Animal Behaviour 186 (2022) 41–55

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Male chimpanzees communicate to mediate competition and cooperation during feeding

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ARTICLE INFO

Article history:
Received 18 May 2021
Initial acceptance 2 August 2021
Final acceptance 7 December 2021

MS. number: 21-00308R

Keywords:
audience effect
food-associated call
Pan troglodytes
social cognition
social cohesion
vocal communication

An ongoing debate in animal behaviour research is whether food calls function to cooperatively inform others or provide the caller with competitive advantages. When feeding, chimpanzees, *Pan troglodytes*, produce two types of call: context-specific, close-range 'rough grunts' and context-general, long-range 'pant hoots'. We investigated this dual signalling behaviour by wild male chimpanzees that were either actively joining others or passively being joined in food trees, considering the effects of the audience composition and the type of food encountered. For arriving individuals, we found that pant hoot production was best explained by the absence of socially important individuals (i.e. social bond partners and/or high-ranking males), suggesting that callers were cooperatively informing them about food availability, probably to strengthen social relationships. In contrast, rough grunts were mostly produced by low-ranking individuals, suggesting they were part of competitive interactions to avoid aggression. For individuals already in a tree, we found that both rough grunt and pant hoot production was most common in low-ranking individuals reacting to the arrival of high-ranking males and there was no significant effect of the presence, or absence, of social bond partners. We discuss these patterns and conclude that, when chimpanzees enter a food tree, their vocal behaviour functions to mediate both cooperative and competitive interactions.

Living in social groups is an evolutionary strategy that carries a range of advantages, such as reduced risk of predation, improved access to food and mating partners or increased protection from ectoparasites through social grooming (Chapman & Chapman, 2000; Crofoot & Wrangham, 2010; Davies et al., 2012; Grinnell, 2002; Jeschke & Tollrian, 2007). Group living also carries costs, such as higher risks of pathogen transmission and increased foraging and mating competition (Davies et al., 2012; Gruber et al., 2016; Krause & Ruxton, 2002; Leendertz et al., 2004; Wrangham et al., 1993).

Some species have evolved mechanisms to mitigate the costs of social living, by allowing individualized spatial decisions, which will inevitably lead to the formation of temporary groups (i.e. subgroups): a fission–fusion society (Conradt & Roper, 2010; Jacobs, 2010; Kerth, 2010). The term fission–fusion was first used to describe the social system of hamadryas baboons, *Papio hamadryas* (Kummer, 1971) and refers to continuous changes in group composition, subgroup size and dispersion of subgroups (Aureli et al., 2008; Ramos-Fernández & Morales, 2014). For example, if food resources are evenly scattered, rather than clumped, travelling in large groups becomes inefficient and leads to fission whereas large food patches can lead to fusion of subgroups (Hartwell et al., 2018; Krebs & Davies, 2009; Lehmann et al., 2007). However, changes in subgroup size are not always responses to food availability (Asensio et al., 2009; Chapman et al., 1995; Kummer, 1971; Symington, 1990) but often also reflections of social affiliations or reproduction strategies (bottlenose dolphins, *Tursiops truncatus*, Lusseau, 2007; Tonkean macaques, *Macaca tonkeana*, and rhesus macaques, *Macaca mulatta*, Sueur et al., 2010; northern muriquis, *Brachyteles hypoxanthus*, Tokuda et al., 2012; spider monkeys, *Ateles geoffroyi*, Busia et al., 2017; chimpanzees, *Pan troglodytes*, Mitani & Amsler, 2003). Although fission–fusion dynamics minimize competition, they also introduce variability in social interaction and uncertainty about social relations (Hinde, 1976; Wey et al., 2008). In species with high degrees of fission–fusion, subgroup composition is the result of individual decisions, in contrast to more stable

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https://doi.org/10.1016/j.anbehav.2022.01.009
0003-3472/

groups where decision making is a collective process (Conradt & List, 2009; Couzin et al., 2005; Ramos-Fernandez & Aureli, 2018).

According to the social intelligence hypothesis (Humphrey, 1976), the size of the brain and the cognitive abilities of a species should be positively correlated with its degree of social complexity (Dunbar, 1998, 2011). For this reason, it has been argued that living in fission–fusion societies favours the evolution of social intelligence compared to social systems with invariable group sizes (Barrett et al., 2003). Indeed, within the haplorrhine primates, fission–fusion dynamics has been reported for spider monkeys (Chapman, 1990), hamadryas baboons (Kummer, 1968), bonobos, *Pan paniscus* (White & Burgman, 1990), chimpanzees (Goodall, 1986) and humans (Marlowe, 2005), all of which have relatively large brains (Stephan et al., 1981). Contrastingly, other studies have found evidence that primate brain size is correlated with ecological (i.e. diet, home range size, terrestriality and activity period), rather than social, variables, thus supporting the ecological intelligence hypothesis (DeCasien et al., 2017; Powell et al., 2017). However, the social and ecological intelligence hypotheses are not necessarily exclusive and could be integrated as complementary ideas that would explain the evolution of different domains of cognition (Rosati, 2017).

In chimpanzees, changes in group composition often occur during transitions from travelling to feeding and vice versa. Arrivals at food trees can be emotionally charged events that are prone to outbreaks of severe aggression (Ischer et al., 2020; Muller & Mitani, 2005). However, the discovery of a food source also brings crucial opportunities to strengthen social bonds, for instance through tolerated co-feeding or occasional food sharing (Samuni et al., 2018; Wittig et al., 2014). In chimpanzees, male bonding has important fitness consequences as it is a basis for trust and support during various activities, such as cooperative hunting (Hobaiter et al., 2017), intergroup aggression (Herbinger et al., 2009; Wilson et al., 2014), predator defence (Boesch, 1991) and intragroup conflicts (Goodall, 1986; Mitani, 2009; Muller & Mitani, 2005). Associating with high-ranking males can therefore be beneficial (Bray et al., 2016; Duffy et al., 2007; Kaburu & Newton-Fisher, 2015). However, not all males are equally successful in establishing social bonds and often differ in their preferred partners, which may have fitness consequences (Boesch et al., 2006; Feldblum et al., 2021; Muller & Mitani, 2005; Newton-Fisher et al., 2009; Wroblewski et al., 2009). It is therefore unsurprising that chimpanzees communicate prior to and during feeding, which provides rich opportunities to determine the function and meaning of the signals involved (for a review see Clay et al., 2012; Chapman & Lefebvre, 1990; Elgar, 1986; Laidre, 2006).

Chimpanzees produce two types of calls in relation to feeding events: long-distance 'pant hoots' and short-distance 'rough grunts' (Goodall, 1986; Marler & Tenaza, 1977; Reynolds & Reynolds, 1965). Pant hoots are structurally complex calls that consist of four distinct units (introduction, build-up, climax, let-down; Fedurek et al., 2016). These calls are mainly produced by adult males, often as choruses and in a variety of situations, although the let-down unit can be discriminated into two variants, one linked to travel and another to food (Fedurek et al., 2016; Notman & Rendall, 2005). Pant hoots travel over long distances, often combined with drumming displays, suggesting that they function to inform distant group members about the presence of food or direction of travel (Babiszewska et al., 2015; Reynolds & Reynolds, 1965; Wrangham, 1977). Pant hoots also convey other information, such as the rank and identity of the caller (Fedurek et al., 2016) and call production is governed by social factors, such as rank or party size and composition (Clark, 1993; Clark & Wrangham, 1994; Mitani & Nishida, 1993; Wrangham et al., 2007). As mentioned, males often join others' pant hoots to take part in group chorusing (Arcadi, 1996), which seems to function in social bonding (Fedurek et al., 2013; Mitani & Brandt, 1994; Mitani & Gros-Louis, 1998), similar to human singing (Keeler et al., 2015).

Compared to pant hoots, chimpanzee rough grunts are much more context specific, as they are produced exclusively in relation to feeding (Slocombe & Zuberbühler, 2005). Interestingly, rough grunts are acoustically similar to 'pant grunts', a greeting call given by lower-ranking to higher-ranking individuals during approaches and other types of encounters (Laporte & Zuberbühler, 2011), suggesting similar psychological processes underlying call production. Rough grunt production is dependent on the quantity of food (Brosnan & De Waal, 2000; Hauser et al., 1993; Hauser & Wrangham, 1987) and acoustic structures vary with the perceived quality or type of food (Slocombe & Zuberbühler, 2005, 2006). As with pant hoots, social factors play a role in call production, notably the audience composition (oestrous females: Kalan & Boesch, 2015; dominance relation: Schel et al., 2013; bond partners: Fedurek & Slocombe, 2013; Schel et al., 2013; Slocombe et al., 2010).

