. 2015; Vernes 2017; Pika et al. 2018). For example, it is well  
71 documented in Japanese macaques (*Macaca fuscata*) that conversational rules such as turn-  
72 taking facilitate social interactions between dyads or group members (Arlet et al. 2015). Also,  
73 in most primate species, these temporally-ruled vocal exchanges are context- and call type-  
74 dependent, typically emerging in peaceful exchanges of contact calls (review in Pougnault et  
75 al. 2020a).

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3 76 Despite recent scientific interest, our knowledge of rule-governed call exchanges in our  
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5 77 closest living great ape relatives is still partial. All confirmatory evidence to date comes from  
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7 78 captive groups of Western lowland gorillas *Gorilla g. gorilla*, and bonobos *Pan paniscus*, and  
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10 79 is limited to one group per species (gorilla: Lemasson et al. 2018; bonobo: Levréro et al. 2019).  
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12 80 The only study investigating rule-governed call exchanges in a wild great ape species (Arcadi  
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14 81 2000) has been conducted on wild chimpanzees *Pan troglodytes schweinfurthii*, which tended  
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16 82 not to respond to most of the calls of their group members (within 5 sec). Rather, wild  
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18 83 chimpanzees often called in chorus, with vocalisations greatly overlapping among individuals  
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20 84 (Arcadi 2000). Thus, from existing scientific knowledge, wild chimpanzees do not appear to  
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22 85 display rule-governed call exchanges, while captive bonobos do.  
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26 86 However, due to differences in environmental conditions (wild versus captive) between  
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28 87 the studied chimpanzees and bonobos, we cannot readily attribute that such variation in their  
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30 88 vocal behaviour reflects species-specific factors rather than study conditions. For example,  
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32 89 Arcadi (2000) focused only on male Eastern chimpanzees, focusing on a small sample of males  
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34 90 (N = 11) across a broad range of social contexts (communication between distant parties,  
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36 91 agonistic interactions, copulations and feeding). In contrast, Levréro et al. (2019) studied both  
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38 92 sexes in bonobos but only in calm contexts (grooming, resting, foraging), that are more  
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40 93 amenable to organised vocal exchanges (Henry et al. 2015; Levinson 2016; Pournault et al.  
41  
42 94 2020a). Interestingly, our primary prediction would have been that non-agonistic vocal  
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44 95 exchanges are more essential in the wild, wherein individuals more often lose visual contact  
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46 96 with one another in closed forest habitats, than in captive groups. The fact that captivity  
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48 97 deprives bonobos from their natural fission fusion social system may indeed reduce the  
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50 98 importance of vocal turn-taking and overlap avoidance, as these vocal behaviours appear to  
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52 99 function to reinforce social bonds and increase community cohesion. At the same time, call  
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54 100 overlap avoidance seems essential when animals must deal with a large number of potential  
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3 101 vocal interlocutors, particularly because their identity is less predictable in the wild, and hence  
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5 102 it may be relatively important to extract vocal identity cues from the calls of conspecifics  
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8 103 (Keenan et al. 2020). Thus, even if we assume that studies of wild chimpanzees and captive  
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10 104 bonobos are comparable, the fact that captive bonobos show organised vocal exchanges and  
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12 105 wild chimpanzees do not is not in line with our predictions, and makes these opposing  
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14 106 observations even more puzzling. Critically, the avoidance of overlap and the reciprocal  
15  
16 107 exchange of alternating short turns remains to be confirmed in wild great ape species. Such  
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18 108 confirmation is of high interest to understand the evolutionary pressures that have shaped rule-  
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20 109 governed communication (Pougnault et al. 2020a).

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24 110 In the present study, we describe the general calling patterns of a wild community of  
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26 111 bonobos in peaceful contexts and within subgroups. To date, the vocal behaviour of wild  
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28 112 bonobos has been mainly investigated in terms of group coordination (e.g. Hohmann & Fruth  
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30 113 1994; White et al. 2015; Schamberg et al. 2016, 2017), which is in the context of long-distance  
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32 114 communication (but see Clay et al. 2015). We thus first aimed to look at intimate vocal  
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34 115 interactions for evidence of conversational-like rules in wild bonobos, and second, to assess  
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36 116 their importance in bonobo communication. To this end, we collected a unique dataset of  
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38 117 individual vocal utterances within subgroups. We predicted to find three calling patterns:  
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40 118 isolated calling (one call is emitted and no other consecutive calls can be heard), repeated  
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42 119 calling (the same caller calls several times in a row), and temporally-ruled vocal exchanges  
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44 120 (with short call interval) between two or more callers. In addition, we examined the potential  
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46 121 influence of the age-sex class of callers and their behavioural activities on calling patterns, with  
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48 122 a special focus on temporally-ruled vocal exchanges. We also investigated whether calling  
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50 123 patterns were call type-dependent. Indeed, while several studies have attempted to link bonobo  
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52 124 call types or call sequences to specific behavioural contexts, these studies have not focused on  
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54 125 calling patterns in which such calls are most often used (e.g., de Waal 1988; Bermejo & Omedes  
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3 126 1999; Clay & Zuberbühler 2009; Clay et al. 2015). In other non-human primate species, there  
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5 127 exists evidence that calling patterns are context- and call-type specific, and vary as a function  
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7 128 of the biological (age, sex) or social characteristics of the caller (Digweed et al. 2007; Chen et  
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9 129 al. 2009; Lemasson et al. 2013, 2018; Levréro et al. 2019). Such relationships, investigated in  
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11 130 the present study, have not been previously demonstrated in wild bonobos.  
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## 17 132 MATERIAL AND METHODS

### 19 133 *Study site*

21 134 The study was carried out in the Manzano forest (2°38'S, 16°23'E) near Embirima village in  
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23 135 the Bolobo Territory of the Western Democratic Republic of the Congo. The study site is part  
24  
25 136 of the Forest Concession of Local Communities of the Mbali River, a community-based  
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27 137 conservation area led by the Non-Governmental Organisation Mbou-Mon-Tour, which has  
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29 138 worked in close connection with the local community since 2001 (Narat et al. 2015a). The forest  
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31 139 is located in the Maï Ndombe Province, 300 km north of Kinshasa. The habitat is a forest-  
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33 140 savanna mosaic with 58% forest and 42% savannah (Pennec et al. 2016) but bonobos spend  
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35 141 more than 97% of their time in the forest (Pennec et al. 2020). The dry season extends from  
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37 142 June to September and the wet season from October to May (Pennec et al. 2020).  
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42 143 The home range of the bonobos in the Manzano forest covers approximately 20 km<sup>2</sup> with a  
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44 144 bonobo density of 1.2 individuals/km<sup>2</sup> (Pennec et al. 2020), thus comprised in the average  
45  
46 145 density of the broader Bolobo Territory, between 0.5 to 2.2 individuals/km<sup>2</sup> (Inogwabini et al.  
47  
48 146 2008; Serckx et al. 2014; Pennec et al. 2020).  
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### 53 148 *Study group*

54 149 Search of regular visual contact with the bonobo community started in 2007 with the presence  
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56 150 of local trackers in the forest twice a week during 3 years and was followed by a pilot study of  
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3 151 habituation that lasted 6 months over 2010-2011 (Narat et al. 2015b). The proper habituation  
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5 152 of the bonobos started in May 2012 (6 days per week; see Narat et al. 2015b for details). The  
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7 153 community is now well habituated and tolerant to human presence (Narat et al. 2015b). An  
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9 154 approach of a minimum distance of 10 m was possible between the closest individual and the  
10  
11 155 observers. This minimum distance was maintained to decrease the risk of disease transmission.  
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13 156 During our pilot study period (February to March 2019), the studied community was composed  
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15 157 of 20 weaned free-ranging individuals. Dependant infants (N = 2) were excluded from our  
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17 158 analyses as in similar studies investigating general patterns of vocal behaviour (Lemasson et al.  
18  
19 159 2018; Levréro et al. 2019). We used the age classes defined by Van Krunkelsven et al. (1999):  
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21 160 juveniles (3–9.9 years), subadults (10–14.9 years) and adults (15 + years). For individuals born  
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23 161 between 2012 and 2019, the exact month of birth was known while for individuals born between  
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25 162 2007 and 2012, the exact year of birth was known. Regarding individuals born before 2007, the  
26  
27 163 year of birth could be estimated for individuals who were still dependent infants in 2007 and  
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29 164 the other individuals were considered as adults at the time of our study (i.e., they were over 15  
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31 165 years old in 2019).

