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1 **Social pressure drives “conversational rules” in great apes**

2

3 Loïc Pougault<sup>1,2,3</sup>, Florence Levréro<sup>2,†</sup>, Maël Leroux<sup>4,5,6</sup>, Julien Paulet<sup>1</sup>, Pablo  
4 Bombani<sup>7</sup>, Fabrice Dentressangle<sup>2</sup>, Laure Deruti<sup>2</sup>, Baptiste Mulo<sup>3</sup> and Alban  
5 Lemasson<sup>1,8,†,\*</sup>

6

7 <sup>1</sup>*Univ Rennes, Normandie Univ, CNRS, EthoS (Éthologie animale et humaine) - UMR 6552,*  
8 *263 avenue du Général Leclerc, 35042 Rennes, France*

9 <sup>2</sup>*Université de Lyon/Saint-Etienne, CNRS, Equipe Neuro-Ethologie Sensorielle, ENES /*  
10 *CRNL, UMR5292, INSERM UMR\_S 1028, 23 rue Paul Michelon, 42023 Saint-Etienne,*  
11 *France*

12 <sup>3</sup>*ZooParc de Beauval & Beauval Nature, Avenue du Blanc, 41110 Saint Aignan, France*

13 <sup>4</sup>*Department of Comparative Linguistics, University of Zürich, Thurgauerstrasse 30, 8050*  
14 *Zürich-Oerlikon, Switzerland*

15 <sup>5</sup>*Budongo Conservation Field Station, Masindi, Uganda*

16 <sup>6</sup>*Center for the Interdisciplinary Study of Language Evolution (ISLE), University of Zürich,*  
17 *Plattenstrasse 54, 8032 Zürich, Switzerland*

18 <sup>7</sup>*NGO Mbou-Mon-Tour, Nkala, Territoire de Bolodo, Mai-Ndombe, Republic Democratic of*  
19 *Congo*

20 <sup>8</sup>*Institut Universitaire de France, 1 rue Descartes, 75231 Paris, France*

21

22 \* Author for correspondence (E-mail: alban.lemasson@univ-rennes1.fr; Tel.: +33223236820).

23 †These authors contributed equally.

24

25 ABSTRACT

26 In the last decade, two hypotheses, one on the evolution of animal vocal communication in  
27 general and the other on the origins of human language, have gained ground. The first  
28 hypothesis argues that the complexity of communication co-evolved with the complexity of  
29 sociality. Species forming larger groups with complex social networks have more elaborate  
30 vocal repertoires. The second hypothesis posits that the core of communication is represented  
31 not only by what can be expressed by an isolated caller, but also by the way that vocal  
32 interactions are structured, language being above all a social act. Primitive forms of  
33 conversational rules based on a vocal turn-taking principle are thought to exist in primates. To  
34 support and bring together these hypotheses, more comparative studies of socially diverse  
35 species at different levels of the primate phylogeny are needed. However, the majority of  
36 available studies focus on monkeys, primates that are distant from the human lineage. Great  
37 apes represent excellent candidates for such comparative studies because of their phylogenetic  
38 proximity to humans and their varied social lives. We propose that studying vocal turn-taking  
39 in apes could address several major gaps regarding the social relevance of vocal turn-taking  
40 and the evolutionary trajectory of this behaviour among anthropoids. Indeed, how the social  
41 structure of a species may influence the vocal interaction patterns observed among group  
42 members remains an open question. We gathered data from the literature as well as original  
43 unpublished data (where absent in the literature) on four great ape species: chimpanzees *Pan*  
44 *troglodytes*, bonobos *Pan paniscus*, western lowland gorillas *Gorilla gorilla gorilla* and  
45 Bornean orang-utans *Pongo pygmaeus*. We found no clear-cut relationship between classical  
46 social complexity metrics (e.g. number of group members, interaction rates) and vocal  
47 complexity parameters (e.g. repertoire size, call rates). Nevertheless, the nature of the society  
48 (i.e. group composition, diversity and valence of social bonds) and the type of vocal  
49 interaction patterns (isolated calling, call overlap, turn-taking-based vocal exchanges) do

50 appear to be related. Isolated calling is the main vocal pattern found in the species with the  
51 smallest social networks (orang-utan), while the other species show vocal interactions that are  
52 structured according to temporal rules. A high proportion of overlapping vocalisations is  
53 found in the most competitive species (chimpanzee), while vocal turn-taking predominates in  
54 more tolerant bonobos and gorillas. Also, preferentially interacting individuals and call types  
55 used to interact are not randomly distributed. Vocal overlap ('chorusing') and vocal exchange  
56 ('conversing') appear as possible social strategies used to advertise/strengthen social bonds.  
57 Our analyses highlight that: (1) vocal turn-taking is also observed in non-human great apes,  
58 revealing universal rules for conversing that may be deeply rooted in the primate lineage; (2)  
59 vocal interaction patterns match the species' social lifestyle; (3) although limited to four  
60 species here, adopting a targeted comparative approach could help to identify the multiple and  
61 subtle factors underlying social and vocal complexity. We believe that vocal interaction  
62 patterns form the basis of a promising field of investigation that may ultimately improve our  
63 understanding of the socially driven evolution of communication.

64

65 *Key words:* communication evolution, vocal communication, social communication, social  
66 structure, social organization, vocal exchange, conversation, turn-taking, Primates,  
67 Hominidae.

68

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## 86 **I. INTRODUCTION**

### 87 **(1) Vocal communication organisation as a mirror of social complexity**

88       Possibly because communication is widespread across the animal kingdom and occurs  
89 in a wide diversity of social contexts (Waser, 1977; McComb, 1991; Geissmann, 1999; Arlet  
90 *et al.*, 2015), the evolutionary forces driving communication are still intensively debated.  
91 Communication is indeed influenced by habitat quality, predation and life-history traits (e.g.  
92 Lemasson, 2011; Freeberg, Dunbar & Ord, 2012; Mouterde *et al.*, 2014; Fischer *et al.*, 2017a;  
93 Hammerschmidt & Fischer, 2019; Pisanski *et al.*, 2016). The hypothesis that social  
94 complexity has been one of the driving forces shaping vocal complexity (or even *the* main  
95 driving force for primates), as suggested by Darwin (1877), has recently received renewed  
96 interest (Freeberg *et al.*, 2012; Bouchet, Blois-Heulin & Lemasson, 2013; Sewall, 2015). One  
97 of the biggest challenges of this ‘social complexity hypothesis’ for communication is to define  
98 and measure ‘complexity’ properly in terms of both social and communicative aspects

99 (Freeberg *et al.*, 2012, 2019; Manser *et al.*, 2014; Fischer, Wadewitz & Hammerschmidt,  
100 2017b; Rebut *et al.*, 2021).

101 Several metrics have been used successfully as proxies for social complexity (Dunbar,  
102 1998; McComb & Semple, 2005). The group's social structure (e.g. size, density and age–sex  
103 composition) and social organisation (e.g. number of roles and variation in social bond  
104 strength) are common key metrics used to quantify the degree of complexity of a social  
105 system (Lemasson, 2011; Freeberg *et al.*, 2012; Pollard & Blumstein, 2012; Freeberg &  
106 Krams, 2015; Fischer *et al.*, 2017a). The 'social brain hypothesis' proposes that the complex  
107 social world of primates is especially cognitively demanding, and that this imposed an intense  
108 selection pressure for increasingly large brains (Dunbar, 1998). It thus predicts that a greater  
109 number of individuals and thus greater diversity of personalities and relationships requires  
110 greater signalling complexity for effective manipulation of the behaviours of others (Freeberg  
111 *et al.*, 2019). A key metric of social complexity is the number of differentiated relationships  
112 that individuals have (Bergman & Beehner, 2015). In baboons, for instance, the diversity of  
113 male–female social bonds may be responsible for the emergence of derived call types in the  
114 vocal repertoires of some species (Gustison, le Roux & Bergman, 2012). An additional  
115 important metric is group stability. Fission–fusion [i.e. group members regularly join (fusion)  
116 or separate from (fission) one another] dynamics, for example, may constrain the regulation of  
117 social relationships, introducing uncertainty in interactions between group members (Ramos-  
118 Fernandez *et al.*, 2018).