Beyond chimpanzees, there is an ongoing debate as to whether animals are capable of cooperatively informing others or whether calling is always part of imperative or competitive interactions. Evidence for a competitive function is from data showing that food calls advertise social status or dominance rank (chimpanzees, Clark & Wrangham, 1994; pinyon jays, *Gymnorhinus cyanocephalus*, Dahlin et al., 2005; ravens, *Corvus corax* Heinrich & Marzluff, 1991) or even ownership and willingness to defend a resource (white-faced capuchins, *Cebus imitator*, Boinski & Campbell, 2010; Gros-Louis, 2004). On the other hand, food calls can also be produced by subordinates towards high-ranking individuals to avoid aggression, with possible cases of 'punishment' after failing to disclose the discovery of a food patch (spider monkeys, Chapman & Lefebvre, 1990; tufted capuchins, *Cebus apella*, Di Bitetti, 2005; rhesus macaques, Hauser & Marler, 1993b).

Evidence for a cooperative function is from data showing that the structure and rate of food-associated calls can vary with food quantity (red-bellied tamarins, *Saguinus labiatus*, Caine et al., 1995; chimpanzees, Hauser et al., 1993) or quality (ravens, Bugnyar et al., 2001; bonobos, Clay & Zuberbühler, 2009; cotton-top tamarins, *Saguinus oedipus*, Elowson et al., 1991). Also, food calls are sometimes directed at preferred audiences, notably kin (rhesus macaques, Hauser & Marler, 1993a; naked mole-rats, *Heterocephalus glaber*, Judd & Sherman, 1996; tufted capuchins, Pollick et al., 2005), mates (chickens, *Gallus gallus domesticus*, Evans & Marler, 1994; bonobos, Krunkelsven et al., 1996) and bond partners (bonobos, Krunkelsven et al., 1996; chimpanzees, Slocombe et al., 2010).

Here, we revisited this cooperation/competition debate by investigating chimpanzee vocal behaviour in the feeding context. The function of both call types given during feeding remains puzzling. Indeed, pant hoots produced in a feeding context have an intimidating effect on nearby listeners and are preferentially initiated by the highest-ranking males in a party (Clark & Wrangham, 1994) while, at the same time, they might provide information about the presence of food and even attract desired partners (Reynolds & Reynolds, 1965; Wrangham, 1977). Similarly, rough grunts have been proposed to convey useful information for others about the presence and type of food (e.g. Slocombe & Zuberbühler, 2005, 2006) which may also facilitate coordinated feeding with preferred partners (e.g. Fedurek & Slocombe, 2013; Schel et al., 2013). However a recent study has shown that these calls are often produced after a history of agonistic interactions, suggesting communication for selfish reasons (Ischer et al., 2020).

As pointed out, feeding in groups is a complex social event that forces individuals to interact in close proximity and under competitive circumstances. We focused on adult males because they are more gregarious than adult females and therefore more often involved in fission–fusion decisions (Gilby and Wrangham, 2008; Mitani, 2009; Nishida, 1983). Moreover, cooperation among males is important since, as previously mentioned, males form strong social relationships that are crucial for their fitness. Competition between males is also essential as dominance relationships are established through aggression and intimidation (Muller & Mitani, 2005). Our strategy was to dissect the feeding event into two chronologically ordered components. First, we investigated the vocal behaviour of males arriving at a food tree, while taking the individuals already in the tree and individuals simultaneously arriving into account. Second, we investigated the vocal behaviour of males already in a tree, while taking the identity of any newly arriving individuals and other individuals already in the tree into account. In both conditions, we were also interested in the impact of the absence of socially relevant individuals (i.e. high-ranking and preferred social partners) and, finally, the type of food present.

Since rough grunts are short-distance calls, we expected these calls to be directed at nearby individuals, while long-distance pant hoots would be directed at distant individuals. For the cooperative function, we predicted increased rough grunt rates in the presence of large parties and, specifically, important social partners, such as high-ranking males and association or bond partners (i.e. to initiate feeding with them). We also predicted increased pant hoot rates in small parties and in the absence of such important social partners (i.e. to inform absent individuals about the presence of food and possibly recruit them to join). For the competitive function, we predicted increased rough grunt rates in the presence of large parties and, specifically, high-ranking males (i.e. to avoid direct aggression) and increased pant hoot rates in small parties and in the absence of such individuals (i.e. to inform absent individuals about the presence of food and thus avoid possible later aggression). We also predicted that call production of both call types would be higher in low-ranking individuals. We also expected that subjects would vocalize in reaction to the newly joined (or joining) individuals or to the absence of specific individuals upon arrival; that is, arriving subjects would vocalize towards either individuals they joined (i.e. rough grunts) or absent ones (i.e. pant hoots), whereas males already feeding would vocalize towards newly joining individuals (i.e. rough grunts).

METHODS

Ethical Note

Our study was approved by the relevant local authorities in Uganda (UWA and UNCST) and complies with the ASAB/ABS guidelines for the Use of Animals in Research. Data collection was entirely observational and noninvasive.

Study Site and Subjects

We collected data on East African chimpanzees, *P. t. schweinfurthii*, of the Sonso community in the Budongo Forest Reserve, Uganda (latitude 1°37′–2°00′N; longitude: 31°22′–31°46′E), between January 2018 and March 2020. At the beginning of the study, the community comprised 75 individuals, 37 of which were adults (>15 years; 11 males; 26 females). In February 2019, three adult males died in an epidemic (Appendix Table A1). The group had been monitored for more than 25 years with all individuals identified and habituated to human observers with daily follows throughout the approximately 7 km^2 home range (Newton-Fisher, 2003). All social and kin relations are known and continuously updated (Reynolds, 2005).

Data Collection

We initially conducted full-day focal follows, usually from 0700 to 1630 local time, for a total observation time of 692 h over 141 days. We followed 11 adult males but then had to exclude one male (ZD) due to a short observation time (Appendix Table A1). During each follow, we continuously recorded the subject's activities with start and end times. During feeding events in trees, we recorded the ‘arrival event’ as the period between an individual approaching in visual range of the food tree (i.e. approximately 30 m) and the moment he started feeding. For each arrival event, we recorded the tree species, the identities of all arriving individuals and all individuals already in the tree, as well as the vocal behaviour (rough grunt and pant hoot production) of all males. We excluded events during which vocalizations were produced by unidentifiable males, which happened frequently due to low visibility.

Owing to a respiratory disease outbreak in 2019, three of the 10 focal animals died within a week, which destabilized the social relations between the remaining males. For this reason, we excluded the data collected in the 3 months after the death of the first individual (26 February 2019 to 31 May 2019) from statistical analyses, which created two data sets (i.e. 4 January 2018 to 26 February 2019 and 1 June 2019 to 16 March 2020).

Social Variables

To determine the social relations between the males, we calculated each subject's dominance rank (Elo-rating; Elo, 1978; Neumann et al., 2011) and identified his most important partners (i.e. bond partners and association partners) using long-term data collected by four trained field assistants during full-day focal follows, which also included 15 min scan samples of party compositions. We did not compute the more commonly known ‘dyadic composite sociality index’ (DSI; Silk et al., 2013) as we were interested in the impact of proximity and grooming separately. We opted for this strategy since a previous study had shown that proximity patterns reflected the strength of relationships whereas grooming patterns reflected the quality of relationships (Mitani, 2009). We therefore defined, for each male separately, his ‘association partners’ as the top three preferred proximity partners and his ‘bond partners’ as the top three preferred grooming partners (Bray & Gilby, 2020; Mitani & Nishida, 1993; Samuni et al., 2018, 2021).

