Male chimpanzee vocal interactions and social bonds

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ABSTRACT

Vocal interactions, such as call exchanges or choruses, are common behaviours in animals and their function has been often linked to social bonding. In this study, I examined the relationship between two types of vocal behaviour common in chimpanzees, pant hoot chorusing and food calling, and social bonds between males. The results of this study, which was conducted on the Kanyawara community of chimpanzees (*Pan troglodytes schweinfurthii*) in the Kibale National Park, Uganda, show that both pant hoot choruses and food-associated calls reliably reflect social bonds between males. For example, males were more likely to join in another male's pant hoot when a well affiliated male was calling. Males, irrespective of the long-term affiliation status between them, were also more likely to be involved in grooming or form coalitions on days when they chorused together, suggesting that chorusing is also a flexible bonding behaviour operating on a short-term basis.

Males were also considerably more likely to produce food-associated calls when feeding in close proximity to well affiliated males than to less affiliated ones or females. Importantly, a male feeding partner was more likely to remain with the focal until the end of a feeding bout if the focal food called at the onset of this bout, suggesting that these vocalisations mediate feeding decisions between affiliated males.

The results of my study suggest that these two types of vocalisations play important functions in chimpanzee fission-fusion societies. Pant hoot chorusing, for example, might facilitate the occurrence of other affiliative interactions between individuals who are not necessarily long-term preferred social partners. Food-associated calls, on the other hand, might facilitate anticipation of each feeding decision which in turn facilitates individuals remaining in proximity or in the same party. Both these types of vocalisations, therefore, might mitigate the costs of living in unstable societies formed by these primates.

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AUTHOR’S DECLARATION

This dissertation is solely my own work, except where indicated in the Acknowledgements and below.

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CHAPTER 1: General introduction

What it is communication?

Interaction of any kind between organisms usually involves communication, which in social animals is crucial for survival at all stages of an individual's life (Bradbury and Vehrencamp 2011). In many animals, and especially in mammals, communication between offspring and parents is crucial for effective rearing of offspring, and all sexually reproducing animals communicate so as to find a mating partner with which to reproduce (Alcock 2009). In many social animals, communication between individuals is important in critical for survival activities such as finding food or avoiding predators (Davies et al. 2012).

Communication is broadly defined as a behaviour produced by one individual (sender) that changes the behaviour or future behaviour of another individual (receiver) (Bradbury and Vehrencamp 2011). If such behaviour is adaptive (i.e., it has been shaped by natural selection for the very purpose of changing the behaviour of other individuals), it is termed as signalling behaviour, and its product as a signal (Davies et al. 2012). For a signal to be effective, it needs to convey information, which is possible if there is a high correlation between the occurrence of a given signal and the behavioural or external context in which it is given. Consequently, the function of signalling is reducing the receiver's uncertainty about sender's future behaviour (e.g., aggressive or affiliative behaviour towards the receiver) or the probability of a given event in the environment (e.g., the presence of a predator) (Searcy and Nowicki 2005; Bradbury and Vehrencamp 2011). In addition, especially in situations where the interests of the sender and the receiver do not converge (and therefore there is a possibility of manipulating receivers by producing signals deceitfully (Johnstone and Grafen 1992)), in the course of evolution receivers shaped the nature of a signalling behaviour in a way that it is costly to produce (and therefore difficult to fake) (Zahavi 1975; Zahavi 1977a; Grafen 1990). Signalling, therefore, usually benefits both the sender and the receiver (Zahavi and Zahavi 1997; Bradbury and Vehrencamp 2011).

Ways to study communication

Signalling behaviour, like other types of adaptive behaviour, can be explained in four different ways (Tinbergen 1963) that are considered proximate or ultimate levels of explanation.

1) Mechanism (proximate): One way to investigate a given behaviour is by understanding its immediate causation or, in other words, how bodies generate this behaviour. For example, a vocal behaviour can be stimulated by certain environmental conditions that in turn trigger hormonal or neural changes stimulating certain muscles and organs to produce a sound.

2) Ontogeny (proximate): We can also study a given behaviour in terms of its development and examine how it is acquired during ontogeny. For example, an animal’s vocal repertoire could be a result of a long-term process of learning acoustic features of calls produced by other individuals.

3) Function (ultimate): Examining why a given behaviour is adaptive is another way of studying it. For example, by vocalising animals might advertise their prime body condition or a high social status, which in turn might attract mates or deter rivals, and therefore increase an individual’s reproductive success.

4) Phylogeny (ultimate): We can also investigate a given behaviour by examining how it has changed during the evolutionary past. For example, by comparing closely related species we can examine how a complexity of a vocal repertoire has been changing in a lineage.

The first two types of explanations are termed as proximate or immediate explanations as they seek to explain how a body produces these behaviours on a physiological basis or how this behaviour develops during an individual’s lifetime. The last two types of explanations are termed as evolutionary or ultimate explanations of a given behaviour as their purpose is to explain its adaptive function or how this behaviour has developed during evolution. To fully understand a given behaviour it needs to be studied on all four levels. However, it is often beyond the scope of a single researcher to tackle all four levels and it is important to note that proximate and ultimate aspects of a given behaviour can be studied independently from each other. For example, to understand why a given behaviour is adaptive we do not need to know how it is produced by the body, and vice versa. Proximate correlates of primate vocal behaviour, such as its cognitive underpinnings, have received a considerable attention partially because of their potential relevance to the evolution of aspects of human language or speech (Fedurek and Slocombe 2011). It is important to highlight, however, that the purpose of this study is to examine the ultimate, and more specifically the adaptive functions, rather than proximate mechanisms, of chimpanzee vocalisations. Nevertheless, this approach also has the potential to contribute to our understanding of human vocal communication. Chimpanzees, for example, are our closest living relatives which, like humans, form fission-fusion societies. Therefore, examining the adaptive value of chimpanzee calls might contribute to our understanding of the selection pressures that have shaped human language.

Primate communication

While monitoring the environment, terrestrial vertebrates use cues conveyed by light, sound, ambient chemicals and touch using senses shaped by natural selection to receive these cues, that is, vision, hearing, olfaction and somatosensation. The same sensory channels or modalities are also used when communicating with other animals. While the relative importance of particular modalities in communicating with other individuals depends mainly on the physical environment inhabited by an animal (Bradbury and Vehrencamp 2011), the overall complexity of communication is often correlated with the complexity of the social environment (e.g., McComb and Semple 2005; Bergman and Sheenan in press). This social complexity appears to be especially pronounced in primates (Dunbar and Shultz 2007), which makes studying communication of these animals challenging but at the same time extremely interesting and rewarding. As mentioned above, this interest is partially generated by the fact that humans belong to the primate lineage, and therefore by studying primate communication we can create more precise hypotheses regarding the evolution of our own communication (Fedurek and Slocombe 2011).

