

Social and ecological correlates of long-distance pant hoot calls in male chimpanzees

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Received: 31 December 2013 / Revised: 19 May 2014 / Accepted: 20 May 2014 / Published online: 3 June 2014
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Abstract Long-distance calls have a variety of functions in different animal species. However, where multiple functions are proposed for a single long-distance call type, little is known about their relative importance. Chimpanzees are one species where several functions have been proposed for their long-distance call, the pant hoot. In this study, we investigated the effect of social factors, including the rank of the caller, party size, fission–fusion rates, and the presence of estrus females as well as ecological factors including the type of food consumed and travel time, on male chimpanzee (*Pan troglodytes schweinfurthii*) pant hooting, in order to identify the key correlates of this behavior. The wild male chimpanzees of the Kanyawara community, Uganda, produced more pant hoots on days when there were frequent changes in the male, but not female, composition of the focal’s party. This factor accounted for the largest amount of variation in pant hoot production, and we found that males were more likely to repeat a call prior to rather than after fusion with other males, suggesting that the calls facilitate fusion. Pant hoots therefore seem to play a pivotal role in regulating grouping dynamics in chimpanzees. Our study also shows that pant hooting was positively correlated with the rank of the caller, the presence of parous females in estrus, and the consumption of high-quality food, suggesting that pant hoots signal social status or social bonds when between-male competition is high. This

study supports the view that pant hoots fulfill a complex social function.

Keywords Chimpanzee · Pant hooting · *Pan troglodytes* · Long-distance call · Fission–fusion

Introduction

Long-distance calls, or long calls, occur in a variety of animal species. Several different functions for such long calls have been suggested, including mate attraction, mate defense, territorial defense, predator avoidance, signaling the location and identity of dispersed individuals, signaling the caller’s social status, and advertising social bonds between callers (Waser 1977; McComb 1991; Geissmann 1999; Furmankiewicz et al. 2001; Zuberbühler 2001; Searcy and Nowicki 2005; Delgado 2006). Species-typical long calls often have several functions. For example, roars produced by male red deer (*Cervus elaphus*) function to both attract females (McComb 1991) and to repel males (Clutton-Brock and Albon 1979). Similarly, roars produced by Guereza colobus monkeys (*Colobus guereza*) might function both to regulate intergroup spacing (Harris 2006) and as alarm calls (Schel et al. 2009). Several functions of long calls, such as maintaining contact and mate guarding, have also been recognized in many bird species (Hall 2004). Such multiple functions of a single-call type are possible because the listener takes into account the context in which the call is produced when responding to it (Smith 1977; Wheeler and Fischer 2012). Therefore, studying contexts in which calls are produced can shed light on their function, and one way of achieving this is identifying social and ecological factors influencing their production.

Several, but not mutually exclusive, hypotheses have been also suggested to explain the function of “pant hoots,” the long-distance calls given by chimpanzees (*Pan troglodytes*).

Communicated by D. P. Watts

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Pant hoots might function to attract conspecifics to food sources or to signal the identity and location of the caller (Reynolds and Reynolds 1965; Marler and Hobbett 1975; Wrangham 1977). Pant hoots by males might also signal social status (Mitani and Nishida 1993; Clark and Wrangham 1994) or, in the case of chorusing, social bonds (Mitani and Brandt 1994; Fedurek et al. 2013). Chimpanzees are also more likely to call in the presence of specific individuals (Clark 1991, 1993; Mitani and Nishida 1993; Wilson et al. 2007). Rather than focusing on a single correlate of pant hooting, examining the relative influence of different factors is arguably a more objective approach that allows us to make predictions as to when these calls are most likely to be produced, and inferences about the functional value of the behavior. In this study, we used data on calling by male chimpanzees to test several hypotheses (summarized in Table 1) about social and ecological influences on pant hoot production.

Given the flexible nature of chimpanzee society (Chapman et al. 1995), pant hoots might play a pivotal role in maintaining contact with community members (Goodall 1986; Mitani and Nishida 1993). Such a role has been proposed for long calls in primates, such as spider monkeys, and other mammals forming fission–fusion societies, such as dolphins, bats, and African elephants (Furmankiewicz et al. 2001; Lammers et al. 2006; Leighty et al. 2008; Spehar and Di Fiore 2013). Producing these calls might therefore facilitate locating and joining other subgroups. Indeed, African elephants (*Loxodonta africana*) produce long-distance rumble

