

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

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3	1	ARTICLE FOR THE SPECIAL ISSUE ON PRIMATE COMMUNICATION
4 5 6	2	A pilot study of calling patterns and vocal turn-taking in wild
7 8	3	bonobos <i>Pan paniscus</i>
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31 32	17	<u>clement.cornec@hotmail.fr</u>).
33 34	18	
35	10	
30 37 38	19 20	 This pilot study shows that wild bonobos display the fundamental temporal rules of vocal
39 40 41	21	turn-taking
42 43	22	• Occurrences of calling patterns are in line with the unique observation collected from a
44 45	23	captive group
46 47	24	• Calling patterns do not differ significantly with age and sex
48 49 50	25	Calling patterns appear context-dependent
51 52 53	26	
54 55	27	
56 57 58 59 60	28	

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

KEY WORDS: wild bonobo, vocal communication, vocal behaviour, calling patterns, vocal turn-taking.

Running head: Vocal turn-taking evidence in wild bonobo

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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 al. 1974; Holler et al. 2015). These vocal turn-taking and overlap avoidance rules, used to 60 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 similarities, and suggest that conversational rules may be an essential prerequisite to maintain 68 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).

Despite recent scientific interest, our knowledge of rule-governed call exchanges in our closest living great ape relatives is still partial. All confirmatory evidence to date comes from captive groups of Western lowland gorillas Gorilla g. gorilla, and bonobos Pan paniscus, and is limited to one group per species (gorilla: Lemasson et al. 2018; bonobo: Levréro et al. 2019). The only study investigating rule-governed call exchanges in a wild great ape species (Arcadi 2000) has been conducted on wild chimpanzees Pan troglodytes schweinfurthii, which tended not to respond to most of the calls of their group members (within 5 sec). Rather, wild chimpanzees often called in chorus, with vocalisations greatly overlapping among individuals (Arcadi 2000). Thus, from existing scientific knowledge, wild chimpanzees do not appear to display rule-governed call exchanges, while captive bonobos do.

However, due to differences in environmental conditions (wild versus captive) between the studied chimpanzees and bonobos, we cannot readily attribute that such variation in their vocal behaviour reflects species-specific factors rather than study conditions. For example, Arcadi (2000) focused only on male Eastern chimpanzees, focusing on a small sample of males (N = 11) across a broad range of social contexts (communication between distant parties, agonistic interactions, copulations and feeding). In contrast, Levréro et al. (2019) studied both sexes in bonobos but only in calm contexts (grooming, resting, foraging), that are more amenable to organised vocal exchanges (Henry et al. 2015; Levinson 2016; Pougnault et al. 2020a). Interestingly, our primary prediction would have been that non-agonistic vocal exchanges are more essential in the wild, wherein individuals more often lose visual contact with one another in closed forest habitats, than in captive groups. The fact that captivity deprives bonobos from their natural fission fussion social system may indeed reduce the importance of vocal turn-taking and overlap avoidance, as these vocal behaviours appear to function to reinforce social bonds and increase community cohesion. At the same time, call overlap avoidance seems essential when animals must deal with a large number of potential

vocal interlocutors, particularly because their identity is less predictable in the wild, and hence it may be relatively important to extract vocal identity cues from the calls of conspecifics (Keenan et al. 2020). Thus, even if we assume that studies of wild chimpanzees and captive bonobos are comparable, the fact that captive bonobos show organised vocal exchanges and wild chimpanzees do not is not in line with our predictions, and makes these opposing observations even more puzzling. Critically, the avoidance of overlap and the reciprocal exchange of alternating short turns remains to be confirmed in wild great ape species. Such confirmation is of high interest to understand the evolutionary pressures that have shaped rule-governed communication (Pougnault et al. 2020a).