Like other mammals, group living primates use several modes of communication. Evolutionarily, chemical communication is the oldest communicative system that remains a key mode of communication in most animals (Bradbury and Vehrencamp 2011). In the course of evolution, however, the role of this modality in primates has been diminished in comparison to other mammals (Martin 1990) and primate olfactory communication has thus been relatively little investigated (Heymann 2006). Nevertheless, this mode of communication is still vital for nocturnal primates, and more important in prosimians than anthropoids (Martin 1990). Scent marking found in nocturnal primates is an example of olfactory communication (Kappeler 1998). However, the role of this mode of communication in sexual behaviour seems important in virtually all primates (Dixson 1998).

As far as tactile communication is concerned, grooming has received a considerable amount of attention as an example of this mode of communication in primates (Hutchins and Barash 1976). Grooming plays a major part in primate social life and these animals can devote to this activity as much as 18 % of their daytime activity budget (Lehmann et al. 2007). Although several functions have been attributed to this behaviour, there is a general agreement that grooming plays a pivotal role as a bonding behaviour, regulating social relationships in primates (Dunbar 1991; Lehmann et al. 2007). The function of grooming is discussed in more detail below.

The role of visual signals in primate communication has also received considerable attention. Examples of signals received visually are red facial coloration in mandrills or sexual swelling in primates such as baboons and chimpanzees (Dixson 1998). These visual signals are products of sexual selection and play an important role in signalling an individual’s social or reproductive status (Setchell 2005; Higham et al. 2008). The role of more flexible, dynamic visual signals, such as facial expressions and various forms of gestures in primate communication, has also been, especially recently, an object of detailed investigation. Facial expressions have been studied both in monkey and ape species, whereas research on gestural communication has been mainly limited to apes (Tomasello 2008; Dobson and Sherwood 2011; Slocombe et al. 2011). While the social importance of ape gestures have been widely recognised in primate literature (Tomasello and Zuberbuehler 1997; Tomasello 2008) recent studies on monkey and ape facial expressions suggest that this modality plays a more complex social function than previously assumed (Waller and Dunbar 2005; Dobson 2012).

As far as vocalisations are concerned, there has been a great deal of research examining the function of this modality in primate communication and sociality. The relatively high importance of this particular modality in primates might be related to the fact that most primates are arboreal forest-dwelling animals and their low-visibility habitat is more suitable for the propagation of auditory rather than visual signals. In such environments, being able to coordinate activities with the group members, especially during travelling or foraging, and maintaining contact with others is crucial (Sugiura 2001; Trillmich et al. 2004; Koda et al. 2008). This coordination function has been often attributed to vocalisations referred to broadly as contact calls, and this kind of call has been an object of investigation in primates (and in other group living animals; see for review Kondo and Watanabe 2009). Although several functions have been attributed to contact calls, such as individual recognition (Rendall et al. 1996; Digweed et al. 2007; Price et al. 2009), kin recognition (Rendall et al. 1996, Rendall et al. 2000) and distance information (Oda 1996; Suguira 2007), the term ‘contact calls’ typically applies to the vocalisations whose overall function is to maintain intra-group cohesion and avoid separation from the group (Masataka and Symmes 1986; Boinski 1993; Sugiura 2007). Thus, vocal communication is a crucial tool for maintaining both contact between group members and intra-group spacing (Palombit 1992; Koda et al. 2008). Nevertheless, the maintenance of cohesion within primate groups might be facilitated by the informative value of calls, regarding especially the identity, location, and possibly the activity of the caller (Boinski 1993; Boinski and Mitchell 1997; Ramos-Fernandez 2005).

Crucially, in primates (as in other mammals) calls can also inform conspecifics about features of the external environment such as the presence of a predator or food (Clay et al. 2012; Zuberbuehler 2012). Primate alarm calling can be especially elaborated, as some species can produce two or three different call types correlating with the presence of different types of predators (Struhsaker 1967; Seyfarth et al. 1980; Zuberbühler 2001). These calls are functionally referential, meaning that receivers’ responses to these calls are very similar to their responses to actual encounters with that type of predator (Marler et al. 1992). Food-associated calls, which are vocalisations produced specifically in feeding contexts (Elowson et al. 1991), are another type of call potentially providing conspecifics with valuable information about the environment, namely the presence of food (Clay et al. 2012). Like alarm calls, food-associated calls may be functionally referential. For example, it has been shown that in primates food calling correlates not only with the presence of encountered food but also with its quantity or quality (Benz 1993; Di Bitetti 2005), and some primates such as chimpanzees can adjust their foraging behaviour in accordance with the calls they hear (Slocombe and Zuberbuhler 2005b). Food calling behaviour is discussed in more detail in Chapter 5.

The above examples suggest that, in primates, vocal communication is crucial for an individual's fitness. However, the functions of vocalisations in primates highlighted above do not differ qualitatively from the function of calls in other group-living mammals (Wheeler and Fischer 2012). The reason for this is that vocal communication seems to be important in facilitating living in groups in many terrestrial vertebrates (Kondo and Watanabe 2009), and group living in turn improves an individual's fitness mainly through predator avoidance and efficient finding of food (Wrangham 1980; van Schaik 1983; Davies et al. 2012). However, living in a group has also negative consequences, and these costs are mainly related to the competition with group members for crucial recourses such as food and mating partners (Bradbury and Vehrencamp 2011). Vocal behaviour has adapted to these challenges of group -living and vocalisations can provide receivers with important information about social interactions. For example, vocalisations such as screams function to recruit help when an individual is aggressed by a group member (e.g., Gouzoules et al. 1984; Slocombe and Zuberbuhler 2005a). Female copulation calls found in many mammalian species, on the other hand, can provide information including the identity of the female, her reproductive state, whether the male has ejaculated and the rank of the male partner (Semple 2001; Semple et al. 2002; Pfefferle et al. 2008; Townsend et al. 2011). Although the type of information provided in the female copulation calls of different species varies, these calls are believed to promote both male-male competition for mating as well as sperm competition so as to secure high-quality offspring for the caller (Semple 1998; Semple and McComb 2000).

