

The function of chimpanzee greeting calls is modulated by their acoustic variation

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Abstract

Signalling plays an important role in mediating social interactions in many animal species. For example, during approaches certain species produce “greetings”, which can take the form of vocal or visual signals, which reduce the probability of aggressive interactions and/or facilitate affiliation when approaching each other. However, in species where greetings are comprised of both vocal and visual signals, little is known about how the vocal component relates to the visual component, or, in species with fission-fusion dynamics, to the time spent together by the dyad in the same subgroup prior to the approach. Similarly, in species with several acoustic variants of greeting calls, it is unclear whether different variants have different functions. We looked at the production of two acoustically distinct greeting call variants, low-fundamental frequency pant grunts and high-fundamental frequency pant barks, during approaches between two individuals in five communities of wild chimpanzees (*Pan troglodytes*) in Uganda and Ivory Coast. More specifically, we explored the relationship between greeting call production and i) aggressive and submissive interactions during the approach ii) preceding and subsequent proximity levels between the involved individuals. Calls were more likely to be produced during aggressive interactions and were associated with postures and gestures linked to submission; these patterns were stronger when the utterance contained a pant bark rather than a pant grunt alone. The production of greeting calls was more likely soon after party fusion and was negatively related to subsequent proximity levels between the caller and receiver. These results expand our knowledge of greeting calls and imply that these calls might be used to re-establish dominance relationships after a period of separation, and that the function of these calls can be modulated by their specific acoustic variants and by visual signals that often accompany them.

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53 **Key words:** call production, fission-fusion, greetings, multimodal signalling, *Pan*
54 *troglydytes*

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56 **Introduction**

57 A universal function of animal signalling is facilitating the predictability of the
58 signaller's subsequent behaviour, which in turn reduces the probability of aggression
59 or/and facilitates affiliative interactions (Andersson, 1994; Smith, 1977). These
60 signals are particularly important where individuals approach each other, as close
61 proximity between individuals increases the risk of physical aggression (Nieburg,
62 1970). "Greetings" – non-aggressive signals specifically employed when approaching
63 or being approached by another individual – are an example of signals that function in
64 this way (Aureli & Schaffner, 2007; Dal Pesco & Fischer, 2020; De Waal & van
65 Roosmalen, 1979).

66

67 Greetings have been observed in a wide variety of animals including mammalian and
68 avian species (Brown, 1967; Schenkel, 1967). These typically highly ritualised
69 behaviours usually involve visual or tactile signals and are linked to several functions.
70 For example, the 'facing away' posture performed by a female when approaching a
71 male facilitates courtship in the lesser black-backed gull (*Larus fuscus*) (Brown,
72 1967). Genital manipulation in spotted hyenas (*Crocuta crocuta*) signals dominance
73 status (East, Hofer, & Wickler, 1993). Embraces and touches reduce tension during
74 stressful events in spider monkeys (*Ateles geoffroyi*) and mantled howler monkeys
75 (*Alouatta palliata*) (Aureli & Schaffner, 2007; Dias, Rodriguez Luna, & Canales
76 Espinosa, 2008). 'Rally' greetings that include sneezing promote communal hunting

in wild dogs (*Lycaon pictus*) (Creel & Creel, 1995; Walker, King, McNutt, & Jordan, 2017). Elaborated greetings involving postural and tactile signals in some baboon (*Papio sp.*) and macaque (*Macaca sp.*) species assess the strength of social relationships and facilitate group cohesion and cooperation (Dal Pesco & Fischer, 2020; De Marco, Sanna, Cozzolino, & Thierry, 2014; Smuts & Watanabe, 1990; Whitham & Maestripieri, 2003).

If greetings involve vocal signals, these are termed “greeting calls” (Laporte & Zuberbühler, 2010; Scheumann, Linn, & Zimmermann, 2017). Greeting calls have been investigated primarily in primates. Primate species are usually highly social and individuals in several species produce calls when approaching each other at a close distance. However, the specific function of these calls may differ depending on the species. Chacma (*Papio ursinus*) and Guinea baboons (*Papio papio*), for example, produce low-pitched grunts when approaching another individual to initiate grooming or infant handling (Cheney, Seyfarth, & Silk, 1995; Faraut, Siviter, Dal Pesco, & Fischer, 2019; Silk, Seyfarth, & Cheney, 2016). Sooty mangabeys (*Cercocebus atys*) produce grunts and twitters prior to affiliative interactions such as grooming or hugging (Range & Fischer, 2004). Vervet monkeys also give low-amplitude grunts when approaching other individuals in affiliative contexts (Cheney & Seyfarth, 1992; Mercier et al., 2017; Struhsaker, 1967).