vocalizations to rejoin group members after periods of separation (Leighty et al. 2008) and long calls of tree-dwelling bats (*Nyctalus noctula*) attract conspecifics to the location from which they are given (Furmankiewicz et al. 2001). In chimpanzees, one study showed that pant hoots produced at feeding trees attract community members to the caller (Wrangham 1977). However, there is little other empirical data available to rigorously test whether pant hoots play a role in coordinating group movement in chimpanzees, especially in nonfeeding contexts. In this study, we tested this hypothesis on a number of different levels. Firstly, we examined the relative influence of fission–fusion rates on pant hoot rates within a given day. As chimpanzee males tend to form strong social bonds and associate more often with other males than females (Nishida 1983; Duffy et al. 2007; Gilby and Wrangham 2008), we predicted that, on a given day, focal pant hooting rates would correlate more with the focal rates of fission–fusion with other males than with females. Second, as pant hoots are sometimes given shortly after reunions with other community members (Reynolds and Reynolds 1965; Bygott 1979; Goodall 1986), they might result from fusion events rather than promoting them. We tested between these two alternative hypotheses by examining whether males were more likely to pant hoot immediately prior to or after fusion with others. Finally, we focused on instances where males called repeatedly and examined whether fusion was more likely to occur immediately after the call sequence or during the call sequence. If a function of pant hooting is to facilitate fusion with community members, males should stop calling once fusion occurs and thus fusion would be observed more after the last call in a sequence, than during a sequence. We also examine whether males pant hooted more on days when they travelled more, a pattern that we predict as males are more likely to fusion with others when they travel.

Pant hoots might also function to maintain individuals within a party (Reynolds and Reynolds 1965) and thus pant hoot rates should correlate positively with party sizes. If this is the case, male pant hoot rates should be associated more strongly with the average number of males than females in the focal's party, as chimpanzee males tend to form strong social bonds with members of the same sex (Gilby and Wrangham 2008).

Pant hoots might also be involved in male–male competition. If so, one factor influencing pant hooting may be social status of the caller. Such rank-related pattern of calling has been recognized in several primate species, including baboons (*Papio cynocephalus*) and black-crested macaques (*Macaca nigra*), where dominant males are more likely to give long calls than low-ranking males, suggesting that such calls may advertise social status and/or male quality (Kitchen et al. 2003; Fischer et al. 2004; Neumann et al. 2010). Similar rank-dependent patterns of long calling have been observed in chimpanzees (Mitani and Nishida 1993; Clark and

Table 1 Summary of the hypotheses on the function of male pant hooting

Hypotheses	Predictions
1. Male pant hooting facilitates fusion with other parties	Male pant hoot rates correlate with his fission–fusion rates with other males After a call, fusion with other males is more likely to occur than fission Fusion with other males is more likely to occur immediately after than before a call Males stop calling after fusion with other males has occurred
2. Male pant hooting facilitates the maintenance of large parties	Male pant hoot rates correlate with the number of males or females in his party
3. Male pant hoots are involved in male–male competition	Male pant hoot rates correlate with his dominance rank Male pant hoot rates are elevated on days when a parous female in estrus is present in his party Male pant hoot rates are elevated on days when he feeds on high-quality food

Wrangham 1994). We, therefore, examined whether pant hooting rates of the Kanyawara males depended on the social rank of the caller.

Male aggression rates increase in the presence of estrus females (Muller and Wrangham 2004). In addition, the level of male–male competition is much higher when a parous (i.e., a sexually mature female that have already given birth before) rather than a nulliparous female (i.e., young but sexually mature females that have not yet reproduced) is in estrus as chimpanzee males prefer to mate with parous females (Muller et al. 2006). Hence, if pant hoots are involved in male–male competition, pant hoot rates by males should be more frequent when a parous estrus female is present in the focal's party.

We also examined whether pant hooting rates varied depending on the type of food consumed. The availability of particular food types varies on a temporal basis and when preferred foods such as fruits are not available, Kanyawara chimpanzees consume less-preferred food such as leaves and piths (Wrangham et al. 1991, 1998). In addition, within the fruit category Kanyawara chimpanzees generally prefer non-fig to fig fruits (Wrangham et al. 1996; Emery Thompson and Wrangham 2008). Chimpanzees tend to form larger groups during seasons of fruit abundance (Conklin-Brittain et al. 1998; Basabose 2002), and the consumption of fruits, especially non-figs, correlates positively with energetic status (Emery Thompson et al. 2009). If pant hooting is involved in male–male competition males should pant hoot more on days when valuable food resources, such as non-fig fruits, are exploited.

