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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.

Key words: call production, fission-fusion, greetings, multimodal signalling, *Pan troglodytes*

Introduction

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

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

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

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

Methods

Study sites and study subjects

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

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

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

Ethical note

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

Data collection

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

During an approach, we noted whether or not the focal animal or the partner produced greeting calls. We distinguished two acoustic variants of greeting calls: pant grunts and pant barks. These variants of greeting calls grade from one to another (Marler & Tenaza, 1977). However, these two calls have distinguishable acoustic characteristics (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).

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

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

Dominance distance

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

Inter-observer reliability data

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

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

Statistical analysis

Generalized linear mixed-effect models (GLMM) were used in statistical analyses (Bolker et al., 2009). In all our analyses, one data point represented a dyadic interaction comprising the focal animal and the approach partner. The first model, hereafter the "pant grunt - behaviour model", examined the relationship between pant grunting and behaviour between two individuals during an approach (N=1959). Using a binomial error structure, we put as the dependent variable whether or not (0/1) a pant grunt utterance (with no pant barks) was produced during an approach. Our predictor variables were: whether or not any of the two individuals behaved aggressively (0/1) or produced visual signals such as postures or gestures linked to submission (0/1) during the approach; latency (minutes) between party fusion between two individuals and the approach; and whether or not (0/1) the focal animal and the approach partner were within 5m of each other during the next 10 min scan. In addition, we included the several control variables. We included the sex category of the approach partners, coded at three levels (male-male (N=448), male-female (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, Waller, Slocombe, & Burrows, 2013; Luef & Pika, 2017; Wilke et al., 2017). Using several modes of communication concurrently is an effective communicative strategy – with the 'back up' hypothesis proposing that by signalling specific information using two or more modalities, the signal is less likely to be missed or misinterpreted (Partan & Marler, 2005; Uetz, Roberts, & Taylor, 2009). Our results show that the high-frequency and high-amplitude pant barks were more likely to be associated with visual signalling than the lower-frequency pant grunts. Utterances with pant barks were also more likely than utterances with pant grunts only to be produced in aggressive contexts. Pant barks arguably require more energy to produce than pant grunts because they involve calling at higher frequencies and amplitude (e.g. Fedurek et al., 2016; Fedurek, Zuberbühler, & Semple, 2017), and therefore, should be produced in more urgent situations than pant grunts. It appears that, at least for some call types, the stronger the motivation or effort to produce a signal from a given modality of communication (e.g. a submissive call), the higher the probability that it will be accompanied by a signal involving another modality (e.g. a gesture). This interpretation is consistent with a study on capuchins monkeys showing that the scream component of greeting embraces produced by males, which apparently signals the strength of affiliative bonds between them, is more often produced during greetings with close social partners rather than with less affiliated individuals (Lynch Alfaro, 2008). A similar interpretation could be applied to the observation that females of the lesser black-backed gull gradually add the call component to their greeting displays as courtship progresses (Brown, 1967). While one previous study showed that in chimpanzees particular call variants are associated with specific visual signals (Luef & Pika, 2017), future studies should explore this relationship in more 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.

References

Albers, P. C., & Vries, H. d. (2001). Elo-rating as a tool in the sequential estimation of dominance strengths. *Animal Behaviour, 61*, 489-495.

Andersson, M. B. (1994). *Sexual selection.* Oxford: Princeton University Press.

Aureli, F., & Schaffner, C. M. (2007). Aggression and conflict management at fusion in spider monkeys. *Biology Letters, 3*(2), 147-149.

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., et al. (2008). Fission-fusion dynamics: New research frameworks. *Current Anthropology, 49*(4), 627-654.

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language, 68*(3), 255-278.

Bates, D., Maechler, M., & Bolker, B. & Walker S. (2012). lme4: linear mixed-effects models using Eigen and S4. R package version, 1.0-4. URL: https://cran.r-project.org/web/packages/lme4/index.html

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï forest: Behavioural ecology and evolution.* Oxford: Oxford University Press.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., et al. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution, 24*(3), 127-135.

Brown, R. G. B. (1967). Courtship behaviour in the lesser black-backed gull, *Larus fuscus*. *Behaviour, 29*, 122-153.