In the present study, we describe the general calling patterns of a wild community of bonobos in peaceful contexts and within subgroups. To date, the vocal behaviour of wild bonobos has been mainly investigated in terms of group coordination (e.g. Hohmann & Fruth 1994; White et al. 2015; Schamberg et al. 2016, 2017), which is in the context of long-distance communication (but see Clay et al. 2015). We thus first aimed to look at intimate vocal interactions for evidence of conversational-like rules in wild bonobos, and second, to assess their importance in bonobo communication. To this end, we collected a unique dataset of individual vocal utterances within subgroups. We predicted to find three calling patterns: isolated calling (one call is emitted and no other consecutive calls can be heard), repeated calling (the same caller calls several times in a row), and temporally-ruled vocal exchanges (with short call interval) between two or more callers. In addition, we examined the potential influence of the age-sex class of callers and their behavioural activities on calling patterns, with a special focus on temporally-ruled vocal exchanges. We also investigated whether calling patterns were call type-dependent. Indeed, while several studies have attempted to link bonobo call types or call sequences to specific behavioural contexts, these studies have not focused on calling patterns in which such calls are most often used (e.g., de Waal 1988; Bermejo & Omedes

1999; Clay & Zuberbühler 2009; Clay et al. 2015). In other non-human primate species, there exists evidence that calling patterns are context- and call-type specific, and vary as a function of the biological (age, sex) or social characteristics of the caller (Digweed et al. 2007; Chen et al. 2009; Lemasson et al. 2013, 2018; Levréro et al. 2019). Such relationships, investigated in the present study, have not been previously demonstrated in wild bonobos.

Study site

MATERIAL AND METHODS

The study was carried out in the Manzano forest (2°38'S, 16°23'E) near Embirima village in the Bolobo Territory of the Western Democratic Republic of the Congo. The study site is part of the Forest Concession of Local Communities of the Mbali River, a community-based conservation area led by the Non-Governmental Organisation Mbou-Mon-Tour, which has worked in close connection with the local community since 2001 (Narat et al. 2015a). The forest is located in the Maï Ndombe Province, 300 km north of Kinshasa. The habitat is a forest-savanna mosaic with 58% forest and 42% savannah (Pennec et al. 2016) but bonobos spend more than 97% of their time in the forest (Pennec et al. 2020). The dry season extends from June to September and the wet season from October to May (Pennec et al. 2020).

The home range of the bonobos in the Manzano forest covers approximately 20 km² with a bonobo density of 1.2 individuals/km² (Pennec et al. 2020), thus comprised in the average density of the broader Bolobo Territory, between 0.5 to 2.2 individuals/km² (Inogwabini et al. 2008; Serckx et al. 2014; Pennec et al. 2020).

> Study group

Search of regular visual contact with the bonobo community started in 2007 with the presence of local trackers in the forest twice a week during 3 years and was followed by a pilot study of

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habituation that lasted 6 months over 2010-2011 (Narat et al. 2015b). The proper habituation of the bonobos started in May 2012 (6 days per week; see Narat et al. 2015b for details). The community is now well habituated and tolerant to human presence (Narat et al. 2015b). An approach of a minimum distance of 10 m was possible between the closest individual and the observers. This minimum distance was maintained to decrease the risk of disease transmission. During our pilot study period (February to March 2019), the studied community was composed of 20 weaned free-ranging individuals. Dependant infants (N = 2) were excluded from our analyses as in similar studies investigating general patterns of vocal behaviour (Lemasson et al. 2018; Levréro et al. 2019). We used the age classes defined by Van Krunkelsven et al. (1999): juveniles (3-9.9 years), subadults (10-14.9 years) and adults (15 + years). For individuals born between 2012 and 2019, the exact month of birth was known while for individuals born between 2007 and 2012, the exact year of birth was known. Regarding individuals born before 2007, the year of birth could be estimated for individuals who were still dependent infants in 2007 and the other individuals were considered as adults at the time of our study (i.e., they were over 15 years old in 2019).

The group composition was thus three adult males, seven adult females, three subadult males, two subadult females and five juvenile females. For the study of their vocal behaviours we considered two age classes: the "immature class" which included juveniles and subadults, and the adult class (see Table 1) because of the limited sample size. Individual identification was based on repetitive direct observations from 2012 and from photographs and film banks (M. Ngofuna and V. Narat). Individual identification relied on body size, face colour, hair growth on the head, anogenital area shape, and particular features such as mutilations caused by poacher traps.

175 Data collection

The field team (one researcher, C. Cornec) accompanied by two to six local trackers patrolled the forest daily between 6:00 am and 6:00 pm, over February 6th to March 8th, 2019. Forest field conditions were harsh with unusual frequent heavy rains for the season that prevented the team from following or recording the bonobos on some days. When we could not follow them until their night nest site, it took 1 to 4 days to relocate the group. In total, we spent 70 hr in visual contact with bonobos during the study period.