Dominance

The rank of each adult male was established using the Elo-rating method, which has the advantage that it depicts rank relations dynamically in contrast to other methods (Elo, 1978; Neumann et al., 2011). The behaviour used to calculate ranks was the production of pant grunt (i.e. a ‘greeting’ vocalization given to higher-ranking individuals). This behaviour accurately reflects dominance relationships (Bygott, 1979) and has traditionally been used to calculate the hierarchy among chimpanzees both in the wild and in captivity (Fedurek et al., 2021; Samuni et al., 2018, 2020, 2021). To have an accurate estimation of dominance ranks at the beginning of the study, we used the data collected from 12 months before the study and then continued to collect data until the end of the study (4 January 2017 to 16 March 2020). In contrast to traditional matrix-based assessments, Elo-rating is based on the Bayesian concept that rank is a dynamic variable that provides an increasingly more accurate description with each observed social interaction. Each male starts the process with a fixed score, which is continuously updated following each dyadic interaction. In particular, each time a male produces pant grunts to another male, he loses points whereas the recipient gains the same number of points. The number of points gained or lost depends on the expected outcome, which is calculated prior to the interaction. Unexpected outcomes lead to more point changes than expected outcomes (Elo, 1978; Neumann et al., 2011). We calculated the Elo-ratings using the ‘EloRating’ R package version 0.46.11 (Neumann & Kulik, 2020). The hierarchy was stable through the two study periods (i.e. before and after the outbreak), enabling us to attribute one Elo-score to each male. For each male, we calculated the mean of the Elo-scores obtained at the end of the two periods (Appendix Table A1). Three individuals had consistently higher Elo-scores than the other males and were thus classified as ‘high-ranking males’ (Appendix Fig. A1, Table A1). Elo-rating scores were standardized for statistical analyses.

Social partners

For each male dyad, we calculated both grooming-based and proximity-based dyadic sociality indices, the DSI_G and the DSI_P, to determine each male's bond and association partners, respectively. The DSI_G and DSI_P calculations were derived from the DSI introduced by Silk et al. (2013), which attributes a value of 1 to the average social bond across all dyads in the group (in our case 55 dyads; $N = 11$ males). If a dyad has a value greater (or less) than 1, the dyad is considered to have a stronger (or weaker) social bond than average. To calculate the DSI_G, we used the duration of grooming interactions between the two males of the dyad (grooming given or received) recorded during the focal follows. To calculate the DSI_P, we used the occurrence of the two males of the dyad being nearest neighbours (i.e. the individual sitting in closest proximity to the focal animal) recorded in 15 min scans. Since three adult males died during the outbreak, we calculated the indices for the periods before and after the outbreak separately. The DSI_G and the DSI_P were calculated using the ‘socialindices2’ R package version 0.50.0 (Neumann, 2017). For each focal male (and for each study period), the social bond partners and the association partners were the top three individuals with the highest DSI_G and DSI_P values, respectively (Appendix Table A2).

Statistical Analyses

We investigated which parameters influenced the production of the two call types (i.e. pant hoot and rough grunt) depending on the role of the individual (i.e. arriving or present in the food tree) during arrival events. We were interested in whether individuals were addressing the joining (or joined) individuals or the entire party. Hence, we considered distinct variables (i.e. the number of individuals, the presence of a high-ranking male, the presence of a social bond partner and the presence of an association partner) to describe both the composition of the joining (or joined) group and the composition of the entire party.

First, we built four generalized linear mixed models (GLMMs) corresponding to the four combinations of vocalizations and roles: production of pant hoot (GLMM1) or rough grunt (GLMM2) when arriving at a food tree, and production of pant hoot (GLMM3) or rough grunt (GLMM4) when being joined (i.e. already present) in a food tree (Appendix Table A3). All GLMMs had a binomial error structure and logit link function, with the call (i.e. pant hoot for GLMM1 and 3 and rough grunt for GLMM2 and 4) production (at least one call produced/no call produced) as the response variable. The test variables were the dominance rank (Elo-rating) of the subject, the food tree species, the total number of individuals in the feeding party and the social composition (presence of a high-ranking male, a male social bond partner or a male association partner) of the entire party (all GLMMs) and of the arriving group (GLMM3 and 4) or of the group already present in the tree (GLMM1 and 2). The subject ID was entered as a random factor in all the GLMMs.

To account for the fact that the subject would sometimes produce both pant hoots and rough grunts during the same arrival events and to disentangle the functions of these two calls, we also built similar models (GLMM1b, 2b, 3b and 4b) on subsets of the data without the other call type produced (i.e. without the production of rough grunt for GLMM1b and 3b, and of pant hoot for GLMM2b and 4b).

We then used a statistical model selection and averaging approach on each GLMM to disentangle the effect of each variable and determine which submodels fitted the data best. To do so, we used the dredge function of the ‘MuMIn’ R package (version 1.43.17; Barton, 2020) to generate a full submodel set (including the null model) from each GLMM previously built. For each submodel set, we used Akaike's information criterion values corrected for small sample size (AICc; Burnham et al., 2011) to rank the submodels from best to worst and conducted model averaging separately, for each GLMM, across the top submodel set, i.e. where $\Delta AICc < 2$ (Burnham & Anderson, 2004; Symonds & Moussalli, 2011). We considered variables as informative if zero was not included within their 95% confidence interval. We used the vif function of the ‘car’ R package (version 3.0–3; Fox & Weisberg, 2019) to derive variance inflation factors (VIF), which revealed no collinearity issues (largest $VIF = 2.01$ across all models). We calculated Cook's distances of single observations using the ‘influence.ME’ R package (version 0.9–9; Nieuwenhuis et al., 2012) and detected no influential cases (all values <1). Lastly, we checked model assumptions by visually checking the distribution of residuals. Additionally, Spearman rank correlation tests confirmed that the productions of both rough grunts and pant hoots by individuals arriving or being joined in the food tree were not significantly correlated with the production of the other call ($P > 0.10$; Appendix Table A4). All GLMMs were built using the glmer function of the ‘lme4’ R package (version 1.1–21; Bates et al., 2015). All analyses were implemented in R v3.6.1 (R Core Team, 2019).

RESULTS

General Patterns

Long-term data analyses allowed us to establish the dominance rank between adult males and to determine the top three high-ranking individuals (Appendix Fig. A1, Table A1) as well as the top three bond partners and association partners for each focal male (Appendix Table A2).

Across subjects ($N = 10$ adult males), we observed 233 arrival events, during which we recorded 190 males joining others and 519 males being joined in a food tree. When actively joining, subjects produced pant hoots or rough grunts in about one-third of events (mean proportion of events ± SD: with pant hoots $= 0.35 \pm 0.14$; with rough grunts $= 0.36 \pm 0.16$; Fig. 1) and, when vocalizing, they often produced both calls during the same events (31 of 104 vocal events). When passively being joined, call rates were much lower (mean proportion of events ± SD: with pant hoots $= 0.08 \pm 0.04$; with rough grunts $= 0.14 \pm 0.08$; Fig. 1) and, when vocalizing, they rarely produced both calls during the same event (seven of 90 vocal events).

Calling Patterns When Joining Others

Pant hoot production was negatively related to party size and the presence of high-ranking individuals and social bond partners;

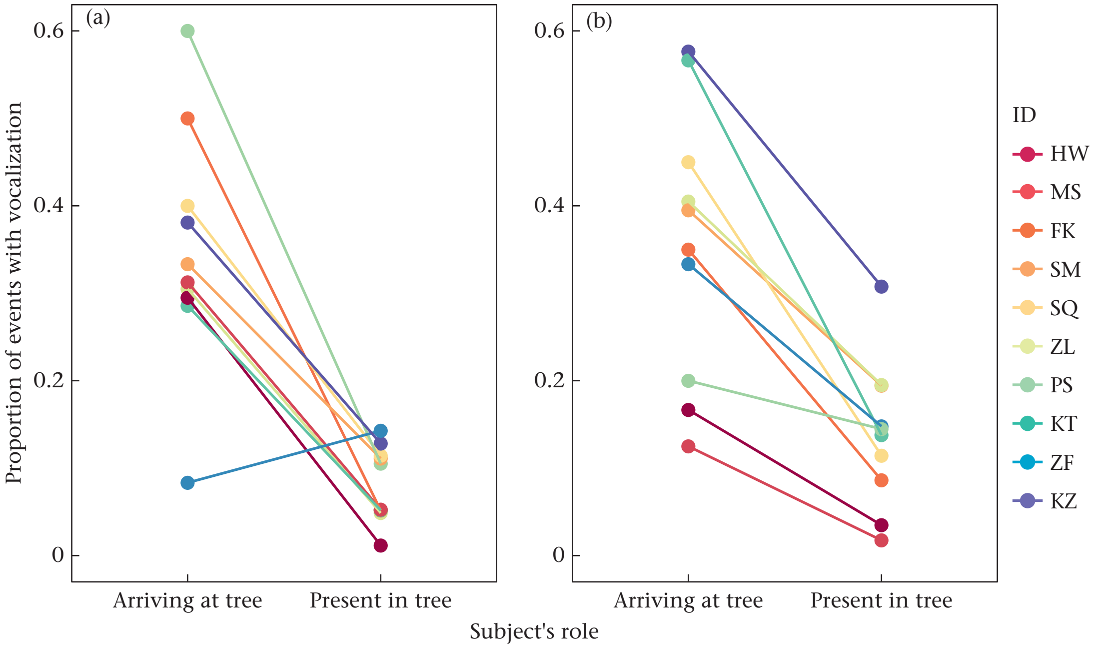

Figure 1. Proportion of events with a vocalization produced by the subject depending on whether he is arriving at the food tree or already present in the tree and being joined by other individuals for (a) pant hoot and (b) rough grunt. The subjects are ordered by dominance rank (from top high ranking to bottom low ranking).