Bygott, J. D. (1979). Agonistic behaviour, dominance, and social structure in wild chimpanzees of the gombe national park. In D. A. Hamburg & E. R. McCown (Eds), *The great apes*. (pp. 405-428). Menlo Park: Benjamin/Cummings.

Cheney, D. L., & Seyfarth, R. M. (1992). *How monkeys see the world: Inside the mind of another species*. Chicago: University of Chicago Press.

Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995). The role of grunts in reconciling opponents and facilitating interactions among adult female baboons. *Animal Behaviour, 50*(1), 249-257.

Creel, S., & Creel, N. M. (1995). Communal hunting and pack size in african wild dogs, *Lycaon pictus*. *Animal Behaviour, 50*(5), 1325-1339.

Crockford, C., & Boesch, C. (2005). Call combinations in wild chimpanzees. *Behaviour, 142*, 397-421.

Crockford, C., Wittig, R. M., & Zuberbühler, K. (2017). Vocalizing in chimpanzees is influenced by social-cognitive processes. *Science Advances, 3*(11), e1701742.

Dal Pesco, F., & Fischer, J. (2018). Greetings in male guinea baboons and the function of rituals in complex social groups. *Journal of Human Evolution, 125*, 87-98.

Dal Pesco, F., & Fischer, J. (2020). On the evolution of baboon greeting rituals. *Philosophical Transactions of the Royal Society B, 375*(1805), 20190420.

De Marco, A., Sanna, A., Cozzolino, R., & Thierry, B. (2014). The function of greetings in male Tonkean macaques. *American Journal of Primatology, 76*(10), 989-998.

De Waal, F. B., & van Roosmalen, A. (1979). Reconciliation and consolation among chimpanzees. *Behavioral Ecology and Sociobiology, 5*(1), 55-66.

Dias, P. A. D., Rodriguez Luna, E., & Canales Espinosa, D. (2008). The functions of the "greeting ceremony" among male mantled howlers (*Alouatta palliata*) on agaltepec island, mexico. *American Journal of Primatology, 70*(7), 621-628.

East, M. L., Hofer, H., & Wickler, W. (1993). The erect 'penis' is a flag of submission in a female-dominated society: Greetings in Serengeti spotted hyenas. *Behavioral Ecology and Sociobiology, 33*(6), 355-370.

Faraut, L., Siviter, H., Dal Pesco, F., & Fischer, J. (2019). How life in a tolerant society affects the usage of grunts: Evidence from female and male guinea baboons. *Animal Behaviour, 153*, 83-93.

Fedurek, P., Neumann, C., Bouquet, Y., Mercier, S., Magris, M., Quintero, F., et al. (2019). Behavioural patterns of vocal greeting production in four primate species. *Royal Society Open Science, 6*(4), 182181.

Fedurek, P., & Slocombe, K. E. (2013). The social function of food-associated calls in male chimpanzees. *American Journal of Primatology, 75*(7), 726-739.

Fedurek, P., Slocombe, K. E., Enigk, D. K., Thompson, M. E., Wrangham, R. W., & Muller, M. N. (2016). The relationship between testosterone and long-distance calling in wild male chimpanzees. *Behavioral Ecology and Sociobiology, 70*(5), 659-672.

Fedurek, P., Slocombe, K. E., & Zuberbühler, K. (2015). Chimpanzees communicate to two different audiences during aggressive interactions. *Animal Behaviour, 110*, 21-28.

Fedurek, P., Zuberbühler, K., & Semple, S. (2017). Trade-offs in the production of animal vocal sequences: Insights from the structure of wild chimpanzee pant hoots. *Frontiers in Zoology, 14*(1), 50.

Firth, R. (1972). Verbal and bodily rituals of greeting and parting. In J. S. La Fontaine (Ed), *The Interpretation of Ritual* (pp. 1-38). London: Tavistock.

Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology, 65*(1), 47-55.

Gilby, I. C., & Wrangham, R. W. (2008). Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. *Behavioral Ecology and Sociobiology, 62*(11), 1831-1842.

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge: Harvard University Press.

Hebets, E. A., & Papaj, D. R. (2005). Complex signal function: Developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology, 57*(3), 197-214.

Hobaiter, C., & Byrne, R. (2011). The gestural repertoire of the wild chimpanzee. *Animal Cognition, 14*(5), 745-767.