Methods

Study subjects and study site

The study was conducted on the Kanyawara community in the Kibale National Park, located in western Uganda (0° 13'–0° 41' N and 30° 19'–30° 32' E). At the beginning of the study in October 2010, the community comprised 54 individuals (including 10 adult males and 14 adult females) and their home range occupied approximately 14 km² of the park in 2006 (Wilson et al. 2012). The Kibale forest is transitional between lowland rainforest and montane forest (Struhsaker 1975). The forest occupied by the Kanyawara chimpanzees is a mosaic of a semideciduous primary forest, regenerated forest, grasslands, and swamps (Chapman and Wrangham 1993). The community is well habituated and has been studied continuously since 1987 by the Kibale Chimpanzee Project and also from 1983 to 1985 (Isabirye-Basuta 1987; Wrangham et al. 1992). The study subjects were nine adult (i.e., ≥16 years old; estimated mean age at the beginning of the study in October 2010=34.77 (SD=13.18) years) and two subadult (15 years old each) males (Reynolds 2005).

Data collection

This study was approved by the Department of Psychology Ethics Committee at the University of York, and permission to conduct the study was granted by the Ugandan Wildlife Authority and the Ugandan National Council for Science and Technology.

Data were collected between October 2010 and September 2011. Focal animal sampling was the main method of data collection, and a randomly chosen male was followed for a whole day (i.e., from nest to nest). We recorded all vocal behavior of the focal male, including the context in which vocalizations were given (see below). In addition, we conducted instantaneous scan samples at 5-min intervals to record (i) the behavior of the focal male (i.e., travelling, feeding, and resting (including grooming)), (ii) the type of any food consumed by the focal (see below), and (iii) the composition of the focal male's party. The focal animal's party was defined as all individuals within 50 m from him.

We also collected data on the all pant grunts received and given by the focal male and all dyadic agonistic interactions (i.e., physical attack, chase, charge, displacements, etc. (Bygott 1979; Goodall 1986; Muller and Wrangham 2004)) involving the focal, where the winner and loser of the interaction were also recorded. Data collection resulted in a total of 185 days of focal observations.

From this total set, only days of data collection in which the focal was followed for at least 6 h were incorporated in the analyses ($N=169$; mean=549.98 min of direct focal observation/day). Table 2 shows a summary of the data collected.

Table 2 The rank, the number of focal follow days, and the number of pant hoots produced by focal males

Male ID	Rank ^b	Focal days	Number of calls
AJ	3	20	175
BB	4	18	59
ES	6	14	173
KK	1	19	220
LK	2	22	188
PB ^a	10	13	40
PG	7	15	68
ST	8	18	232
TJ ^a	5	12	95
TU	9	3	7
YB	11	15	63
Total		169	1,320

^a Subadult male

^b No. 1 denotes the highest rank

Data collected and calculation of measures

Pant hoots

A pant hoot usually consists of four distinctive phases: introduction, build-up, climax, and let down (Mitani and Gros-Louis 1998). In this study, a call was defined as a pant hoot only if it included the climax phase (which is the loudest part of the call that may include one or several “screams” given in succession (Mitani and Gros-Louis 1998)).

We divided the context of pant hooting into four categories: (i) travel (caller travelling), (ii) feeding (caller feeding or arriving at a feeding site), (iii) displaying (caller performing an intimidation display which consisted of the male running (sometimes bipedal) pilo-erect, and may include shaking vegetation, drumming on tree buttresses, or slapping the ground (Goodall 1986)), and (iv) resting (caller resting—not travelling, feeding, or displaying).

Focal pant hoot rates were calculated by dividing the total number of pant hoots produced by the focal individual on a given day by the duration of focal observation on that day.

Fission-fusion rates

The focal individual’s fission–fusion rates with males and females were based on the number of changes in the presence of males and females in the focal’s party, as recorded in the instantaneous scan samples of party composition over 1 day of data collection. For example, consecutive party composition scans were considered and if one or more males left or joined the party in one scan, compared with the previous scan, this was recorded as a single change in the composition of males in the focal’s party. The total number of changes in the composition of males (mean=6.33 changes/day, SD=3.95) and females (mean=6.52, SD=3.90) in the focal’s party on a given day was then divided by the number of hours of focal observation on that day. This represented the focal’s overall rate of fission–fusion with male or female community members.

Fission and fusion with other males before and after the call

1. Temporal association between pant hoot and fission–fusion events

To investigate whether pant hooting was temporally associated with male fission and fusion events and then whether calls are more likely to precede or to follow a caller’s fusion or fission with other males, we calculated the average number of males joining and leaving the focal’s party within two scans before and after the call. In this analysis, we incorporated only the data points where there were no other pant hoots given by the focal within two scans before and two scans after the call ($N=368$ calls, mean=36.80, and SD=20.69 calls/focal male)

so as to eliminate the potential influence of these calls on the investigated patterns. In other words, if several calls were given within a short period of time, we were not able to effectively establish which one of these calls resulted in a potential fusion event that followed, so we excluded these cases from analysis. We also excluded pant hoots given during feeding ($N=115$ out of 368) because of the possibility that independent attraction to food sources would confound the effects of pant hoots on fusion events.