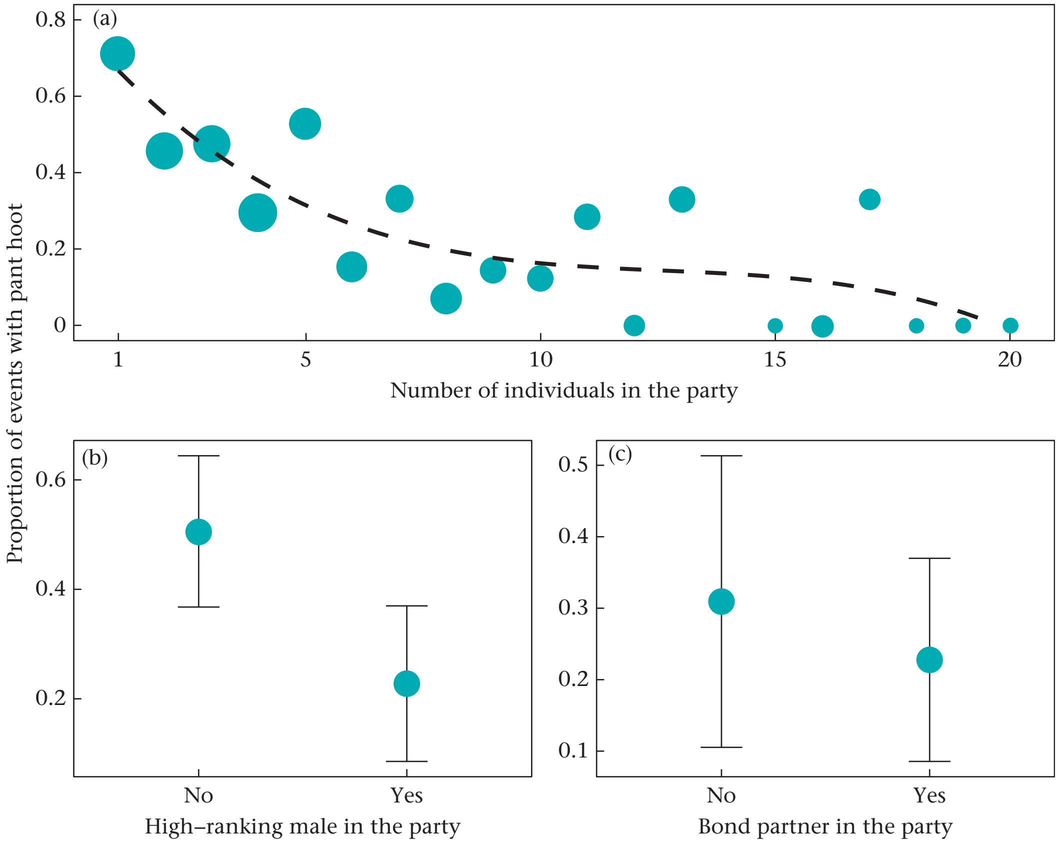

Figure 2. Relationship between the proportion of events with pant hoot produced by the subject arriving at the food tree and (a) the party size and (b) the presence of a high-ranking male or (c) a social bond partner in the party. Larger points in (a) denote a larger number of observations. Points in (b) and (c) represent the mean proportion of events ± SD.

i.e. higher in smaller than larger parties ($\beta = -0.19$, SE = 0.06, 95% CI = −0.31 to −0.07; Fig. 2a), higher when high-ranking individuals were absent ($\beta = -1.30$, SE = 0.50, 95% CI = −2.28 to −0.31; Fig. 2b) and higher when social bond partners were absent ($\beta = 1.08$, SE = 0.50, 95% CI = 0.10 to 2.07; Fig. 2c; GLMM1; Appendix Table A5).

Rough grunt production was negatively related to party size and caller rank, i.e. lower in large parties (β = −0.12, SE = 0.05, 95% CI = −0.22 to −0.03; Fig. 3a) and higher for low than high-ranking males (β = −0.62, SE = 0.18, 95% CI = −0.97 to −0.27; Fig. 3b; GLMM2; Appendix Table A5).

Calling Patterns When Being Joined

Pant hoot production was negatively related to party size and caller rank, and positively related to the presence of a high-ranking male in the joining group, i.e. higher in smaller than larger parties (β = −0.17, SE = 0.06, 95% CI = −0.29 to −0.05; Fig. 4a), higher in low-ranking callers (β = −0.52, SE = 0.22, 95% CI = −0.95 to −0.09; Fig. 4b) and higher when a high-ranking male joined (β = 1.26, SE = 0.40, 95% CI = 0.46 to 2.05; Fig. 4c; GLMM3; Appendix Table A5).

Rough grunt production, similarly to pant hoot, was also negatively related to party size and caller rank, and positively related to the presence of a high-ranking male in the joining group, i.e. higher in smaller than larger parties (β = −0.17, SE = 0.05, 95% CI = −0.26 to −0.08; Fig. 5a), higher in low-ranking callers (β = −0.83, SE = 0.19, 95% CI = −1.21 to −0.45; Fig. 5b) and higher when a high-ranking male joined (β = 1.74, SE = 0.33, 95% CI = 1.10 to 2.38; Fig. 5c; GLMM4; Appendix Table A5).

Overall, we did not find any significant effect of the type of food consumed (i.e. tree species) on the production of both calls.

To further explore the data, we reran all models for both call types produced separately (Appendix Table A6). Here, we found overall the same production patterns although some variables, i.e. presence of a preferred grooming partner in the party in the model exploring pant hoot production by arriving individuals (GLMM1b; Appendix Table A6), party size in the model exploring rough grunt production by arriving individuals (GLMM2b; Appendix Table A6) and the Elo-rating in the model exploring pant hoot production when being joined at a food tree (GLMM3b; Appendix Table A6), were no longer informative. However, results still showed a high relative importance of these variables in their models (0.82, 0.74 and 1.00, respectively; Appendix Table A6), suggesting that lack of significance was due to low sample sizes.

DISCUSSION

There is something paradoxical about advertising the discovery of food. Rather than taking advantage of encountering a new resource, many social animals announce their discovery before starting to feed or, when already feeding, produce signals when new group members arrive. This behaviour is prominent in chimpanzees, with individuals producing two types of calls in the feeding context, the rough grunt and the pant hoot, both when joining and when being joined in food trees. Food calling has been observed in many species and several hypotheses have been suggested to explain the adaptive function of these vocalizations (see Clay et al., 2012 for a review). One of the most popular hypotheses is based on the assumption that callers perceive feeding as a social event and seek to inform others about, or include others at, a valuable resource suggesting that the caller will benefit from such selfless behaviour in some other way (Chapman, 1990; Dahlin et al., 2005; Heinrich & Marzluff, 1991; Pollick et al., 2005). In primates,