119 Communicative complexity within a signalling system is commonly measured as the  
120 number of structurally and functionally distinct elements (e.g. Jansen, Cant & Manser, 2012)  
121 and/or the amount of bits of information in a call (Freeberg *et al.*, 2012). Interestingly, the  
122 different call types of a given vocal repertoire have different potential for information coding.  
123 For instance, in some species 'social' calls (such as contact calls) are more individually

124 variable than alarm calls (e.g. Lemasson & Hausberger, 2011; Bouchet *et al.*, 2013).  
125 Nonetheless, it is not always easy to quantify communicative complexity using these features.  
126 Very often, signals exist in a graded form, leading to difficulties in interpreting their functions  
127 (Keenan, Lemasson & Zuberbühler, 2013; Fischer *et al.*, 2017b; Keenan *et al.*, 2020). On the  
128 one hand, the existence of gradation may allow coding of information with greater subtlety,  
129 including emotional states, but on the other hand it increases the risk of message confusion  
130 due to physical constraints on acoustic structure during sound propagation in forested habitats.  
131 Recently, Rebout *et al.* (2020) studied two components of vocal complexity: diversity (i.e.  
132 number of call categories) and flexibility (i.e. degree of gradation between categories), and  
133 compared the acoustic structure of vocal signals in groups of macaques belonging to four  
134 species with varying levels of uncertainty in social tolerance (i.e. the higher the degree of  
135 tolerance, the higher the degree of uncertainty). Tolerant macaques displayed higher levels of  
136 diversity and flexibility than did intolerant macaques in situations with a greater number of  
137 options and consequences (i.e. agonistic and affiliative contexts). Beyond the level of the call  
138 structure, other relevant measures of communication complexity can be found at the level of  
139 the vocal sequence (i.e. more- or less-complex strings of sounds) (Kershenbaum *et al.*, 2016).  
140 In male gelada baboons *Theropithecus gelada*, sequence complexity and size function to  
141 counteract the challenges of living in a large group (overcoming conspecific noise and  
142 crowding) to maintain bonds with females (Gustison *et al.*, 2019).

143         The limits of these communication measures also come from the fact that they are  
144 emitter-centred, while communication is two-sided (Freeberg *et al.*, 2019). First, focusing on  
145 what a receiver perceives from the observed acoustic variations of a vocal signal is necessary  
146 to assess how much meaningful information is encoded within that signal (Freeberg *et al.*,  
147 2012; Manser *et al.*, 2014; Levréro *et al.*, 2015; Garcia *et al.*, 2020). Second, communicating  
148 and socialising are above all acts of interaction. To explore the link between the

149 requirements/characteristics of social life and the expression/structure of vocal interactions is  
150 another way to assess the social complexity hypothesis for communication. All the  
151 aforementioned studies focused on vocal repertoire sizes and variations in acoustic structure,  
152 thus with a focus on individuals as if they were isolated callers. However, the social core of  
153 communication may also be found in the patterns and rules of vocal interactions among two  
154 or more individuals (Lemasson, Hausberger & Zuberbühler, 2005; Lemasson, 2011; Fedurek  
155 *et al.*, 2013a; Arlet *et al.*, 2015; Henry *et al.*, 2015; Pika *et al.*, 2018). Focusing on the co-  
156 evolution of social lifestyle and vocal interaction patterns, as we do here, offers a promising  
157 new field of investigation.

158

## 159 **(2) Vocal interactions in primates: a remarkable diversity of temporal calling patterns**

160 A vocal interaction is primarily defined by its temporal pattern, with comparisons  
161 among species attracting interest due to the extensive diversity of existing temporal patterns.

162 When focusing on the temporal rules guiding call production in primates, three main  
163 types of temporal calling patterns are typically found (Pougnault, Levréro & Lemasson,  
164 2020a): (i) isolated calls (when only one individual produces a single call); (ii) a series of  
165 consecutive calls (where a given individual repeats a call several times in a row); and (iii)  
166 vocal interactions (when at least two individuals temporally coordinate their vocal  
167 production). The frequency of use of these different calling patterns may depend on the  
168 context and call type, but also on the identity (i.e. age, sex) and social characteristics of the  
169 caller (Pougnault *et al.*, 2020a). But what motivates and structures the organisation of vocal  
170 interactions still remains an open question.

171 Researchers distinguish several types of vocal interactions with more or less  
172 predictable temporal patterns: (1) disorganised phonoresponses, occurring when one  
173 individual produces a call, typically an alarm call that triggers calls in an apparently chaotic

174 way from other group members (e.g. blue monkey *Cercopithecus mitis stuhlmanni*; Papworth  
175 *et al.*, 2008); (2) choruses, which result from simultaneous production of the same call type by  
176 two or more individuals, implying causal interactions between individuals joining the chorus  
177 in a synchronised way (Yoshida & Okanoya, 2005; Ravignani, Bowling & Fitch, 2014); (3)  
178 duets, when two individuals synchronise or overlap long series of calls or songs with a  
179 stereotyped temporal association (e.g. gibbon *Hylobates syndactylus*; Geissmann &  
180 Orgeldinger, 2000), and (4) vocal exchanges involving individuals who alternate their calling  
181 and vocally ‘respond’ to one another.

182         Among the different patterns of vocal interactions, vocal exchanges have recently  
183 attracted a great deal of attention because of their complex organisation, possible prosocial  
184 function, and implications for our understanding of language evolution (Chow, Mitchell &  
185 Miller, 2015). Vocal exchanges are based on a turn-taking principle, and have been  
186 documented in all main primate branches [e.g. Catarrhini: Campbell’s monkey *Cercopithecus*  
187 *campbelli* (Lemasson *et al.*, 2011a), Japanese macaque *Macaca fuscata* (Sugiura, 1993);  
188 Platyrrhini: squirrel monkey *Saimiri sciureus* (Masataka & Biben, 1987), pygmy marmoset  
189 *Cebuella pygmaea* (Snowdon & Elowson, 1999), spider monkey *Ateles geoffroyi* (Briseño-  
190 Jaramillo *et al.*, 2018); for a review, see Pougnault *et al.* (2020a)]. Turn-taking is defined as  
191 the orderly exchange of communicative signals between individuals adjusting the timing of  
192 their vocal responses by respecting a minimum silence gap (preventing call overlap), and a  
193 maximum silence gap (allowing call coordination) (for a review see Pika *et al.*, 2018). They  
194 are typically composed of one to three turns with individuals alternating their calls (e.g.  
195 Lemasson, Gandon & Hausberger, 2010a; Levréro *et al.*, 2019), and thus are characterised by  
196 short vocal sequences. The common response delay is rarely shorter than the average call  
197 duration [e.g. Diana’s monkey *Cercopithecus diana* (Candiotti, Zuberbuhler & Lemasson,  
198 2012); squirrel monkey (Masataka & Biben, 1987); Japanese macaque (Sugiura, 1993); spider

199 monkey (Briseño-Jaramillo *et al.*, 2018); western lowland gorilla *Gorilla gorilla gorilla*  
200 (Lemasson, Pereira & Levréro, 2018); bonobo *Pan paniscus* (Levréro *et al.*, 2019).  
201 Interestingly, speech overlap avoidance and turn-taking also represent the social core of  
202 human vocal interactions and are found in all human cultures (Stivers *et al.*, 2009; Levinson,  
203 2016).

204 In sum, turn-taking-based vocal exchanges represent one of a variety of methods that  
205 allow group members to interact with one another. Vocal exchanges in some non-human  
206 primate species appear highly similar to temporally and socially organised vocal interactions  
207 in humans. How social structure influences the evolution of vocal turn-taking across the  
208 primate phylogeny remains a focus of research interest.