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33 166 The group composition was thus three adult males, seven adult females, three subadult males,  
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35 167 two subadult females and five juvenile females. For the study of their vocal behaviours we  
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37 168 considered two age classes: the “immature class” which included juveniles and subadults, and  
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39 169 the adult class (see Table 1) because of the limited sample size. Individual identification was  
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41 170 based on repetitive direct observations from 2012 and from photographs and film banks (M.  
42  
43 171 Ngofuna and V. Narat). Individual identification relied on body size, face colour, hair growth  
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45 172 on the head, anogenital area shape, and particular features such as mutilations caused by  
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47 173 poacher traps.

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58 175 *Data collection*

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3 176 The field team (one researcher, C. Cornec) accompanied by two to six local trackers patrolled  
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5 177 the forest daily between 6:00 am and 6:00 pm, over February 6th to March 8th, 2019. Forest  
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7 178 field conditions were harsh with unusual frequent heavy rains for the season that prevented the  
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9 179 team from following or recording the bonobos on some days. When we could not follow them  
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11 180 until their night nest site, it took 1 to 4 days to relocate the group. In total, we spent 70 hr in  
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13 181 visual contact with bonobos during the study period.  
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17 182 Wild bonobos live in a fission-fusion social system (Kano 1982; White 1988; Van Elsacker et  
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19 183 al. 1995) where individuals form temporary subgroups, or parties, that travel and forage  
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21 184 separately from other parties. Parties are unpredictable in size (ranging from one individual to  
22  
23 185 the entire community), longevity and composition. We decided each time to follow the larger  
24  
25 186 subgroup (on average 10 individuals) and focused on intra-subgroup vocal behaviour. Over the  
26  
27 187 study period, all the group members had been monitored at least 2 days (mean: 4.7  
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29 188 days/individual, range: 2-7 days).  
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33 189 Vocalisations were collected with ad libitum sampling (Altmann 1974) as the rapid move of  
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35 190 individuals through dense vegetation did not permit the method of focal sampling for collecting  
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37 191 vocal data. Recordings began systematically when the target group was close enough (20 m on  
38  
39 192 average) to ensure quality audio recordings and reliable identification of individuals using  
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41 193 binoculars. One local tracker (M. Ngofuna) remained with the researcher (C. Cornec) to check  
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43 194 the identification of individuals and behavioural observations, while the other trackers remained  
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45 195 at a distance to reduce disturbance.  
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49 196 We focused on vocalisations produced when the group was peaceful (e.g., resting, foraging,  
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51 197 playing, moving and positive social interactions like grooming) similar to protocols used in  
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53 198 captive population studies. Indeed, it has been previously shown, as in humans, that effective  
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55 199 temporally organised vocal exchanges require calmness and attention toward others and so have  
56  
57 200 a higher probability to occur in quiet contexts (Levinson 2016; Pournault et al. 2020a). We thus  
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3 201 excluded calls recorded during agonistic interactions (e.g., threatening or chasing behaviours)  
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5 202 and any synchronized group responses to external events (for example, falling branches). Due  
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7 203 to the sudden and brief nature of vocal exchanges, vocal interactions were defined by their  
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9 204 temporal characteristics regardless of behavioural parameters, similar to studies on captive  
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11 205 populations (see Lemasson et al. 2018; Levréro et al. 2019). Nevertheless, we describe the  
12  
13 206 general activity of the group because the behaviour of individual callers could not always be  
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15 207 identified (e.g., when hidden by vegetation), and thus group dynamics can offer additional  
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17 208 context. We distinguished two main broad behavioural contexts: sedentary behaviour (the  
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19 209 majority of the group was feeding or half of the group was feeding while the other half was  
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21 210 resting or grooming), and moving behaviour (about half of the individuals moved calmly  
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23 211 towards other group members or played, or general calm movement of all group members). For  
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25 212 each recording, we noted, in a notebook, the age and sex class of callers and the broad  
26  
27 213 behavioural context.

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29 214 Calls were recorded using a digital Zoom H4n Handy Recorder (Zoom, Japan: 44.1 kHz  
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31 215 sampling frequency, 32-bits resolution, mono, .WAV format) connected to a directional  
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33 216 Sennheiser MKH70-1 microphone (Sennheiser Electronic KG, Germany) with windscreen.  
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#### 41 42 218 *Calling patterns*

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44 219 In order to define calling patterns (see below for definitions), we investigated inter-call delays  
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46 220 between two successive vocalisations within a timespan up to 10 sec. This time delay  
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48 221 corresponds to 2 or 3 times the maximum response delay recorded in great apes (5 sec in wild  
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50 222 chimpanzees: Arcadi 2000; 2.5 sec in captive bonobos: Levréro et al. 2019; 3 sec in captive  
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52 223 gorillas: Lemasson et al. 2018). Calls that occurred more than 10 sec apart were thus considered  
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54 224 as- resulting from independent vocal events. We studied the distribution of all inter-call  
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56 225 durations within each vocal event using spectrograms produced in PRAAT (Boersma &  
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3 226 Weenink 2018). Inter-call duration corresponded to the silent gap between two consecutive  
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5 227 calls, from the offset of the first call to the onset of the second call (e.g., Lemasson et al. 2018;  
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7 228 Levréro et al. 2019). Interval call duration could be negative when there was an overlap between  
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9 229 two calls. All calls with poor spectrographic quality, thus preventing measurement of call onset  
10  
11 230 (e.g., due to overlapping forest noises), were excluded from analysis.  
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14 231 To determine if the calls of two consecutive callers belonged to a vocal exchange, we analysed  
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16 232 the distribution of call intervals to define a baseline threshold of the occurrence of inter-call  
17  
18 233 durations. Then, relying on this temporal baseline threshold and taking into account the identity  
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20 234 of callers, we determined whether the recorded calls were isolated calls or repeated calls from  
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22 235 a single caller, or rather, belonged to a vocal interaction (i.e. two successive calls from two  
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24 236 individuals with a short inter-vocalisation delay or a negative inter-call duration). Vocal  
25  
26 237 exchange analyses focused on dyadic interactions, in which the identity of one or both  
27  
28 238 individuals was always known (see Fig. 1 for details). In a subset of cases that involved different  
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30 239 consecutive callers, but in which the identity of one caller was uncertain, we noted his/her sex  
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32 240 and/or age class when possible.  
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37 241 In summary, we considered the following possible calling patterns (following Lemasson et al.  
38  
39 242 2018; Levréro et al. 2019; see Fig. 1) distinguishing between calls produced in non-interactive  
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41 243 contexts versus interactive contexts:  
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44 244 (1) Calls produced by the same individual (subsequently termed ‘non-exchanged calls’), which  
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46 245 could be:  
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49 246 (1.a) Isolated calls: a call not followed by a consecutive call within a maximum delay  
50  
51 247 obtained by analysing the inter-call distributions in our data (see Fig. 1 and Results for  
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53 248 value of maximum delay).  
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55 249 (1.b) Repeated calls: a call followed by a consecutive call produced by the same  
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57 250 individual within a maximum delay (see Fig. 1 and Results).  
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3 251 (2) Calls produced during a vocal interaction involving at least two individuals (subsequently  
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5 252 termed ‘vocal exchanges’), which could be:

7 253 (2.a) Vocal turn-taking: a call followed by a consecutive call produced by another  
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10 254 individual within a maximum delay (see Fig. 1 and Results).

12 255 (2.b) Overlapping calls: negative time interval between two calls produced by two  
13  
14 256 different individuals.

16  
17 257

19 258 *Call types*

21 259 Because we can never be sure that we captured the very first call of a vocal interaction  
22  
23 260 (undetected soft calls and/or unpredictability of the vocal interaction), the call types produced  
24  
25 261 were investigated independently of the temporal order of call utterances. Using PRAAT  
26  
27 262 software (Boersma & Weenink 2018), all calls were categorised into call types based on visual  
28  
29 263 comparisons between our data and spectrograms provided by Bermejo and Omedes (1999) and  
30  
31 264 de Waal (1988). The bonobo vocal repertoire is highly graded (Keenan et al. 2020), however  
32  
33 265 researchers agree on a number between 12 and 15 call types (de Waal 1988; Bermejo & Omedes  
34  
35 266 1999). Because of the well-known difficulty of classifying the graded calls of bonobos (Keenan  
36  
37 267 et al. 2020), we considered seven broad call type categories, that together represented all the  
38  
39 268 calls produced by all individuals in peaceful contexts:

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43 269 - “Peep” category: relatively unmodulated calls with a fundamental frequency peak between  
44  
45 270 500 and 2500 Hz and a slope below 400 Hz, with a duration below 400 msec (grouping  
46  
47 271 peep/peep-yelp: Bermejo & Omedes 1999; and peep-yelp/food peep/alarm peep: de Waal  
48  
49 272 1988), or, a downward modulated call with a frequency peak that can reach 3000 Hz and a  
50  
51 273 negative slope between – 500 to – 1000 Hz, with a duration below 300 msec (corresponding to  
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53 274 yelp: Bermejo & Omedes 1999).  
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3 275 - “Bark” category: chevron-shaped modulated call with a fundamental frequency peak between  
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5 276 500 and 2500 Hz and a slope above 400 Hz, the duration is between 100 and 300 msec (grouping  
6  
7 277 soft bark/bark/composed bark: Bermejo & Omedes 1999; and staccato hoot/legato hoot/wieww  
8  
9 bark: de Waal 1988).