Wild bonobos live in a fission-fusion social system (Kano 1982; White 1988; Van Elsacker et al. 1995) where individuals form temporary subgroups, or parties, that travel and forage separately from other parties. Parties are unpredictable in size (ranging from one individual to the entire community), longevity and composition. We decided each time to follow the larger subgroup (on average 10 individuals) and focused on intra-subgroup vocal behaviour. Over the study period, all the group members had been monitored at least 2 days (mean: 4.7 days/individual, range: 2-7 days).

Vocalisations were collected with ad libitum sampling (Altmann 1974) as the rapid move of individuals through dense vegetation did not permit the method of focal sampling for collecting vocal data. Recordings began systematically when the target group was close enough (20 m on average) to ensure quality audio recordings and reliable identification of individuals using binoculars. One local tracker (M. Ngofuna) remained with the researcher (C. Cornec) to check the identification of individuals and behavioural observations, while the other trackers remained at a distance to reduce disturbance.

We focused on vocalisations produced when the group was peaceful (e.g., resting, foraging,
playing, moving and positive social interactions like grooming) similar to protocols used in
captive population studies. Indeed, it has been previously shown, as in humans, that effective
temporally organised vocal exchanges require calmness and attention toward others and so have
a higher probability to occur in quiet contexts (Levinson 2016; Pougnault et al. 2020a). We thus

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excluded calls recorded during agonistic interactions (e.g., threatening or chasing behaviours) and any synchronized group responses to external events (for example, falling branches). Due to the sudden and brief nature of vocal exchanges, vocal interactions were defined by their temporal characteristics regardless of behavioural parameters, similar to studies on captive populations (see Lemasson et al. 2018; Levréro et al. 2019). Nevertheless, we describe the general activity of the group because the behaviour of individual callers could not always be identified (e.g., when hidden by vegetation), and thus group dynamics can offer additional context. We distinguished two main broad behavioural contexts: sedentary behaviour (the majority of the group was feeding or half of the group was feeding while the other half was resting or grooming), and moving behaviour (about half of the individuals moved calmly towards other group members or played, or general calm movement of all group members). For each recording, we noted, in a notebook, the age and sex class of callers and the broad behavioural context.

Calls were recorded using a digital Zoom H4n Handy Recorder (Zoom, Japan: 44.1 kHz
sampling frequency, 32-bits resolution, mono, .WAV format) connected to a directional
Sennheiser MKH70-1 microphone (Sennheiser Electronic KG, Germany) with windscreen.

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Calling patterns

In order to define calling patterns (see below for definitions), we investigated inter-call delays between two successive vocalisations within a timespan up to 10 sec. This time delay corresponds to 2 or 3 times the maximum response delay recorded in great apes (5 sec in wild chimpanzees: Arcadi 2000; 2.5 sec in captive bonobos: Levréro et al. 2019; 3 sec in captive gorillas: Lemasson et al. 2018). Calls that occurred more than 10 sec apart were thus considered as- resulting from independent vocal events. We studied the distribution of all inter-call durations within each vocal event using spectrograms produced in PRAAT (Boersma & Weenink 2018). Inter-call duration corresponded to the silent gap between two consecutive calls, from the offset of the first call to the onset of the second call (e.g., Lemasson et al. 2018; Levréro et al. 2019). Interval call duration could be negative when there was an overlap between two calls. All calls with poor spectrographic quality, thus preventing measurement of call onset (e.g., due to overlapping forest noises), were excluded from analysis.

To determine if the calls of two consecutive callers belonged to a vocal exchange, we analysed the distribution of call intervals to define a baseline threshold of the occurrence of inter-call durations. Then, relying on this temporal baseline threshold and taking into account the identity of callers, we determined whether the recorded calls were isolated calls or repeated calls from a single caller, or rather, belonged to a vocal interaction (i.e. two successive calls from two individuals with a short inter-vocalisation delay or a negative inter-call duration). Vocal exchange analyses focused on dyadic interactions, in which the identity of one or both individuals was always known (see Fig. 1 for details). In a subset of cases that involved different consecutive callers, but in which the identity of one caller was uncertain, we noted his/her sex and/or age class when possible.