Social bonding in primates and its function

Group-living in animals such as primates is especially challenging. The reason for this is that the social environment of primates living in groups is very complex. This complexity is related not only to the relatively large number of individuals typically comprising a primate group, but also to highly sophisticated social relationships within a group (Dunbar 1988). In contrast to other mammals such as ungulates or avian species living in groups, most primate groups consist of a relatively stable number of individuals who rarely migrate between groups. This allows group living primates to develop complex networking patterns with group members. The relative stability of a primate group also means that an animal's behaviour towards another individual often depends on the relationship of this individual with third parties, making the sociality of these animals even more intricate (Cheney and Seyfarth 1990). The social complexity of group living primates imposes on these animals a pressure to develop an efficient form of communication (e.g., McComb and Semple 2005) so as to coordinate the behaviour of individuals joined by complex social relationships.

At the same time, however, the relative stability of a primate group over time allows these animals to mitigate the costs of group-living by selectively associating with some group members for prolonged periods of time. Such long-term relationships between specific individuals characterised by a high degree of affiliative interactions between them are often termed as 'bonds', and the process in which these relationships are established and maintained as 'social bonding' (Dunbar and Shultz 2010). The term 'social bonding' has been traditionally associated with monogamous animals, such as pair living birds, in which maintaining a relationship and coordinating activities between a male and a female are crucial for a successful rearing of offspring (Shultz and Dunbar 2010). However, in contrast to monogamous animals, in primates [but also in some other mammals, such as horses, dolphins, hyenas and elephants (see review by Seyfarth and Cheney 2012)] such long-term bonded relationships extend beyond reproductive units (Dunbar and Shultz 2007). As far as group-living primates are concerned, the aspect of social bonding and its effect on an individual's fitness has been closely studied in baboons. Baboons form female-philopatric societies in which females, usually kin, form close relationships expressed mainly by a high degree of proximity, grooming rates, and coalitions between females within a matriline (Seyfarth 1977; Silk 2012). Several studies on baboons showed that social bonds facilitate an individual's progression within a group. For instance, females who concentrate their affiliative interactions on a small but stable number of female partners deal better with social stress (Crockford et al. 2008; Wittig et al. 2008). In baboons, females also seem to form long-term social bonds with males as a strategy against infanticide (Palombit et al. 1997). Furthermore, more recent studies show that there might also be profound long-term consequences of social bonding in baboons. For instance, females who form strong social bonds produce offspring with a higher rate of survival (Silk et al. 2003) and with higher longevity (Silk et al. 2009) than those forming weaker social bonds with others.

Social bonds in chimpanzees

Social bonds seem to play a crucial role also in chimpanzee sociality. In order to understand the function of social bonds in this species, it is important to understand the social structure characterising this species. Chimpanzees live in highly flexible societies termed as fission-fusion. In these societies the basic social unit is a party – a temporary collection of individuals separated from other individuals within the same home range by certain distance (Clark and Wrangham 1994). The collection of all parties within a home range is termed a community (Goodall 1986). On average a chimpanzee community includes between 20 and 120 individuals, whereas a party might comprise between 1 and 50 individuals (Newton-Fisher 2002; Muller and Mitani 2005). The party size and composition changes frequently on both a daily and seasonal basis, and the rate of these fluctuations is highly dependent on the availability of preferred food for these primates – ripe fruits (Chapman et al. 1995). For example, during seasons when ripe fruit is available in abundance, chimpanzees tend to form larger groups than when this food type is scarce (Chapman et al. 1995). Chimpanzees are highly territorial and protecting food sources from other communities seems to be a key reason for chimpanzee territoriality (Mitani et al. 2010). The territorial behaviour is exhibited mainly by boundary patrols, during which a group of chimpanzees, mainly males, visit the edges of their territory and sometimes make incursions into neighbouring territories. Such patrols are extremely risky and might result in fatalities (Mitani 2009a). The primary function of boundary patrolling is not only to protect own territory but also to acquire territory from neighbouring communities (Wrangham 1999; Mitani et al. 2010; Wilson et al. 2012).

Chimpanzees are a male-philopatric species, which means that males remain in their natal community through their lifetime whereas females usually transfer to neighbouring communities upon reaching sexual maturity (Nishida 1969; Wrangham and Smuts 1980). On a proximate level, this might explain why males are usually considerably more gregarious than females. Similarly, since males spend all their lives in the same community, providing them with more time and opportunities to interact with other males than females, the pattern of sex dispersal in this species might also explain why males form strong affiliative relationships with other males than with females. Males also form these affiliative relationships, measured by grooming interactions and proximity levels, with particular males, and these relationships or alliances are often stable over a period of ten and more years (Gilby and Wrangham 2008; Mitani 2009b). It is believed that these long-term affiliative relationships between males have a deep adaptive value. For instance, maintaining afiliative relationships between males might improve effectiveness in defending or acquiring territories from neighbouring communities (e.g., Van Hooff and Van Schaik 1994). Indeed, some researchers suggested that participation in boundary patrols might be mediated by the level of social bonding between males (Watts and Mitani 2001).

It is not, however, just inter-community competition that makes strong male-male social bonds adaptive in chimpanzees. Intra-community competition may have been an even greater evolutionary pressure that made the formation of such affiliative relationships adaptive. The reason for this is that while the inter-group competition can explain why males in chimpanzees in general form strong social bonds, the intra-group competition can explain why these bonds are formed between specific individuals. In this species (as in other species where it is the female who invests substantially more in producing and rearing offspring), there is an intensive male-male competition for a high social status. High-ranking males often monopolise resources crucial for an individual’s fitness such as access to receptive females (Muller and Mitani 2005). Therefore, males fiercely compete to obtain a high social position within the community. This competition might have a form of direct physical aggression directed at other males (with high-ranking individuals being more aggressive), but it is usually ritualised into various forms of agonistic displays (Goodall 1986; Muller and Mitani 2005). The consequence of this competition is a strict and linear male dominance hierarchy, which is often manifested by pant-grunt vocalisations (i.e., calls by subordinate individuals to higher ranking males).

In order to be successful in building and maintaining a high social status, the ability to form efficient alliances with other males is crucial (Muller and Mitani 2005). The fact that in this species high-ranking individuals have on average more allies than low-ranking ones seems to support this view (Duffy 2006). It has also been shown that males with strong social bonds between them are more likely to support each other in conflicts (de Waal 1982; Hemelrijk and Ek 1991; Mitani 2009a). Since the ability to form coalitions with other males is crucial to succeeding in competition with other males for a high social position, social bonds might ultimately function to facilitate the acquisition and maintenance of a high social status and associated reproductive benefits (Muller and Mitani 2005).