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12 279 - “Whistle” category: Long call (may be longer than 1 sec) with variable frequency contour  
13  
14 280 normally indicating a single peak, seldom two or three peaks (corresponding to whistle:  
15  
16 281 Bermejo & Omedes 1999; and legato high hoot: de Waal 1988).

17 282 - “Low hooting”: lowest-pitched call, with a fundamental frequency hardly ever above 800 Hz  
18  
19 283 and a short duration rarely longer than 200 msec (low hooting: de Waal 1988; Bermejo &  
20  
21 284 Omedes 1999).

22 285 - “Hiccup”: Similar to an upward frequency modulated call with a short duration rarely longer  
23  
24 286 than 200 msec (hiccup: Bermejo & Omedes 1999).

25 287 - “Grunt” category: Short call (50 to 200 msec) consisting of a column of wide frequency noise  
26  
27 288 (grouping grunt: Bermejo & Omedes 1999; and greeting grunt: de Waal 1988).

28 289 - “Pout moan”: Short call (less than 200 msec) with variably shaped frequency contour and a  
29  
30 290 fundamental frequency always below 1500 Hz (pout moan: de Waal 1988; Bermejo & Omedes  
31  
32 291 1999).

33 292 All these vocalizations are produced in a large range of contexts, but most often in a feeding  
34  
35 293 context. Compared to “peeps” and “barks”, other vocalisation types including “grunts”,  
36  
37 294 “hiccup”, “hoots”, “pout moan” and “whistles” are relatively rare vocalisations in the bonobo  
38  
39 295 vocal repertoire (de Waal 1988; Bermejo & Omedes 1999; Keenan 2016). To confirm the inter-  
40  
41 296 rater reliability of call classification, we calculated the Fleiss’ Kappa coefficient between two  
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43 297 independent raters (C. Cornec and F. Levréro) on a subset of 72 randomly selected calls (around  
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45 298 30% of the calls).

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3 300 *Statistical analysis*  
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5 301 All statistical analyses were performed using R version 3.6.1 (R Core Team 2019).  
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7 302 We conducted a series of Generalised Linear Mixed Models (GLMMs) in R software. A first  
8  
9 303 GLMM tested whether the sex and/or age of bonobos were significant predictors of calling  
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11 304 patterns. Two additional GLMMs tested the contribution of the two behavioural contexts and  
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13 305 call type categories on calling patterns. The sex, age, behavioural context and call type  
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15 306 categories were respectively included as fixed factors. We coded a binary pattern where 1 was  
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17 307 attributed to a vocal exchange and 0 to a vocal non-exchange. The models were run using a  
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19 308 logit link function with a binomial distribution. Because one individual could be involved in  
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21 309 several vocal interactions and vocal interactions could come from the same or different vocal  
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23 310 events, the identity of the emitters and the code of the vocal event were included as random  
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25 311 factors in all GLMMs to avoid pseudo-replication. We used likelihood ratio tests (LRTs) and  
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27 312 Akaike Information Criteria (AIC) to determine best fitting models. GLMMs were performed  
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29 313 using the function glmer of the 'lme4' package (Bates et al. 2015).  
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37 315 RESULTS  
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40 316 In total we analysed 259 call intervals from 63 independent vocal events during peaceful  
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42 317 activities (on average 5.72 vocal events per day, range 0 to 31 per day). Among these 259 call  
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44 318 intervals, there were 217 call intervals for which callers were identified. Among the remaining  
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46 319 intervals, there were two call intervals for which the sex and age category of the callers were  
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48 320 known, six call intervals for which only the age of the callers was determined, and 34 call  
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50 321 intervals for which we had no information about the age category, sex, or identity of the callers  
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52 322 but we were certain that they were distinct callers. We excluded 382 call intervals from analysis  
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54 323 due to poor acoustic quality that did not allow us to define the onset of the call or to reliably  
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56 324 identify the vocalisers (see Fig. 1).  
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5 326 *General description of calling patterns*6  
7 327 The distributions of all call intervals between two consecutive calls are shown in Figure 2,  
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9 328 revealing a baseline threshold of 2.1 sec on which we relied to define a vocal exchange between  
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11 329 two callers.12  
13 330 Based on this temporal threshold, we found that 52.9% (N = 137/259) of calls were produced  
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15 331 within a vocal exchange (vocal turn-taking or overlapping calls) (Table 2). A vocal exchange  
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17 332 involved on average of 2.34 distinct individuals and up to four individuals. Among these vocal  
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19 333 exchanges, the avoidance of call overlap seemed to be the rule, as 94.2% of calls (N = 129/137)  
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21 334 had a positive short inter-call delay. The mean overlap duration was  $54 \pm \text{SD } 42.2$  ms (range:  
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23 335 16-130 msec, N = 8 call intervals) whereas the inter-call duration of vocal exchanges without  
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25 336 overlap lasted on average  $590.1 \pm \text{SD } 468.8$  msec (range: 5-2093 msec, N = 129 call intervals).  
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27 337 The remaining 47.1% (N = 122/259) of calls showed that the vocal 'responses' of the group  
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29 338 members did not occur systematically (Table 2). Isolated calls and repeated calls represented  
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31 339 respectively 51.6% (N = 63/122) and 48.4% (N = 59/122) of these non-exchanged calls.  
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40 341 *Differences in calling patterns by age and sex*41  
42 342 We found that neither age (GLMM:  $\beta = -0.27$ , SE = 0.63,  $z(219) = -0.43$ ,  $P = 0.67$ ) nor sex  
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44 343 ( $\beta = 0.6$ , SE = 0.64,  $z(219) = 0.94$ ,  $P = 0.35$ ) had a significant influence on individual calling  
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46 344 patterns (N = 219 call intervals, 16 different individuals: 7 adult females and 3 adult males, 3  
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48 345 immature females and 3 immature males). Examining the raw data, it is however interesting to  
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50 346 note that adult bonobos seem to produce slightly more calls in the context of vocal turn-taking  
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52 347 (6.6 calls/individual) than did immature bonobos (3.7 calls/individual), whereas adult and  
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54 348 immature individuals contributed similarly to the production of isolated and repeated calls  
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56 349 (Table 3). Regardless of age class, females tended to be less vocal than males [mean 7.2 calls  
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3 350 per female (14 females and 101 calls) and 19.7 calls per male (six males and 118 calls)]. Among  
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5 351 adult bonobos, both sexes participated equally in vocal turn-taking (7.3 and 6.4 calls/individual,  
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7 352 for males and females respectively) while among immature bonobos, none of the seven young  
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9 353 immature females were recorded producing vocal exchanges. All vocal turn-taking observed in  
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11 354 immature bonobos was indeed uttered by the three young males (Table 3).  
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### 17 356 *Differences in calling patterns across behavioural contexts*

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19 357 The behavioural context of call production was determined in 234 out of 259 call intervals.  
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21 358 The occurrence of vocal exchanges and non-exchanged calls differed significantly according to  
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23 359 behavioural context (GLMM:  $\beta = 2.24$ ,  $SE = 0.58$ ,  $z(195) = 3.88$ ,  $P < 0.001$ ). Most vocal  
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25 360 exchanges occurred during sedentary behaviours (91.2%,  $N = 114/125$  vocal exchanges), while  
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27 361 non-exchanged calls occurred in similar proportions in both contexts (53.2%,  $N = 58/109$  non-  
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29 362 exchanged calls occurred during sedentary behaviours, Table 4).  
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### 35 364 *Contribution of call type to calling patterns*