In summary, we considered the following possible calling patterns (following Lemasson et al. 2018; Levréro et al. 2019; see Fig. 1) distinguishing between calls produced in non-interactive contexts versus interactive contexts:

(1) Calls produced by the same individual (subsequently termed 'non-exchanged calls'), which could be:

- Isolated calls: a call not followed by a consecutive call within a maximum delay (1.a)obtained by analysing the inter-call distributions in our data (see Fig. 1 and Results for value of maximum delay).
- Repeated calls: a call followed by a consecutive call produced by the same (1.b)individual within a maximum delay (see Fig. 1 and Results).

(2) Calls produced during a vocal interaction involving at least two individuals (subsequently
termed 'vocal exchanges'), which could be:

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

255 (2.b) Overlapping calls: negative time interval between two calls produced by two256 different individuals.

Call types

Because we can never be sure that we captured the very first call of a vocal interaction (undetected soft calls and/or unpredictability of the vocal interaction), the call types produced were investigated independently of the temporal order of call utterances. Using PRAAT software (Boersma & Weenink 2018), all calls were categorised into call types based on visual comparisons between our data and spectrograms provided by Bermejo and Omedes (1999) and de Waal (1988). The bonobo vocal repertoire is highly graded (Keenan et al. 2020), however researchers agree on a number between 12 and 15 call types (de Waal 1988; Bermejo & Omedes 1999). Because of the well-known difficulty of classifying the graded calls of bonobos (Keenan et al. 2020), we considered seven broad call type categories, that together represented all the calls produced by all individuals in peaceful contexts:

- "Peep" category: relatively unmodulated calls with a fundamental frequency peak between
500 and 2500 Hz and a slope below 400 Hz, with a duration below 400 msec (grouping
peep/peep-yelp: Bermejo & Omedes 1999; and peep-yelp/food peep/alarm peep: de Waal
1988), or, a downward modulated call with a frequency peak that can reach 3000 Hz and a
negative slope between – 500 to – 1000 Hz, with a duration below 300 msec (corresponding to
yelp: Bermejo & Omedes 1999).

- "Bark" category: chevron-shaped modulated call with a fundamental frequency peak between
500 and 2500 Hz and a slope above 400 Hz, the duration is between 100 and 300 msec (grouping
soft bark/bark/composed bark: Bermejo & Omedes 1999; and staccato hoot/legato hoot/wieew
bark: de Waal 1988).

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

- "Low hooting": lowest-pitched call, with a fundamental frequency hardly ever above 800 Hz
and a short duration rarely longer than 200 msec (low hooting: de Waal 1988; Bermejo &
Omedes 1999).

- "Hiccup": Similar to an upward frequency modulated call with a short duration rarely longer
 than 200 msec (hiccup: Bermejo & Omedes 1999).

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

- "Pout moan": Short call (less that 200 msec) with variably shaped frequency contour and a
fundamental frequency always below 1500 Hz (pout moan: de Waal 1988; Bermejo & Omedes
291 1999).

All these vocalizations are produced in a large range of contexts, but most often in a feeding context. Compared to "peeps" and "barks", other vocalisation types including "grunts", "hiccup", "hoots", "pout moan" and "whistles" are relatively rare vocalisations in the bonobo vocal repertoire (de Waal 1988; Bermejo & Omedes 1999; Keenan 2016). To confirm the interrater reliability of call classification, we calculated the Fleiss' Kappa coefficient between two independent raters (C. Cornec and F. Levréro) on a subset of 72 randomly selected calls (around 30% of the calls).

300 Statistical analysis

301 All statistical analyses were performed using R version 3.6.1 (R Core Team 2019).

We conducted a series of Generalised Linear Mixed Models (GLMMs) in R software. A first GLMM tested whether the sex and/or age of bonobos were significant predictors of calling patterns. Two additional GLMMs tested the contribution of the two behavioural contexts and call type categories on calling patterns. The sex, age, behavioural context and call type categories were respectively included as fixed factors. We coded a binary pattern where 1 was attributed to a vocal exchange and 0 to a vocal non-exchange. The models were run using a logit link function with a binomial distribution. Because one individual could be involved in several vocal interactions and vocal interactions could come from the same or different vocal events, the identity of the emitters and the code of the vocal event were included as random factors in all GLMMs to avoid pseudo-replication. We used likelihood ratio tests (LRTs) and Akaike Information Criteria (AIC) to determine best fitting models. GLMMs were performed using the function glmer of the 'lme4' package (Bates et al. 2015).