In some species greetings comprise both visual and acoustic signalling, and variation in these signal combinations might modulate their function. Indeed, in capuchin monkeys, embrace greetings that are accompanied by screams reflect stronger affiliative relationships than silent embraces (Lynch Alfaro, 2008). The addition of

‘landing calls’ to greeting postures by females of the lesser black-backed gull depends on courtship status (Brown, 1967). Whether or not vocalisations are involved in baboon greetings seems to depend on their function and the species (Dal Pesco & Fischer, 2018; Dal Pesco & Fischer, 2020). Nonetheless, the relationship between the vocal and gestural component of greetings and its relevance to their function remains largely unexplored for most species. Furthermore, in species that produce several acoustic variants of greeting calls, little is known about how particular variants relate to visual signalling. It is also unclear whether and how the time spent apart by the signaller and the receiver prior to the approach modulates the production of greetings. A considerable number of animal species are characterised by at least some degree of fission-fusion dynamics (Aureli et al., 2008). In such species, and particularly in those at a higher level on the fission-fusion spectrum such as chimpanzees, greetings might have an important function of re-establishing relationships between individuals upon reunion and therefore might be especially elaborated. This hypothesis, however, has not been tested yet.

Chimpanzees commonly produce specific calls associated with greeting interactions and these calls are given predominantly towards higher-ranking individuals (Goodall, 1986; Laporte & Zuberbühler, 2010; Luef & Pika, 2017). Therefore, it has been proposed that these calls function to signal submission in order to avoid aggression (Bygott, 1979; Fedurek et al., 2019; Wittig & Boesch, 2003). To our knowledge, however, there have been no systematic studies investigating in detail the relationship between greeting call production and aggressive or submissive interactions, or separation time prior to approach, between two individuals. Chimpanzee greeting calls are acoustically very distinct and context-specific, i.e. used when approaching or

being approached by another individual (Fedurek et al., 2019). At the same time, however, greeting calls in chimpanzees have distinct acoustic variants, such as low-fundamental frequency grunts, which are frequently emitted in sequences joined by voiced inhalations, or pants (hereafter pant grunts (Fig. 1a)) and high-fundamental frequency barks, which are also frequently emitted in sequences joined by voiced inhalations, or pants (hereafter pant barks (Goodall, 1986) (Fig. 1b)). These acoustic variants may provide flexibility in moderating social interactions; however, how these variants relate to interactions between the caller and receiver remains unknown.

Since chimpanzee greeting calls are usually given within sight of the receiver, they are likely to be associated with visual signalling. Using several modalities of communication concurrently, such as acoustic and visual signalling, is an effective way of communicating under certain conditions (Partan & Marler, 2005). We should expect that increased signalling effort, including multi-modal signalling, is particularly common during potentially risky situations involving close proximity between individuals, such as when approaching a dominant individual, to prevent receiving aggression. These risks may particularly apply to chimpanzees, where dominant individuals often direct unprovoked aggression towards lower-ranking individuals (Muller, 2002). Indeed, in this species, individuals often use specific postures and gestures when signalling submission towards higher-ranking individuals (e.g. crouching, extended hand), and such signals are commonly employed when individuals approach each other (Hobaiter & Byrne, 2011; Luef & Pika, 2017). However, the association between greeting calls, or their particular acoustic variants, and visual signals has not yet been explored in detail in chimpanzees, or other animal

species, and is required to establish the specific function of these different signal forms.

The aim of this study was to explore the relationship between chimpanzee greeting calls and both aggressive and submissive behaviours between two individuals during approaches (i.e. situations where one individual approaches another at a close distance), as well as previous and subsequent spatial proximity levels between them, in five communities from two populations and subspecies of wild chimpanzees in Uganda (*P. t. schweinfurthii*) and Ivory Coast (*P. t. verus*).

First, we investigated whether the production of pant grunts – the low pitched and more commonly produced variant of greeting calls, was related to the presence of aggressive behaviour (i.e. when one of the individuals behaved aggressively at the time of the approach), and visual signals such as postures or gestures linked to submission, during an approach. We predicted that pant grunts would be positively associated with both aggression and postural or gestural signalling. Second, we directly compared pant grunt only greeting variants with greeting variants that contained pant barks to evaluate the relative importance of aggression and visual signalling in the production of these two call variants. Since pant barks are higher-pitched and higher-amplitude calls than pant grunts, they probably reflect a higher motivation to signal submission than pant grunts (Owings & Morton, 1998). Accordingly, we predicted that pant barks would be more strongly associated with submissive gestures and postures, as well as with aggressive contexts, when compared to pant grunts.

176 Third, we also explored whether the production of these calls was associated with
177 subsequent tolerance by examining the proximity level between two individuals after
178 the approach. Post-greeting proximity is an aspect of particular interest as it has been
179 shown in some primate species, such as baboons, that calls produced during
180 approaches function to facilitate proximity and affiliative interactions (Silk et al.,
181 2016; Silk, Seyfarth, Stadele, & Strum, 2018). If chimpanzee greeting calls are
182 affiliative signals that facilitate proximity, we would expect that after producing these
183 calls, the producer and receiver are more likely to be in close proximity than after
184 silent approaches. This hypothesis, however, has not yet been tested in chimpanzees,
185 and so we did not form specific predictions about the impact of greetings on
186 proximity.