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37 365 Specific call types could be assigned to 235 calls. We obtained a high and significant  
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39 366 concordance in call classification between raters (Fleiss' kappa coefficients = 0.81,  $P < 0.001$ ).  
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41 367 The calls belonging to the “peep” category were the most frequently produced, both in vocal  
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43 368 exchanges (58.4%,  $N = 130$ ) and in non-exchanged calls (63.8%,  $N = 105$ , Table 5), followed  
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45 369 by calls from the “bark” category, representing nearly 30% of calls produced in vocal exchanges  
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47 370 ( $N = 130$ ) and non-exchanges ( $N = 105$ ). Other call types (“hoots”, “hiccup”, “grunt” category,  
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49 371 “pout moan”, and “whistle” category) were rarely recorded (Table 5). Call type contributions  
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51 372 to calling patterns did not differ significantly between vocal exchanges and vocal non-  
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53 373 exchanges (GLMM:  $\beta = 0.28$ ,  $SE = 0.22$ ,  $z(194) = 1.24$ ,  $P = 0.22$ ). It is however worth noting  
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55 374 that calls produced in isolation and in vocal turn-taking mainly belonged to the “peep” category  
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3 375 (76.8%, N = 43/56 for isolated calls and 60.5%, N = 75/124 for vocal turn-taking, Table 5).  
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5 376 Repeated calls were equally composed of calls from the “peep” and “bark” categories (49%, N  
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7 377 = 24/49 and 44.9%, N = 22/49 respectively). Only overlapping calls more often included those  
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9 378 from the “bark” (4/6) than “peep” category.  
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## DISCUSSION

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17 381 This pilot study provides the first valuable data on the general calling patterns of a wild great  
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19 382 ape species, the bonobo. Focusing on peaceful contexts, we found that bonobos in our study  
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21 383 population exchanged calls that followed fundamental temporal rules of vocal turn-taking.  
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23 384 Vocal exchanges represented half of the calls produced and bonobos almost systematically  
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25 385 avoided overlapping the call of a previous caller, leaving a short delay of on average 2.1 sec  
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27 386 between callers. This call delay was consistent with that observed in other ape studies (2.5 sec  
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29 387 in captive bonobos: Levréro et al. 2019; 3 sec in captive gorillas: Lemasson et al. 2018).  
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33 388 First, this pilot study largely corroborates the findings of the only other studied bonobo  
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35 389 group, which was in captivity (Levréro et al. 2019). Both studies followed a similar  
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37 390 methodology and analogous definitions, except for repeated calls that were not recorded in  
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39 391 captivity. Excluding these repeated calls for comparison, the general vocal behaviour of wild  
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41 392 and captive bonobos appears very similar, with 68.5% vs 73.6% of all coded calls respectively  
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43 393 produced within vocal exchanges (the remaining calls were isolated calls, see Levréro et al.  
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45 394 2019 for values in captive bonobos). Within vocal exchanges, overlapping calls appear more  
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47 395 frequent in captivity than in the wild (32.8% vs 5.8%, see Levréro et al. 2019 for captive values).  
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49 396 Call overlap may increase the risk of confusion during message transmission and so, makes  
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51 397 individual recognition uncertain. However, this risk is limited in captivity where the group  
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53 398 composition is stable and individuals are more often in visual contact, and thus individual  
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55 399 recognition can be achieved through visual cues. Despite this, we acknowledge that the sample  
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3 400 size is limited in both studies. While the higher frequency of call overlap in captivity suggests  
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5 401 that such temporal rule violation may be less crucial in captivity, it has been experimentally  
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7 402 demonstrated that such rule violation remains relevant even to captive primates (Campbell's  
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9 403 monkeys *Cercopithecus campbelli*: Lemasson et al. 2011; gorillas: Pournault et al. 2020b;  
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11 404 bonobos: Levréro et al. 2017).

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14 405 Second, we found no differences in calling patterns between adult and immature  
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16 406 bonobos, while other primate studies suggest that adults emit significantly more calls during  
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18 407 social interactions than do immature individuals (Common marmosets *Callithrix jacchus*, Chen  
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20 408 et al. 2009; wild spider monkeys *Ateles geoffroyi*, Briseño-Jaramillo et al. 2018; captive  
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22 409 gorillas: Lemasson et al. 2018). We cannot rule out the possibility that the lack of differences  
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24 410 across ages was due to the small sample size and notably the low number of juveniles, who  
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26 411 consequently were included in the same category than subadults, as immature individuals.  
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28 412 Similar to age, we found that calling patterns did not vary between males and females.  
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30 413 Regarding vocal turn-taking specifically, adult males and females seemed to be equally  
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32 414 involved, but interestingly no immature females were involved in exchanged calls.  
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37 415 Third, our results suggest that vocal exchanges are context-specific, at least during  
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39 416 sedentary or moving activities. The softest calls of the bonobo repertoire ("peep" category)  
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41 417 were most often produced in vocal turn-taking without overlap as found in captive bonobos  
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43 418 (Levréro et al. 2019) and other primate species (reviewed in Pournault et al. 2020a). Such soft  
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45 419 calls in bonobos convey information about caller identity (Keenan et al. 2020) and receivers  
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47 420 can extract such information (Keenan 2016). In the wild, because callers are not always in visual  
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49 421 contact, overlap avoidance appears crucial for transmitting information that can enable  
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51 422 individual recognition and ensure subgroup cohesion and affiliative bonding between  
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53 423 conspecifics. The fact that vocal exchanges, as opposed to non-exchanged calls, are used  
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55 424 preferentially during non-travelling contexts that typically favour socialising, may support the  
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3 425 “grooming-at-distance” hypothesis of vocal exchanges (Dunbar 1996). We further showed that  
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5 426 overlapping and repeated calls were mostly composed of “barks”, which may be related to  
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7 427 subtly higher-arousal emotional states (de Waal 1988; Bermejo & Omedes 1999; Clay &  
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9 428 Zuberbühler 2009; Keenan et al. 2020) keeping in mind that the studied bonobos were always  
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11 429 in calm contexts.  
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14 430 Fourth, this study suggests that bonobos display vocal turn-taking in the wild, as they  
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16 431 do in captivity (Levréro et al. 2019). Interestingly, a similar recent approach confirmed that  
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18 432 captive chimpanzees do not often display temporally-organized vocal exchanges in peaceful  
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20 433 contexts (Pougnault et al. 2021). This difference between chimpanzee and bonobo vocal  
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22 434 behaviour, two phylogenetically close forest species (Prufer et al. 2012), may reflect their  
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24 435 intrinsically different social organization and thus needs of communication. Bonobos show  
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26 436 greater levels of tolerance and cooperative behaviours wherein individuals repeatedly interact  
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28 437 with numerous other group members in a range of different contexts (review in Gruber & Clay  
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30 438 2016). This could promote selection for temporally-ruled vocal exchanges in bonobos. In  
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32 439 contrast, chimpanzees show lower cooperation and higher competition (Hare & Tomasello  
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34 440 2004; Hare et al. 2007; Surbeck & Hohmann 2013; see for an extensive review Muller & Mitani  
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36 441 2005). However, turn-taking skills in chimpanzees are not questioned, as they readily  
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38 442 demonstrate communicative gestural interactions within mother-offspring pairs (Fröhlich et al.  
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40 443 2016). To understand the origin of this difference in vocal behaviour between chimpanzees and  
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42 444 bonobos is of great interest to understand the origin and evolution of human language, and the  
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44 445 coevolution between communicative behaviours and sociality. A comparative study of several  
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46 446 African starling species with different social systems – ranging from solitary pairs to colonial  
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48 447 groups and communally-breeding species – showed that the species’ social organisation may  
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50 448 be a key factor in developing temporal regulation of vocal exchanges (Henry et al. 2015).  
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3 449 In conclusion, this pilot study supports the existence of coordinated vocal exchanges in  
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5 450 a wild great ape species. We acknowledge that our findings are based on a small sample size,  
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8 451 nevertheless these data corroborate the observations obtained from a captive bonobo group, and  
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10 452 pave the road for replication studies. Although preliminary, these new data will serve future  
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12 453 comparative studies investigating the temporal and social patterns of call exchanges in primates  
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14 454 along their natural range of social systems, and can potentially provide further insight into the  
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17 455 function of turn-taking in primates, and ultimately, the evolution and origins of language  
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19 456 (Levinson 2006, 2016).  
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#### DISCLOSURE STATEMENT

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41 466 The authors declare no competing interests.  
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#### ETHICAL STANDARD

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3 473 All methods were carried out in accordance with the relevant international guidelines and  
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5 474 regulations, and were approved by the Institutional Animal Ethical Committee of the University  
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9  
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11  
12 477 the community-based conservation project. This study involved only behavioural observations  
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14 478 and spontaneous vocal recordings of animals in their natural social group and environment. No  
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17 479 experimental protocols nor invasive methods were used in this study.  
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## 481 AUTHOR CONTRIBUTION