Hobaiter, C., Byrne, R., & Zuberbühler, K. (2017). Wild chimpanzees' use of single and combined vocal and gestural signals. *Behavioral Ecology and Sociobiology, 71*(6), 96.

Laporte, M. N., & Zuberbühler, K. (2010). Vocal greeting behaviour in wild chimpanzee females. *Animal Behaviour, 80*(3), 467-473.

Liebal, K., Waller, B. M., Slocombe, K. E., & Burrows, A. M. (2013). *Primate communication: A multimodal approach.* Cambridge: Cambridge University Press.

Luef, E. M., & Pika, S. (2017). Reciprocal greeting in chimpanzees (*Pan troglodytes*) at the ngogo community. *Journal of Neurolinguistics, 43*, 263-273.

Luef, E. M., & Pika, S. (2019). Social relationships and greetings in wild chimpanzees (*Pan troglodytes*): Use of signal combinations. *Primates, 60*(6), 507-515.

Lynch Alfaro, J. (2008). Scream–embrace displays in wild black-horned capuchin monkeys. *American Journal of Primatology, 70*(6), 551-559.

Marler, P., & Tenaza, R. R. (1977). Signaling behavior of apes with special reference to vocalization. In T. A. Sebeok (Ed.), *How animals communicate* (pp. 965-1033). Bloomington: Indiana University Press.

Mercier, S., Neumann, C., van de Waal, E., Chollet, E., de Bellefon, J. M., & Zuberbühler, K. (2017). Vervet monkeys greet adult males during high-risk situations. *Animal Behaviour, 132*, 229-245.

Muller, M. N. (2002). Agonistic relations among Kanyawara chimpanzees. In C Boesch, G. Hohmann, L.F. Marchant (Eds), *Behavioural Diversity in Chimpanzees and Bonobos* (pp. 112– 23). Cambridge: Cambridge University Press.

Muller, M. N. (2017). *Chimpanzees and human evolution.* Harvard University Press.

Muller, M. N., & Mitani, J. C. (2005). Conflict and cooperation in wild chimpanzees. *Advances in the Study of Behavior, 35*, 275-331.

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., et al. (2011). Assessing dominance hierarchies: Validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour, 82*(4), 911-921.

Newton-Fisher, N. (1999). Association by male chimpanzees: A social tactic? *Behaviour, 136*(6), 705-730.

Nieburg, H. L. (1970). Agonistics—rituals of conflict. *The Annals of the American Academy of Political and Social Science, 391*(1), 56-73.

Nishida, T., Kano, T., Goodall, J., McGrew, W. C., & Nakamura, M. (1999). Ethogram and ethnography of Mahale chimpanzees. *Anthropological Science, 107*(2), 141-188.

Owings, D. H., & Morton, E. S. (1998). *Animal vocal communication: A new approach.* Cambridge: Cambridge University Press.

Partan, S. R., & Marler, P. (2005). Issues in the classification of multimodal communication signals. *The American Naturalist, 166*(2), 231-245.

R Core Team. (2014). *R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.2013.* URL: http://www.R-project.org/

Range, F., & Fischer, J. (2004). Vocal repertoire of sooty mangabeys (*Cercocebus torquatus atys*) in the Taï national park. *Ethology, 110*(4), 301-321.

Reynolds, V. (2005). *The chimpanzees of the Budongo forest: Ecology, behaviour and conservation*. Oxford: Oxford University Press.

Rowe, C. (1999). Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour, 58*(5), 921-931.

Samuni, L., Mundry, R., Terkel, J., Zuberbühler, K., & Hobaiter, C. (2014). Socially learned habituation to human observers in wild chimpanzees. *Animal Cognition, 17*(4), 997-1005.

Schenkel, R. (1967). Submission: Its features and function in the wolf and dog. *American Zoologist, 7*(2), 319-329.

Scheumann, M., Linn, S., & Zimmermann, E. (2017). Vocal greeting during mother-infant reunions in a nocturnal primate, the gray mouse lemur (*Microcebus murinus*). *Scientific Reports, 7*(1), 10321.

Shrout, P. E., & Fleiss, J. L. (1979). Intraclass correlations: Uses in assessing rater reliability. *Psychological Bulletin, 86*(2), 420-428.