2. Fusion with other males after and during a pant hoot sequence

A pant hoot sequence was defined as at least two calls, where the calls were separated by a time interval equal to or smaller than 10 min. We identified 273 call sequences (mean=24.73 and SD=15.13 call sequences/focal male). We tested the prediction that the focal is more likely to stop pant hooting once fusion with other males has occurred. In order to do this, we examined if fusion was more likely to occur in the two scans after the last call in the sequence (mean duration ‘after’ sequence=479.12 s, SD=86.39 s, sum of “after” sequence durations=130,800 s), compared with scans during the sequence (i.e., between the first and last call in the sequence; mean sequence duration=483.74 s, SD=443.64 s, sum of “within” sequence durations=132,060 s).

The number of males and females in the focal’s party

Average number of males and females in the focal’s party on a given day was calculated as the mean numbers of males or females in their party recorded across all scans on that day.

Time spent travelling

The proportion of time spent travelling by the focal male during a given day of data collection was established by dividing the number of scans in which the focal was observed travelling by the total number of scans.

Social rank

Each male was assigned an ordinal linear rank (1–11, where 1 is the highest ranking; Table 2). Following Muller and Wrangham (2004), the linear hierarchy was based on the outcomes of win–lose interactions combining pant grunt and agonistic interactions recorded during the study period using focal animal sampling. The analysis was carried out using Matman Software Package (version 1.1, Noldus Information Technology; de Vries 1993), and all male dominance hierarchies were significantly linear using a two-step randomization procedure with 10,000 iterations (de Vries 1993, 1995).

Food type consumed

If during the scan the focal male was observed feeding, the species and type of food consumed were recorded. We focused on three categories of food most commonly consumed by the Kanyawara chimpanzees: (i) ripe non-fig fruits, (ii) ripe fig fruits, and (iii) piths and leaves. Days of data collection were divided into three categories in terms of the type of food consumed by the focal (e.g., Emery Thompson et al. 2009). If more than 50 % of the focal's feeding time was spent consuming piths and leaves, the day was labeled as a "piths and leaves" day ($N=26$). If on a given day more than 50 % of focal's feeding time was allocated to consuming ripe fruits, the day was labeled either as a "fig fruit day" ($N=81$) or as a "non-fig fruit day" ($N=61$), depending on which of these two types of fruits accounted for the majority of the focal's feeding time within the fruit category.

The presence of an estrus female

Females are considered in estrus when their sexual swelling is maximally swollen and males tend to mate only with these females. For each day of data collection, we recorded whether ($N=61$) or not ($N=107$) a parous female ($N=12$) in estrus was present (i.e., during at least one party composition scan) in the focal male's party.

Statistical analysis

Linear mixed models (LMM) and generalized linear mixed models (GLMM) were the main statistical tools used in the analyses. In the analyses, focal ID was inserted into all the models as a random effect. There was no collinearity between the examined independent variables (variance inflation factor (VIF) of the independent variables were considerably below the value of 10 (mean=1.75)) allowing for the inclusion of all the independent variables in the same model. If multiple post hoc tests were carried out to determine differences between levels of a variable, we corrected the α level for significance using Sidak's adjustment equation (Sidak 1967) to control for family-wise error. All statistical analyses were carried out using STATA 12.0 software (StataCorp LP, College Station, TX, USA).

Models created

We first created an initial LMM with the rate of pant hoots given by the focal male in 1 day of data collection (i.e., pant hoots/hour) as the continuous dependent variable. We entered the following variables as independent variables: (i) the rank of the focal male (1–11), (ii) the average number of males in the focal's party, (iii) the average number of females in the focal's party, (iv) the focal's fission–fusion rates with males,

(v) the focal's fission–fusion rates with females, (vi) the presence of a parous female in estrus (0/1), (vii) the type of food consumed (i.e., non-fig fruits, fig fruits, and piths/leaves), and (viii) proportion of time spent traveling. We then selected an optimal model using the Akaike information criterion (AIC) method, which measures the goodness of fit and model complexity (Akaike 1974) with terms considered to improve the fit only if their exclusion from the model inflated AIC value by more than two units (Burnham and Anderson 2004).

Once the optimal model had identified the most relevant factors influencing pant hoot production rates, we created another model containing the optimal model variables and three key interactions that allowed us to better understand if these variables were exerting independent influences on pant hoot rates.

To investigate whether pant hooting preceded or followed fusion or fission with other males, we used exact Wilcoxon signed-rank tests. For these analyses, we averaged the number of fusion or fission events immediately before and after calls for each male ($N=10$).