23  
24 482 C. Cornec and F. Levréro conceived, designed and coordinated the study. F. Levréro allocated  
25  
26 483 research funding. C. Cornec and M. Ngofuna collected data. C. Cornec and F. Levréro carried  
27  
28 484 out the statistical analyses and interpreted the data. C. Cornec, F. Levréro and A. Lemasson  
29  
30 485 drafted the manuscript. V. Narat and C. M Monghiemo supported the study implementation in  
31  
32  
33 486 the Manzano forest. All authors gave final approval for publication and agree to be held  
34  
35 487 accountable for the work performed therein.  
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## 496 DATA ACCESSIBILITY

53  
54 497 The raw data supporting this research are openly available on the Open Science Framework  
55  
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## REFERENCES

- 1  
2  
3 500  
4  
5 501  
6  
7 502 Altmann J. 1974. Observational study of behaviour: Sampling methods. *Behaviour*. 49:227-  
8  
9 503 267. doi:<https://doi.org/10.1163/156853974X00534>
- 10 504 Arcadi AC. 2000. Vocal responsiveness in male wild chimpanzees: implications for the  
11  
12 505 evolution of language. *J Hum Evol.* 39(2):205–223.  
13  
14 506 doi:<https://doi.org/10.1006/jhev.2000.0415>
- 15 507 Arlet M, Jubin R, Masataka N, Lemasson A. 2015. Grooming-at-a-distance by exchanging calls  
16  
17 508 in non-human primates. *Biol Lett.* 11(10):20150711–20150714.  
18  
19 509 doi:<https://doi.org/10.1098/rsbl.2015.0711>
- 20 510 Bates D, Mächler M, Bolker B, Walker S (2015). “Fitting Linear Mixed-Effects Models Using  
21  
22 511 lme4.” *Journal of Statistical Software*, 67(1), 1–48. R Package Version. 1.1–26.  
23  
24 512 doi:<https://10.18637/jss.v067.i01>
- 25 513 Bermejo M, Omedes A. 1999. Preliminary vocal repertoire and vocal communication of wild  
26  
27 514 bonobos (*Pan paniscus*) at Lilungu. *Folia Primatol.* 70(6):328–357.  
28  
29 515 doi:<https://doi.org/10.1159/000021717>
- 30 516 Boersma P, Weenink D. 2018. Praat: doing phonetics by computer (version 6.0.19,  
31  
32 517 15/06/2016). Available from: <http://www.praat.org/>
- 33 518 Briseño-Jaramillo M, Ramos-Fernández G, Palacios-Romo TM, Sosa-López JR, Lemasson A.  
34  
35 519 2018. Age and social affinity effects on contact call interactions in free-ranging spider  
36  
37 520 monkeys. *Behav Ecol Sociobiol.* 72:192. doi:[https://doi.org/10.1007/s00265-018-](https://doi.org/10.1007/s00265-018-2615-2)  
38  
39 521 [2615-2](https://doi.org/10.1007/s00265-018-2615-2)
- 40 522 Chen HC, Kaplan G, Rogers LJ. 2009. Contact calls of common marmosets (*Callithrix*  
41  
42 523 *jacchus*): Influence of age of caller on antiphonal calling and other vocal responses.  
43  
44 524 *Am J Primatol.* 71(2):165–170. doi:<https://doi.org/10.1002/ajp.20636>
- 45 525 Clay Z, Archbold J, Zuberbühler K. 2015. Functional flexibility in wild bonobo vocal behaviour.  
46  
47 526 *PeerJ.* 3:e1124. doi:10.7717/peerj.1124
- 48 527 Clay Z, Zuberbühler K. 2009. Food-associated calling sequences in bonobos. *Anim Behav.*  
49  
50 528 77(6):1387–1396. doi:<https://doi.org/10.1016/j.anbehav.2009.02.016>
- 51 529 de Waal FBM. 1988. The communicative repertoire of captive bonobos (*Pan paniscus*),  
52  
53 530 compared to that of chimpanzees. *Behaviour.* 106:183–251.  
54  
55 531 doi:<https://doi.org/10.1163/156853988X00269>
- 56  
57  
58  
59  
60

- 1  
2  
3 532 Digweed SM, Fedigan LM, Rendall D. 2007. Who cares who calls? Selective responses to the  
4  
5 533 lost calls of socially dominant group members in the white-faced capuchin (*Cebus*  
6  
7 534 *capucinus*). *Am J Primatol.* 69(7):829–835. doi:<https://doi.org/10.1002/ajp.20398>  
8  
9 535 Dunbar R. 1996. Grooming, gossip, and the evolution of language. Cambridge (MA): Harvard  
10 536 University Press.  
11  
12 537 Fröhlich M, Kuchenbuch P, Müller G, Fruth B, Furuichi T, Wittig RM, Pika S. 2016. Unpeeling  
13 538 the layers of language: Bonobos and chimpanzees engage in cooperative turn-taking  
14 539 sequences. *Sci Rep.* 6(1):25887. doi:<https://doi.org/10.1038/srep25887>  
15  
16 540 Gruber T, Clay Z. 2016. A comparison between bonobos and chimpanzees: A review and  
17 541 update. *Evol Anthropol.* 25(5):239-252.  
18  
19 542 Hare B, Melis AP, Woods V, Hastings S, Wrangham R. 2007. Tolerance allows bonobos to  
20 543 outperform chimpanzees on a cooperative task. *Curr Biol.* 17(7):619–623.  
21 544 doi:<https://doi.org/10.1016/j.cub.2007.02.040>  
22  
23 545 Hare B, Tomasello M. 2004. Chimpanzees are more skilful in competitive than in cooperative  
24 546 cognitive tasks. *Anim Behav.* 68(3):571–581.  
25  
26 547 Henry L, Craig AJ, Lemasson A, Hausberger M. 2015. Social coordination in animal vocal  
27 548 interactions. Is there any evidence of turn-taking? The starling as an animal model.  
28 549 *Front Psychol.* 6:1416. doi:10.3389/fpsyg.2015.01416  
29  
30 550 Hohmann G, Fruth B. 1994. Structure and use of distance calls in wild bonobos (*Pan paniscus*).  
31 551 *Int J Primatol.* 15:767–782. doi:<https://doi.org/10.1007/BF02737430>  
32  
33 552 Holler J, Kendrick KH, Casillas M, Levinson SC. 2015. Turn-taking in human communicative  
34 553 interaction. *Front Psychol.* 6:1919. doi:10.3389/fpsyg.2015.01919  
35  
36 554 Inogwabini BI, Bewa M, Longwango M, Abokome M, Vuvu M. 2008. The bonobos of the Lake  
37 555 Tumba–Lake Maindombe hinterland: threats and opportunities for population  
38 556 conservation. In: Furuichi T, Thompson J, editors. *The bonobos: behavior, ecology*  
39 557 *and conservation.* New York (NY): Springer; p. 273–290.  
40  
41 558 Kano T. 1982. The social group of pygmy chimpanzees (*Pan paniscus*) of Wamba. *Primates.*  
42 559 23:171–188.  
43  
44 560 Keenan S. 2016. identity information in bonobo vocal communication: from sender to receiver.  
45 561 [Doctoral Dissertation]. Saint-Étienne (France): Saint-Étienne University. Available  
46 562 from: [hal.archives-ouvertes.fr](http://hal.archives-ouvertes.fr).  
47  
48 563 Keenan S, Mathevon N, Stevens JMG, Nicolè F, Zuberbühler K, Guéry JP, Levréro F. 2020.  
49 564 The reliability of individual vocal signature varies across the bonobo's graded  
50 565 repertoire. *Anim Behav.* 169:9-21. doi:<https://doi.org/10.1016/j.anbehav.2020.08.024>