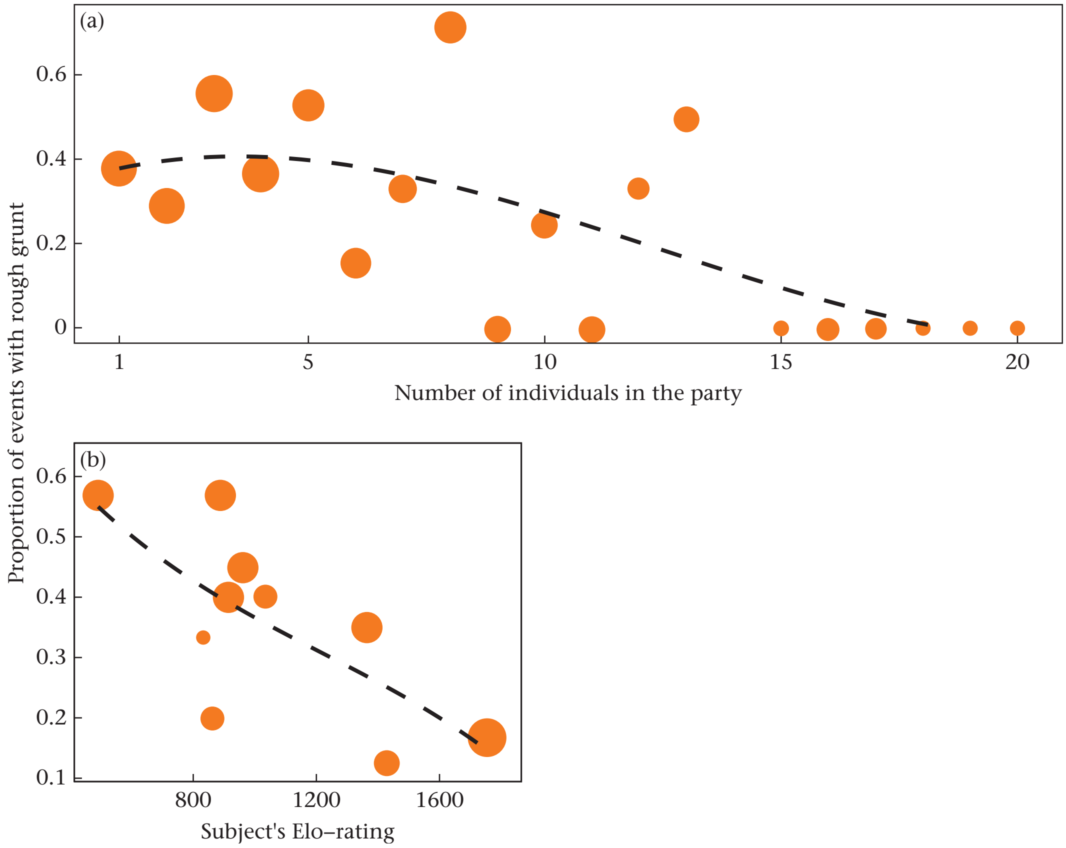

Figure 3. Relationship between the proportion of events with rough grunt produced by the subject arriving at the food tree and (a) the party size and (b) the dominance rank of the subject (Elo-rating). Larger points denote a larger number of observations.

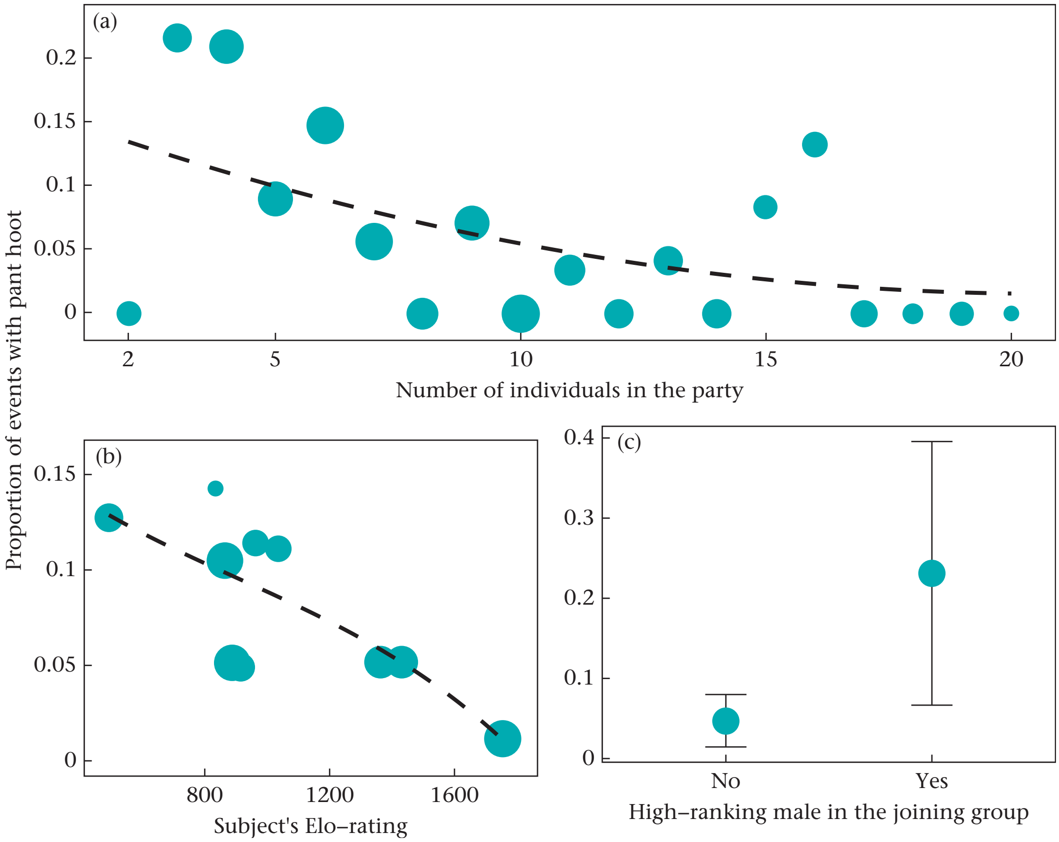

Figure 4. Relationship between the proportion of events with pant hoot produced by the subject being joined in the food tree and (a) the party size, (b) the dominance rank of the subject (Elo-rating) and (c) the presence of a high-ranking male in the group arriving in the food tree. Larger points in (a) and (b) denote a larger number of observations. Points in (c) represent the mean proportion of events ± SD.

another supported hypothesis posits that the function of food-associated calls is to reduce foraging competition (Caine et al., 1995; Di Bitetti, 2005; Gros-Louis, 2004; Hauser & Marler, 1993b).

We monitored the vocal behaviour of 10 adult male chimpanzees either when arriving or when being joined at a food tree. For both call types, we found that call production was higher in the actively joining than passively joined role. Both call rates were also higher in smaller than larger parties, regardless of whether the caller actively joined others or was passively joined.

Beyond these general patterns, there were some call type-specific effects. First, we found that arriving individuals were most likely to produce long-distance pant hoots when socially important individuals (i.e. high-ranking males and social bond partners) were absent, whereas males already in the tree were most likely to produce this call when high-ranking males joined and they themselves were lower ranking. We interpret these patterns as evidence for a cooperative function, i.e. calls are produced to inform distant group members about a valuable food source and, once they approach, to strengthen social relationships.

Second, for close-range rough grunts, we found that low-ranking males were generally more likely to call than high-ranking males. Arriving males were less likely to call if many others were in the tree and those in the tree were more likely to call when joined by a high-ranking male. We interpret these patterns as evidence for a greeting or appeasement function, similar to greeting calls (i.e. pant grunts; Goodall, 1986). When producing rough grunts, males may attempt to manage socially difficult situations, i.e. co-feeding with competitors in the confined space of a tree crown, where individuals only have limited choice in terms of spatial decisions and proximity to others.

Do Pant Hoots Recruit Absent Partners?

When joining a feeding party, males produced pant hoots in about a third of events. One surprising finding was that pant hoot call production by these newly arriving individuals was related to the absence of specific individuals. Our results show that subjects called more often when they were in small parties, and especially when high-ranking males and social bond partners were absent. Since pant hoots travel over long distances (>1 km), it is possible that callers sought to inform absent high-ranking males and social bond partners to recruit them to the food tree. It has been argued that sharing information about feeding events provides opportunities to feed together or even share food, which is correlated with high levels of oxytocin and thus plays a key role in social bonding (Samuni et al., 2018; Wittig et al., 2014). These social bonds are crucial to the fitness of male chimpanzees (Gilby & Wrangham, 2008; Mitani, 2009; Muller & Mitani, 2005; Nishida, 1983; Nishida & Hosaka, 1996). This interpretation is in line with previous studies that have shown that pant hoots play a role in maintaining group cohesion and regulating spatial dynamics between males (Eckhardt et al., 2015; Fedurek et al., 2014; Mitani & Nishida, 1993).