To examine whether the focal is more likely to stop a calling sequence once fusion with other males has occurred, we created a GLMM with a binomial error structure. In this model, the dependent variable was the time period examined (0=the two scans after the last call in the sequence; 1=the scans between the first and last call in the sequence) and the independent variable was whether or not (0/1) other males joined the focal's party during the relevant scans. Focal ID and call sequence ID were set as random effects.

Results

The general context of pant hooting

Males pant hooted more while traveling (50.30 %) than while feeding (25.45 %), resting (16.60 %), or displaying (7.65 %).

The initial and optimal model of male pant hoot rates

In the full model, only the proportion of time spent traveling, fission–fusion rates with males, and the type of food consumed had significant effect (Table 3). The model with the lowest AIC also included the presence of parous estrus females (Table 4). Variables such as the average number of males and females in focal's party were not significant in either model.

Focal's fission–fusion rates with males and females

There was a positive relationship between male pant hoot rates on a given day and his fission–fusion rates with males but not

Table 3 The relationship between pant hoot rates and the investigated (independent) variables—the initial model

Independent variables	Coefficient	Standard error	z value	95 % conference interval	
Rank	-0.05	0.03	-1.88	-0.10	0.00
Time travel	0.02	0.01	2.83**	0.01	0.05
Average number of males	0.00	0.03	0.06	-0.05	0.06
Average number of females	0.02	0.03	0.85	-0.03	0.08
Fission–fusion rates with males	0.77	0.20	3.80***	0.37	1.17
Fission–fusion rates with females	-0.07	0.21	-0.37	-0.48	0.33
Presence of estrus female	0.26	0.14	1.87	-0.01	0.52
Food type	0.17	0.07	2.43*	0.03	0.31

Dependent variable: pant hoot rates; all independent variables included; random effect: focal ID; AIC=358.35

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$ (LMM)

females (Tables 3 and 4). Fission–fusion rates with other males accounted for the greatest amount of variation in the data (Table 4), and males also pant hooted more on days when they traveled more (Table 4).

Chimpanzee grouping dynamics and fission–fusion rates can be influenced by both the availability of particular food types and the presence of a female in estrus (Reynolds 2005). In order to examine if these factors interacted with male fission–fusion rates to influence chimpanzee pant hoot rates, we examined interaction terms between them. While there was no significant interaction between the effects fission–fusion rates with males and food type consumed had on the rate of pant hooting (LMM: $\beta \pm SE = -0.23 \pm 0.17$, $z = 1.36$, $P = 0.174$), there was a significant interaction between fission–fusion rates with males and the presence of an estrus female in terms of their effect on pant hoot rates ($\beta \pm SE = 0.90 \pm 0.26$, $z = 3.51$, $P < 0.001$). The positive relationship between pant hoot rates and fission–fusion rates with males was stronger on days when a parous estrus female was present (Fig. 1).

Temporal association between pant hoot and fission-fusion events

Of pant hoot events, 31.25 % ($N = 115$ out of 368) were associated with a change in the composition of males in the

focal's party immediately before or after the call. On a finer level, pant hoots were significantly more associated with males joining (25.27 % ($N = 93$)) than leaving (10.32 % ($N = 38$)) the caller's party (exact Wilcoxon signed-rank tests: $Z = -2.80$, $N = 10$, $P = 0.002$).

When only fusion events were analyzed, more males tended to join the caller's party immediately after (median = 0.27, IQR = 0.40) than before (median = 0.15, IQR = 0.24) the call (exact Wilcoxon signed-rank tests: $Z = -1.68$, $N = 10$, $P = 0.105$).

Fusion with other males after and during a pant hoot sequence

If males called repeatedly, they were likely to stop calling once fusion with other males had occurred. Fusion was significantly more likely to occur in the period immediately after the last call in a sequence, than during the sequence (GLMM: $\beta \pm SE = -0.65 \pm 0.27$, $z = -2.37$, $P = 0.018$; Fig. 2).

The presence of a female in estrus

Males pant hooted more often on days when a parous female in estrus was present (Table 4) and, as described above, there was a significant interaction between the presence of a parous estrus female and male fission-fusion rates (Fig 1).