209

### 210 **(3) Turn-taking-based vocal exchange in primates: a social function**

211 Beyond temporal aspects, turn-taking-based vocal exchanges in non-human primates  
212 differ from other types of vocal interactions in several ways. First, they involve a diversity of  
213 recurrent vocal partners [differing from duets (MacKinnon & MacKinnon, 1980; Geissmann  
214 & Orgeldinger, 2000)]. Second, vocal exchange interlocutors can be of any age or either sex  
215 (differing from choruses; Haimoff, 1986). Third, vocal exchanges are not restricted to a  
216 specific context, time of day, or season, which differs from long-distance collective  
217 communication associated with mate attraction, territory protection and environmental  
218 disturbance (Gros-Louis & Mitani, 1998; Schel & Zuberbühler, 2012; Briseño-Jaramillo *et*  
219 *al.*, 2017). Most commonly, vocal exchanges are observed daily in short-distance  
220 communication, occur throughout the day, and consist mostly of soft calls exchanged in  
221 peaceful and relaxed contexts (Pougnault *et al.*, 2020a).

222 Due to their role in within-group socio-spatial coordination (Pougnault *et al.*, 2020a),  
223 turn-taking-based vocal exchanges represent an interesting vocal interaction metric to test the

224 proposed links between sociality and vocal complexity. The ‘grooming-at-distance’  
225 hypothesis proposed by Dunbar (1996) highlighted the possible role played by vocal  
226 exchanges during the evolution of primates. This hypothesis suggested that, in large social  
227 groups and in groups with long-lasting bonds, the function of gestural grooming was partially  
228 transferred to vocal exchanges. Gestural grooming plays an important role in forming new  
229 bonds and strengthening existing ones in all primate species (Dunbar, 1991). As group size  
230 and social network increased during our ancestral history, vocal exchanges may have  
231 developed, as it ultimately would have become impossible to allocate sufficient time to  
232 grooming all partners physically.

233         Vocal exchanges do indeed occur mostly between interlocutors that are non-randomly  
234 chosen, depending on their affiliative bonds [e.g. bonobo (Levréro *et al.*, 2019), spider  
235 monkey *Ateles geoffroyi* (Briseño-Jaramillo *et al.*, 2018), Japanese macaque (Arlet *et al.*,  
236 2015), pygmy marmoset (Snowdon & Cleveland, 1984)] or ages [common marmoset  
237 *Callithrix jacchus* (Chen, Kaplan & Rogers, 2009), Campbell’s monkey (Lemasson *et al.*,  
238 2010a); for a review see Pougnault *et al.* (2020a)]. The temporal [squirrel monkey (Biben,  
239 Symmes & Masataka, 1986; Masataka & Biben, 1987)] and acoustic [Japanese macaque  
240 (Sugiura & Masataka, 1995); Diana monkey (Candiotti *et al.*, 2012); spider monkey (Briseño-  
241 Jaramillo *et al.*, 2018)] organisation of vocal exchanges in monkeys is socially guided. These  
242 vocal exchanges represent a significant cognitive demand, implying cooperation (Takahashi,  
243 Narayanan & Ghazanfar 2013; Levinson & Holler, 2014; Levinson, 2016).

244         However, despite growing interest, many knowledge gaps remain to be filled to  
245 comprehend fully the social relevance of vocal exchanges in non-human primates and the  
246 evolutionary trajectory of this type of vocal interaction. One of the major missing elements is  
247 comparative studies that are necessary to characterise the vocal exchange phenotype of a wide  
248 diversity of primate species (Pika *et al.*, 2018).

249

250 **(4) Selection for vocal turn-taking systems from monkeys to humans: an open question**

251         The growing interest in turn-taking vocal exchanges in animals is partly due to their  
252 many parallels with human conversations (Snowdon & Cleveland, 1984; Sugiura & Masataka,  
253 1995; Lemasson *et al.*, 2011*b*; Henry *et al.*, 2015). Overlap avoidance, turn-taking, social  
254 selection of interlocutors, varied contexts beyond a strict message-transmission function, and  
255 acoustic convergence are all found in both non-human primate vocal exchanges and human  
256 conversations. Researchers have thus questioned the role played by social factors during both  
257 the development and evolution of vocal exchanges.

258         During development or ontogeny, the extent to which the abilities to converse in  
259 primates are socially acquired or learned remains debated. The few available studies on  
260 monkeys show that juveniles break conversational rules more often than do adults [howler  
261 monkey *Alouatta pigra* (Briseño Jaramillo *et al.*, 2017); Campbell's monkey (Lemasson *et*  
262 *al.*, 2011*a*)]. A recent study conducted on common marmosets (*Callithrix jacchus*) suggested  
263 that, rather than parental influence (Chow *et al.*, 2015), the ability to participate in vocal turn-  
264 taking might be due to self-monitoring that increases with age (Takahashi, Fenley &  
265 Ghazanfar, 2016). Despite the lack of empirical evidence to answer this question, results from  
266 playback experiments using a violation-of-expectation paradigm showed that adult monkeys  
267 clearly discriminated between conversationally appropriate and inappropriate vocal-exchange  
268 patterns, whereas socially inexperienced juveniles did not [Japanese macaque (Bouchet,  
269 Koda, & Lemasson, 2017); Campbell's monkey (Lemasson *et al.*, 2011*a*)]. These findings  
270 show that the social rules in vocal interactions are not a simple neurobiologically determined  
271 behaviour, but rather, may represent an awareness of social rules.

272         Concerning their evolution, the debate likewise remains open, mainly because most  
273 published research on vocal interactions has focused on Platyrrhini and Catarrhini monkeys or

274 lesser apes [e.g. agile gibbon *Hylobates agilis* (Koda *et al.*, 2013); siamang *Hylobates*  
275 *syndactylus* (Geissmann & Orgeldinger, 2000)]. Remarkably, researchers have largely  
276 neglected vocal interactions among great apes for decades. However, they are also excellent  
277 candidates for such research given their well-described complex social structures with long-  
278 term bonds and intricate social interactions [e.g. orang-utan *Pongo pygmaeus* (Delgado & van  
279 Schaik, 2000); gorilla (Stokes, 2004); chimpanzee *Pan troglodytes* (van Lawick-Goodall,  
280 1968; Goodall, 1986); bonobo (Kano, 1982, 1992)]. Moreover, vocal communication plays a  
281 central role in their daily lives [e.g. orang-utan (Hardus *et al.*, 2009); gorilla (Salmi,  
282 Hammerschmidt & Doran-Sheehy, 2013); chimpanzee (Slocombe & Zuberbühler, 2010);  
283 bonobo (De Waal, 1988, Bermejo & Omedes, 1999)]. Great apes are also of interest because  
284 of their close phylogenetic proximity to humans. As a result, the selective pressures that  
285 maintain such vocal behaviours in non-human primates remain unclear, notably because the  
286 current state of knowledge still prevents us from concluding in favour of a convergent-  
287 evolution scenario (turn-taking has been favoured in some species more than others by the  
288 requirements of social life) or a shared-inheritance scenario (turn-taking is universal  
289 suggesting an ancient mechanism present deep within the primate lineage).

290         In the following section, we explore further explore how the requirements of a social  
291 life may match the use of turn-taking, as well as other types of vocal interaction patterns, in  
292 great apes. While comparisons between a limited number of species should be interpreted  
293 cautiously, similar studies at the genus level have enabled a better understanding of some  
294 aspects of social–vocal coevolution (see the studies cited above on macaques and baboons, for  
295 example). The four species of great apes described herein are valuable candidates for a  
296 comparative analysis of social and vocal features because they exhibit four very different and  
297 well-described social systems.