When males were already feeding in a tree, they only produced pant hoots 8% of the time when other individuals joined them. These calls were mainly produced by low-ranking males when being joined by high-ranking ones and in small parties. In the same context, the rough grunt production pattern was similar and one hypothesis is that both these calls are produced by low-ranking individuals to avoid aggression by joining high-ranking males (see the section below for further development of this hypothesis). On the other hand, why would these two calls (i.e. pant hoots and

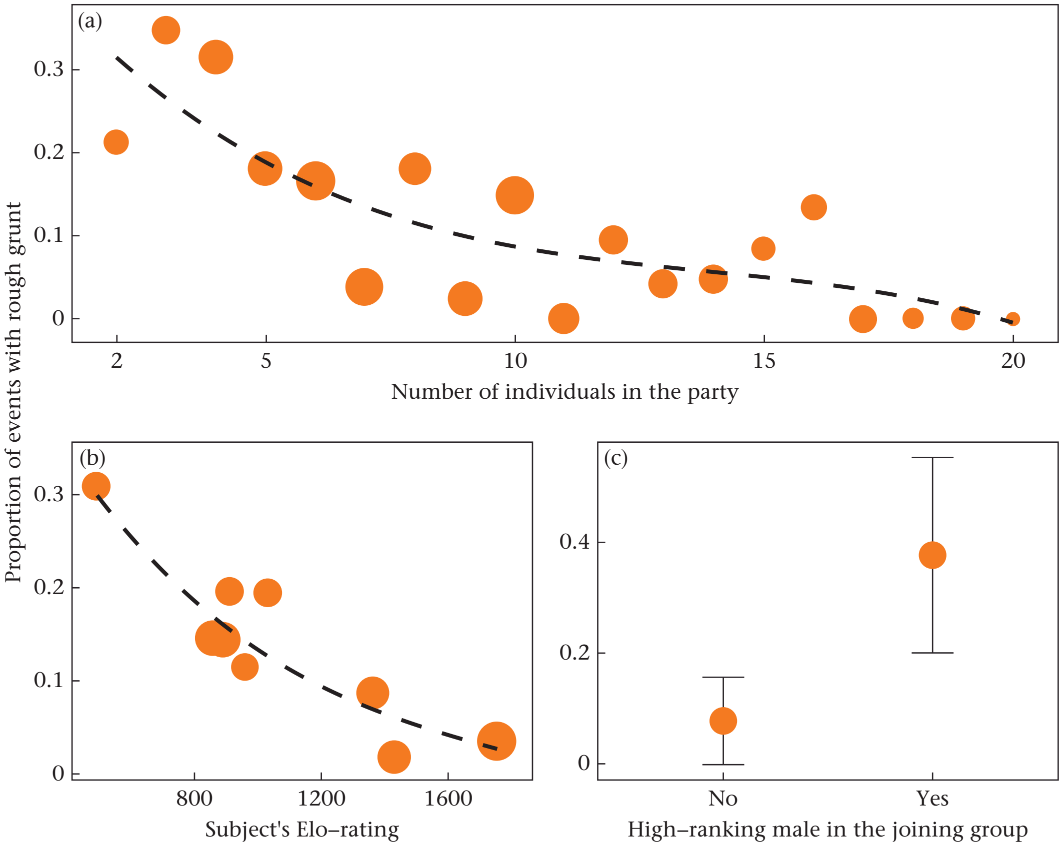

Figure 5. Relationship between the proportion of events with rough grunt produced by the subject being joined in the food tree and (a) the party size, (b) the dominance rank of the subject (Elo-rating) and (c) the presence of a high-ranking male in the group arriving in the food tree. Larger points in (a) and (b) denote a larger number of observations. Points in (c) represent the mean proportion of events ± SD.

rough grunts) be produced with the same function? Since individuals sometimes produced both calls during the same arrival event, the two calls could be produced in combination. Indeed Leroux et al. (2021) recently showed that chimpanzees produce these calls in combination, mainly when high-ranking individuals join the feeding party. Even though their study did not specifically investigate the function of these call combinations, their results suggested that the meaning of the combination seems to be related to the meaning of the two calls produced in isolation. Further research is needed to disentangle the function of the calls when produced alone or in combination.

However, in our study, when subjects were being joined in the tree, they only produced these two calls during the same events in approximately 8% of the events during which they vocalized and their patterns of production remained the same when produced in isolation. Moreover, no correlation was found between the production of these two calls (Table A4). These calls must therefore have distinct functions when produced alone. One hypothesis is that pant hoot production could have a different function. Indeed, if the intended recipients are in the same party (i.e. joining high-ranking males) then why use a long-distance call? We think that these calls might be uttered in response to pant hoots produced by arriving high-ranking males. Pant hoots are often produced in response (or in chorus) to a pant hoot initiated by another individual and these call exchanges might be socially relevant (Arcadi, 1996; Fedurek et al., 2013). So far, pant hoot chorusing has been proposed to be a low-cost bonding behaviour, adaptive to a species with a high degree of fission–fusion, and would thus play a role in maintaining social relationships (Fedurek et al., 2013; Mitani & Brandt, 1994; Mitani & Gros-Louis, 1998). We hypothesize that low-ranking individuals might chorus with high-ranking individuals' pant hoots to strengthen their relationships. Indeed, pant hoot chorusing might be important during co-feeding events since Fedurek et al. (2013) showed that male chimpanzee dyads engaged in pant hoot choruses more often on days when they spent time co-feeding. Overall, no study has yet investigated pant hoot response patterns or pant hoot choruses produced specifically in a feeding context so further research would be necessary.

Contrary to our findings, several studies have shown that pant hoots are mainly produced by high-ranking individuals and would advertise their social status (Clark & Wrangham, 1993; Fedurek et al., 2014). But these studies were investigating pant hoots produced across all contexts whereas it has since been shown that pant hoots are structurally complex and can encode information about the identity, age, dominance rank and activity of the caller (Fedurek et al., 2016). Notman and Rendall (2005) even hypothesized that there could be different subtypes of pant hoots according to the context of production. Therefore, the production patterns of these pant hoot subtypes might differ, and future research should consider the context of production of pant hoots. We also think that the recruitment effect of pant hoots produced upon arrival at food trees should be tested by observing potential recipients and their behavioural response to these calls.

Do Rough Grunts Appease Dominant Competitors?

Male chimpanzees produced rough grunts more frequently when joining a feeding party (i.e. 36% of events) than when being joined in a food tree (i.e. 14% of events). Remarkably, in both situations, this behaviour was largely seen in lower-ranking males and when party size was small, suggesting that overall feeding competition was not the driving force. Instead, we hypothesize that, in small parties, individual identity was more likely to play a role than in larger, more anonymous groups, similar to a 'dilution' effect, that is, the idea that the chances of each specific individual being targeted by an opponent (or predator) are inversely related to group size (Lehtonen & Jaatinen, 2016; Pappano et al., 2012). Also, victims of aggression can count on the support of allies (de Waal & Harcourt, 1992), suggesting that this is more probable when the party is large. Furthermore, males produced rough grunts more often when being joined by high-ranking males, suggesting that these calls could be directed at them, to avoid potential aggression.

We hypothesize that male chimpanzees produce rough grunts to inform others of the presence of food and therefore avoid misunderstandings or eventual aggression. The idea that animals disclose the possession of food to avoid aggression has been proposed for food calling in spider monkeys (Chapman & Lefebvre, 1990), tufted capuchin monkeys (Di Bitetti, 2005) and rhesus macaques (Hauser & Marler, 1993b; see also ; Clutton-Brock & Parker, 1995). In chimpanzees, rough grunt production depends on food quantity (Brosnan & De Waal, 2000; Hauser et al., 1993; Hauser & Wrangham, 1987) and encodes information about food type and quality (Slocombe & Zuberbühler, 2005, 2006), suggesting that these calls provide information about the food source, albeit not necessarily as a cooperative attempt to inform others but as a way to avoid conflict. Although rough grunts are short-distance signals, they can still be heard beyond the immediate visual range and could thus address individuals who are not in the immediate party. This would explain why the production of rough grunts when arriving at a food tree is correlated with dominance rank but not with the presence, or absence, of high-ranking individuals, since these calls could be directed at high-ranking individuals either present in the tree (i.e. to avoid direct aggression) or absent and potentially joining (i.e. to avoid later aggression). Ischer et al. (2020) showed that rough grunt production was higher after agonistic interactions, supporting the hypothesis that the function of this call is related to aggression. However, more detailed studies investigating the relationship between calling and aggression are needed to confirm, or refute, our hypotheses. Future research should also investigate the effect of party size and would need to take variables such as fruit availability or tree crown size into account to control for differences in competitive pressures.