187
188 As chimpanzees live in complex societies with a high degree of fission-fusion
189 dynamics, where individuals form temporary subgroups or parties, and reunions
190 between parties are often associated with aggression (Aureli et al., 2008; Muller,
191 2002; Nishida, Kano, Goodall, McGrew, & Nakamura, 1999), producing these
192 apparently aggression-alleviating calls, particularly shortly after party fusion, should
193 be adaptive. Accordingly, we predicted that the probability of calling would be
194 negatively related to the time between party reunion and approach. If this were the
195 case, it would suggest that greeting calls function to reassess or re-establish
196 dominance relationships between the producer and recipient of the signal after a
197 period of separation – a hypothesis that, to our knowledge, has not yet been tested on
198 animal greetings.

200 **Methods**

201 Study sites and study subjects

202 To examine the universality of the investigated patterns of greeting signals in
203 chimpanzees, we included data from several communities of chimpanzees from the
204 two geographically most separated subspecies of chimpanzees: *P.t. verus* in Taï
205 National Park, Ivory Coast, and *P.t. schweinfurthii* in Budongo Forest, Uganda. In
206 Budongo, data were collected on the Waibira (January 2017 - January 2018) and
207 Sonso (January 2018 - November 2018) communities of Eastern chimpanzees (*Pan*
208 *trogodytes schweinfurthii*). The Sonso group is fully habituated to human presence
209 (Reynolds, 2005) and at the time of the study community contained 75 individuals.
210 Habituation of the Waibira community started in 2011 and, during the study,
211 comprised 95 named individuals with all the community members identifiable at the
212 time of the study and the with majority of individuals habituated to human presence
213 (Samuni, Mundry, Terkel, Zuberbühler, & Hobaiter, 2014).

214 In Taï, data were collected on the East, North and South communities of Western
215 chimpanzees (*Pan troglodytes verus*) between December 2016 and June 2018. During
216 the study period, the East, North and South communities consisted of 32-34, 19-20,
217 and 41-42 individuals respectively. All communities in Taï are fully habituated to
218 human presence, regular observations of the North community commenced in 1982,
219 South community in 1993 and East in 2000 (Boesch & Boesch-Achermann, 2000;
220 Wittig, 2018).

221 Study subjects were adult and late adolescent males ($N=50:\geq 13$ years; (Goodall,
222 1986)) and females ($N=65:\geq 11$ years) (see Table A1 for the number of subject
223 individuals per age-sex category and community).

224 Ethical note

225 The study was approved by the Uganda Wildlife Authority and the Uganda National
226 Council for Science and Technology in Uganda, and the Ministère de l'Enseignement
227 supérieur et de la Recherche Scientifique, the Ministère des Eaux et Forêts, and the
228 Office Ivoirien des Parcs et Réserves in Côte d'Ivoire.

229 Data collection

230 A randomly chosen individual was followed for half a day (up to five hours). In total,
231 3086 hours of observation were used in the study (see Table A1 for more details on
232 observation time per community and per focal animal). Rotating focal samples evenly
233 is challenging with wild chimpanzees as not all individuals are equally available at the
234 same time. However, to the best of our capacities, we aimed not to sample the same
235 individual twice during the same day, and to have samples from individuals collected
236 during both morning and afternoon periods. *Approaches* were defined as events
237 where the focal individual approached, or was approached by, another individual
238 (hereafter: *partner*) to within a distance of 10m – a distance within which these calls
239 are typically produced perhaps because being within this distance of another
240 individual makes them vulnerable to receiving aggression (e.g. Fedurek et al., 2019;
241 Laporte & Zuberbühler, 2010).

242

243 During an approach, we noted whether or not the focal animal or the partner produced
244 greeting calls. We distinguished two acoustic variants of greeting calls: pant grunts
245 and pant barks. These variants of greeting calls grade from one to another (Marler &
246 Tenaza, 1977). However, these two calls have distinguishable acoustic characteristics
247 (Goodall, 1986). Pant grunts are sequences of low-pitched grunts that systematically

alternate with voiced, inhaled elements usually of similar pitch (Goodall, 1986; Marler & Tenaza, 1977). Pant barks are sequences of high-pitched barks that systematically alternate with voiced, inhaled elements usually of lower pitch. The bark elements are more tonal, louder, and have higher amplitude than pant grunts, and on spectrograms, bark elements have dome-shaped fundamental frequency compared with grunt element, which have a relatively flat fundamental frequency and a noisy spectral quality (Crockford & Boesch, 2005; Goodall, 1986) (Fig. 1a, b; see supplementary material Audio S1 and Audio S2 for examples of recordings). Where combinations of different call variants were emitted in the same greeting, that is, pant grunts and pant barks (Fig. 1c; see Audio S3 and Audio S4 for examples of recordings), the call was coded as the loudest call variant, i.e. pant bark (e.g. Fedurek & Slocombe, 2013).