298

299 **II. THE SOCIO ECOLOGY OF GREAT APES: SIMILARITIES AND**  
300 **DIFFERENCES**

301 Current knowledge on the socio-ecology of great ape species, particularly in terms of  
302 vocal communication, varies among species. We selected four species/sub-species for which  
303 sufficient literature is available to perform a comparative analysis: (i) bonobo, (ii)  
304 chimpanzee, (iii) western lowland gorilla, and (iv) Bornean orang-utan. All key references for  
305 the phylogenetic and socio-ecological information discussed below are provided in Table 1.

306

307 **(1) Origins and habitat**

308 The evolution of vocal communication in great apes is likely to have been influenced  
309 by phylogenetics, habitat use and social life-related factors. Genetic evidence indicates that  
310 the last common ancestor to Ponginae and Homininae lived about 9–18 million years ago  
311 (Mya) (Castellano & Munch, 2020). A second speciation, between ~8.6 and 11.5 Mya, led to  
312 the separation of Gorillini and Hominini, and a final differentiation, between ~4.2 and 9 Mya,  
313 gave rise to the Panina and Hominina clades. Given their phylogenetic proximity, the *Pan*  
314 genus thus represent our closest living relatives. An evolutionary hypothesis based on  
315 phylogeny would thus predict more vocal similarities between chimpanzees and bonobos than  
316 between other pairs of these species, as well as more similarities between *Pan* spp. and  
317 gorillas than with orang-utans.

318 Despite a growing body of evidence for an European origin of great apes (e.g. Begun,  
319 2010; Böhme *et al.*, 2019), all currently living non-human great apes are located in tropical  
320 and equatorial rain forests of Asia and Africa. The four species considered herein usually  
321 occupy habitats with reduced visibility due to the density of the surrounding vegetation, and  
322 travel, to some extent at least, in a three-dimensional space. These characteristics are known  
323 to be suitable for vocal communication (Bradbury & Vehrencamp, 2011). However, these

324 four species do show differences in habitat preferences and modes of locomotion, which  
325 could also influence vocal communication (Marler, 1965; Lemasson, 2011). Bornean orang-  
326 utans live almost exclusively in the canopy of humid forests, while western lowland gorillas  
327 are mainly terrestrial and inhabit both humid and *terra firma* lowland forests (Table 1).  
328 Chimpanzees and bonobos mainly occupy primary and secondary humid forests but can  
329 sometimes be found on savannah woodland mosaics. They travel in the trees as well as on the  
330 ground according to their age. Therefore, a habitat-based evolutionary hypothesis would again  
331 predict more similarities between chimpanzees and bonobos than between any other pair of  
332 species.

333

## 334 **(2) Social systems**

335 The four great apes considered herein live in four different social systems that differ in  
336 group size, group structure, and social organisation (see Table 1 for details and references).

337 Bornean orang-utans are known as the most solitary great ape species. Males  
338 (particularly flanged males) generally live alone whereas females are typically found with  
339 their infants. Orang-utans can be described as an individual-based fission–fusion species with  
340 a mean party size of less than two independent individuals (usually related females or  
341 unflanged males). Temporary groupings are peaceful, typically observed near food sources  
342 (van Schaik, Marshall & Wich, 2009). Physical interactions are rare and a high level of  
343 intolerance is generally reported between adult males for access to females (Galdikas, 1985).

344 In contrast to orang-utans, which are female-philopatric, chimpanzees and bonobos are  
345 male-philopatric species that live in large multi-male multi-female and highly flexible fission–  
346 fusion societies (i.e. with subgroups of variable size and composition; Kummer, 1971). Sub-  
347 groups are typically composed of 20–100 individuals. Both species have a high rate of  
348 physical interactions, notably very high grooming rates compared to the two other great apes

349 considered herein. Male chimpanzees are highly territorial. Related males form strong social  
350 bonds on which they rely to manage inter- and intra-community competition, while females  
351 have weaker social bonds with each other. This high level of competition leads to more  
352 aggressive conflicts in chimpanzees and to the highest recorded death rate due to intra-  
353 specific conflict among great apes (Table 1). Chimpanzees appear to perform fewer  
354 cooperative behaviours than their bonobo relatives (Hare & Tomasello, 2004; Jensen *et al.*,  
355 2006; Melis, Hare & Tomasello, 2006; Hare *et al.*, 2007; Hirata & Fuwa, 2007; Pelé *et al.*,  
356 2009; Gruber & Clay, 2016; Suchak *et al.*, 2016), for whom inter- and intragroup interactions  
357 are mostly tolerant. In bonobos, members from different communities regularly mix  
358 peacefully to feed, and females have a central role in the community. They establish strong  
359 affiliative bonds with other females independently of their kinship and also form bonds with  
360 unrelated males.

361         Western lowland gorillas live in single-male/multi-female medium-sized groups of  
362 10–20 individuals, and both sexes disperse. The sole adult male in a group develops strong  
363 social bonds with adult females. He is the leader of the group, coordinating activities,  
364 protecting the group and managing social interactions between females (Parnell, 2002;  
365 Harcourt & Stewart, 2007). Despite the strong social bonds between the male and females,  
366 individual gorillas appear to cooperate only rarely (Harcourt & Stewart, 2007; Pelé *et al.*,  
367 2009).

368         Living in different society types will obviously require different daily social  
369 interactions and it is important to consider how this may influence vocal interaction patterns.  
370 Interestingly, all great ape species are known to have comparably high cognitive and social  
371 skills (Chalmeau *et al.*, 1997; Pelé *et al.*, 2009; Dufour *et al.*, 2009), suggesting that any  
372 differences in vocal communication among these species may be related more to social  
373 differences than to habitat or cognitive differences.

374

### 375 **III. TESTING THE SOCIAL COMPLEXITY HYPOTHESIS FOR**

### 376 **COMMUNICATION IN GREAT APES**

#### 377 **(1) Traditional vocal metrics (repertoire size, call rate)**

378           The social complexity hypothesis for communication predicts a higher number of  
379 distinct call types in the vocal repertoires of more social species, hence increasing from orang-  
380 utans to gorillas and then to bonobos and chimpanzees if group sizes and time spent grooming  
381 are representative indices of social complexity (e.g. McComb & Semple, 2005; Gustison *et*  
382 *al.*, 2012). Table 2 summarises findings from the literature on the vocal behaviour of the four  
383 great ape species considered herein, supplemented where necessary with new data (see online  
384 Supporting Information, Appendix S1–S3). Previous studies on wild free-ranging animals  
385 show that the vocal repertoire size of Bornean orang-utans and chimpanzees is very similar  
386 (25 for orang-utans and 13–29 for chimpanzees; Table2). A comparable vocal repertoire size  
387 is reported for wild bonobos (15 call types) and gorillas (16 call types). In captivity, the  
388 repertoire size of these great ape species contains fewer distinct call types than in wild  
389 populations, with all species using only 8–12 distinct call types.

390           The hourly rate of vocal production is high for all great ape species. Even if the two  
391 species forming multi-male multi-female groups appear to have higher call rate than the two  
392 others, at least compared to gorillas in the wild, there are strong variations among study  
393 populations and environmental contexts (Table 2). The relative richness of the environments  
394 encountered by wild animals compared with those in captivity typically result in more call  
395 types and higher call rates in free-ranging populations (Lameira & Call, 2020). As for vocal  
396 repertoire size, any link between hourly vocalisation rate and social complexity appears very  
397 weak (Table 2). This is particularly striking when considering the very large vocal repertoire  
398 size of orang-utans, which are the most solitary species (Hardus *et al.*, 2009). This questions

399 the use of group size and grooming rate as measures of social complexity in the debated  
400 hypotheses (McComb & Semple, 2005; Freeberg *et al.*, 2012; Kershenbaum, Freeberg &  
401 Gammon, 2015).