- 1  
2  
3 566 Lemasson A, Glas L, Barbu S, Lacroix A, Guilloux M, Remeuf K, Koda H. 2011. Youngsters  
4 do not pay attention to conversational rules: also, in non-human primates? *Sci Rep.*  
5 567 1:22. doi:<https://doi.org/10.1038/srep00022>  
6 568  
7  
8 569 Lemasson A, Guilloux M, Rizaldi, Barbu S, Lacroix A, Koda H. 2013. Age- and sex- dependent  
9 contact call usage in Japanese macaques. *Primates.* 54(3):283–291.  
10 570 doi:<https://doi.org/10.1007/s10329-013-0347-5>  
11 571  
12 572 Lemasson A, Pereira H, Levréro F. 2018. Social basis of vocal interactions in Western lowland  
13 gorillas (*Gorilla g. gorilla*). *J Comp Psychol.* 132(2):141–151.  
14 573 doi:<https://doi.org/10.1037/com0000105>  
15 574  
16 575 Levinson SC. 2006. Cognition at the heart of human interaction. *Discourse Stud.* 8(1):85-93.  
17 576 doi:<https://doi.org/10.1177/1461445606059557>  
18 577 Levinson SC. 2016. Turn-taking in human communication – origins and implications for  
19 language processing. *Trends Cogn Sci.* 20(1):6-14.  
20 578 doi:<https://doi.org/10.1016/j.tics.2015.10.010>  
21 579  
22 580 Levréro F, Clerc O, Touitou S, Fredet J, Guéry JP, Lemasson A. 2017. Bonobos converse and  
23 pay attention to breaking conversational rules. In: *Behaviour 2017 – 35th International*  
24 581 *Ethological Conference.* Estoril (Portugal): Instituto Universitário de Ciências  
25 582 Psicológicas, Sociais e da Vida (ISPA); Association for the Study of Animal  
26 583 Behaviour (ASAB).  
27 584  
28 585 Levréro F, Touitou S, Frédet J, Nairaud B, Guéry JP, Lemasson A. 2019. Social bonding drives  
29 586 vocal exchanges in Bonobos. *Sci Rep.* 9:711. doi:[https://doi.org/10.1038/s41598-018-](https://doi.org/10.1038/s41598-018-36024-9)  
30 587 [36024-9](https://doi.org/10.1038/s41598-018-36024-9)  
31 588  
32 589 Muller MN, Mitani JC. 2005. Conflict and cooperation in wild chimpanzees. *Adv Stud Behav.*  
33 590 35:275-331. doi:[https://doi.org/10.1016/S0065-3454\(05\)35007-8](https://doi.org/10.1016/S0065-3454(05)35007-8)  
34 591  
35 592 Narat V, Pennec F, Ledo-Bisson L, Bokika Ngawolo JC, Dumez R, Krief S. 2015a. Bonobo  
36 593 conservation as a means for local development: an innovative local initiative of  
37 594 community-based conservation in Democratic Republic of Congo. *J Primatol.*  
38 595 4(2):1000127. doi:<https://doi.org/10.4172/2167-6801.1000127>  
39 596  
40 597 Narat V, Pennec F, Simmen B, Ngawolo JCB, Krief S. 2015b. Bonobo habituation in a forest–  
41 598 savanna mosaic habitat: influence of ape species, habitat type, and sociocultural  
42 599 context. *Primates.* 56:339–349. doi:<https://doi.org/10.1007/s10329-015-0476-0>  
43 600  
44 601 Pennec F, Gérard C, Meterreau L, Monghiemo C, Bokika Ngawolo JC, Laurent R, Narat V.  
45 602 2020. Spatiotemporal variation in bonobo (*Pan paniscus*) habitat use in a forest–  
46 603  
47 604  
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3 599 savanna mosaic. *Int J Primatol.* 41:775–799. doi:<https://doi.org/10.1007/s10764-020->  
4 600 00180-5
- 6 601 Pennec F, Krief S, Hladik A, Lubini Ayingweu C, Bortolamiol S, Bokika Ngawolo JC, Narat  
7 602 V. 2016. Floristic and structural vegetation typology of bonobo habitats in a forest-  
8 603 savanna mosaic (Bolobo Territory, D.R. Congo). *Plant Ecol Evol.* 149(2):199-215.  
9 604 doi:<https://doi.org/10.5091/plecevo.2016.1157>
- 13 605 Pika S, Wilkinson R, Kendrick KH, Vernes SC. 2018. Taking turns: bridging the gap between  
14 606 human and animal communication. *Proc R Soc Lond B.* 285:20180598.  
15 607 doi:<http://dx.doi.org/10.1098/rspb.2018.0598>
- 18 608 Pougnault L, Lemasson A, Mulot B, Levréro F. 2021. Temporal calling patterns of a captive  
19 609 group of chimpanzees. *Int J Primatol.* 42:809-832.
- 22 610 Pougnault L, Levréro F, Lemasson A. 2020a. Conversation among primate species. In:  
23 611 Masataka N, editor. *The origins of language revisited. Differentiation from music and*  
24 612 *the emergence of neurodiversity and autism.* Singapore: Springer; p. 73-96.
- 27 613 Pougnault L, Levréro F, Mulot B, Lemasson A. 2020b. Breaking conversational rules matters  
28 614 to captive gorillas: A playback experiment. *Sci Rep.* 10(1):6947.
- 31 615 Prufer K, Munch K, Hellmann I, Akagi K, Miller JR, Walenz B, Koren S, Sutton G, Kodira C,  
32 616 Winer R, et al. 2012. The bonobo genome compared with the chimpanzee and human  
33 617 genomes. *Nature.* 486:527–531. doi: <https://doi.org/10.1038/nature11128>
- 36 618 R Core Team. 2019. R: A language and environment for statistical computing. Vienna  
37 619 (Austria): R Foundation for Statistical Computing. Version 1.3.1093, 20/09/2020.  
38 620 Available from: <https://www.R-project.org/>
- 41 621 Sacks H, Schegloff EA, Jefferson G. 1974. A simplest systematics for the organization of turn-  
42 622 taking for conversation. *Language.* 50(4):696–735.  
43 623 doi:<https://doi.org/10.1353/lan.1974.0010>
- 46 624 Schamberg I, Cheney DL, Clay Z, Hohmann G, Seyfarth RM. 2016. Call combinations, vocal  
47 625 exchanges and interparty movement in wild bonobos. *Anim Behav.* 122:109-116.  
48 626 doi:<https://doi.org/10.1016/j.anbehav.2016.10.003>
- 51 627 Schamberg I, Cheney DL, Clay Z, Hohmann G, Seyfarth RM. 2017. Bonobos use call  
52 628 combinations to facilitate inter-party travel recruitment. *Behav Ecol Sociobiol.* 71:75.  
53 629 doi:<https://doi.org/10.1007/s00265-017-2301-9>
- 56 630 Serckx A, Huynen MC, Bastin JF, Hambuckers A, Beudels-Jamar RC, Vimond M, Raynaud E,  
57 631 Kühl HS. 2014. Nest grouping patterns of bonobos (*Pan paniscus*) in relation to fruit  
58  
59  
60

- 1  
2  
3 632 availability in a forest-savannah mosaic. PLoS ONE. 9(4):e93742.  
4  
5 633 doi:<https://doi.org/10.1371/journal.pone.0093742>  
6  
7 634 Stivers T, Enfield NJ, Brown P, Englert C, Hayashi M, Heinemann T, Hoymann G, Rossano F,  
8  
9 635 de Ruiter JP, Yoon KE, Levinson SC. 2009. Universals and cultural variation in turn-  
10  
11 636 taking in conversation. PNAS. 106(26):10587–10592.  
12  
13 637 doi:<https://doi.org/10.1073/pnas.0903616106>  
14  
15 638 Surbeck M, Hohmann G. 2013. Intersexual dominance relationships and the influence of  
16  
17 639 leverage on the outcome of conflicts in wild bonobos (*Pan paniscus*). Behav Ecol  
18  
19 640 Sociobiol. 67:1767-1780. doi:<https://doi.org/10.1007/s00265-013-1584-8>  
20  
21 641 Van Elsacker L, Vervaecke H, Verheyen RF. 1995. A review of terminology on aggregation  
22  
23 642 patterns in bonobos (*Pan paniscus*). Int J Primatol. 16(1):37-52.  
24  
25 643 doi:<https://doi.org/10.1007/BF02700152>  
26  
27 644 Van Krunkelsven E, Dupain J, Van Elsacker L, Verheyen R. 1999. Habituation of bonobos  
28  
29 645 (*Pan paniscus*): first reactions to the presence of observers and the evolution of  
30  
31 646 response over time. Folia Primatol. 70(6):365–368.  
32  
33 647 Vernes SC. 2017. What bats have to say about speech and language. Psychon Bull Rev. 24:111–  
34  
35 648 117. doi:<https://doi.org/10.3758/s13423-016-1060-3>  
36  
37 649 White FJ. 1988. Party composition and dynamics in *Pan paniscus*. Int J Primatol. 9:179–193.  
38  
39 650 White FJ, Waller M, Boose K, Merrill MY, Wood KD. 2015. Function of loud calls in wild  
40  
41 651 bonobos. J Anthropol Sci. 93:1-13.  
42  
43  
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3 653**TABLES**4  
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Table 1.

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Composition of the studied community of wild bonobos from Manzano forest, Democratic Republic of the Congo.