Silk, J., Seyfarth, R., & Cheney, D. (2016). Strategic use of affiliative vocalizations by wild female baboons. *PLoS One, 11*(10), e0163978.

Silk, J., Seyfarth, R., Stadele, V., & Strum, S. (2018). To grunt or not to grunt: Factors governing call production in female olive baboons, papio anubis. *PloS One, 13*(11), e0204601.

Slocombe, K. E., & Zuberbuhler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences of the United States of America, 104*(43), 17228-17233.

Smith, W. J. (1977). *The behavior of communicating: An ethological approach.* Cambridge: Harvard University Press.

Smuts, B. B., & Watanabe, J. M. (1990). Social relationships and ritualized greetings in adult male baboons (*Papio cynocephalus anubis*). *International Journal of Primatology, 11*(2), 147-172.

Struhsaker, T. T. (1967). Auditory communication among vervet monkeys (*Cercopithecus aethiops*). In S.A. Altmann (Ed), *Social Communication among Primates* (pp. 281–324). Chicago: University of Chicago Press.

Titze, I. (1989). On the relation between subglottal pressure and fundamental frequency in phonation. *The Journal of the Acoustical Society of America, 85*(2), 901-906.

Titze, I., & Riede, T. (2010). A cervid vocal fold model suggests greater glottal efficiency in calling at high frequencies. *PLoS Computational Biology, 6*(8), 10.1371/journal.pcbi.1000897.

Uetz, G. W., Roberts, J. A., & Taylor, P. W. (2009). Multimodal communication and mate choice in wolf spiders: Female response to multimodal versus unimodal signals. *Animal Behaviour, 78*(2), 299-305.

Walker, R. H., King, A. J., McNutt, J. W., & Jordan, N. R. (2017). Sneeze to leave: African wild dogs (*Lycaon pictus*) use variable quorum thresholds facilitated by sneezes in collective decisions. *Proceedings of the Royal Society B: Biological Sciences, 284*(1862), 20170347.

Whitham, J. C., & Maestripieri, D. (2003). Primate rituals: The function of greetings between male guinea baboons. *Ethology, 109*(10), 847-859.

Wilke, C., Kavanagh, E., Donnellan, E., Waller, B. M., Machanda, Z. P., & Slocombe, K. E. (2017). Production of and responses to unimodal and multimodal signals in wild chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour, 123*, 305-316.

Wittig, R. M. (2018). Taï chimpanzees. In J. Vonk, & T. Shackelford (Eds.), *Encyclopedia of animal cognition and behavior* (pp. 1-7) Springer International Publishing.

Wittig, R. M., & Boesch, C. (2003). Food competition and linear dominance hierarchy among female chimpanzees of the tai national park. *International Journal of Primatology, 24*(4), 847-867.

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 ± SE**	**Z value**	***P* value**	**95% confidence intervals**
Intercept	-3.31±0.83	-3.96		-4.38 to 0.17
Male-female dyads	1.27±0.80	1.58	0.113	-1.70 to 2.28
Male-male dyads	0.75± 0.83	0.90	0.369	-2.87 to 2.31
Aggressor by caller	**1.22 ±2.02**	**0.61**	**0.543**	**-8.23 to 6.85**
Aggressor by recipient	**2.60±0.23**	**11.22**	**<0.001**	**1.72 to 3.12**
Visual signalling by caller	**1.18±0.19**	**6.19**	**<0.001**	**0.57 to 1.51**
Visual signalling by recipient	**0.53±0.28**	**1.92**	**0.055**	**-0.18 to 1.11**
Latency between fusion and approach	**-0.30±0.11**	**-2.75**	**0.006**	**-0.54 to -0.04**
Subsequent proximity	**-0.71±0.30**	**-2.33**	**0.020**	**-1.34 to 0.03**
Elo rating difference	-0.73±0.16	-4.63	<0.001	-1.03 to -0.35
Community North	0.32±0.44	0.73	0.467	-0.83 to 1.46
Community Sonso	0.35±0.44	0.78	0.437	-0.98 to 1.56
Community South	-0.34±0.32	-1.05	0.292	-1.04 to 0.26
Community Waibira	0.49±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).