RESULTS

In total we analysed 259 call intervals from 63 independent vocal events during peaceful activities (on average 5.72 vocal events per day, range 0 to 31 per day). Among these 259 call intervals, there were 217 call intervals for which callers were identified. Among the remaining intervals, there were two call intervals for which the sex and age category of the callers were known, six call intervals for which only the age of the callers was determined, and 34 call intervals for which we had no information about the age category, sex, or identity of the callers but we were certain that they were distinct callers. We excluded 382 call intervals from analysis due to poor acoustic quality that did not allow us to define the onset of the call or to reliably identify the vocalisers (see Fig. 1).

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5 6	326	General description of calling patterns
7 8 0	327	The distributions of all call intervals between two consecutive calls are shown in Figure 2,
9 10 11	328	revealing a baseline threshold of 2.1 sec on which we relied to define a vocal exchange between
12 13	329	two callers.
14 15 16	330	Based on this temporal threshold, we found that 52.9% (N = $137/259$) of calls were produced
10 17 18	331	within a vocal exchange (vocal turn-taking or overlapping calls) (Table 2). A vocal exchange
19 20	332	involved on average of 2.34 distinct individuals and up to four individuals. Among these vocal
21 22 22	333	exchanges, the avoidance of call overlap seemed to be the rule, as 94.2% of calls (N = $129/137$)
25 24 25	334	had a positive short inter-call delay. The mean overlap duration was $54 \pm SD 42.2$ ms (range:
26 27	335	16-130 msec, $N = 8$ call intervals) whereas the inter-call duration of vocal exchanges without
28 29	336	overlap lasted on average 590.1 \pm SD 468.8 msec (range: 5-2093 msec, N = 129 call intervals).
30 31 32	337	The remaining 47.1% (N = $122/259$) of calls showed that the vocal 'responses' of the group
33 34	338	members did not occur systematically (Table 2). Isolated calls and repeated calls represented
35 36	339	respectively 51.6% (N = $63/122$) and 48.4% (N = $59/122$) of these non-exchanged calls.
37 38 39	340	
40 41	341	Differences in calling patterns by age and sex
42 43	342	We found that neither age (GLMM: $\beta = -0.27$, SE = 0.63, z(219) = -0.43 , P = 0.67) nor sex
44 45 46	343	$(\beta = 0.6, SE = 0.64, z(219) = 0.94, P = 0.35)$ had a significant influence on individual calling
47 48	344	patterns (N = 219 call intervals, 16 different individuals: 7 adult females and 3 adult males, 3
49 50	345	immature females and 3 immature males). Examining the raw data, it is however interesting to
51 52 53	346	note that adult bonobos seem to produce slightly more calls in the context of vocal turn-taking
55 54 55	347	(6.6 calls/individual) than did immature bonobos (3.7 calls/individual), whereas adult and
56 57	348	immature individuals contributed similarly to the production of isolated and repeated calls
58 59	349	(Table 3). Regardless of age class, females tended to be less vocal than males [mean 7.2 calls

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per female (14 females and 101 calls) and 19.7 calls per male (six males and 118 calls)]. Among adult bonobos, both sexes participated equally in vocal turn-taking (7.3 and 6.4 calls/individual, for males and females respectively) while among immature bonobos, none of the seven young immature females were recorded producing vocal exchanges. All vocal turn-taking observed in immature bonobos was indeed uttered by the three young males (Table 3).

Differences in calling patterns across behavioural contexts

The behavioural context of call production was determined in 234 out of 259 call intervals.

The occurrence of vocal exchanges and non-exchanged calls differed significantly according to behavioural context (GLMM: $\beta = 2.24$, SE = 0.58, z(195) = 3.88, P < 0.001). Most vocal exchanges occurred during sedentary behaviours (91.2%, N = 114/125 vocal exchanges), while non-exchanged calls occurred in similar proportions in both contexts (53.2%, N = 58/109 non-exchanged calls occurred during sedentary behaviours, Table 4).