402 Some methodological issues involved in the classification of call types, also need to be  
403 addressed. Many reports of communicative repertoires reveal intermediate forms between  
404 specific signals as well as variations within signal types. These so-called ‘graded repertoires’  
405 are characteristic of great apes, particularly chimpanzees and bonobos, leading to difficulties  
406 in identifying a specific number of stereotypic signals in a species’ repertoire (Keenan *et al.*,  
407 2020). Experimental approaches using playback and systematic contextual studies of call  
408 emission are still needed to test whether overly simplistic acoustic analyses may lead to  
409 overestimation or underestimation of repertoire size, and thus bias interspecific comparisons.  
410 Interestingly, a comparative study on macaques found more gradation of vocal  
411 communication in tolerant than in despotic species (Rebout *et al.*, 2020). Thus whether vocal  
412 interaction pattern measures are suitable candidates to assess the social complexity hypothesis  
413 for communication remains unclear at this stage, and is considered in more detail in Section  
414 III.2.

415

## 416 **(2) Vocal interaction patterns**

417 Vocal interaction patterns are not randomly distributed across the four great apes  
418 studied herein (Table 2). Vocal interactions are most frequent in bonobos (53% of their calls  
419 in wild animals; 74% in captivity), followed by gorillas (38% in captive animals; unstudied in  
420 the wild) and then chimpanzees (19% in wild animals; 16% in captivity), and they seem to be  
421 extremely rare in orang-utans. Vocal interactions, regardless of the species’ average group  
422 size, typically concern only two or three coordinating partners. This parallels results for  
423 monkeys’ conversation-like vocal exchanges (Pougnault *et al.*, 2020a). The typical pattern of

424 vocal production in the orang-utan is isolated calling. Chimpanzees also often emit isolated  
425 calls, but most of their vocal production consists of series of repeated calls. However, all our  
426 data on vocal interaction in orang-utans come from two captive groups, and this has never  
427 been investigated in the wild. To draw firm conclusions about this species, future  
428 investigations should focus on their call patterns in the wild during fusion periods.

429 Differences do exist among the three other great ape species. Considering the vocal  
430 interactions (namely excluding isolated and repeated calls), most of chimpanzees'  
431 vocalizations overlapped (58%) while it occurred in 27.5% in gorillas and 19% in bonobos  
432 (Table 2 and Fig. 1c). Arcadi (2000) also identified an intriguing rarity of turn-taking in free-  
433 ranging chimpanzees. Chimpanzees are known for their structured choruses, mainly based on  
434 a superimposed pant-hoots (Gros-Louis & Mitani, 1998; Fedurek, Schel & Slocombe, 2013b;  
435 Ravignani *et al.*, 2014), which seem to play a role in territory defence and in regulating group  
436 dynamics facilitating fusion and changes in sub-group composition (Fedurek, Donnellan &  
437 Slocombe, 2014). A pant-hoot vocalisation is composed of four distinct phases (Gros-Louis &  
438 Mitani, 1998; Slocombe & Zuberbühler, 2010). During pant-hoot chorusing, interlocutors  
439 adjust the duration of constituent phases, promoting choruses by mirroring the partner's call,  
440 and revealing that the temporal structure of this rather stereotyped vocalisation is sensitive to  
441 fine details of the vocal behaviour of the audience (Fedurek *et al.*, 2013b).

442 Conversely, bonobos, and to lesser extent gorillas, tend to avoid overlap when they  
443 interact vocally (about 67% and up to 94% of the vocal interactions without overlap in  
444 bonobos in captivity and in the wild, respectively (81% on average for both populations), and  
445 72% in gorillas; Table 2 and Fig. 1c). As found in several monkey species and in humans,  
446 gorillas and bonobos engage frequently in vocal exchanges that involve a turn-taking rule.  
447 Their vocal exchanges are call-type dependent. For both species, soft contact calls, known to  
448 be characteristic of peaceful contexts (grunts/double grunt in gorillas; peeps/peep-yelps in

449 bonobos), are predominantly used. The inter-call duration between two consecutive  
450 interlocutors is also similar: a maximum of 3 s in gorillas (0.5 s median; Lemasson *et al.*,  
451 2018) and a maximum between 2.1 and 2.5 s in bonobos [wild bonobos 0.7 s median (Cornec  
452 *et al.*, in press); captive bonobos 0.4 s median (Levréro *et al.*, 2019). This inter-call duration is  
453 consistent with those found in monkeys, i.e. it is rarely shorter than the mean duration of a  
454 call, although most published maximum response delays appear slightly shorter in monkeys  
455 (around 1 or 1.5 s). Recent playback experiments using violation-of-expectations on gorillas  
456 and bonobos revealed that individuals could perceive whether a short silent gap between  
457 vocalisations produced by different interlocutors is present (Levréro *et al.*, 2017; Pournault *et*  
458 *al.*, 2020b). These results suggest that the presence of a response delay matters to the audience  
459 (Levréro *et al.*, 2017; Pournault *et al.*, 2020b).

460 Our analysis does not support a strict correlation between group size, grooming rate  
461 and vocal exchange rate, as would be expected from Dunbar's grooming-at-distance  
462 hypothesis (Dunbar, 1996). However, a subtler link between social structure and type of vocal  
463 interaction emerges from our comparative data. Call overlap and turn-taking exchanges may  
464 represent two possible vocal alliance strategies to advertise or strengthen social bonds as  
465 detailed in Section III.3.

466

### 467 **(3) Social structure as a defining factor of vocal interaction patterns**

468 In chimpanzees, pant-hoot choruses are mainly produced by high-ranking males  
469 (Mitani & Nishida, 1993; Clark & Wrangham, 1994), with the aim of recruiting and  
470 maintaining the company of close associates (Mitani & Nishida, 1993). Researchers highlight  
471 that choruses occur between allies without consideration of kinship or age (Mitani & Nishida,  
472 1993). Indeed, this vocal behaviour appears to be a strong indicator of affiliation between  
473 males (Fedurek *et al.*, 2013a), and during a chorus, allies tend to match vocally the acoustic

474 features of a partner's calls (Mitani & Brandt, 1994; Gros-Louis & Mitani, 1998). Pant-hoot  
475 choruses thus might represent a reliable social bonding signal in highly fluid fission–fusion  
476 societies (Fedurek *et al.*, 2013a). The prevalence of pant-hoot chorusing in chimpanzee vocal  
477 interactions could be explained by the fact that, in a context of highly risky intra- and inter-  
478 community competition, opponents seem able to perceive the number of participants of a  
479 pant-hoot chorus and to adapt their behaviour accordingly (Wilson, Hauser & Wrangham,  
480 2001). By attesting to social affinities, such loud calls produced in a chorus might deter  
481 potential rivals and avoid a costly fight (Wilson *et al.*, 2001).

482         In western lowland gorillas, the adult male responds vocally more to adult females  
483 with whom he establishes durable social bonds, and less to individuals distant in age such as  
484 sub-adults or juveniles (Lemasson *et al.*, 2018). The same is true for bonobos for which vocal  
485 turn-taking occurs mainly between interlocutors with strong social affinities, and is not  
486 influenced by the age, sex, hierarchical rank or kinship of interlocutors (Levréro *et al.*, 2019).  
487 Experimental approaches using violation-of-expectation paradigms have been used to test the  
488 relevance of social rules previously described in bonobos and western lowland gorillas. These  
489 studies compared the attentional response of the audience towards vocal exchanges of  
490 individuals with or without strong social affinities in bonobos (Levréro *et al.*, 2017) and close  
491 or distant in age in gorillas (Pougnault *et al.*, 2020a). It seems clear that individuals have  
492 some expectations about which individuals will interact vocally with them (Pougnault *et al.*,  
493 2020a). Additional playback experiments are now needed to explore the social function of  
494 vocal interaction patterns in more detail.

