



Pant hoot chorusing and social bonds in male chimpanzees



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Vocal interactions, such as call exchanges or chorusing, are common behaviours in many animal species and their function has often been attributed to social bonding. However, few studies have investigated the effectiveness of vocalizations as bonding signals in comparison to other affiliative behaviours. We tested the hypothesis that male chimpanzee, *Pan troglodytes schweinfurthii*, pant hoot chorusing, a common behaviour in these primates, is a reliable but also flexible signal of affiliative relationships. The results of our study, conducted on the Kanyawara community of chimpanzees in Uganda, show that males were more likely to join in with the pant hoot of preferred long-term social partners to form a chorus. This supports the hypothesis that this behaviour is a good indicator of strong or long-term social bonds between male chimpanzees. However, our results also show that pant hoot chorusing reliably reflects short-term affiliations between males. For instance, male dyads were more likely to be involved in affiliative behaviours, such as reciprocated grooming, joint nonvocal displays and coalitions, on days when they chorused together, compared to days when they did not. This pattern applied to both preferred and neutral social partners. Moreover, on a short-term basis chorusing was a better indicator of other affiliative behaviours than grooming. We suggest that in male chimpanzees pant hoot choruses are efficient signals of short-term affiliative relationships. We conclude that potentially low-cost bonding behaviours such as coordinated vocal displays might be especially adaptive in highly fluid fission–fusion societies where grouping patterns are often unpredictable.

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Vocal interactions such as call exchanges, choruses or duets, are common phenomena in the animal kingdom, ranging from insect to mammal species (Oda 1996; Gerhardt et al. 2000; Geissmann 2002; Bailey 2003; Hall 2004; Schulz et al. 2008). The ultimate function of vocal displays such as duet songs has often been attributed to social bonding, for example in many pair-living bird species (Hall 2004). In primates, the evolutionary function of call exchanges or chorusing has also been linked to social bonding because well-affiliated individuals or kin are more likely to interact vocally than less affiliated ones (gorillas, *Gorilla gorilla*: Harcourt & Stewart 1996; rhesus macaques, *Macaca mulatta*: Hauser & Marler 1993; squirrel monkeys, *Saimiri* spp.: Biben 1993; Soltis et al. 2002; spider monkeys, *Ateles geoffroyi*: Ramos-Fernandez 2005; ring-tailed lemurs, *Lemur catta*: Oda 1996; and siamangs, *Symphalangus syndactylus*: Geissmann & Orgeldinger 2000). More specifically, it has been suggested that in primates vocal interactions play a similar bonding role to grooming (Dunbar 1993; McComb & Semple 2005; Greeno & Semple 2009), which is a well-

established bonding behaviour in these animals (Dunbar 1988). However, few studies have addressed the specific question of how reliably vocal interactions reflect strong social bonds between individuals in comparison to other well-established bonding indicators in primates. We aimed to address this issue using data on chimpanzee chorusing.

Male chimpanzees, *Pan troglodytes*, form strong and durable social bonds that appear crucial in facilitating coalitions and alliances, which are in turn necessary to obtain high social status and associated benefits (Nishida 1983; Duffy et al. 2007; Gilby & Wrangham 2008; Mitani 2009). In chimpanzees, several indicators of social bonds have been recognized. As in other primates, both reciprocated grooming and mutual support in agonistic interactions are widely considered to reflect strong social bonds (Hemelrijk & Ek 1991; Muller & Mitani 2005; Mitani 2009). However, these well-established bonding behaviours in primates are costly. For example, interactions such as grooming are time consuming and both grooming and the formation of coalitions require certain circumstances to take place. Grooming, for instance, takes place mainly during resting time, whereas coalition formation can only occur during agonistic interactions. One could imagine, therefore, that a more flexible bonding behaviour, which incurs fewer costs and could be deployed in a wider variety of

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situations than the above-mentioned behaviours, would be advantageous. Vocal interactions are a good candidate for this (Dunbar 1993), mainly because calls can be exchanged during activities such as travelling or foraging, which are incompatible with standard affiliative interactions, such as grooming. In contrast to grooming, vocal interactions also take less time and do not necessitate potentially risky close physical proximity between partners.

One type of vocalization that may reflect social bonds in chimpanzees is the pant hoot: the long-distance species-specific call that is commonly produced by male chimpanzees. Traditionally, it has been suggested that these calls function to attract conspecifics to food sources or to maintain contact with or localize other parties within a community, and maintain intercommunity spacing (Reynolds & Reynolds 1965; Marler & Hobbet 1975; Wrangham 1977; Ghiglieri 1984; Mitani & Nishida 1993; Wilson et al. 2007). Other studies have suggested, however, a more complex social role for pant hoots. For example, party size and composition have been put forward as important factors influencing the frequency with which individuals pant hoot (Clark 1991, 1993; Mitani & Nishida 1993; Wilson et al. 2007).