Social grooming as a bonding behaviour

In primates social bonds are usually manifested by a high degree of grooming between individuals. Social grooming is basically defined as removing dirt and parasites from the fur of another individual, and therefore the basic function of this behaviour is to reduce the load of external parasites (Hutchins and Barash 1976). However, the fact that primates (especially Old World primates (Dunbar 1991)) spend considerably more time on social grooming than is required by its hygienic function suggests that it also plays another role. Indeed, many studies showed that grooming might play an important role in primate sociality. It has been suggested, for example, that primates directly exchanging grooming for other benefits such as tolerance or support in agonistic interactions (Seyfarth 1977; Barrett et al. 1999). Others suggested that the function of grooming is building familiarity or establishing ‘trust’ between grooming partners, which in turn facilitates the occurrence of other affiliative interactions (Dunbar 1988). In the latter case grooming is perceived not as a commodity but rather as a signal which function is to test or facilitate the bond between individuals (Fedurek and Dunbar 2009). Finally, grooming has a calming effect on animals (Aureli et al. 1999) and the proximate correlates of the tension-reducing function of this behaviour have also been revealed. In primates grooming activity is correlated with an elevated production of the neurotransmitter Beta-endorphin (Keverne et al. 1989) and the hormone oxytocin (Snowdon et al. 2010), both of which have been shown to mitigate stress in animals including humans (Dunbar 2010). Importantly, oxytocin plays also an important role in establishing and maintaining social bonds across many animals such as monogamous birds, voles or humans (Insel and Shapiro 1992; Curley and Keverne 2005; Schneiderman et al. 2012; Klatt and Goodson 2013), which, on a proximate level, might link grooming to social bonding. It has also been shown that providing grooming reduces levels of the stress hormone cortisol (Shutt et al. 2007).

Social grooming seems to be a very important tool for maintaining affiliative relationships between males in chimpanzees. For example, males (who are more social than females and who associate more often with members of the same sex than with females) allocate substantially more time to grooming than females do and groom considerably more frequently with each other than with females (Nishida 1969; Bygott 1979). Males also tend to distribute their grooming behaviour towards valuable social partners (Watts 2000), and grooming interactions seem to be crucial for building and maintaining alliances between males (de Waal 1982; Nishida 1983; Nishida and Hosaka 1996). Males who tend to groom each other, for example, also tend to support each other in agonistic interactions (Hemelrijk and Ek 1991). Recent studies show that balanced grooming relationships in terms of grooming reciprocation are an especially good indicator of stable long-term relationships between males (Mitani 2009b). Such balanced grooming outcomes could be either a result of keeping track of previous grooming interactions between males over a long period of time (Gomes et al. 2009) or could be an effect of more balanced grooming distribution between partners within grooming bouts (Fedurek and Dunbar 2009). The degree of grooming reciprocation within a grooming bout correlates with bout duration in chimpanzees and, if reciprocated and uninterrupted, male-male grooming bouts can last more than one hour (P.Fedurek, unpublished data). Because reciprocated grooming bouts are usually time consuming, they might incur opportunity costs or impair vigilance (Dunbar and Sharman 1984; Maestripieri 1993). These costs might make reciprocated grooming an efficient signal or test of a bond, which might explain why on average kin and allies are more likely to groom reciprocally than others.

The costs associated with grooming might make it a reliable but at the same time a conservative affiliative interaction in terms of partner choice. It is possible, therefore, that a more flexible behaviour facilitating the formation of temporary affiliative relationships between individuals, who are not necessarily affiliated on a long-term basis, would also be adaptive. This especially might the case in species forming fusion-fission societies. For example, the majority of group living primates live in stable groups in which group size and composition do not vary greatly with time. Chimpanzees, in contrast, form highly fluid and flexible societies in which party size and composition change on both seasonal and daily bases (Nishida 1979; Sakura 1994; Chapman et al. 1995; Lehmann and Boesch 2004). This means that chimpanzees, along with other species forming fission-fusion societies, face a different set of social challenges than most group living primates (Aureli et al. 2008; Lehmann and Dunbar 2009). For example, the fact that party composition changes so frequently means that grouping patterns are often unpredictable and therefore valuable social partners are not always around. A behaviour that would signal short-term affiliations between individuals available in the party, not necessary long-term preferred social partners, would be advantageous for effective social progression. Coordinated vocal behaviour may act as a signal of positive or benign intent between the callers, which might facilitate cooperative activities between them (e.g., support in agonistic interaction, tolerated co-feeding, or a decreased likelihood of aggression between them). In contrast to grooming, call interactions are less time consuming and do not require a great deal of proximity between the involved individuals. I would expect therefore a chorus to be a weaker ‘bonding’ signal than, for example, grooming, but that this behaviour would be an efficient means of signalling temporary bonds between individuals (Chapter 3).

Vocalisations and social bonding in pair-living birds and primates

Coordinated vocal exchanges have been recognised in many classes across the animal kingdom, including mammals, birds, amphibians, and insects (Gerhardt et al. 2000; Burt et al. 2001; Schulz et al. 2008). However, the role of vocalisations, especially vocal duetting, in social bonding has been investigated mainly in monogamous animals, and most of these studies focused on avian species (Hall 2009). In many monogamous birds, male and females often participate in so-called duets in which both sexes produce highly coordinated calls simultaneously (Hall 2009). Many functions have been attributed to vocal duetting in monogamous birds, such as recognising the identity and location of the partner (Lamprecht et al. 1985), maintaining contact with the partner (Wickler 1980), repelling others from the pair's territory (Hall 2006), synchronising reproductive physiology (Wickler 1980), and mate guarding (Rogers 2005). Nevertheless, the potentially crucial role of this behaviour in maintaining long-term social bonds across many monogamous bird species seems to find considerable support (Hall 2004). Interestingly, the bonding function of bird duetting is not always confined to reproductive pairs. In long-tailed manakins, for example, two top ranking males develop long-term alliances to achieve a high social status and associated mating opportunities, and these cooperative relationships are built mainly through participation in highly coordinated duet songs (Trainer and McDonald 1995). This is an interesting finding because the function of duetting in stimulating coalitions between males in these birds might be parallel to the potential bonding function of convergent vocalisations performed by males in other animals, such as primates.