495         Our focused phylogenetic comparison provides evidence both in support of and  
496 against the social complexity hypothesis for communication (Blumstein & Armitage, 1997;  
497 Freeberg *et al.*, 2012; Pollard & Blumstein, 2012; Manser *et al.*, 2014). If we focus our  
498 attention only on the number of different call types composing the vocal repertoire of each

499 great ape species and the nature of social interactions or the number of group members, the  
500 results are not convincing. Such a comparison can be criticised for omitting potentially  
501 important variables, such as relationship types between group members, or a subjective  
502 classification of calls from a graded repertoire (Fischer *et al.*, 2017*a,b*; Hammerschmidt &  
503 Fischer, 2019). However, by considering a more complex set with more subtle features, it  
504 seems possible to structure a gradation in social–vocal complexity using the three social–  
505 vocal patterns (see Fig. 1). Bornean orang-utans form dispersed single/multi-male groups with  
506 extended solitary periods and favour the production of isolated calls. In chimpanzee societies,  
507 which are mainly despotic with a strong male influence, consecutive calls from single callers  
508 [i.e. characteristic of emotional discharge (Lemasson *et al.*, 2010*b*; Owren & Rendall, 1997;  
509 Scherer, 2003)] are particularly common, and vocal interactions occur frequently in the form  
510 of choruses of pant-hoots. On the contrary, gorillas and bonobos, who are more social than  
511 orang-utans and have more peaceful intra-group interactions than do chimpanzees, show a  
512 majority of vocal interactions characterised by overlap avoidance and turn-taking.

513         Interestingly, chimpanzees spend more time in social grooming than the other three  
514 species (see Fig. 1). They appear to use dyadic mutual grooming (Fedurek & Dunbar, 2009)  
515 in a fluid way to access a large number of grooming partners, changing partners more often  
516 than do bonobos (Girard-Buttoz *et al.*, 2020). Moreover, a large part of their time spent in  
517 social grooming is allocated to polyadic grooming [16% of total grooming time in  
518 chimpanzees (Nakamura, 2003) against only 3% in bonobos (Sakamaki, 2013)]. Polyadic  
519 grooming also involves a larger number of partners in chimpanzees than in bonobos (Girard-  
520 Buttoz *et al.*, 2020). In this way, chimpanzees can reach the same efficiency as human  
521 conversations in terms of number of partners accessed simultaneously in polyadic grooming  
522 clusters (a mean of 2.72 partners in humans *versus* 2.18 partners in chimpanzees; Nakamura,  
523 2000). These clusters occur particularly between males of similar hierarchical rank in

524 chimpanzees, while bonobos engage more often with conspecifics distant in dominance rank  
525 (Girard-Buttoz *et al.*, 2020). Thus, at a first glance, the low rate of vocal exchanges in  
526 chimpanzees appears counter-intuitive given their high rate of social grooming (see Fig. 1).  
527 However, it is possible that the apparent efficiency of polyadic social grooming, its focus on a  
528 limited number of close social partners, and high levels of intra-group competition could  
529 explain why this species does not need to ‘groom-at-distance’ using vocal exchanges to  
530 maintain their relationships (Dunbar, 1996). By contrast, in species displaying more tolerance  
531 among group members, as bonobos and gorillas, vocal exchanges that follow temporal and  
532 social rules may be favoured during vocal interactions. This interpretation must be considered  
533 preliminary, given the representation of each social system by a single species here, but it  
534 does highlight the potential for integrative approaches to investigate diverse complementary  
535 social parameters.

536

#### 537 **IV. CONCLUSIONS**

538 (1) Our goal herein was to highlight the necessity to include metrics at the vocal interaction  
539 level when investigating the coevolution between social and vocal complexity in primates or  
540 other animals. The limited number of species included here, and the limited number of  
541 sampled populations per species, make our description of the potential relationships between  
542 social bonds and vocal interaction patterns essentially qualitative. Although it does not allow  
543 us to provide any evolutionary scenario across primate genera, we believe that this analysis  
544 has several major implications for the field and opens interesting perspectives for future  
545 studies.

546 (2) Vocal interaction patterns broadly map onto the quality of social bonds in apes, in  
547 agreement with the predictions of a socially driven evolution of communication. A well-  
548 targeted comparative approach could help to identify the multiple and probably subtle social

549 factors underlying social and vocal complexity, beyond a consideration of only social  
550 structure or organisation. While focusing on four great apes provides only one template for  
551 each different social system, we believe that focusing on our nearest living relatives is a  
552 necessary step to a better understand of the social factors influencing different vocal  
553 interaction patterns.

554 (3) It will be a difficult task to derive a scenario of the evolution of vocal interaction skills,  
555 from the Strepsirhini to the genus *Homo*, because the emergence of social and vocal  
556 complexity is found throughout the primate lineage and probably results from multiple  
557 evolutionary pressures. However, some great apes (mainly bonobos and gorillas) and  
558 monkeys share some temporal and social rules regulating their vocal exchanges that may  
559 indicate similar constraints between primate ‘conversational’ vocal exchanges and human  
560 conversations. It is possible that chimpanzees and orang-utans have been subject to different  
561 selection pressures, due respectively to a strong male-despotic hierarchy and an extended  
562 solitary life, leading to the appearance of derived traits.

563 (4) It is somewhat reductive to discuss the evolution of social life and vocal communication  
564 without considering other modalities of communication (e.g. see the social complexity  
565 hypothesis proposed for visual and chemical signals; Freeberg *et al.*, 2012). Human language  
566 is likely to have multimodal origins (Prieur *et al.*, 2020). This is particularly true for some  
567 great apes who are known to communicate intensively with gestures, with reported cases of  
568 gestural turn-taking (Fröhlich *et al.*, 2016). Further research may extend this comparison to  
569 visual and tactile communication and thereby highlight alternative options to vocal  
570 interactions for short-range communication, adding even more complexity (Smith & Evans,  
571 2013; Peckre, Kappeler & Fichtel, 2019).

572

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590

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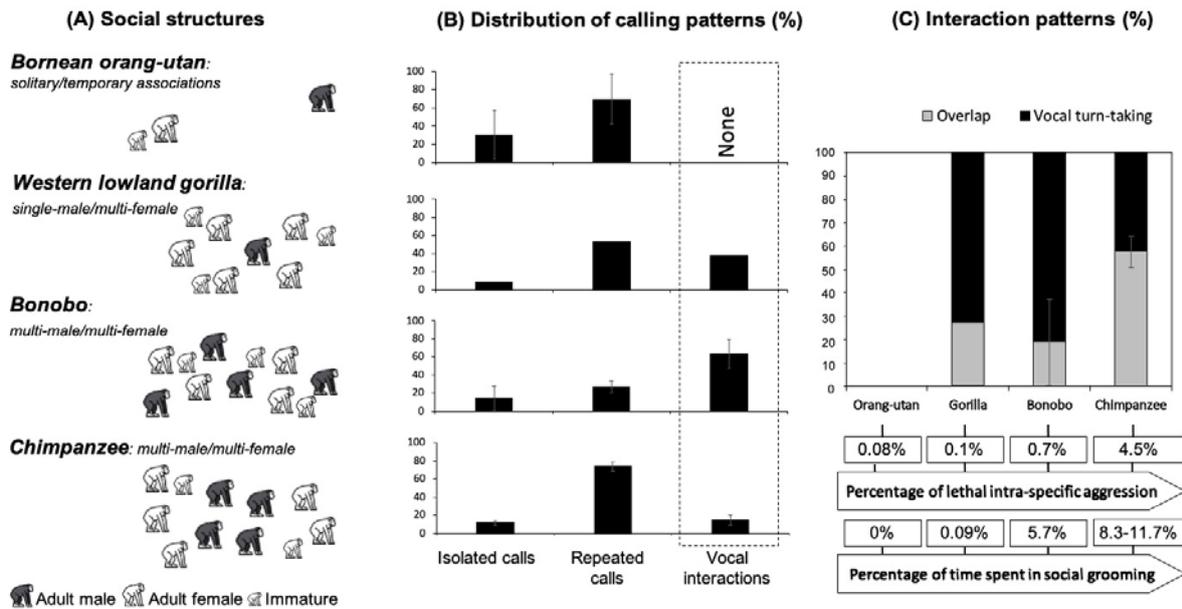
1123 **VII. SUPPORTING INFORMATION**

1124 Additional supporting information may be found online in the Supporting Information section  
1125 at the end of the article.