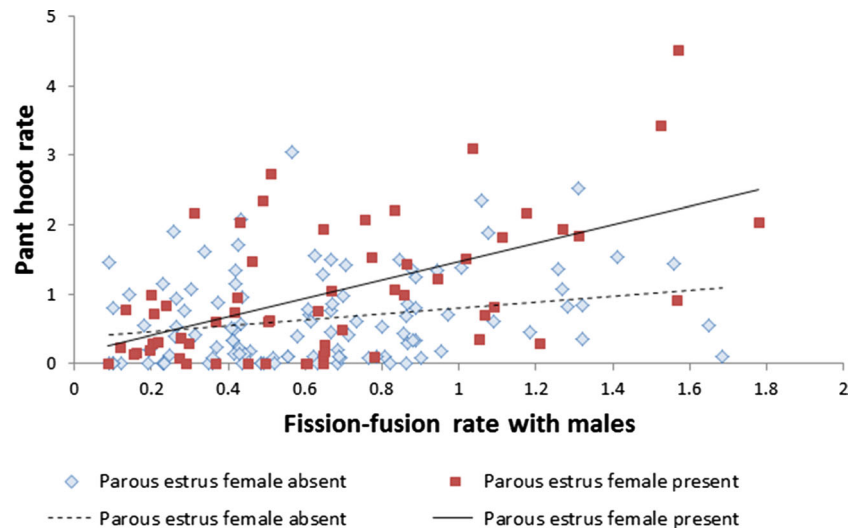
Table 4 The relationship between pant hoot rates and the investigated (independent) variables—the optimal model

Independent variables	Coefficient	Standard error	z value	95 % conference interval	
Time travel	0.02	0.01	2.74**	0.01	0.04
Fission–fusion rates with males	0.72	0.13	5.39***	0.46	0.98
Presence of estrus female	0.32	0.10	3.04**	0.11	0.53
Food type	0.16	0.07	2.27*	0.02	0.30

Dependent variable: pant hoot rates; random effect: focal ID; AIC=354.46

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$ (LMM)

Fig. 1 The relationship between daily pant hoot rates (call/h) and fission–fusion rates with males (fission–fusion/h) depending on whether or not a parous estrus female was present in the focal male party on that day. Lines represent linear regression lines



Type of food consumed

Another strong predictor of male pant hooting was the type of food consumed (Table 4). Figure 3 shows that males pant hooted more often on days when they consumed mostly non-fig fruits rather than fig fruits (LMM: $\beta \pm \text{SE} = 0.852 \pm 0.13$, $z = 4.07$, $P < 0.001$) or, although not significantly, piths/leaves ($\beta \pm \text{SE} = -0.40 \pm 0.19$, $z = -2.09$, $P = 0.036$; Sidak-corrected α level = 0.025).

This pattern might be however confounded by the possibility that males were more likely to pant hoot when arriving at feeding trees (e.g., Clark and Wrangham 1994) containing non-fig fruits than other food types, so as to attract others to high-quality food. However, a similar pattern emerged when pant hoots produced in feeding contexts were excluded from the analyses: males produced more pant hoots on days when their diet was dominated by non-fig fruits than by figs ($\beta \pm \text{SE} = 3.87 \pm 1.13$, $z = 3.44$, $P = 0.001$) or, although not significantly, piths and leaves ($\beta \pm \text{SE} = -3.41 \pm 1.71$, $z = -2.00$, $P = 0.046$; Sidak-corrected α level = 0.025).

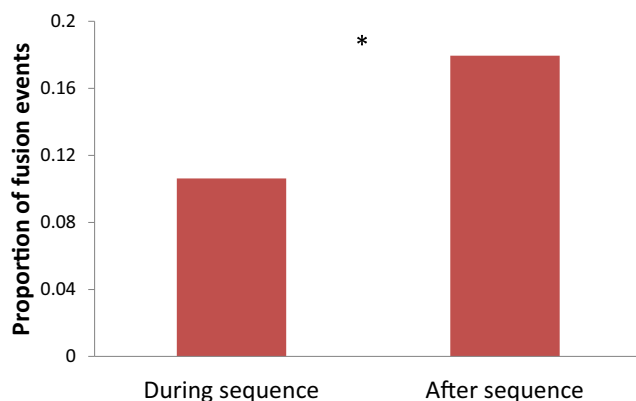


Fig. 2 The proportion of events in which males joined the caller's party during a pant hoot sequence and after the last call in a pant hoot sequence (GLMM; $*P \leq 0.05$; random effects: focal ID and call sequence ID)

Although different food sources may require different travel times, there was no significant interaction between the type of food consumed and travel time in terms of their effect on pant hoot rates ($\beta \pm \text{SE} = -0.01 \pm 0.01$, $z = -1.11$, $P = 0.269$).

Rank

Although the variable rank was not included in the optimal model, in the initial model, high-ranking males tended to call more often than low-ranking ones ($P = 0.060$).

Pant hooting and the number of males and females in the party

There was no significant relationship between the average number of either males or females in the focal's party and pant hoot rates produced by him (Tables 3 and 4).