Joint vocal displays are also common behaviours in some pair-living primates such as gibbons (Geissmann 2002), pair-living lemurs (Schulke and Kappeler 2003; Mendez-Cardenas and Zimmermann 2009), titi monkeys (Muller and Anzenberger 2002) or tarsiers (Nietsch 1999)]. The function of duetting in primates has been suggested to play such roles as maintaining social bonds, territorial defence, mate guarding as well as coordinating activities between individuals (Mendez-Cardenas and Zimmermann

2009). However, among primates, gibbons, and especially siamangs, are believed to be one of few primates that produce duet songs that resemble avian duets in their sophistication (Geissmann 1999). Gibbons are also one of the several primate species that form durable monogamous reproductive pairs. It has been traditionally argued therefore that the function of gibbon duettings does not differ substantially from the role of duet songs of monogamous birds. As in the case of monogamous avian species, territoriality and social bonding have been typically attributed as two main reasons for coordinated singing in gibbons (Chivers 1976; Wickler and Seibt 1980; Geissmann 1986).

Vocalisations and social bonds in group living primates

Recent studies suggest that in primates vocalisations might be involved in social bonding not only in the case of monogamous species but also in group living primates (McComb and Semple 2005; Greeno and Semple 2009). This is not surprising considering the fact that, as mentioned above, within primate groups individuals form close affiliative relationships with some group members and these relationships resemble in many respects those characterising reproductive pair relationships in monogamous animals (Dunbar 2009). One might expect therefore that some mechanisms involved in strengthening bonds in group living primates, including vocalisations, are parallel to those found in monogamous ones. Indeed, there is a large body of literature showing that in primates forming multi-male multi-female groups, contact calls tend to be exchanged mainly between well affiliated individuals such as close social partners and kin [gorillas (Harcourt and Stewart 1996), rhesus macaques (Hauser and Marler 1993a), squirrel monkeys (Biben 1993; Soltis et al. 2002), spider monkeys (Ramos-Fernandez 2005), ring-tailed lemurs (Oda 1996)]. Although one might argue that the informative value of contact calls might indicate they have been shaped by both kin-selection and reciprocal altruism (Hamilton 1964; Trivers 1971), there is a reason to believe that in primates these vocalisations might be involved in signalling affiliative relationships. Indirect evidence for the bonding role of vocalisations in multi-male multi-female primate groups has been also suggested by more recent studies. For example, it has been recognised that among rhesus macaques contact calls play a role in reconciliation (Rendall et al. 1999), which is behaviour traditionally associated with grooming (Aureli et al. 1989). Another study showed that in Rhesus macaques, where females are involved in grooming more often than males do, females also vocalise socially more frequently than males (Greeno & Semple 2009). It has also been shown that in primates the size of vocal repertoire correlates with both group size and time spent grooming (McComb and Semple 2005), with primates characterised by especially intricate social structures, such as gelada baboons, having particularly elaborated vocal communication (see also Richman 1993; Gustison et al. 2012). These studies are consistent with the claim that more complex social structures bring about more complex communication [not only within vocal communication but also within other modalities (delBarco-Trillo et al. 2012; Dobson 2012; Freeberg et al. 2012)].

Flexibility over call structure and social bonds

A certain degree of flexibility and control over call structure might be required in order to produce effective duets or choruses, which in turn might facilitate social bonding. Such flexibility might be possible either as a result of a long-term learning of how to coordinate a call with the partner (Wickler 1980) or it might a result of a short-term process of active, dynamic vocal coordination when calling together with another individual (e.g., Smith 1994). As far as the former is concerned, it has been suggested that, on a proximate level, the time and energy invested in learning how to perform coordinated duet singing, make duetting a signal of commitment to the partner (Wickler 1980). Indeed, in some duetting birds it might take several years before a pair learn how to perform coordinated duet songs (Trainer et al. 2002).

Another type of flexibility over a call structure is related to a short-term process of dynamically coordinating a call with a partner. Such coordination might be achieved by both replying in time to the partner’s call (Smith 1994) or/and by adjusting the acoustic structure of a call to match the partner’s one (Hall 2009). This process has also been linked to social bonding. For instance, it has been suggested that by coordinated responding to each other calls, an animal assesses the partner’s attention to its calls and, in turn, the level of its involvement in the relationship (see also von Helversen 1980; Smith 1994). Therefore, well affiliated partners should be on average more likely to coordinate their vocal displays than less bonded ones

(Smith 1994). Literature, especially on avian species, shows that duetting partners do coordinate their calls when calling together. For instance, birds often match tempos of their calls when calling together with a partner (Hall 2009). Some birds also prolong a vocal display when calling with a partner (Hall 2009). Importantly, there is some evidence that at least in some duetting birds the level of vocal coordination between singing partners is a good indicator of the pair's relationship status (Trainer & McDonald 1995).

Modification of call structure also occurs in primates. In contrast to avian calls, however, the primate vocal repertoire seems to be highly constrained genetically (Winter et al. 1973; Owren et al. 1992). In primates, therefore, we do not observe acquisitions of completely novel vocalisations (Janik and Slater 1997). Nevertheless, a number of studies showed that despite their inability to generate new calls, primates can modify subtle acoustic features of their existing calls. Such acoustic modification can occur in response to a change in social circumstances. For example, one study showed that after placing two unfamiliar populations of pygmy marmosets in the same environment, after 10 weeks in proximity the two populations modified certain acoustic parameters of their contact calls such as the peak frequency, making them acoustically more similar to each other (Elowson and Snowdon 1994). The authors suggested that this process of call modification is a result of learning (Elowson and Snowdon 1994). A similar convergence of call structure over time was observed in the trill calls of newly paired pygmy marmosets (Snowdon and Elowson 1999) and might occur during the process of pair-bonding in gibbons (Geissmann 1986). Similarly, in Campbell's monkeys the acoustic structure of calls is very sensitive to changes in social environment (Lemasson et al. 2003; Lemasson and Hausberger 2004). More interestingly, it has been suggested that in these monkeys individuals who are affiliated are more likely to share similar acoustic structure of their calls than those who are not (Lemasson et al. 2005). It is possible therefore that the long-term process of adjusting calls to match those of a partner is also linked to social bonding in primates. Some studies also show that in these animals short-term vocal flexibility over the call structure can occur too. For example, if played back coo calls, Japanese macaques reply with calls that match the acoustic features of the calls they heard

(Sugiura 1993; Sugiura 1998). Similarly, when chorusing, males in chimpanzees adjust some acoustic features of their pant hoots to match the partner's one (Mitani and Gros-Louis 1998see below).