Contribution of call type to calling patterns

Specific call types could be assigned to 235 calls. We obtained a high and significant concordance in call classification between raters (Fleiss' kappa coefficients = 0.81, P < 0.001). The calls belonging to the "peep" category were the most frequently produced, both in vocal exchanges (58.4%, N = 130) and in non-exchanged calls (63.8%, N = 105, Table 5), followed by calls from the "bark" category, representing nearly 30% of calls produced in vocal exchanges (N = 130) and non-exchanges (N = 105). Other call types ("hoots", "hiccup", "grunt" category, "pout moan", and "whistle" category) were rarely recorded (Table 5). Call type contributions to calling patterns did not differ significantly between vocal exchanges and vocal non-exchanges (GLMM: $\beta = 0.28$, SE = 0.22, z(194) = 1.24, P = 0.22). It is however worth noting that calls produced in isolation and in vocal turn-taking mainly belonged to the "peep" category

375 (76.8%, N = 43/56 for isolated calls and 60.5%, N = 75/124 for vocal turn-taking, Table 5). 376 Repeated calls were equally composed of calls from the "peep" and "bark" categories (49%, N 377 = 24/49 and 44.9%, N = 22/49 respectively). Only overlapping calls more often included those 378 from the "bark" (4/6) than "peep" category.

DISCUSSION

This pilot study provides the first valuable data on the general calling patterns of a wild great ape species, the bonobo. Focusing on peaceful contexts, we found that bonobos in our study population exchanged calls that followed fundamental temporal rules of vocal turn-taking. Vocal exchanges represented half of the calls produced and bonobos almost systematically avoided overlapping the call of a previous caller, leaving a short delay of on average 2.1 sec between callers. This call delay was consistent with that observed in other ape studies (2.5 sec in captive bonobos: Levréro et al. 2019; 3 sec in captive gorillas: Lemasson et al. 2018).

First, this pilot study largely corroborates the findings of the only other studied bonobo group, which was in captivity (Levréro et al. 2019). Both studies followed a similar methodology and analogous definitions, except for repeated calls that were not recorded in captivity. Excluding these repeated calls for comparison, the general vocal behaviour of wild and captive bonobos appears very similar, with 68.5% vs 73.6% of all coded calls respectively produced within vocal exchanges (the remaining calls were isolated calls, see Levréro et al. 2019 for values in captive bonobos). Within vocal exchanges, overlapping calls appear more frequent in captivity than in the wild (32.8% vs 5.8%, see Levréro et al. 2019 for captive values). Call overlap may increase the risk of confusion during message transmission and so, makes individual recognition uncertain. However, this risk is limited in captivity where the group composition is stable and individuals are more often in visual contact, and thus individual recognition can be achieved through visual cues. Despite this, we acknowledge that the sample Page 17 of 35

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size is limited in both studies. While the higher frequency of call overlap in captivity suggests
that such temporal rule violation may be less crucial in captivity, it has been experimentally
demonstrated that such rule violation remains relevant even to captive primates (Campbell's
monkeys *Cercopithecus campbelli*: Lemasson et al. 2011; gorillas: Pougnault et al. 2020b;
bonobos: Levréro et al. 2017).

Second, we found no differences in calling patterns between adult and immature bonobos, while other primate studies suggest that adults emit significantly more calls during social interactions than do immature individuals (Common marmosets Callithrix jacchus, Chen et al. 2009; wild spider monkeys Ateles geoffroyi, Briseño-Jaramillo et al. 2018; captive gorillas: Lemasson et al. 2018). We cannot rule out the possibility that the lack of differences across ages was due to the small sample size and notably the low number of juveniles, who consequently were included in the same category than subadults, as immature individuals. Similar to age, we found that calling patterns did not vary between males and females. Regarding vocal turn-taking specifically, adult males and females seemed to be equally involved, but interestingly no immature females were involved in exchanged calls.

Third, our results suggest that vocal exchanges are context-specific, at least during sedentary or moving activities. The softest calls of the bonobo repertoire ("peep" category) were most often produced in vocal turn-taking without overlap as found in captive bonobos (Levréro et al. 2019) and other primate species (reviewed in Pougnault et al. 2020a). Such soft calls in bonobos convey information about caller identity (Keenan et al. 2020) and receivers can extract such information (Keenan 2016). In the wild, because callers are not always in visual contact, overlap avoidance appears crucial for transmitting information that can enable individual recognition and ensure subgroup cohesion and affiliative bonding between conspecifics. The fact that vocal exchanges, as opposed to non-exchanged calls, are used preferentially during non-travelling contexts that typically favour socialising, may support the

> 425 "grooming-at-distance" hypothesis of vocal exchanges (Dunbar 1996). We further showed that 426 overlapping and repeated calls were mostly composed of "barks", which may be related to 427 subtly higher-arousal emotional states (de Waal 1988; Bermejo & Omedes 1999; Clay & 428 Zuberbühler 2009; Keenan et al. 2020) keeping in mind that the studied bonobos were always 429 in calm contexts.