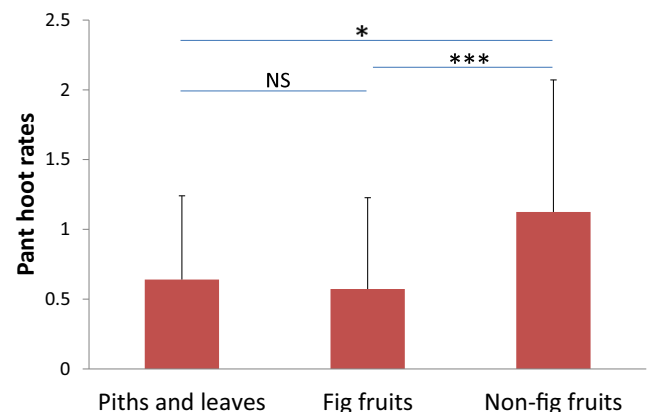


Fig. 3 Mean pant hoot rates (call/h) as a function of the type of food that the focal male spent most of his feeding time consuming on a given day (LMM; $***P \leq 0.001$; $*P \leq 0.05$; NS not significant; random effect: focal ID; error bars represent 1 SD)

Discussion

Overall, our study supports the idea that pant hoots play an important role in facilitating fusion with other individuals and regulating grouping dynamics (Reynolds and Reynolds 1965; Goodall 1986). Daily fission–fusion rates with other males was the most important factor in both our initial and optimal models and explained the most variance in pant hooting behavior. Pant hooting was more likely to be temporally associated with fusion than fission events, and more male fusion events tended to occur immediately after than before a focal pant hoot. Importantly, males were more likely to stop calling once fusion has occurred. These results suggest that although pant hoots are sometimes produced immediately after reunion with community members (Goodall 1986), these calls usually facilitate rather than are a consequence of fusion.

Our findings are in line with other studies on mammals, including primates, that live in groups with high fission–fusion dynamics (Aureli et al. 2008), indicating a pivotal role of long-distance calls in modulating grouping patterns (Furmankiewicz et al. 2001; McComb et al. 2003; Spehar and Di Fiore 2013). For example, in white-bellied spider monkeys (*Ateles belzebuth*), subgroups that produced long-distance calls were more likely to fusion with community members than those that did not (Spehar and Di Fiore 2013). The fact that chimpanzee pant hoots are individually distinctive also makes these calls good candidates for mediating grouping decisions between dispersed individuals (Marler and Hobbett 1975; Mitani et al. 1996).

The finding that the number of changes in the composition of males rather than females in the focal parties was associated with male pant hoot production is in line with the fact that male chimpanzees tend to form stronger social bonds with males than with females. Therefore, signals mediating grouping decisions such as pant hoots are more likely directed to members of the same sex. In this respect, pant hoots are similar to other calls frequently given by males, such as food-associated calls (Fedurek and Slocombe 2013). This does not mean that female grouping dynamics are not influenced by male pant hooting, but rather that male pant hoots are more associated with mediating grouping decisions with other males than females. Given that food-associated calls have been recently shown to be produced selectively to specific males (e.g., high-ranking friends (Schel et al. 2013)), future research could investigate whether pant hoots are given to facilitate fusion with specific individual males (e.g., close friends) within the community.

An alternative interpretation, however, is that pant hoots rather than being involved in localizing community members, function to reduce the costs of fusion with a party that has already been located by the caller. Aggression commonly occurs after a reunion between community members (Nishida et al. 1999; Muller 2002). Therefore, on days when

the rates of fission and fusion are high, the uncertainty with regard to the occurrence of aggression between party members is high (e.g., Aureli and Schaffner 2007). Signaling social bonds between pant hooting individuals (e.g., Fedurek et al. 2013) or the social status of the caller might be potentially effective strategies minimizing the costs of potential male–male aggressive interactions that often follow fusion.

As shown in a previous study on chimpanzees (Mitani and Nishida 1993), there was no relationship between the number of other males in the focal's party and the rates of pant hoots (Mitani and Nishida 1993). Therefore, there is little support for the hypothesis that pant hooting coordinates the maintenance of large male parties in chimpanzees (Reynolds and Reynolds 1965).

Our study is in line with previous studies showing that high-ranking males tend to produce more pant hoots than low-ranking ones (Clark 1993; Mitani and Nishida 1993; Clark and Wrangham 1994). Although the rank of the focal did not predict pant hoot rates as strongly as, for example, fission–fusion rates, high-ranking males tended to call more than low-ranking ones. Therefore, pant hoots may have been shaped by sexual selection to advertise high quality of the caller or his competitive ability, a function that has been attributed to long-distance calls in a variety of animals, including tree frogs (*Hyla microcephala*) (Schwartz 1986), pied flycatchers (*Ficedula hypoleuca*) (Gottlander 1987), red deer (McComb 1991), and baboons (Kitchen et al. 2003). However, more studies are needed, focusing on receiver reactions to pant hoots, to address this hypothesis thoroughly in chimpanzees.