In sum, two models have been proposed to explain why coordinated vocal interactions such as choruses might be bonding behaviours. Wicker's (1980) model suggests that the bonding function attached to such interactions arises as a result of a long-term learning process (Geissmann 1999), whereas Smith (1994) proposes that the bonding function of this behaviour is attached to the costs of constant testing of a partner's attention: a process which could be executed instantly without the need of time-consuming learning. The second explanation for the bonding nature of duets or choruses, although rather neglected in the literature, might be convincingly applied to choruses in many animals including those living in multi-male multi-female groups, such as chimpanzees.

Vocalisations and social bonds in chimpanzees

The purpose of this study is to examine whether chimpanzee vocalisations are involved in social bonding in this species. Chimpanzees produce a number of vocalisations and their calls are graded rather than discrete, meaning that one call type can grade into another. Chimpanzee calls are typically graded within and between call types (Marler 1976). While this grading provides a large number of call variants that have the potential to provide a wide array of information (provided that that these call variants reliably correlate with the context in which they are produced), it also makes it challenging to precisely establish the vocal repertoire in this species. Attempts to classify chimpanzee vocalisations have been made since the onset of research on wild chimpanzees (Reynolds and Reynolds 1965), but the first reliable and quantitative description of vocal repertoire in this species was offered by Marler and Tenaza (1977). Based on the acoustic features of calls and behavioural context in which they are produced, Marler and Tenaza (1977) distinguished 14 broad types of chimpanzee vocalisations: pant hoot, pant grunt, laughter, squeak, scream, whimper, bark, waa bark, cough, rough grunts, pant, grunt, wraa and huu. Although the social function of all these vocalisations is an extremely interesting research prospect, the two particular vocalisations investigated in this study are pant hoots and rough grunts (labelled in this study as food-associated calls). Pant hoots are probably the most empirically examined chimpanzee vocalisations and several social functions have been attributed to this call (see below). In contrast, the function of chimpanzee food-associated calls had been historically neglected in behavioural sciences and has only recently gained more interest. In this study I test the hypothesis that these two types of vocalisations, although acoustically and contextually different from each other, facilitate social bonds between males by both promoting behavioural coordination and facilitating the occurrence of other affiliative interactions between males in a fission-fusion society.

Pant hoots

Pant hoots are long-distance species-specific calls. Traditionally the function of these calls is associated with attracting conspecifics to food sources in addition to providing information regarding the identity of the caller and location of a travelling individual or party (Reynolds and Reynolds 1965; Marler and Hobbet 1975; Wrangham 1977b; Ghiglieri 1984). Other studies, however, suggest a more complex social role of these vocalisations. For example, party size and composition might be important factors influencing the frequency with which individuals pant hoot (Clark 1991, Clark 1993; Wilson et al. 2007). Importantly, some studies suggest that these calls might be involved in social bonding. Males, for instance, are more likely to produce a pant hoot when well affiliated individuals are nearby (Mitani and Nishida 1993). However, despite these studies there are still important but unanswered questions regarding the socio-ecology of these calls, such as the potential influence of food availability and fission-fusion rates on the production of these calls. One of the aims of this study is therefore to explore the basic social and ecological correlates of these calls (Chapter 2). Importantly, males in the same party often produce pant hoots at the same time to perform a chorus and affiliated males tend to produce such joint pant hoots more often than less affiliated ones (Mitani and Brandt 1994; Mitani and Gros-Louis 1998). In Chapter 3 I build on these studies and examine whether joint pant-hooting is indeed a reliable indicator of long-term social bonds in chimpanzees. In this chapter I also test the hypothesis, which is not mutually exclusive with the previous one, that pant hoot chorusing is a flexible bonding behaviour operating on a short-term basis. The rationale for this hypothesis is that, as mentioned above, vocal interactions are less costly than the well-established indicators of strong social bonds in chimpanzees such as grooming, making these behaviours a good candidate to signal such temporary affiliations between males. I also suggest that flexible and relatively low cost bonding interactions such as chorusing might make this behaviour an especially effective signal in unstable fusion-fission societies. Hence, I predict that pant hoot choruses are often employed by both long-term preferred and neutral social partners, and that males are more likely to be involved in other affiliative interactions on days when they pant hoot jointly. Crucially, I examine whether on a short-term basis pant hoot chorusing is a more accurate predictor of other affiliative interactions than grooming.

Another aspect investigated in this study is whether males coordinate their pant hoot behaviour when calling in a chorus with a partner. As mentioned before, a certain degree of vocal flexibility over call structure might be required to make vocal interactions an efficient bonding behaviour. Such flexibility seems to characterise pant-hooting. For example, several studies show that some acoustic structures of a chimpanzee pant hoot are population-specific, which prompted some researchers to suggest that these acoustic differences are the result of learning (Mitani et al. 1992; Clark Arcadi 1996; but see Mitani et al. 1999; Crockford et al. 2004). Moreover, some studies show that in chimpanzees, flexible control over the acoustic structure of a pant hoot can also be manifested on a short-term basis. For instance, Mitani and Gros-Louis (1998) focussed on a single chimpanzee dyad and found that while producing a joint pant hoot these close social partners adjusted certain acoustic structure of their calls to match elements of their partner’s call. The results of this study are especially interesting as they suggest that chorusing in chimpanzees signal social bonds in a way initially suggested by Smith (1994). For example, the level of acoustic adjustment of a male’s call to the partner’s one might reflect his attention to the partner’s call and consequently his level of affiliation towards him. However, no study to date has addressed the specific question of whether chimpanzees modulate the temporal structure of their calls to promote joint pant-hooting. If male joint pant-hooting plays an important role in signalling affiliations between males, I would imagine that such a mechanism facilitating joint pant hooting exists. Indeed, considering the basic acoustic structure of a pant hoot, with a gradual onset of the call leading a loud climax (Chapter 4), males might adjust the duration of particular phases of the call to both facilitate the occurrence and prolong a chorus with the partner. This specific hypothesis is examined in Chapter 4.