Fourth, this study suggests that bonobos display vocal turn-taking in the wild, as they do in captivity (Levréro et al. 2019). Interestingly, a similar recent approach confirmed that captive chimpanzees do not often display temporally-organized vocal exchanges in peaceful contexts (Pougnault et al. 2021). This difference between chimpanzee and bonobo vocal behaviour, two phylogenetically close forest species (Prufer et al. 2012), may reflect their intrinsically different social organization and thus needs of communication. Bonobos show greater levels of tolerance and cooperative behaviours wherein individuals repeatedly interact with numerous other group members in a range of different contexts (review in Gruber & Clay 2016). This could promote selection for temporally-ruled vocal exchanges in bonobos. In contrast, chimpanzees show lower cooperation and higher competition (Hare & Tomasello 2004; Hare et al. 2007; Surbeck & Hohmann 2013; see for an extensive review Muller & Mitani 2005). However, turn-taking skills in chimpanzees are not questioned, as they readily demonstrate communicative gestural interactions within mother-offspring pairs (Fröhlich et al. 2016). To understand the origin of this difference in vocal behaviour between chimpanzees and bonobos is of great interest to understand the origin and evolution of human language, and the coevolution between communicative behaviours and sociality. A comparative study of several African starling species with different social systems – ranging from solitary pairs to colonial groups and communally-breeding species – showed that the species' social organisation may be a key factor in developing temporal regulation of vocal exchanges (Henry et al. 2015).

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449 In conclusion, this pilot study supports the existence of coordinated vocal exchanges in 450 a wild great ape species. We acknowledge that our findings are based on a small sample size, 451 nevertheless these data corroborate the observations obtained from a captive bonobo group, and 452 pave the road for replication studies. Although preliminary, these new data will serve future 453 comparative studies investigating the temporal and social patterns of call exchanges in primates 454 along their natural range of social systems, and can potentially provide further insight into the 455 function of turn-taking in primates, and ultimately, the evolution and origins of language 456 (Levinson 2006, 2016). 457 458 **ACKNOWLEDGMENTS** 459 We are very grateful to the NGO Mbou-Mon-Tour for logistical support and for providing 460 access to the Manzano forest, to field assistants who accompanied us in forest, as well as the 461 Embirima inhabitants and their Chief for a warm welcome. We thank two anonymous reviewers 462 who provided helpful comments on the previous version of this manuscript. Lastly, we thank 463 Katarzyna Pisanski for English corrections and scientific input. 464

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ETHICAL STANDARD

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All methods were carried out in accordance with the relevant international guidelines and

regulations, and were approved by the Institutional Animal Ethical Committee of the University

of Lyon/Saint-Etienne, under the authorization no. 42-218-0901-38 SV 09 (Lab ENES) and by

the Congolese partner Mbou-Mon-Tour (MMT) that supervises the local research programs of

the community-based conservation project. This study involved only behavioural observations

and spontaneous vocal recordings of animals in their natural social group and environment. No

AUTHOR CONTRIBUTION

C. Cornec and F. Levréro conceived, designed and coordinated the study. F. Levréro allocated

research funding. C. Cornec and M. Ngofuna collected data. C. Cornec and F. Levréro carried

out the statistical analyses and interpreted the data. C. Cornec, F. Levréro and A. Lemasson

drafted the manuscript. V. Narat and C. M Monghiemo supported the study implementation in

the Manzano forest. All authors gave final approval for publication and agree to be held

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DATA ACCESSIBILITY

The raw data supporting this research are openly available on the Open Science Framework

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experimental protocols nor invasive methods were used in this study.

accountable for the work performed therein.