Dual Function of Food-associated Calls

In socially complex situations, chimpanzees can produce distinct calls with different functions to address different audiences. Indeed, during aggressive interactions, the victims often produce two calls: screams to try and recruit support from bystanders and 'waa' barks to deter their aggressors by signalling their willingness to retaliate (Fedurek et al., 2015).

Feeding events are often associated with competitive or aggressive interactions (Muller & Mitani, 2005) but they can also present an opportunity to cooperate and strengthen social bonds (Samuni et al., 2018; Wittig et al., 2014). Here, we have provided evidence that, when arriving at food trees, chimpanzees produce both pant hoots and rough grunts to achieve different social functions and help mediate both cooperative and competitive interactions. Indeed, on the one hand, pant hoots seem to be directed towards socially important absent individuals (i.e. high-ranking males and social bond partners) to recruit them when arriving at a food tree, or towards arriving high-ranking males probably to chorus with them and strengthen their relationships. On the other hand, the function of rough grunts, when joining or being joined in a food tree, would be to avoid aggression, especially by higher-ranking males.

When chimpanzees arrive in a food tree, both pant hoot and rough grunts are produced towards specific individuals. The production of these calls seems to be recipient directed and thus meets one of the key criteria for intentionality (Townsend et al., 2017). Moreover, since both calls were produced in small rather than large parties and pant hoot production was higher in the absence of high-ranking males, it seems unlikely that the production of these calls would be based on arousal alone. These findings are adding to the corpus of evidence that chimpanzees have some voluntary control over their vocal production, which can be driven by intentional cognitive mechanisms (Crockford et al., 2012; Gruber & Zuberbühler, 2013; Schel et al., 2013). Investigating the recipients' behavioural response to these calls would allow us to determine whether they are also produced in a goal-directed way, another key criterion for intentionality.

Previous studies presented conflicting results regarding the effect of food type on call production. Indeed, contrary to some studies (Fedurek & Slocombe, 2013; Kalan et al., 2015; Schel et al., 2013) but consistently with others (Ischer et al., 2020; Leroux et al., 2021), our results did not show any effect of this ecological variable on call production. Feeding events are complex events composed of several phases, which are associated with different social and ecological factors. Our study focused on the production of calls during arrival events, which can be socially challenging. In this context, we expect individuals who vocalize to respond to this specific event and may, therefore, explain why call production was mainly driven by social variables. Future research should consider more detailed levels of context during feeding.

Our study focused on call production by adult males, but females also produce pant hoots and food grunts during feeding. However, the stakes of food competition and cooperation are different for females and their calling behaviour might differ accordingly. Again, further studies investigating food-associated call production by females are necessary to develop a more comprehensive understanding of the function of these calls.

Overall, our study shows that pant hoot and rough grunt vocalizations are produced to regulate cooperative and competitive interactions upon arrival at food trees, therefore playing an important role in chimpanzee fission–fusion societies. These results underline the importance of considering both cooperation and competition, especially when studying complex social events such as feeding. As already suggested by Muller and Mitani (2005), these two processes should not be opposed and examined separately but should rather be considered as complementary since animals often cooperate to compete with conspecifics.

Author Contributions

Alice Bouchard: Conceptualization, Methodology, Investigation, Formal analysis, Writing. **Klaus Zuberbühler:** Conceptualization, Methodology, Resources, Writing.

Acknowledgments

We are grateful to the Sonso field assistants (Sam Adue, Geresomu Muhumuza, Monday Gideon, and Chandia Bosco) and all the staff of the Budongo Conservation Field Station for assistance with data collection in Uganda. We thank the Uganda Wildlife Authority, the Ugandan National Council for Science and Technology, and the President's office for research permissions, as well as the Royal Zoological Society of Scotland for providing core funding for Budongo Conservation Field Station. Thanks to Bilgé Kimyonok for his technical support. We also thank Auriane Le Floch for comments on the manuscript. This research was supported by the University of Neuchâtel and the Swiss National Science Foundation (Project Grant #310030_185324 and NCCR Evolving Language, Agreement #51NF40_180888).

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Appendix

Table A1

IDs of the adult male chimpanzee subjects, with their age (at the beginning of the study), total focal time, Elo-rating scores and associated dominance rank

Focal ID	Age (years)	Focal time (h)	Elo-rating	Dominance
HW	24	88	1755	High-ranking
MS	26	87	1431	High-ranking
FK	18	60	1365	High-ranking
SM	24	63	1035	Nondominant
SQ	26	55	962	Nondominant
ZL	21	66	914	Nondominant
KT	23	83	890	Nondominant
PS	19	87	864	Nondominant
ZF	35	22	834	Nondominant
KZ	22	71	493	Nondominant
ZD*	16	10	482	Nondominant

Subjects in italics died in the respiratory disease outbreak in 2019.

* ZD was excluded from the analysis due to the short focal time (the subject was notoriously difficult to follow).

Table A2
Preferred grooming partners and preferred proximity partners, with the associated grooming-based and proximity-based dyadic sociality indices, DSI_G and DSI_P, respectively, for each study subject and each study period

Focal ID	Preferred grooming partners						Preferred proximity partners					
	ID1	DSI_G	ID2	DSI_G	ID3	DSI_G	ID1	DSI_P	ID2	DSI_P	ID3	DSI_P
Study period before outbreak (4 January 2018 to 26 February 2019)												
FK	HW	2.51	MS	0.82	ZL	0.72	HW	1.94	PS	1.23	SM	1.12
HW	MS	7.42	ZL	3.57	SQ	2.86	KT	3.15	MS	2.96	ZL	2.74
KT	HW	2.11	MS	1.87	ZL	0.92	HW	3.15	MS	1.55	FK	1.09
KZ	ZL	1.18	PS	0.87	SM	0.81	SQ	1.39	PS	0.95	ZF	0.91
MS	HW	7.42	PS	2.71	SQ	2.06	HW	2.96	SQ	1.98	KT	1.55
PS	MS	2.71	HW	2.36	ZL	1.85	HW	1.58	FK	1.23	MS	1.15
SM	HW	1.59	ZL	1.48	PS	0.81	HW	1.93	ZD	1.27	ZL	1.15
SQ	HW	2.86	MS	2.06	PS	1.33	MS	1.98	HW	1.79	KZ	1.39
ZD	ZL	2.14	PS	1.35	SQ	1.18	ZL	1.50	SM	1.27	SQ	1.01
ZF	MS	0.83	HW	0.66	ZL	0.46	HW	1.78	SQ	0.98	KZ	0.91
ZL	HW	3.57	ZD	2.14	PS	1.85	HW	2.74	ZD	1.50	SM	1.15
Study period after outbreak (1 June 2019 to 16 March 2020)												
FK	HW	1.51	ZL	0.65	SM	0.62	PS	1.43	HW	1.26	SM	1.14
HW	MS	5.17	ZL	3.26	FK	1.51	ZL	3.39	KT	2.83	MS	2.62
KT	MS	1.43	HW	1.41	PS	0.52	HW	2.83	MS	1.14	PS	0.77
MS	HW	5.17	PS	2.90	KT	1.43	HW	2.62	PS	1.26	KT	1.14
PS	MS	2.90	ZL	1.85	HW	1.07	FK	1.43	MS	1.26	HW	1.14
SM	HW	1.37	FK	0.62	MS	0.44	HW	1.73	FK	1.14	ZL	0.98
ZD	ZL	1.99	PS	0.46	HW	0.02	ZL	0.94	SM	0.24	PS	0.12
ZL	HW	3.26	ZD	1.99	PS	1.85	HW	3.39	PS	1.04	SM	0.98

Table A3
Structure of the generalized linear mixed models (GLMMs) used in this study

Subject's role	Call	GLMM	Response variable	Test variables	Random factor
Arriving in the food tree	Pant hoot Rough grunt	GLMM1 GLMM2	Call production (yes / no)	Dominance rank + food tree species + (number of individuals, presence of a high-ranking individual, a social bond partner or an association partner) in the entire party and in the group already present in the tree	Subject ID
Present in the food tree	Pant hoot Rough grunt	GLMM3 GLMM4		Dominance rank + food tree species + (number of individuals, presence of a high-ranking individual, a social bond partner or an association partner) in the entire party and in the arriving group	

All GLMMs have a binomial error structure and logit link function.