Food-associated calls

Another type of chimpanzee vocalisation on which this study is focused is food-associated calls. As mentioned above, food-associated calls are broadly defined as calls given specifically in the feeding context and these vocalisations have been recognised in a variety of animals (Clay et al. 2012). Traditionally, it has been proposed that the function of these calls is to attract group members to food, which in turn, among other benefits (see Chapter 5) improves anti-predator vigilance and feeding efficiency (Chapman and Lefebvre 1990; Caine et al. 1995; Boinski and Campbell 1996). Food calling is also a common behaviour in chimpanzees with feeding individuals commonly producing ‘rough grunts’ (Marler and Tenaza 1977), which grade from low-pitched ‘food grunts’ to high-pitched ‘food barks’ (Chapter 5). Studies showed that the acoustic structure of these calls correlates with the quality of food consumed (Slocombe and Zuberbuhler 2006; Slocombe et al. 2010). It has also been shown that males are more likely to produce these calls when valuable social partners are in the same party, suggesting that these vocalisations might play a role in social bonding in these primates (Slocombe et al. 2010). However, the question of why food calling might be involved in social bonding has not yet been answered convincingly. For example, the hypothesis that by food calling males inform each other about the presence, quality or quantity of encountered food has theoretical drawbacks and is not consistent with some observations of chimpanzees in the wild (Chapter 5). In this study a new hypothesis with regard to the social function of food-associated calls is tested. The specific hypothesis tested here is that food calling signals that the calling individual is likely to initiate and prolong a feeding bout. I propose that ultimately these calls facilitate feeding coordination between feeding males, especially well affiliated ones, which in turn facilitates them remaining in proximity and the same party. The key prediction of this hypothesis is that males are more likely to remain in close proximity during a feeding bout after giving food-associated calls. I suggest that such signals allowing anticipation of each others' behaviours facilitate grouping decisions in chimpanzee societies characterised by a high degree of fusion-fission.

In sum, in this study I test the hypothesis that pant hoot choruses reflect short-term social bonds between males. Given the potential social importance of pant hoot chorusing, I also examine whether call structure is dynamically modified to facilitate and enhance such joint vocal displays. With regard to food calling behaviour, I investigate the possibility that these calls facilitate anticipation of each other's feeding decisions which in turn facilitates remaining in proximity.

CHAPTER 2: General social and ecological correlates of pant-hooting behaviour in male chimpanzees

ABSTRACT

The production of pant hoots, the long-distance species-specific call, is a common behaviour in chimpanzees. It has been suggested that examining social and ecological correlates of this behaviour can provide insight into the function of these vocalisations. Although there have been several studies looking at this research issue, there is an ongoing debate concerning the factors that affect male chimpanzee pant-hooting and their relative importance in this respect. In this study I investigated the effect of basic social factors, including the rank of the caller, party size, fusion-fission rates and the presence of oestrous females, as well as ecological factors including food availability and travel time, on male pant-hooting behaviour. The results of this study show that males produced more pant hoots on days when they travelled more and when there were frequent changes in the male, but not female, composition of the focal's party, and when there was a female in oestrus present. Males were also more likely to produce pant hoots on days when they fed on high quality food types, such as non-fig fruits, rather than on less preferred foods, such as figs or piths/leaves. My results suggest that male chimpanzee pant-hooting might be influenced by a number of social and ecological factors, supporting the view that pant-hoots are a vocalisation fulfilling a complex social role.

INTRODUCTION

Pant hoots are a very common vocalisation in chimpanzees. As mentioned in Chapter 1, early studies of this behaviour suggested that these calls function to attract conspecifics to food sources or to provide information regarding the identity of the caller and location of a travelling individual or party (Reynolds and Reynolds 1965; Marler and Hobbet 1975; Wrangham 1977b; Ghiglieri 1984). Studying social and ecological correlates of pant-hooting behaviour might be an especially effective way of determining the function of these vocalisations and there were several studies that successfully employed this approach. For instance, previous studies showed that when arriving at feeding trees the probability of giving a pant hoot depends on the size and quality of the food source (Wrangham 1977b; Clark and Wrangham 1994). Other studies showed that party size and composition might be important factors influencing the frequency with which individuals pant hoot (Clark 1991; Clark 1993; Mitani and Nishida 1993; Wilson et al. 2007). Chimpanzees often pant hoot in choruses (Mitani and Gros-Louis 1998) and such chorusing has also been suggested to play an important role in mediating social bonds between males (Chapter 3). Chimpanzee pant-hooting might thus play a complex role in chimpanzee sociality fulfilling probably several functions.

The purpose of this study was to build on the previous studies on chimpanzee pant-hooting by examining basic social and ecological correlates of this behaviour. There are two reasons why I believe this study might contribute to our understanding of chimpanzee pant-hooting. Firstly, in this study I incorporated several factors that might affect chimpanzee pant hoot production, such as fission-fusion rates and food availability, which were not considered in detail in previous studies. Secondly, the currently available statistical tools, such as multivariate mixed models, allow for testing several alternative hypotheses regarding factors affecting pant-hooting at the same time by incorporating several variables into a single model (Pinheiro and Bates 2000). Such approach might therefore establish the relative importance of particular factors correlating with chimpanzee pant-hooting while at the same time controlling for potential confounds; something previous statistical techniques employed to answer similar questions were not capable of doing. In addition, in contrast to previous studies on male pant-hooting, I analysed data collected during all-day, usually nest-to-nest focal follows. This allowed me to capture the pant-hooting behaviour of males more accurately than previous studies. Below I outline the social and ecological factors that I examined in my study and that might be relevant to chimpanzee pant hoot production, while at the same time summarising what has been done in this respect in previous studies.

As discussed in Chapter 1, chimpanzees live in very flexible fission-fusion societies in which party size and composition can change on both daily and seasonal bases. Therefore, it has been suggested that in such unstable societies pant hoots, as long-distance calls, play a pivotal role in maintaining contact with or facilitating reunions between community members (Goodall 1986; Mitani and Nishida 1993). Indeed, chimpanzees upon hearing pant hoots given by individuals in other parties often respond by pant-hooting (Goodall 1986). Producing these calls might therefore facilitate locating and joining other parties. However, few studies provided a direct support for the claim that pant-hooting facilitates fusion in these primates. In this study I tested this hypothesis more directly by looking whether pant hoot rates on a given day correlated with rates of fission-fusion on that day. Because, as discussed in Chapter 1, chimpanzee males tend to form strong social bonds and associate more often with other males than females, I predict that, on a given day, pant-hooting rates of the focal correlate more with the focal’s rates of fission-fusion with other males than with females.