We noted whether or not an approach occurred in an aggressive context, i.e. whether either of the two individuals involved in an approach behaved aggressively towards each other during the approach ($N=208$ of 2267 approaches). We defined aggressive behaviour as a physical assault (e.g. hitting, pulling, biting) or non-contact aggression (such as chasing, charging, directed charging displays, or threats (Fedurek, Slocombe, & Zuberbühler, 2015)).

We also noted whether during an approach any of the partners produced visual signals linked to submission ($N=564$ of 2267), including postures or gestures, during an approach: crouching, bowing, arm-reaching, reach-touching, presenting, kissing, genital touching. These behaviours or visual signals are often associated with submission (Goodall, 1986; Hobaiter & Byrne, 2011).

273

274 Every 10 min, we noted the identities of individuals that were within 5m of the focal
275 individual.

276

277 We noted the time of the focal animal joining another party, as well as the time of any
278 individual joining the party of the focal animal. “Party” was defined as all individuals
279 present within a visual range of the focal individual, typically 35m (Newton-Fisher,
280 1999).

281

282 Dominance distance

283 Data on dominance relationships were based on the production of greeting calls - a
284 behaviour that accurately reflects dominance relationships (Bygott, 1979). To ensure
285 that these data were independent from the data on greeting calls collected during
286 approaches used in this study, for dominance calculations, we used a separate dataset
287 on greeting calls collected during the same time period per site, between 2014 and
288 2018 by field assistants of the Budongo Conservation Field Station and the Tai
289 Chimpanzee Project, and researchers associated with these field sites. Dominance
290 status was calculated using the Elo rating procedure (Albers & Vries, 2001; Neumann
291 et al., 2011; see Fedurek et al., 2015 for details). Rank difference between two
292 partners was calculated by deducting the Elo rating of the focal animal from the Elo
293 rating of the approach partner.

294

295 Inter-observer reliability data

296 Inter-observer reliability tests were conducted between individuals involved in data
297 collection to ensure that the data were collected in systematic and consistent ways. In

298 Budongo, data were collected by one of the authors and one field assistant. In Tai,
299 data were collected by one of the authors and three research assistants. Inter-observer
300 reliability tests using intra-class coefficient tests (ICC; (Shrout & Fleiss, 1979)) were
301 initially conducted between the two authors at Budongo and Tai, with the frequency
302 and duration of variables recorded by each significantly correlated ($ICC > 0.80$).
303 Research assistants started collecting behavioural data only once they had recorded
304 two consecutive tests with variables significantly correlated with those recorded by
305 the authors ($ICC > 0.80$).

306

307 Statistical analysis

308 Generalized linear mixed-effect models (GLMM) were used in statistical analyses
309 (Bolker et al., 2009). In all our analyses, one data point represented a dyadic
310 interaction comprising the focal animal and the approach partner. The first model,
311 hereafter the “pant grunt - behaviour model”, examined the relationship between pant
312 grunting and behaviour between two individuals during an approach ($N=1959$). Using
313 a binomial error structure, we put as the dependent variable whether or not (0/1) a
314 pant grunt utterance (with no pant barks) was produced during an approach. Our
315 predictor variables were: whether or not any of the two individuals behaved
316 aggressively (0/1) or produced visual signals such as postures or gestures linked to
317 submission (0/1) during the approach; latency (minutes) between party fusion
318 between two individuals and the approach; and whether or not (0/1) the focal animal
319 and the approach partner were within 5m of each other during the next 10 min scan.
320 In addition, we included the several control variables. We included the sex category
321 of the approach partners, coded at three levels (male-male ($N=448$), male-female
322 ($N=1546$), and female-female ($N=65$)), and Elo rating dominance difference between

two partners, since these factors may be associated with greeting call production (Fedurek et al., 2019). The five study communities differ considerably in terms of, for example, sex ratios and the number of individuals comprising them - demographic features that might affect the probability of greeting call production. Therefore, we included the identity of the community as another control variable.

To directly compare between approaches with pant grunts and approaches which included pant barks in terms of the above factors, we created another GLMM with a binomial error structure ($N=1067$) with the independent variables used in the previous model and with the variant of greeting call (0-pant grunt only utterance, 1-utterance containing pant barks) as the dependent variable, hereafter called the “call variant - behaviour model”. In contrast to the previous model, however, we differentiated between whether the caller or the recipient exhibited aggressive behaviour and visual (gesturing and posturing) signalling, resulting in four (rather than two) variables related to these two behaviours. This procedure, which was not possible for the pant grunt-behaviour model due to the inclusion in this model of data from approaches with no calls, allowed us to establish whether it was the caller or the recipient that behaved aggressively or submissively. Also in contrast to the “pant grunt-behaviour” model, the variable “Elo rating dominance difference” included the directionality of this difference (rather than only the difference) between the caller and the recipient (which, again, was not possible for the pant grunt-behaviour model due to the model also containing data from silent approaches).