Males were more likely to give pant hoots on days when the majority of food consumed consisted of high-quality food, such as non-fig fruits. On a proximate level, one explanation of this result might be that a higher energetic value of non-fig fruits in comparison to other food types (Emery Thompson et al. 2009) allows males to perform pant hoot displays (which may be arousal driven) more often on days when the diet is dominated by energy-rich foods. On an ultimate level, the elevated level of male pant hooting might be the result of an increased degree of competition for preferred food such as non-fig fruits. More specifically, pant hoots as potentially both signals of social status (e.g., Clark and Wrangham 1994) and tools for building coalitions against other males (e.g., Fedurek et al. 2013), might enhance male effectiveness in competing for these valuable food sources.

The fact that males were more likely to pant hoot on days when a parous female in estrus was present further supports the view that these calls are signals involved in male–male competition. Therefore, as in the case of the type of food consumed, male pant hooting might contribute positively to male effectiveness in competing for a valued resource. Indeed, when a parous female in estrus was present, the relationship between male pant hoot rates and his fission–fusion rates with

other males was stronger. Thus, as males joining a party containing a parous estrus female are potential competitors for males already present in that party, it is possible that pant hoots mitigate the costs of fusion with such parties. More research, however, is needed to test this hypothesis directly.

Our results contrast with those of Mitani and Nishida (1993) who failed to find an association between pant hoot rates and the presence of estrus females. However, it is important to note that Mitani and Nishida (1993) did not distinguish between parous and nulliparous females in estrus, which may explain this inconsistency. As we focused on the calling behavior of males when a parous estrus female was present in the focal male's party, future research is required to investigate whether pant hoots attract estrus females into the party if they are available in the community (e.g., Wrangham 1977).

The multiple social and ecological correlates of pant hooting we have identified indicate that pant hoots fulfill several functions. This finding is consistent with other studies on long-distance calls, especially in other primates. For example, loud calls in white-bellied spider monkeys function to regulate grouping decisions between dispersed individuals and also as a signal of social status of the caller (Spehar and Di Fiore 2013). Multiple functions, such as facilitating group cohesion, mate attraction, mate defense, and predator avoidance, have been attributed to long-distance "pyow" calls in male blue monkeys (*Cercopithecus mitis stuhlmanni*) (Fuller 2013), and similar functional versatility of "pyow" calls has been recognized in putty-nosed monkeys (*Cercopithecus nictitans martini*) (Arnold and Zuberbühler 2013). Such multiple functions within a single type of vocalization can be supported by listeners taking into account the context of emission when responding to the call (Smith 1977; Wheeler and Fischer 2012) or subtle context-specific acoustic differences occurring within the call type (e.g., Fischer et al. 2002; Slocombe and Zuberbühler 2006). Although chimpanzee pant hoots have been shown to vary in fine acoustic structure according to broad context of emission (Clark and Wrangham 1993; Notman and Rendall 2005), further research is required to examine if the different possible functions identified here are marked by differences in fine acoustic structure.

Taken together, our results suggest that pant hooting plays several social functions. Facilitating fusion with community members seems to be an especially important function of these calls. These results are consistent with the view that a pant hoot, as a long-distance call, plays an important role in mediating movements of the community and facilitating reunions between parties. However, the fact that pant hoots were more likely to be given when high-quality food or a female in estrus was present, suggests that these calls fulfill other social functions, such as signaling male social status or social bonds on days when competition for valuable resources is high.

Acknowledgments The authors would like to thank the directors of the Kibale Chimpanzee Project, Richard Wrangham and Martin Muller, for allowing them to conduct this research on the Kanyawara chimpanzees as well as for commenting on a previous version of the paper. The KCP field manager Emily Oтали and KCP field assistants Francis Mugurusi, Solomon Musana, James Kyomuhendo, Wilberforce Tweheyo, Sunday John, and Christopher Irumba, who were extremely helpful during the fieldwork are also thanked. The authors also thank Stuart Semple and Geoffrey Hall for helpful comments on a previous version of the draft and Simon Townsend for statistical advice. Comments and suggestions were provided by the editor David Watts, and two anonymous reviewers substantially improved the paper. PF was funded by a BBSRC studentship, a Leakey Foundation General Grant, and an American Society of Primatologists General Small Grant.

Ethical standards Permission to conduct the study was granted by the Ugandan Wildlife Authority and the Ugandan National Council for Science and Technology. The study complied with the current laws of Uganda.

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