1126 **Appendix S1.** Details of new data for wild free-ranging chimpanzees.

1127 **Appendix S2.** Details of new data for wild free-ranging bonobos.

1128 **Appendix S3.** Details of new data for captive orang-utans.



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**Fig. 1.** Synthesis of the social structure, distribution of calling patterns and interaction

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patterns (percentage of lethal intra-specific aggression and time spent in social grooming) for

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each of the four great ape species considered herein. The data used for B and C were obtained

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by averaging data collected from the wild and captivity ((2 groups for each species except for

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gorillas, for which data came from one group; see Tables 1 and 2 for data and references).

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Values are means + SD.

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1138 Table 1. Socio-ecology of four great ape species. Mya, million years ago.

	<b>Bornean orang-utan</b> ( <i>Pongo pygmaeus</i> )	<b>Western lowland gorilla</b> ( <i>Gorilla gorilla gorilla</i> )	<b>Chimpanzee</b> ( <i>Pan troglodytes</i> )	<b>Bonobo</b> ( <i>Pan paniscus</i> )
<b>Last common ancestor with humans</b>	~9 Mya to ~18 Mya (Hobolth <i>et al.</i> , 2011; Castellano & Munch, 2020)	~8.6 to ~11.5 Mya (Upham <i>et al.</i> , 2019; Castellano & Munch, 2020)	~4.2 to ~9 Mya (Patterson <i>et al.</i> , 2006; Hobolth <i>et al.</i> , 2011; Prüfer <i>et al.</i> , 2012; Rogers & Gibbs, 2014; Upham <i>et al.</i> , 2019)	~4.2 to ~9 Mya (Patterson <i>et al.</i> , 2006; Hobolth <i>et al.</i> , 2011; Prüfer <i>et al.</i> , 2012; Rogers & Gibbs, 2014; Upham <i>et al.</i> , 2019)
<b>Geographical distribution</b>	South-east equatorial Asia (Ancrenaz <i>et al.</i> , 2018)	Western equatorial Africa (Maisels <i>et al.</i> , 2018)	Western, central and eastern Africa (Oates <i>et al.</i> , 2007)	Central Africa (Kano, 1992; Idani <i>et al.</i> , 2008; Fruth <i>et al.</i> , 2016)
<b>Main habitat type</b>	Humid forest (Delgado & van Schaik, 2000; Ancrenaz <i>et al.</i> , 2018)	Humid and <i>terra firma</i> lowland forests (Gatti <i>et al.</i> , 2004; Levréro <i>et al.</i> , 2006; Maisels <i>et al.</i> , 2018; Forcina <i>et al.</i> , 2019)	Humid forest (sometimes savannah woodland) (Nishida, 1968; van Lawick-Goodall, 1968; Goodall, 1986; Oates <i>et al.</i> , 2007)	Humid forest (sometimes forest-savannah mosaics) (Kano, 1982; Narat <i>et al.</i> , 2015; Fruth <i>et al.</i> , 2016)
<b>Group size</b>	Small (1–2 adults) (Delgado & van Schaik, 2000; van Noordwijk <i>et al.</i> , 2012)	Medium (10, occasionally up to 20) (Williamson & Butynski, 2013)	Large (20 to 120) (Muller & Mitani, 2005)	Large (30 to 80) (Fruth <i>et al.</i> , 2013, 2016)
<b>Social group pattern</b>	Mix of solitary life and temporary ♂ / ♀ grouping (fission–fusion society) (Delgado & van Schaik, 2000; van Noordwijk <i>et al.</i> , 2012; van Schaik 1999)	Single ♂/multi ♀ and temporary grouping composed mainly of immature ♂♂ (Gatti <i>et al.</i> , 2004; Robbins <i>et al.</i> , 2004; Levréro <i>et al.</i> , 2006; Harcourt & Stewart, 2007)	Multi-♂/multi-♀ (fission–fusion society) (Wrangham & Smuts, 1980; Muller & Mitani, 2005)	Multi-♂/multi-♀ (fission–fusion society) (Kano, 1982; van Elsacker <i>et al.</i> , 1995; Furuichi <i>et al.</i> , 2012)
<b>Sex dispersal</b> ♂	Disperse	Disperse (Stokes <i>et al.</i> , 2003; Forcina <i>et al.</i> , 2019)	Philopatric (Nishida, 1968; Wrangham & Smuts, 1980)	Philopatric (Kano, 1982; van Elsacker <i>et al.</i> , 1995; Furuichi <i>et al.</i> , 2012)

	(Morrogh-Bernard <i>et al.</i> , 2011; van Noordwijk <i>et al.</i> , 2012)			
♀	Philopatric (Arora <i>et al.</i> , 2010; Morrogh-Bernard <i>et al.</i> , 2011; Nater <i>et al.</i> , 2011)	Disperse (Stokes <i>et al.</i> , 2003; Forcina <i>et al.</i> , 2019)	Disperse (Nishida, 1968; Wrangham & Smuts, 1980)	Disperse (Kano, 1982; van Elsacker <i>et al.</i> , 1995; Furuichi <i>et al.</i> , 2012)
♂-♂	Weak [medium if immature (unflanged)] (Delgado & van Schaik, 2000)	Weak (Robbins <i>et al.</i> , 2004; Hagemann <i>et al.</i> , 2018)	Strong (van Hooff & van Schaik, 1994; Watts & Mitani, 2001; Gilby & Wrangham, 2008; Mitani, 2009b; Surbeck <i>et al.</i> , 2017)	Weak (Kano, 1992; De Waal, 1995; Surbeck <i>et al.</i> , 2017)
♀-♀	Weak (medium if kin) (Delgado & van Schaik, 2000; Knott <i>et al.</i> , 2008; Singleton <i>et al.</i> , 2009)	Weak (medium if kin) (Robbins <i>et al.</i> , 2004; Hagemann <i>et al.</i> , 2018)	Medium (Lehmann & Boesch, 2008, 2009; Langergraber <i>et al.</i> , 2013; Surbeck <i>et al.</i> , 2017)	Strong (Kano, 1992; De Waal, 1995; Surbeck <i>et al.</i> , 2017)
♂-♀	Weak (medium if kin) (Delgado & van Schaik, 2000; Knott <i>et al.</i> , 2008; Singleton <i>et al.</i> , 2009)	Strong (Robbins <i>et al.</i> , 2004; Hagemann <i>et al.</i> , 2018)	Medium (van Hooff & van Schaik, 1994; Watts & Mitani, 2001; Lehmann & Boesch, 2008; Gilby & Wrangham, 2008; Mitani, 2009b; Langergraber <i>et al.</i> , 2013; Surbeck <i>et al.</i> , 2017)	Strong (Kano, 1992; De Waal, 1995; Surbeck <i>et al.</i> , 2017)
<b>Inter-group competition</b>	Medium (♀) to strong (♂) (Poole, 1987; Delgado & van Schaik, 2000; Knott <i>et al.</i> , 2008; van Noordwijk <i>et al.</i> , 2012)	Medium (Levréro, 2005; Harcourt & Stewart, 2007; Forcina <i>et al.</i> , 2019)	Strong (Wrangham, 1999; Mitani, 2009a; Mitani <i>et al.</i> , 2010; Wilson <i>et al.</i> , 2012)	Weak (Kuroda, 1980; Furuichi, 2011)

<b>Percentage of lethal intra-specific aggression</b>	0.08% (Gómez <i>et al.</i> , 2016)	0.14% (Gómez <i>et al.</i> , 2016)	4.49% (Gómez <i>et al.</i> , 2016)	0.68% (Gómez <i>et al.</i> , 2016)
<b>Percentage of time spent on social grooming</b>	0% (Dunbar, 1991; McComb & Semple, 2005)	0.09% (Lehmann <i>et al.</i> , 2007)	8.3-11.7% (Lehmann <i>et al.</i> , 2007)	5.7% (Lehmann <i>et al.</i> , 2007))

Table 2. Vocal behaviour of four great ape species.