Since, as with greeting calls (Fedurek et al., 2019), the production of both visual signalling (linked to submissive behaviour) and aggressive interactions between two

individuals can be related to dominance distance between them (i.e. the larger the dominance distance between two individuals, the higher the probability of producing these behaviours), in the pant grunt-behaviour model we also included interactions between dominance distance and both visual signalling and aggressive behaviour. In addition, since subsequent proximity levels between two individuals after an approach could depend on whether or not there was an aggressive interaction between them during the approach, we included an interaction between aggression and proximity during the next ten-minute scan in the pant grunt-behaviour model, and an interaction between aggression by the recipient of call and proximity during the next ten-minute scan in the call variant-behaviour model.

There was no collinearity between the examined independent variables (variance inflation factors of the independent variables were below the value of 1.5). The values of all quantitative variables were z transformed into a mean of 0 and standard deviation of 1. We used a likelihood ratio test (LRT) to test the full model against a null model (comprising the intercept, random effects, and control independent variables (sex type, community, and Elo rating difference). To test the significance of individual independent variables, we used the drop1 function from the 'lme4' R package (Barr, Levy, Scheepers, & Tily, 2013; Forstmeier & Schielzeth, 2011).

We first ran the two models with the interactions described above and then reran them without interactions if these interactions were not significant. In both models, we put the identity of the focal individual, the identity of the partner, and the identity of the dyad as random effects. Since many interactions occurred during the same day, we also included date as an additional random effect. In addition, to reduce type I error

rate and to account for potential non-uniform variation of our predictor variables within the random effects (Barr et al., 2013), we included a maximal random slope structure, incorporating random slopes for the variable ‘latency between party fusion and the approach’, sex type, and Elo rating dominance difference within focal identity and partner identity, and ‘latency between party fusion and the approach’ and Elo rating dominance difference within date (Barr et al., 2013; Forstmeier & Schielzeth, 2011).

All statistical analyses were conducted using R, version 3.3.0 and the lme4 package, version 1.1-17 (Bates, Maechler, & Bolker, 2012; R Core Team, 2014).

Results

In total, we collected data on 2267 approaches (See Table A1 for the number of approaches per community). Greeting calls were produced during 1067 approaches (47.07%). Utterances with pant grunts only were produced during 759 approaches while utterances containing pant barks during 308 approaches (Fig. 2a).

For both models, the full model was significantly different from the null model (pant grunt - behaviour model: LRT: $\chi^2=280.53_{(31)}$, $P<0.001$; call variant - behaviour model: LRT: $\chi^2=175.11_{(36)}$, $P<0.001$).

Pant grunts were produced in all three types of sex-class dyads, but were more likely in mixed-sex dyads than during male-male and particularly female-female approaches (Fig. 2b, Table 1). The production of utterances with pant barks relative to that of pant grunts only was not related to the sex-class of dyads (Table 2). During mixed-sex

approaches in which greeting calls were produced, females emitted calls to males in 99.13% (799 of 806) of cases.

Greeting calls, aggressive behaviour, and submission-related visual signals

Greeting calls, and particularly those including pant barks, were associated with both aggressive contexts (Fig. 2c, 2d, 2a, 3a) and visual signalling (Fig. 2e, 2f, 3b, 4b, Table 1, 2). Aggressive behaviour was predominantly exhibited by the recipient of the call, and gestures and postures by the caller (Table 2). The larger the dominance distance between two individuals was, the higher was the probability of producing a greeting call, and a pant bark in particular (Table 1, 2).

The interactions between dominance distance and visual signalling or aggressive behaviour did not predict the production of pant grunts ($P=0.329$ and 0.311 , respectively), suggesting that the production of greeting calls related to aggression and visual signalling independently from dominance distance.

Greeting calls and proximity levels

The production of greeting calls, and particularly those containing pant barks, was negatively related to the time between party reunion and approach: the sooner the approach after party reunion between two individuals, the more likely the production of greeting calls containing pant barks (Fig. 3c, 4d, Table 1, 2). There was no relationship between the production of pant grunts (Table 1) and the probability with which the two involved individuals were recorded within 5m of each other within the next ten-minute scan. However, when compared directly by the call variant-behaviour model, two individuals were less likely to be within 5m during the next ten-minute

scan after producing utterances with pant barks than after producing pant grunts only (Fig. 4c, Table 2). The interaction between aggression and subsequent proximity between two individuals was not significant (pant grunt-behaviour model: $P=0.176$, call variant-behaviour model: $P=0.593$), suggesting that calls related to subsequent proximity independently from their relationship to aggression.

Discussion

The results of our study show that the production of greeting calls whilst approaching or being approached by a dominant individual was positively associated with visual signals linked to submission and was more likely in aggressive contexts. Individuals were more likely to produce a greeting call shortly after a reunion between two parties. The production of greeting calls was related positively to the dominance distance between two individuals. These patterns were stronger when the utterance contained a pant bark rather than only a pant grunt. In addition, utterances containing pant barks were negatively related to the probability of being spatially close to each other shortly after the approach.