Name	Sex	Age class (2019)	Age category (2019)
Ngampeï	Male	Adult	Adult
Roger	Male	Adult	Adult
Dodo	Male	Adult	Adult
Clémentine	Female	Adult	Adult
Pam	Female	Adult	Adult
Flèche	Female	Adult	Adult
Obia	Female	Adult	Adult
Kimono	Female	Adult	Adult
Ngwana	Female	Adult	Adult
Lili	Female	Adult	Adult
Charlie	Male	Subadult	Immature
Popeye	Male	Subadult	Immature
Filou	Male	Subadult	Immature
Kawa	Female	Subadult	Immature
Not named yet (New immigrant)	Female	Subadult	Immature
Primus	Female	Juvenile	Immature
Faki	Female	Juvenile	Immature
Okay	Female	Juvenile	Immature
Kiteke	Female	Juvenile	Immature
Nguli	Female	Juvenile	Immature

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Table 2.

Distribution of call intervals for different calling patterns. In italics we give the percentage of occurrence for each given calling pattern.

Non-exchanged calls		Vocal exchanges		
Isolated calls	Repeated calls	Vocal turn-taking	Overlapping calls	Total call intervals
63 <i>24.3%</i>	59 <i>22.8%</i>	129 <i>49.8%</i>	8 <i>3.1%</i>	259

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Table 3.

Distributions of calling patterns per caller sex and age. Numbers in brackets refer to individual vocal rate production obtained by dividing the total number of recorded calls by the number of individuals within each age and sex class.

	Non-exchanged calls		Vocal exchanges		Total calls N = 219
	Isolated calls N = 51	Repeated calls N = 59	Vocal turn-taking N = 104	Overlapping calls N = 5	
Adult males (N = 3)	14 (4.7)	5 (1.7)	22 (7.3)	2 (0.7)	43
Adult females (N = 7)	16 (2.3)	26 (3.7)	45 (6.4)	0	87
Subtotal adult inds (N = 10)	30 (3)	31 (3.1)	66 (6.6)	2 (0.2)	131
Immature males (N = 3)	19 (6.3)	16 (5.3)	37 (12.3)	3 (1)	75
Immature females (N = 7)	2 (0.3)	12 (1.7)	0	0	14
Subtotal immature inds (N = 10)	21 (2.1)	28 (2.8)	37 (3.7)	3 (0.3)	89

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Table 4.

Distribution of calling patterns as a function of behavioural context. Percentages in italics correspond to the contribution of each behavioural context to each calling pattern.

Behaviour	Non-exchanged calls		Vocal exchanges		Total calls N = 234
	Isolated calls N = 57	Repeated calls N = 52	Vocal turn-taking N = 117	Overlapping calls N = 8	
Sedentary behaviour <sup>a</sup>	39 <i>68.4%</i>	19 <i>36.5%</i>	108 <i>92.3%</i>	6 <i>75%</i>	172
Movement <sup>b</sup>	18 <i>31.6%</i>	33 <i>73.5%</i>	9 <i>7.7%</i>	2 <i>25%</i>	62

676 <sup>a</sup>The majority of the group was feeding or half of the group was feeding while the other half  
677 was resting or grooming.

678 <sup>b</sup>About half of the group moved towards other group members or played or there was a  
679 general movement of the group members.

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Table 5.

Contribution of the seven broad call type categories (defined from Bermejo & Omedes 1999 and de Waal 1988) to calling patterns. Percentages in italics correspond to the contribution of each call type category to each calling pattern.

Call type category	Non-exchanged calls		Vocal exchanges		Total calls N = 235
	Isolated calls N = 56	Repeated calls N = 49	Vocal turn-taking N = 124	Overlapping calls N = 6	
Peep category	43 <i>76.8%</i>	24 <i>49%</i>	75 <i>60.5%</i>	1 <i>16.7%</i>	143
Bark category	9 <i>16.1%</i>	22 <i>44.9%</i>	34 <i>27.4%</i>	4 <i>66.7%</i>	69
Whistle category	1 <i>1.8%</i>	3 <i>6.1%</i>	4 <i>3.2%</i>	0 <i>0%</i>	8
Low hooting	1 <i>1.8%</i>	0 <i>0%</i>	4 <i>3.2%</i>	1 <i>16.7%</i>	6
Hiccup	1 <i>1.8%</i>	0 <i>0%</i>	4 <i>3.2%</i>	0 <i>0%</i>	5
Grunt category	0 <i>0%</i>	0 <i>0%</i>	3 <i>2.4%</i>	0 <i>0%</i>	3
Pout moan	1 <i>1.8%</i>	0 <i>0%</i>	0 <i>0%</i>	0 <i>0%</i>	1

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**FIGURE CAPTIONS**

689 Fig. 1. — Distinct calling patterns considered in the study. The baseline threshold of 2100 msec  
690 between two calls was determined by an analysis of the distribution of call intervals (see Results  
691 and Fig. 2) and was used to define the calling patterns.

692  
693 Fig. 2. — Distribution of inter-call durations between two successive calls from different callers  
694 (not all non-exchanged calls are represented in this figure for visual clarity). The dotted line  
695 corresponds to the baseline of the occurrence of inter-call durations. The black arrow  
696 corresponds to the threshold indicating the maximum response delay for defining a vocal  
697 exchange, and was placed at the location where inter-call delays start rising above the baseline  
698 when moving from long delays to the peak observed at around 2 sec (as in Lemasson et al.  
699 2018; Levréro et al. 2019).

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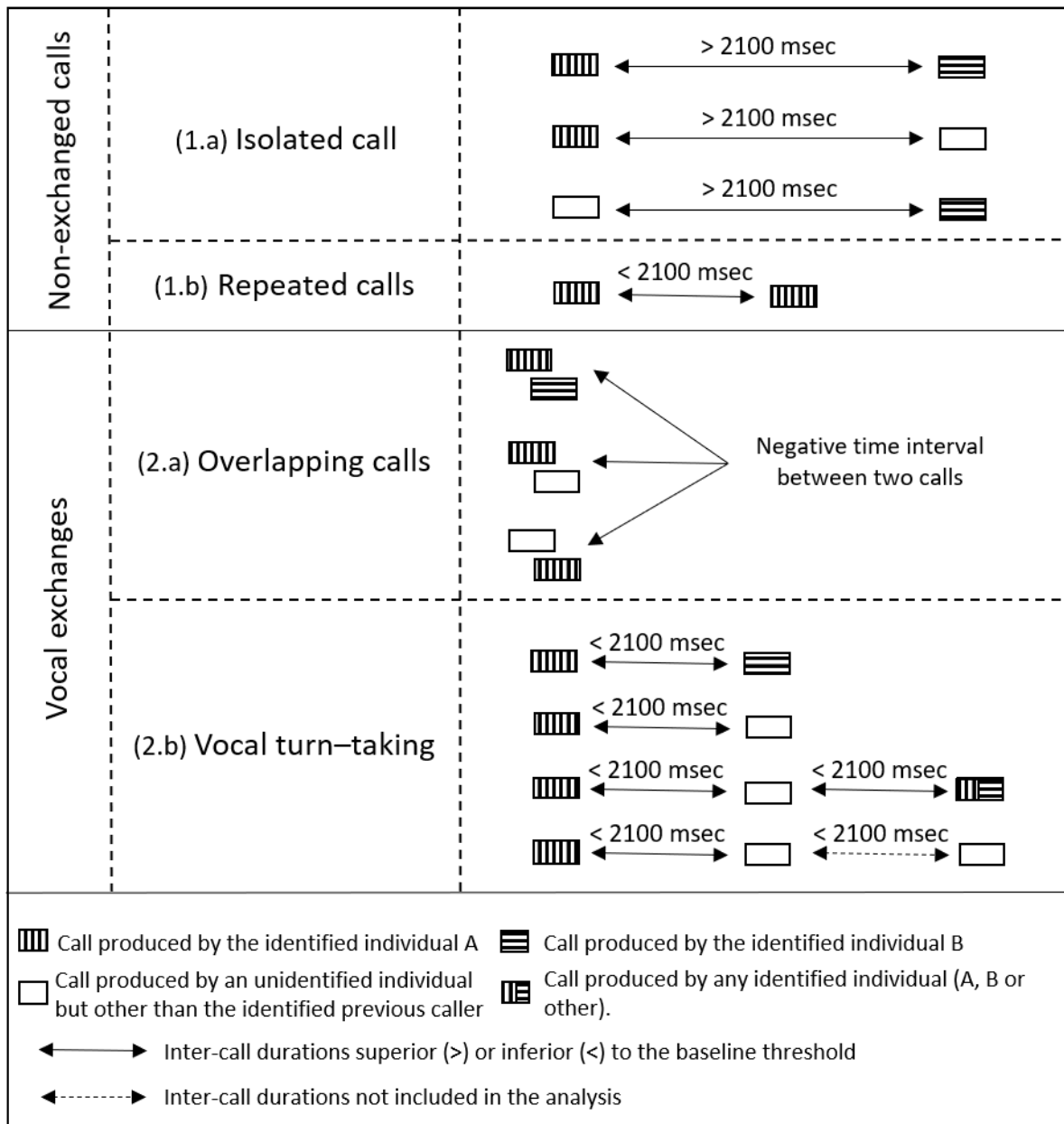
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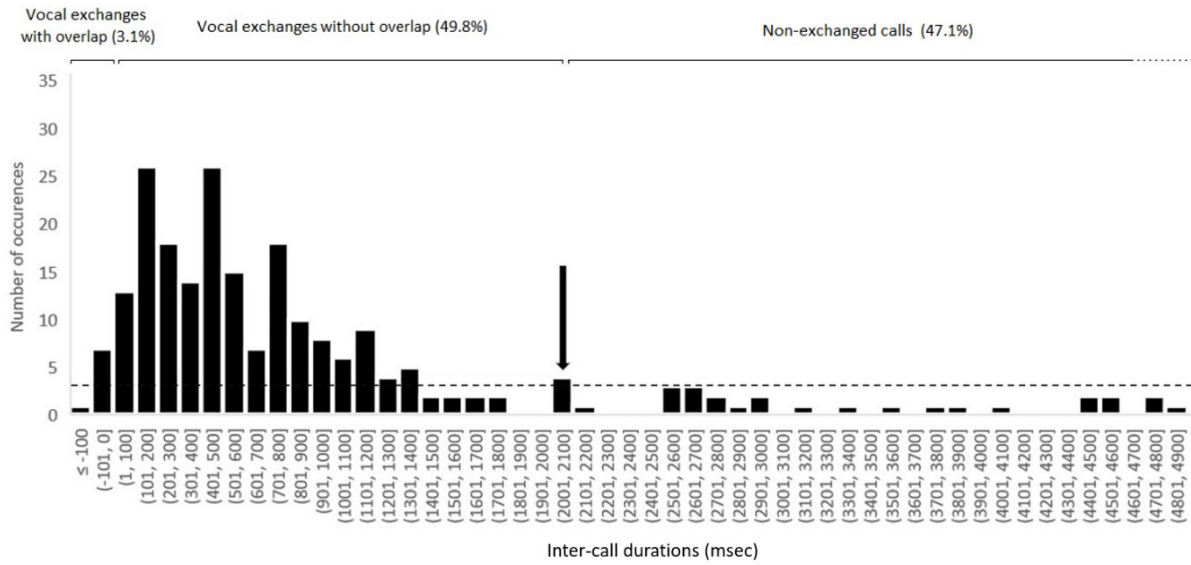
**FIGURES**