		<b>Bornean orang-utan</b> ( <i>Pongo pygmaeus</i> )	<b>Western lowland gorilla</b> ( <i>Gorilla gorilla gorilla</i> )	<b>Chimpanzee</b> ( <i>Pan troglodytes</i> )	<b>Bonobo</b> ( <i>Pan paniscus</i> )
<b>Vocal repertoire size (number of call types)</b>	<b>Wild</b>	25 (Hardus <i>et al.</i> , 2009)	16 (Salmi <i>et al.</i> , 2013)	13–29 (Marler & Tenaza, 1977; Goodall, 1986; Arcadi, 2000; Slocombe & Zuberbühler, 2010)	15 (Bermejo & Omedes, 1999)
	<b>Captivity</b>	8 (new data <sup>#3</sup> )	11 (Lemasson <i>et al.</i> , 2018)	10 (Pougnault <i>et al.</i> , in press)	12 (De Waal, 1988)
<b>Hourly rate of vocal production: entire group call rate (G) or individual call rate (I)</b>	<b>Wild</b>	?	G: 12.8 I: 8.7 (Salmi <i>et al.</i> , 2013)	G: 29.4 I: 2.3–2 (Arcadi, 2000; new data <sup>#1</sup> )	G: 23.3 (new data <sup>#2</sup> )
	<b>Captivity</b>	G: 0.7–1.9 I: 0–5.3 (new data <sup>#3</sup> )	G: 65 (Lemasson <i>et al.</i> , 2018)	G: 22.8 I: 0.15–0.8 (Pougnault <i>et al.</i> , in press)	G: 4.8–8.4 (De Waal, 1988; Levréro <i>et al.</i> , 2019)
<b>Percentage of calls uttered in vocal interaction</b>	<b>Wild</b>	?	?	19% (new data <sup>#1</sup> )	53 % (Cornec <i>et al.</i> , in press)
	<b>Captivity</b>	0% (new data <sup>#3</sup> )	38% (Lemasson <i>et al.</i> , 2018)	16% (Pougnault <i>et al.</i> , in press)	74% (Levréro <i>et al.</i> , 2019)

<b>Main call type used during vocal interactions</b>			None (new data <sup>#3</sup> )	Grunts (turn-taking) (Harcourt & Stewart, 1996; Hedwig <i>et al.</i> , 2015a,b)	Pant-hoots (overlap) (Mitani & Nishida, 1993; Mitani & Brandt, 1994; Gros-Louis & Mitani, 1998; Fedurek <i>et al.</i> , 2013a,b, 2014; new data <sup>#1</sup> )	Hooting and barks (overlap); peeps (turn-taking) (De Waal, 1988; Hohmann & Fruth, 1994; Bermejo & Omedes, 1999)
<b>Mean number of interacting partners</b>			0 (new data <sup>#3</sup> )	2.4±0.06 (Lemasson <i>et al.</i> , 2018)	0.34±0.7 (new data <sup>#1</sup> )	2.2±0.5 (Levréro <i>et al.</i> , 2019)
<b>Outside vocal interactions</b>	<b>Percentage of isolated calls</b>	<b>Wild</b>	?	?	11% (new data <sup>#1</sup> )	52% (Cornec <i>et al.</i> , in press)
		<b>Captive</b>	11–50% (new data <sup>#3</sup> )	15% (calculated from Lemasson <i>et al.</i> , 2018)	14% (calculated from Pougnauld thesis's data, 2020)	14% (calculated from Pougnauld thesis's data, 2020)
	<b>Percentage of repeated calls</b>	<b>Wild</b>	?	?	89% (new data <sup>#1</sup> )	48% (Cornec <i>et al.</i> , in press)
		<b>Captive</b>	89–50% (new data <sup>#3</sup> )	85% (calculated from Lemasson <i>et al.</i> , 2018)	86% (calculated from Pougnauld thesis's data, 2020)	31% (calculated from Pougnauld thesis's data, 2020)
<b>Within vocal interactions</b>	<b>Percentage of calls in overlap</b>	<b>Wild</b>	?	?	53% (new data <sup>#1</sup> )	6% (Cornec <i>et al.</i> , in press)
		<b>Captive</b>	0% (new data <sup>#3</sup> )	27.5% (Lemasson <i>et al.</i> , 2018)	63% (calculated from Pougnauld thesis's data, 2020)	33% (Levréro <i>et al.</i> , 2019)
	<b>Temporal organisation of overlap</b>		None (new data <sup>#3</sup> )	?	♂♂ adjust constituent phrases to promote chorusing (Fedurek <i>et al.</i> , 2013b)	Perfect synchronisation/alternation of <i>high-hoot</i> vocalisation (De Waal, 1988; Hohmann & Fruth, 1994)

	<b>Social organisation of overlap</b>	None (new data <sup>#3</sup> )	?	Interlocutors are mainly adult ♂♂ with affiliative bonds (Fedurek <i>et al.</i> , 2013a)	Interlocutors can be ♂ or ♀ with strong affiliative bonds (Hohmann & Fruth, 1994)	
	<b>Percentage of calls in turn-taking</b>	<b>Wild</b>	?	?	47% (new data <sup>#1</sup> )	94% (Cornec <i>et al.</i> , in press)
		<b>Captive</b>	0% (new data <sup>#3</sup> )	72.5% (Lemasson <i>et al.</i> , 2018)	37% (Pougnault <i>et al.</i> , in press)	67% (Levréro <i>et al.</i> , 2019)
	<b>Temporal organisation of turn-taking</b>	None (new data <sup>#3</sup> )	Maximum inter-call delay of 3 s (mean 0.5 s) (Lemasson <i>et al.</i> , 2018)	Maximum inter-call delay of 1.5 s (mean 0.5 s) (Pougnault <i>et al.</i> , in press; new data <sup>#1</sup> )	Maximum inter-call delay of 2.5 s (mean 0.4 s) (Levréro <i>et al.</i> , 2019)	
	<b>Playback experiment confirmation of turn-taking</b>	?	Yes (Pougnault <i>et al.</i> , 2020b)	?	Yes (Levréro <i>et al.</i> , 2017)	
	<b>Social organisation of turn-taking</b>	None (new data <sup>#3</sup> )	High rate of interactions between the dominant adult ♂ and adult ♀♀, and low rate of interactions between ♀♀ (Lemasson <i>et al.</i> , 2018; Pougnault <i>et al.</i> , 2020b)	None (Arcadi, 2000; Pougnault <i>et al.</i> , in press)	Adults of both sexes (66%) and sub-adults ♂ (37%) (Cornec <i>et al.</i> , in press)  Interlocutors with strong affiliative social bonds (Levréro <i>et al.</i> , 2019)	

?: no information available.

Definitions of calling patterns (Pougnault *et al.*, 2020a): **isolated calls** occur when one call is emitted in isolation with no other calls in close proximity; **repeated calls** occur when the same individual calls several times in a row; **calls in overlap** involve partial (or total) superposition of calls from two or more callers; **calls in turn-taking** involve an orderly exchange of vocalisations between individuals, adjusting the timing of their vocal responses by including a minimum silence gap (preventing call overlap), and a maximum silence gap (ensuring call coordination).

New data: #1 for wild chimpanzees, Budongo Forest Reserve, Uganda, details of these unpublished data are given as online Supporting Information in Appendix S1, N=1 wild chimpanzee group including 35 identified individuals; #2 for wild bonobos, Nkala forest in Bolobo Territory, Democratic Republic of Congo, see Appendix S2, N=1 wild bonobo group including 19 identified individuals; #3 for orang-utans, ZooParc de Beauval (France) and Ouweland Dierenpark (Netherlands), see Appendix S3, N=2 captive orang-utan groups including 8 identified individuals in each zoo.