As predicted, the production of greeting calls was negatively associated with the time between party reunion and approach, with greeting calls being more often produced shortly after party reunions between two individuals. A likely reason for this is that reunions between parties in chimpanzees often involve threats or aggression (Muller, 2002; Nishida et al., 1999). Therefore, submissive signals, such as greeting calls, might ultimately reduce the probability of receiving aggression, or the severity of aggression, during these potentially risky events. This vocal approach to mitigating risk may particularly apply to pant barks, since these calls were more likely to be

produced than pant grunts shortly after party fusion. Periods of separation between individuals in chimpanzee communities can range from hours to months, therefore, greeting calls produced upon party reunions might also function to re-establish dominance relationships after a period of separation.

Producing greeting signals shortly after reunions is also common in other species that form societies with high fission-fusion dynamics (Aureli et al., 2008). In spider monkeys (*Ateles geoffroyi*), for example, embraces during reunions are common and apparently reduce tension and inhibit aggression during these events (Aureli & Schaffner, 2007). A similar function has been attributed to human greeting rituals such as verbal greetings or handshakes (Firth, 1972). Vocal greetings also facilitate reunions after separation between mother and infant in grey mouse lemurs, a species where mothers park their infants in tree holes or dense vegetation while foraging (Scheumann et al., 2017). In species with unstable grouping patterns, therefore, greeting signals probably alleviate aggression upon reunion or/and are involved in testing or re-establishing dominance or affiliative relationships after separation. This use of greetings to manage risk may particularly apply to species at the upper end of the fission-fusion spectrum, including humans (Aureli et al., 2008), where there may be a higher selection pressure to communicate additional information during reunions, and therefore a need for greater sophistication or nuance in greeting signals, than in species with more stable societies – a hypothesis that needs to be tested by future studies.

Greeting calls were not associated with close proximity between two individuals following an approach, suggesting that greeting calls in chimpanzees are unlikely to

promote tolerance and subsequent friendly interactions. Furthermore, after producing utterances with pant barks individuals were less likely to subsequently maintain close proximity than after pant grunting, and this pattern was independent of any aggression that occurred during the approach. Since pant barking is associated with an increased subsequent spatial distance between the signaller and recipient, it might also reduce the probability of future aggression – a possibility that should be explored in the future. Alternatively, pant barks might be employed within dyads with insecure relationships, and therefore less predictable interactions, in a similar way as grunts in baboons (Silk et al., 2016). The subsequent greater distance between the producer and recipient of pant barks might then be a strategy by the former to minimize the probability of receiving aggression from the latter. Since these calls are not associated with subsequent close proximity between two partners, our findings are consistent with a recent study suggesting that these calls do not reflect affiliation between individuals (Fedurek et al., 2019). Considering, however, that chimpanzees produce shorter pant grunt sequences when approaching bonded individuals than when approaching less closely affiliated ones (Luef & Pika, 2019), more studies are needed to investigate the relationship between greeting calls and social bonds in chimpanzees.

During an approach between two individuals, greeting calls were associated with visual signals, specifically postures and gestures typically linked to submission (such as extended hand or bowing (Hobaiter & Byrne, 2011)). This is an example of multimodal communication where more than one modality is used when signalling – a common occurrence in animals (Hebets & Papaj, 2005; Rowe, 1999) including chimpanzees and other primates (Hobaiter, Byrne, & Zuberbühler, 2017; Liebal,

498 Waller, Slocombe, & Burrows, 2013; Luef & Pika, 2017; Wilke et al., 2017). Using
499 several modes of communication concurrently is an effective communicative strategy
500 – with the ‘back up’ hypothesis proposing that by signalling specific information
501 using two or more modalities, the signal is less likely to be missed or misinterpreted
502 (Partan & Marler, 2005; Uetz, Roberts, & Taylor, 2009). Our results show that the
503 high-frequency and high-amplitude pant barks were more likely to be associated with
504 visual signalling than the lower-frequency pant grunts. Utterances with pant barks
505 were also more likely than utterances with pant grunts only to be produced in
506 aggressive contexts. Pant barks arguably require more energy to produce than pant
507 grunts because they involve calling at higher frequencies and amplitude (e.g. Fedurek
508 et al., 2016; Fedurek, Zuberbühler, & Semple, 2017), and therefore, should be
509 produced in more urgent situations than pant grunts. It appears that, at least for some
510 call types, the stronger the motivation or effort to produce a signal from a given
511 modality of communication (e.g. a submissive call), the higher the probability that it
512 will be accompanied by a signal involving another modality (e.g. a gesture). This
513 interpretation is consistent with a study on capuchins monkeys showing that the
514 scream component of greeting embraces produced by males, which apparently signals
515 the strength of affiliative bonds between them, is more often produced during
516 greetings with close social partners rather than with less affiliated individuals (Lynch
517 Alfaro, 2008). A similar interpretation could be applied to the observation that
518 females of the lesser black-backed gull gradually add the call component to their
519 greeting displays as courtship progresses (Brown, 1967). While one previous study
520 showed that in chimpanzees particular call variants are associated with specific visual
521 signals (Luef & Pika, 2017), future studies should explore this relationship in more
522 detail, for example by looking at how the production of such specific signals (e.g.

extended hand or crouching) during calling relate to dominance relationships between two individuals. Future studies should also explore the relationship between greeting calls, or their variants, and aggression over longer timescales. For example, it would be interesting to examine whether the production of greeting calls reduces the likelihood of receiving aggression later on that day, or whether receiving aggression increases the probability of producing these calls during a subsequent encounter with the aggressor.