703 *Figure 1*



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705 *Figure 2*



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Peer Review Only

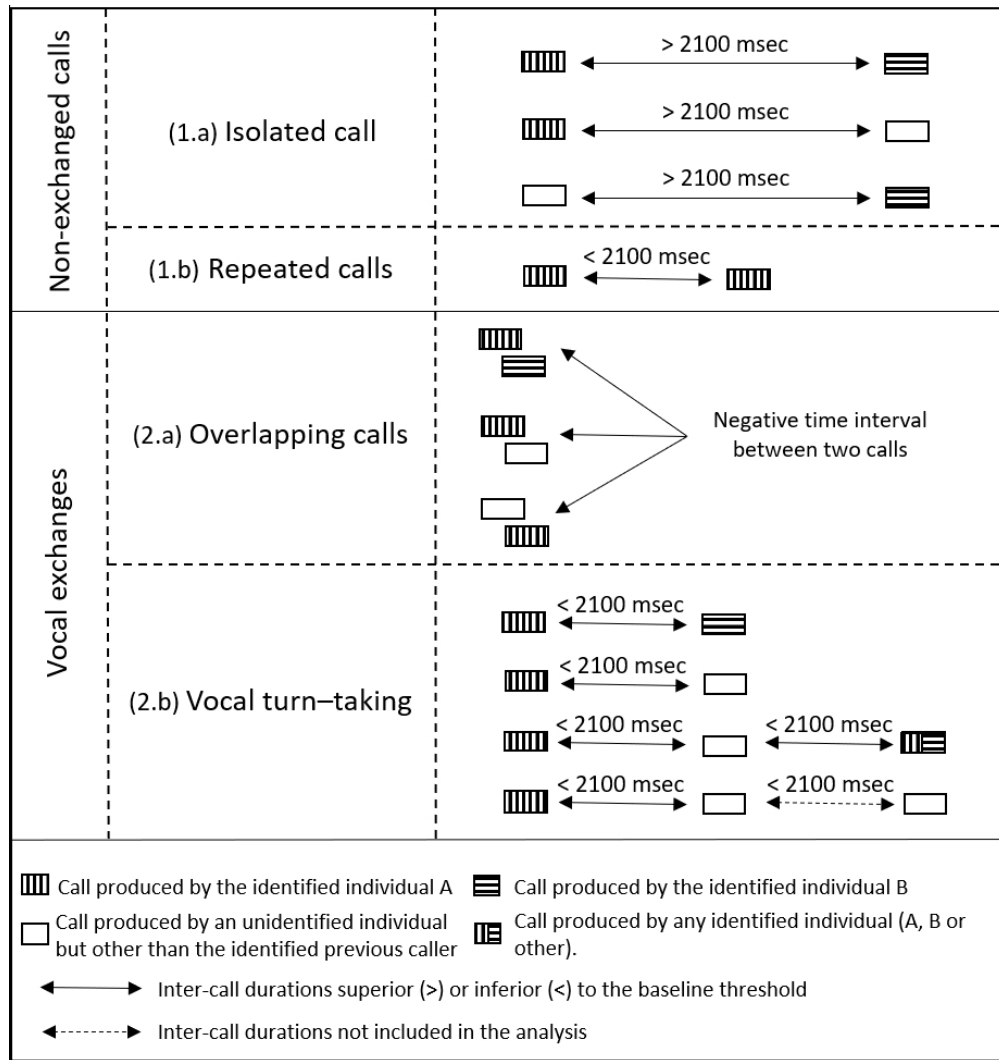


Fig. 1. — Distinct calling patterns considered in the study. The baseline threshold of 2100 msec between two calls was determined by an analysis of the distribution of call intervals (see Results and Fig. 2) and was used to define the calling patterns.

396x418mm (59 x 59 DPI)

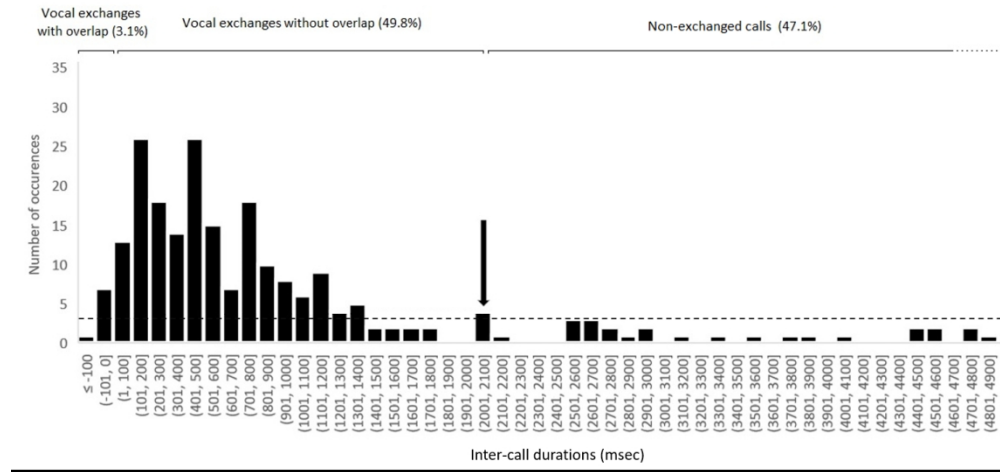


Fig. 2. — Distribution of inter-call durations between two successive calls from different callers (not all non-exchanged calls are represented in this figure for visual clarity). The dotted line corresponds to the baseline of the occurrence of inter-call durations. The black arrow corresponds to the threshold indicating the maximum response delay for defining a vocal exchange, and was placed at the location where inter-call delays start rising above the baseline when moving from long delays to the peak observed at around 2 sec (as in Lemasson et al. 2018; Levréro et al. 2019).

655x316mm (59 x 59 DPI)