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2 3 4	653	TABLES					
5	654	Table 1.					
7 8	655	Composition of the studied community of wild bonobos from Manzano forest, Democratic Republic of the Congo.					
9		Name	Sex	Age class (2019)	Age category (2019)		
10		Ngampei	Male	Adult	Adult		
11		Roger	Male	Adult	Adult		
12		Dodo	Male	Adult	Adult		
13		Clémentine	Female	Adult	Adult		
14		Pam	Female	Adult	Adult		
15		Flèche	Female	Adult	Adult		
16		Obia 🔨	Female	Adult	Adult		
17		Kimono	Female	Adult	Adult		
10		Ngwana	Female	Adult	Adult		
19 20		Lili	Female	Adult	Adult		
20		Charlie	Male	Subadult	Immature		
21		Popeye	Male	Subadult	Immature		
23		Filou	Male	Subadult	Immature		
24		Kawa	Female	Subadult	Immature		
25		Not named yet (New immigrant)	Female	Subadult	Immature		
26		Primus	Female	Juvenile	Immature		
27		Faki	Female	Juvenile	Immature		
28		Okay	Female	Juvenile	Immature		
29		Kiteke	Female	Juvenile	Immature		
30		Nguli	Female	Juvenile	Immature		
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660			Table 2.					
661 662	Distribution of ca	Distribution of call intervals for different calling patterns. In italics we give the percentage of occurrence for each given calling pattern.						
	Non-exch	anged calls	Vocal ex	xchanges				
-	Isolated calls	Repeated calls	Vocal turn-taking	Overlapping calls	Total call interva			
	63 24.3%	59 22.8%	129 49.8%	8 3.1%	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.

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	Non-exchanged calls		Vocal ex	Total calls	
	Isolated calls N = 51	Repeated calls N = 59	Vocal turn–taking N = 104	Overlapping calls $N = 5$	N = 219
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
670					

1						
2	672					
4 5	673			Table 4.		
6 7 8	674 Distributio 675	n of calling patterns as a	a function of behaviou each behavioural co	ral context. Percentages in it ontext to each calling patter	talics correspond to the contri n.	bution of
10 11		Non-exchar	nged calls	Vocal ex	changes	Total calls
12 13 14	Behaviour –	Isolated calls N = 57	Repeated calls $N = 52$	Vocal turn–taking N = 117	Overlapping calls $N = 8$	N = 234
15 16 17	Sedentary behaviour ^a	39 68.4%	19 36.5%	108 <i>92,3%</i>	6 75%	172
18 19 20	Movement ^b	18 31.6%	33 73.5%	9 7.7%	2 25%	62
22 23 24 25 27 28 29 31 33 34 35 37 38 90 41 42 44 45 46 7 89 51 52 34 55 56 57	 677 was rest 678 ^bAbout I 679 general 1 680 681 	ing or grooming. half of the group n movement of the g	noved towards of group members.	her group members of	r played or there was a	

682						
683			Table 5.			
684 685	Contribution of the seven b patterns. Percentages	proad call type categor in italics correspond t	ries (defined from Berme o the contribution of eac	jo & Omedes 1 h call type cate	999 and de Waal 19 gory to each calling	988) to calling pattern.
		Non-exc	hanged calls	Vocal	exchanges	Total calls
	Call type category	Isolated calls N = 56	Repeated calls N = 49	Vocal turn– taking N = 124	Overlapping calls N = 6	N = 235
	Peep category	43 76.8%	24 49%	75 60.5%	1 16.7%	143
	Bark category	9 16.1%	22 44.9%	34 27.4%	4 66.7%	69
	Whistle category	1 1.8%	3 6.1%	4 3.2%	0 0%	8
	Low hooting	1 1.8%	0 0%	4 3.2%	1 16.7%	6
	Hiccup	1 1.8%	0 0%	4 3.2%	0 <i>0%</i>	5
	Grunt category	0 0%	0 0%	3 2.4%	0 0%	3
	Pout moan	1 1.8%	0	0	0	1
686		1.070	0,0	0,0	070	
687						

1 2 3	688	FIGURE CAPTIONS
4 5 6 7 8	689 690 691	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.
5 6 7 8 9 10 11 23 14 15 16 17 8 9 20 21 22 32 4 25 26 27 28 29 30 31 22 33 34 35 36 37 38 9 40 41 42 43 44 5 6 7	689 690 691 692 693 694 695 696 697 698 699 700 701	 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. 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).
48 49 50 51 52 53 54		
55 56 57 58		



FIGURES

703 Figure 1









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 nonexchanged 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)