However, most of these studies neglected the chorusing aspect of pant hooting when investigating the function of this call. A characteristic feature of pant hooting is that chimpanzees in the same party often pant hoot at the same time by performing a so-called 'pant hoot chorus' or 'joint pant hoot' (Ghiglieri 1984; Clark Arcadi 1996). The basic acoustic structure of the call, especially the gradual build-up phase, seems to have been shaped in a way that allows others to join in the display (P. Fedurek, unpublished data). A previous study showed that bonded males, who associate and support each other in conflicts, pant hoot in choruses more often than nonbonded males (Mitani & Gros-Louis 1998). Males can also actively adjust the acoustic structure of their calls to the partner's one (Mitani & Brandt 1994; Mitani & Gros-Louis 1998). These studies suggest that pant hoot chorusing plays a role in social bonding between male chimpanzees (Mitani & Brandt 1994).

In this study, we built on previous research into pant hoot chorusing and examined in detail whether pant hoot chorusing is a reliable indicator of strong long-term social bonds among male chimpanzees (Mitani & Brandt 1994; Mitani & Gros-Louis 1998). To test this bonding hypothesis, we investigated whether a male was more likely to form a chorus by joining a pant hoot produced by a long-term preferred social partner, rather than a neutral social partner.

We also tested the hypothesis that joint pant hooting reflects short-term affiliations between males. The fission–fusion social structure of chimpanzee society (Nishida 1979; Chapman et al.

1995) means that grouping patterns in this species tend to be fluid and unpredictable and valuable long-term social partners are not always available. A flexible, in terms of partner choice, signal that indicates short-term affiliations between individuals, who are not necessarily well affiliated on a long-term basis but find themselves in the same party, may therefore be advantageous.

To test this hypothesis we examined whether dyad partners were more likely to be involved in interactions that are generally regarded as markers for strong social bonds in chimpanzees, such as reciprocated grooming, support in agonistic interaction and joint nonvocal displays (Hemelrijk & Ek 1991; Muller & Mitani 2005; Fedurek & Dunbar 2009; Mitani 2009), on days when they chorused together than on days when they did not. We then investigated whether these short-term correlates differed between long-term preferred and 'neutral' social partners. Second, we compared joint pant hooting and reciprocated grooming in terms of the probability with which these two behaviours co-occurred with other affiliative interactions, such as tolerated co-feeding and the formation of coalitions, on a short-term basis. If, in fact, pant hoot chorusing is a more flexible bonding behaviour than grooming, we expected that, on a short-term basis, chorusing would be a better indicator of these affiliative interactions than grooming.

METHODS

Study Subjects

The study was conducted on the Kanyawara community of wild chimpanzees in the Kibale National Park in Uganda. At the beginning of the study in October 2010 the community comprised 54 individuals (including 10 adult males and 14 adult females). The home range of the community was approximately 14 km² in 2006 (Wilson et al. 2012). The community is well habituated and has been studied regularly since 1987 by the Kibale Chimpanzee Project (Wrangham et al. 1992). Study subjects were 11 males, including nine adults and two subadults (see Table 1). Permission to conduct the study was granted by the Ugandan Wildlife Authority and the Ugandan National Council for Science and Technology.

Data Collection

The focal animal was followed for a whole day (i.e. from nest to nest). Fieldwork was conducted between October 2010 and September 2011 and resulted in 185 days of focal observations (mean = 549.13 min of direct focal observation per day and

Table 1
Summary of the data collected on the focal males

Male ID	Age (years)	Rank	Focal days	Chorus days	Grooming days	Coalition days	Display days	Co-feeding days
AJ	36	3	20	12	17	6	9	19
BB	44	4	18	7	16	2	1	16
ES	16	6	14	12	7	2	4	13
KK	25	1	19	17	19	5	4	19
LK	28	2	22	19	20	5	7	18
PB*	15	10	13	7	9	1	3	10
PG	22	7	15	10	12	1	6	12
ST	55	8	18	15	15	7	2	18
TJ*	15	5	12	7	6	0	1	12
TU	50	9	3	2	3	1	0	3
YB	37	11	15	9	11	1	2	10

Age: estimated age of the male in October 2010 (in years; an asterisk denotes subadult male); rank: dominance rank (1–11); focal days: number of focal follow days (where focal animal was followed for at least 6 h ($N = 169$)); chorus days: number of days on which the focal animal was involved in a pant hoot chorus with another male; grooming days: number of days on which the focal animal was involved in reciprocated grooming with another male; coalition days: number of days on which the focal animal formed a coalition with another male; display days: number of days on which the focal animal performed a joint nonvocal display with another male; co-feeding days: number of days on which the focal animal was involved in tolerated co-feeding with another male.

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