Table A4
Summary results of Spearman rank correlation tests to explore the correlation between the productions of both calls depending on the subject's role

Subject's role	Correlation tested	r_S	P
Arriving in the food tree	Pant hoot ~ Rough grunt	0.01	0.86
	Rough grunt ~ Pant hoot	0.01	0.84
Present in the food tree	Pant hoot ~ Rough grunt	0.07	0.14
	Rough grunt ~ Pant hoot	0.07	0.11

Table A5

Summary results of the model averaging for each variable included in the top set of submodels (ΔAICc < 2) and for each model used in this study

	Estimate	SE	LCI	UCI	Relative importance
GLMM1: Probability of producing a pant hoot when joining a food tree					
Number of individuals in the feeding party	−0.19	0.06	−**0.31**	−**0.07**	1.00
Presence of a preferred grooming partner in the feeding party	1.08	0.50	**0.10**	**2.07**	1.00
Presence of a high-ranking individual in the feeding party	−1.30	0.50	−**2.28**	−**0.31**	1.00
Presence of a preferred proximity partner in the feeding party	−0.11	0.31	−1.45	0.47	0.23
Presence of a high-ranking individual in the tree	0.05	0.27	−0.91	1.53	0.21
Dominance rank (Elo-rating)	−0.03	0.10	−0.49	0.16	0.16
GLMM2: Probability of producing a rough grunt when joining a food tree					
Number of individuals in the feeding party	−0.12	0.05	−**0.22**	−**0.03**	1.00
Dominance rank (Elo-rating)	−0.62	0.18	−**0.97**	−**0.27**	1.00
Presence of a high-ranking individual in the feeding party	0.26	0.42	−0.21	1.47	0.42
Presence of a preferred grooming partner in the tree	−0.28	0.52	−1.92	0.47	0.39
Presence of a preferred grooming partner in the feeding party	0.20	0.43	−0.38	1.81	0.27
Presence of a high-ranking individual in the tree	0.06	0.33	−1.01	1.50	0.24
Presence of a preferred proximity partner in the tree	−0.02	0.13	−1.06	0.49	0.07
GLMM3: Probability of producing a pant hoot when being joined in a food tree					
Number of individuals in the feeding party	−0.17	0.06	−**0.29**	−**0.05**	1.00
Dominance rank (Elo-rating)	−0.52	0.22	−**0.95**	−**0.09**	1.00
Presence of a high-ranking individual in the joining group	1.26	0.40	**0.46**	**2.05**	1.00
Presence of a preferred grooming partner in the feeding party	−0.27	0.51	−1.91	0.49	0.48
Presence of a preferred proximity partner in the feeding party	0.47	0.69	−0.38	2.35	0.38
Presence of a preferred grooming partner in the joining group	−0.03	0.18	−1.20	0.70	0.12
GLMM4: Probability of producing a rough grunt when being joined in a food tree					
Number of individuals in the feeding party	−0.17	0.05	−**0.26**	−**0.08**	1.00
Dominance rank (Elo-rating)	−0.83	0.19	−**1.21**	−**0.45**	1.00
Presence of a high-ranking individual in the joining group	1.74	0.33	**1.10**	**2.38**	1.00
Presence of a preferred grooming partner in the feeding party	0.04	0.20	−0.64	0.96	0.22
Presence of a preferred grooming partner in the joining group	−0.02	0.19	−0.90	0.68	0.21

LCI: lower 95% confidence interval; UCI: upper 95% confidence. Informative variables are in bold.

Table A6

Summary results of the model averaging for each variable included in the top set of submodels (ΔAICc < 2) and for each previously presented model (Table A5) rerun on a subset of the data without the other call type produced

	Estimate	SE	LCI	UCI	Relative importance
GLMM1b: Probability of producing a pant hoot when joining a food tree					
Number of individuals in the feeding party	−0.15	0.07	−**0.28**	−**0.02**	1.00
Presence of a high-ranking individual in the feeding party	−1.12	0.51	−**2.12**	−**0.12**	1.00
Presence of a preferred grooming partner in the feeding party	0.83	0.65	−0.11	2.15	0.82
Presence of a preferred proximity partner in the feeding party	−0.20	0.44	−1.83	0.33	0.27
Presence of a preferred proximity partner in the tree	−0.04	0.19	−1.21	0.59	0.13
Dominance rank (Elo-rating)	−0.01	0.07	−0.49	0.31	0.11
GLMM2b: Probability of producing a rough grunt when joining a food tree					
Dominance rank (Elo-rating)	−0.61	0.20	−**0.99**	−**0.22**	1.00
Number of individuals in the feeding party	−0.06	0.05	−0.17	0.02	0.74
Presence of a high-ranking individual in the tree	0.05	0.20	−0.54	1.07	0.17
Presence of a preferred grooming partner in the feeding party	0.03	0.19	−0.64	1.06	0.16
GLMM3b: Probability of producing a pant hoot when being joined in a food tree					
Number of individuals in the feeding party	−0.18	0.07	−**0.31**	−**0.05**	1.00
Dominance rank (Elo-rating)	−0.43	0.23	−0.88	0.02	1.00
Presence of a high-ranking individual in the joining group	1.09	0.46	**0.19**	**1.99**	1.00
Presence of a preferred proximity partner in the feeding party	0.21	0.50	−0.61	2.10	0.28
Presence of a preferred grooming partner in the feeding party	−0.15	0.40	−1.80	0.65	0.26
Presence of a high-ranking individual in the feeding party	0.09	0.33	−0.71	1.87	0.16
Presence of a preferred grooming partner in the joining group	−0.07	0.27	−1.54	0.60	0.15
GLMM4b: Probability of producing a rough grunt when being joined in a food tree					
Number of individuals in the feeding party	−0.17	0.05	−**0.27**	−**0.08**	1.00
Dominance rank (Elo-rating)	−0.78	0.20	−**1.17**	−**0.40**	1.00
Presence of a high-ranking individual in the joining group	1.72	0.37	**0.99**	**2.44**	1.00
Presence of a preferred proximity partner in the joining group	−0.08	0.26	−1.24	0.52	0.22
Presence of a preferred grooming partner in the feeding party	0.03	0.19	−0.63	1.02	0.18
Presence of a high-ranking individual in the feeding party	−0.03	0.21	−1.15	0.79	0.17

LCI: lower 95% confidence interval; UCI: upper 95% confidence. Informative variables are in bold. GLMMs 1b, 2b, 3b and 4b correspond to previously presented models GLMMs 1, 2, 3 and 4, respectively.

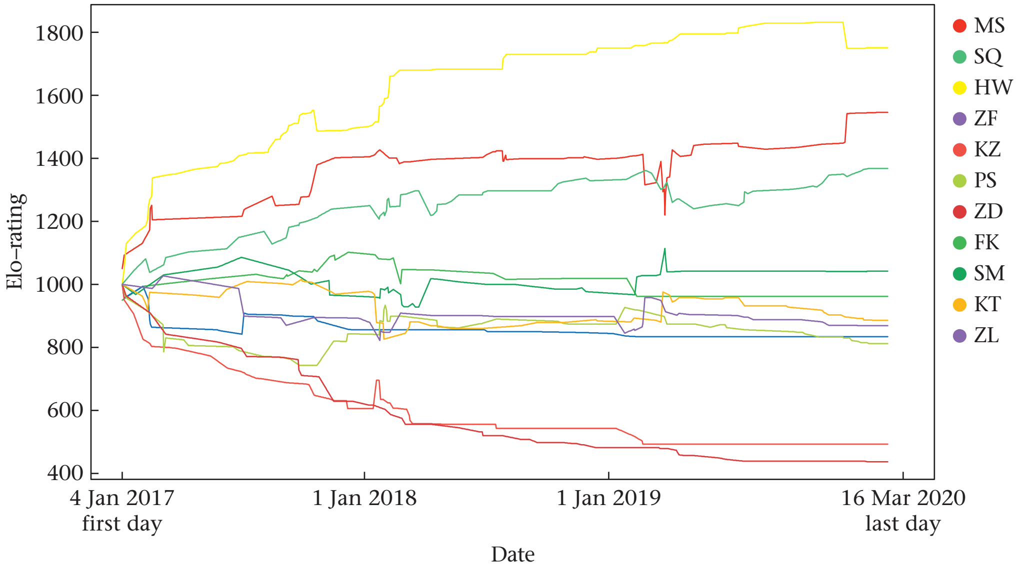

Figure A1. Changes in the Elo-rating scores of the 11 adult males of the Sonso community from 12 months before the study (4 January 2017) to the end of the first study period (16 March 2020).