Our results show that the larger the dominance distance between two individuals, the higher the probability of producing utterances with pant barks as opposed to pant grunts only. In chimpanzees, the likelihood of aggression is positively linked to dominance distance (Muller & Mitani, 2005). It appears that pant barks reflect a higher motivation to signal submission than pant grunts, a view also supported by the finding that utterances with pant barks were more likely than pant grunts only to be produced in aggressive contexts and with submissive visual signals. The function of greeting calls in chimpanzees seems to be mediated by their acoustic structure, with pant barks being more likely to be produced as risk of aggression increases, and being a stronger predictor of dominance relationships between two individuals, than pant grunts. In this respect, our results are consistent with a recent study on chimpanzee greeting calls showing that these calls, and particularly sequences comprising pant barks, correlate positively with dominance distance between two individuals (Luef & Pika, 2019). Sequences including pant barks (which typically graded from pant grunts) likely reflect a stronger physical effort (compared to sequences comprising only pant grunts) by the signaller to produce the signal (Titze, 1989; Titze & Riede, 2010). On a proximate level, that effort could be mediated by an elevated arousal

level, which may explain why the production of pant barks is mediated by dominance distance between two individuals (Luef & Pika, 2019) and is associated more strongly with aggression. A promising research avenue would be investigating whether in other species that also produce several kinds of greeting calls, such as the grunts and twitters in sooty mangabeys (Fedurek et al., 2019), different calls have different functions.

Given that greetings often occur over short distances between the signaller and recipient, the visual component of chimpanzee greetings alone might be sufficient on these occasions to communicate submission. Nonetheless, vocal signals are also given during approaches, with the signaller often ceasing the production of greeting calls once physical contact with the aggressor has been established (Pers. observation). Thus, it is possible that the vocal component carries an additional function, to inform nearby individuals of the dominance relationship (e.g. Slocombe & Zuberbuhler, 2007). This extension of the audience might apply particularly to the high amplitude – louder – pant barks. For example, greeting calls might recruit support from bystanders (e.g. Fedurek et al., 2015), or reduce the probability of receiving aggression from them. Greeting calls might also advertise the dominance relationship between the producer and recipient of the signal to nearby individuals. The potential role of greeting calls in informing third-party individuals should be examined by future studies.

One potential limitation of our study is that in our analysis, sequences with pant barks also included sequences with pant grunts grading into pant barks. As the function of pant grunts and pant barks is not identical, we encourage future studies to differentiate

in their data collection and analyses those sequences comprising pant grunts, sequences comprising both pant grunts and pant barks, and sequences comprising only pant barks (e.g. Luef & Pika, 2019). It is possible, for example, that sequences comprising both call variants have a function that is intermediate between those comprising only pant grunts and those that include only pant barks. Such analysis would provide further insight into how the acoustic structure of greeting calls modulates their function.

The structural complexity of chimpanzee greetings, with the acoustic variation within the greeting call and several types of gestures and postures that accompany it, might reflect the complex nature of societies that these animals form. Chimpanzee societies, for example, are characterised by a dynamic fission-fusion structure as well as by networks of complex kin and non-kin social relationships between individuals (Aureli et al., 2008; Gilby & Wrangham, 2008; Muller & Mitani, 2005). It is thus possible that the elaborate communication system involved in chimpanzee greetings has evolved in response to the challenges associated with such complex societies (e.g. Crockford, Wittig, & Zuberbühler, 2017). Considering the evolutionary closeness of chimpanzees to humans and that there are considerable similarities between the societies of these two species (Muller, 2017), looking into chimpanzee communication has the potential to shed light on the evolution of human communication.

To conclude, our results suggest that greeting calls can function to re-assert existing dominance relationships after a period of separation and may ultimately reduce aggression between the signaller and recipient. Our study also shows that the above

processes can be moderated by the acoustic variants of calls. These results thus support the view that animal greetings can form a sophisticated signalling system, with the function of greeting calls modulated by their acoustic structure and involving signals from several different modalities.

Supplementary Material

Supplementary material associated with this article is available.

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Independent variable	Estimate ± SE	Z value	P value	95% confidence intervals
Intercept	0.74±0.55	1.35		-0.48 to 1.42
Male-female dyads	1.03±0.37	2.81	0.005	0.49 to 1.73
Male-male dyads	0.40±0.36	1.11	0.267	-0.35 to 1.12
Aggression (0/1)	2.05±0.34	6.09	<0.001	1.10 to 2.68
Visual signalling (0/1)	2.94±0.24	12.42	<0.001	2.41 to 3.44
Latency between fusion and approach	-0.18±0.09	-2.12	0.034	-0.34 to 0.01
Subsequent proximity	0.30±0.22	1.36	0.173	-0.07 to 0.79
Elo rating difference	1.00±0.14	6.87	<0.001	0.69 to 1.29
Community North	-0.23±0.44	-0.52	0.604	-1.01 to 0.61
Community Sonso	-0.19±0.46	-0.42	0.677	-1.23 to 0.70
Community South	-0.59±0.36	-1.62	0.106	-1.14 to 0.32
Community Waibira	-0.28±0.37	-0.74	0.459	-1.04 to 0.66

Tables

Table 1. The relationship between pant grunt production during approaches and test predictors (pant grunt-behaviour model).

Test variables are in bold. GLMM; dependent variable: pant grunt only utterance (0/1); random effects: focal animal ID, partner ID, dyad ID, date ID). Test variables are in bold.

Table 2. The relationship between greeting call variants (pant grunt only utterances or utterances with pant barks) emitted during approaches and test predictors (call variant-behaviour model).

Independent variable	Estimate \pm SE	Z value	P value	95% confidence intervals
Intercept	-3.31 \pm 0.83	-3.96		-4.38 to 0.17
Male-female dyads	1.27 \pm 0.80	1.58	0.113	-1.70 to 2.28
Male-male dyads	0.75 \pm 0.83	0.90	0.369	-2.87 to 2.31
Aggressor by caller	1.22 \pm2.02	0.61	0.543	-8.23 to 6.85
Aggressor by recipient	2.60\pm0.23	11.22	<0.001	1.72 to 3.12
Visual signalling by caller	1.18\pm0.19	6.19	<0.001	0.57 to 1.51
Visual signalling by recipient	0.53\pm0.28	1.92	0.055	-0.18 to 1.11
Latency between fusion and approach	-0.30\pm0.11	-2.75	0.006	-0.54 to -0.04
Subsequent proximity	-0.71\pm0.30	-2.33	0.020	-1.34 to 0.03
Elo rating difference	-0.73 \pm 0.16	-4.63	<0.001	-1.03 to -0.35
Community North	0.32 \pm 0.44	0.73	0.467	-0.83 to 1.46
Community Sonso	0.35 \pm 0.44	0.78	0.437	-0.98 to 1.56
Community South	-0.34 \pm 0.32	-1.05	0.292	-1.04 to 0.26
Community Waibira	0.49 \pm 0.43	1.04	0.299	-0.72 to 1.70

Test variables are in bold. GLMM; dependent variable: (0-pant grunt only utterance/1-utterance containing pant barks); random effects: focal animal ID, partner ID, dyad ID, date ID). Test variables are in bold.

Table A1. The number of study subjects per age and sex category, observation time, and the number of approaches per each community

Community	Budongo Sonso	Budongo Waibira	Taï East	Taï North	Taï South
Number of adult and late adolescent males	14	22	5	4	5
Number of adult and late adolescent females	18	16	9	7	15
Observation time (h)	329.87	567.56	610.60	546.64	1031.09
Observation time (h) per focal animal (Mean±SD)	10.31±5.94	14.93±10.74	46.97±9.02	49.69±1.82	51.55±7.24
Number of approaches	146	364	290	210	1257

Figure legends

Figure 1. Spectrographic representation of an utterance comprising (a) pant grunts, (b) pant barks, (c) both pant grunts and pant barks, given by an adult female.

Figure 2. (a) Percentage of approaches with pant grunt greeting calls, greeting calls containing pant barks, and no greeting calls. (b) Percentage of greeting calls given by male-female, male-male and female-female dyads. (c) Percentage of approaches in agonistic contexts that were associated with pant barks, pant grunts only, and no greeting calls. (d) Percentage of approaches in non-agonistic contexts that were associated with pant barks, pant grunts only, and no greeting calls. (e) Percentage of approaches with visual signalling that were associated with pant barks, pant grunts only, and no greeting calls. (f) Percentage of approaches with no visual signalling that were associated with pant barks, pant grunts only, and no greeting calls.

Figure 3: The likelihood of chimpanzees to emit pant grunts under varying social conditions, specifically: (a) aggression occurring during an approach, (b) co-occurrence of submission-related postures and gestures. (c) latency between party fusion and the approach between two individuals. Circles (figures a and b) and line (figure c) represent model estimates. Error bars represent standard error (figures a, b), shaded area represents 95% confidence intervals (figures c).

Figure 4: The likelihood of chimpanzees to emit greeting call variants depending on varying social conditions. (a) The relationship between the variant of greeting calls (0-pant grunt only utterance, 1-utterance containing pant barks) and aggression during an approach produced by the recipient of the call. Error bars represent standard error.

(b) The relationship between the variant of greeting calls and postural or gestural signalling produced by the caller. (c) The relationship between the variant of greeting calls and whether or not the two individuals were in close proximity during next scan. (d) The relationship between the variant of greeting calls and latency between party fusion and the approach between two individuals. Circles (figures a, b and c) and line (figure d) represent model estimates. Error bars represent standard error (figures a, b and c), shaded area represents 95% confidence intervals (figure d).