Another way, although more indirect, to investigate whether pant-hooting mediates grouping dynamics in chimpanzees is to look at how pant hoot production correlates with time spent travelling. A previous study, for example, showed that after giving a pant hoot males are likely to resume travelling (Mitani and Nishida 1993) possibly to facilitate fusion with other group members. In this study I tested this prediction by comparing pant hoot rates given by a male on a given day with time that male spent travelling on the same day.

Another social factor that has been suggested to affect chimpanzee pant-hooting is party size. It has been proposed that since pant-hooting may facilitate the formation and maintenance of parties, the rates of these calls should correlate positively with party sizes (Reynolds and Reynolds 1965). If this was the case, we might expect that male pant-hooting correlates especially with the number of males rather than females in the party. This is because males tend to associate more strongly with other males than females and so they may be more motivated than females to join the party of the calling male. However, this hypothesis was not supported by Mitani and Nishida (1993) who showed that the number of males in the focal’s party did not correlate with male calling behaviour. Since the study by Mitani and Nishida (1993) is the only study to date that has examined this particular aspect of male pant-hooting, I replicated it and investigated the relationship between male pant-hooting rates and the average number of males in focal's party on a given day. In contrast to the previous study (Mitani and Nishida 1993), however, I also looked at the relationship between male pant-hooting and the average number of females in the focal's party on a given day. If pant-hooting facilitates the preservation of parties containing valuable social partners, we should expect that male pant hoot rates are associated stronger with the average number of males rather than females in the focal's party since, as mentioned above, in chimpanzees males tend to form strong social bonds with members of the same sex.

Several studies suggested that in primates long-distance calls might function to signal the high social status of the individuals producing them. In baboons and black-crested macaques, for instance, dominant males are more likely to give long calls than low-ranking males and such calls might function to advertise male quality (Kitchen et al. 2003; Fischer et al. 2004; Neumann et al. 2010). Studies on male chimpanzee pant hoots also suggest that these vocalisations signal the high social status of the caller. For example, it has been shown that high-ranking males of both the M unit in the Mahale Mountains National Park in Tanzania (Mitani and Nishida 1993) and the Kanyawara community in the Kibale National Park in Uganda pant hoot more often than low-ranking males (Clark and Wrangham 1994). The social rank of a male seems to be a social factor that strongly correlates with pant hoot rates and therefore I incorporated this factor in my study. I predicted that I would replicate previous findings, but also be able to analyse how important this factor is in relation to other social and ecological factors.

Male chimpanzees display a substantially elevated level of aggressive behaviour towards conspecifics during periods when a female is in oestrous (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 oestrous as in chimpanzees males prefer to mate with parous females (Muller et al. 2006). Hence, signals, such as pant hoots, that may function to advertise the high social status of the caller (Clark and Wrangham 1994) or/and to facilitate male-male coalition formation (Chapter 3), both of which might influence the outcome of competition for mating opportunities (Muller and Mitani 2005), might be displayed more often on days when an oestrous female is available. However, to date only one study tested this hypothesis. This study showed that males at Mahale did not pant hoot more in the presence of an oestrous female. Considering the above rationale and the fact that this hypothesis so far has been tested only on one population of chimpanzees, in this study I investigated whether the pant-hooting behaviour of the Kanyawara chimpanzees correlates with the presence of a female in oestrous.

Another factor that might affect chimpanzee pant-hooting behaviour is food availability. As mentioned in Chapter 1, the availability of particular food types is highly seasonal and when preferred foods such as fruits are not available chimpanzees consume less preferred food such as leaves and piths (Wrangham et al. 1991; Wrangham et al. 1998). In addition, within the fruit category chimpanzees prefer non-fig to fig fruits (Wrangham et al. 1996; Emery Thompson and Wrangham 2008). It has been shown that chimpanzees tend to form larger groups during seasons of fruit abundance (Conklin-Brittain et al. 1998; Basabose 2002), and that the consumption of fruits, especially non-figs, correlates positively with energetic status of these primates (Emery Thompson et al. 2009). Because fruit availability affects both grouping patterns and energetic condition in chimpanzees (both of which might affect chimpanzee social behaviour) I examined whether this factor also correlates with rates of chimpanzee pant hoots. Since previous studies showed that males are more likely to produce pant hoots when arriving at large feeding trees (Clark and Wrangham 1994), this pattern might therefore be driven by pant hoots given in this context. To control for this I also looked at the relationship between the type of food consumed on a given day and pant hoot rates produced on that day after excluding calls given in the feeding context.

METHODS

Study subjects

The study was conducted on the Kanyawara community in the Kibale National Park located in western Uganda (0” 13’-0” 41” 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 occupied around 38 km^2 of the forest (Wilson 2001). The Kibale forest is a transitional forest between lowland rainforest and montane forest (Struhsaker 1975). The forest occupied by the chimpanzees is a mosaic of a semi-deciduous primary forest, regenerated forest, grasslands and swamps (Chapman and Wrangham 1993). The community is well habituated and has been studied regularly since 1987 by the Kibale Chimpanzee Project (Isabirye-Basuta 1987; Wrangham et al. 1992). The study subjects were 9 adult and 2 sub-adult (Table 2.1) males (Reynolds 2005). The reason why data on one adult male (MS) were not included in the analysis was that he was difficult to find during the study period (I managed to collect only 1 day of data on this male).

Data collection

Fieldwork was conducted between October 2010 and September 2011. Continuous 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). I recorded vocal behaviour of the focal male, including the context in which vocalisations were given (see below). In addition, 5-minute scans (i.e., scan samples conducted in 5-minute intervals) were employed to record the behaviour of the focal male (i.e., travelling, feeding and resting [including grooming]) as well as the type of any food consumed (see below). Data collection resulted in a total of 185 days of focal observations. However, only days of data collection in which the focal was followed for at least 6 hours were incorporated in the analyses (*N*=168; Mean=549.98 (SD=148.19) minutes of direct focal observation per day).

Table 2.1: The rank and estimated age (at the beginning of the study in October 2010) of the focal males (*donate sub-adult male).

Male ID	Age (years)	Rank
AJ	36	3
BB	44	4
ES	16	6
KK	25	1
LK	28	2
PB*	15	10
PG	22	7
ST	55	8
TJ*	15	5
TU	50	9
YB	37	11

Definitions

Pant hoots

A typical pant hoot consists of four acoustically distinctive phases that occur in the following succession: the introduction, the build-up, the climax and the let down (Fig. 2.1).

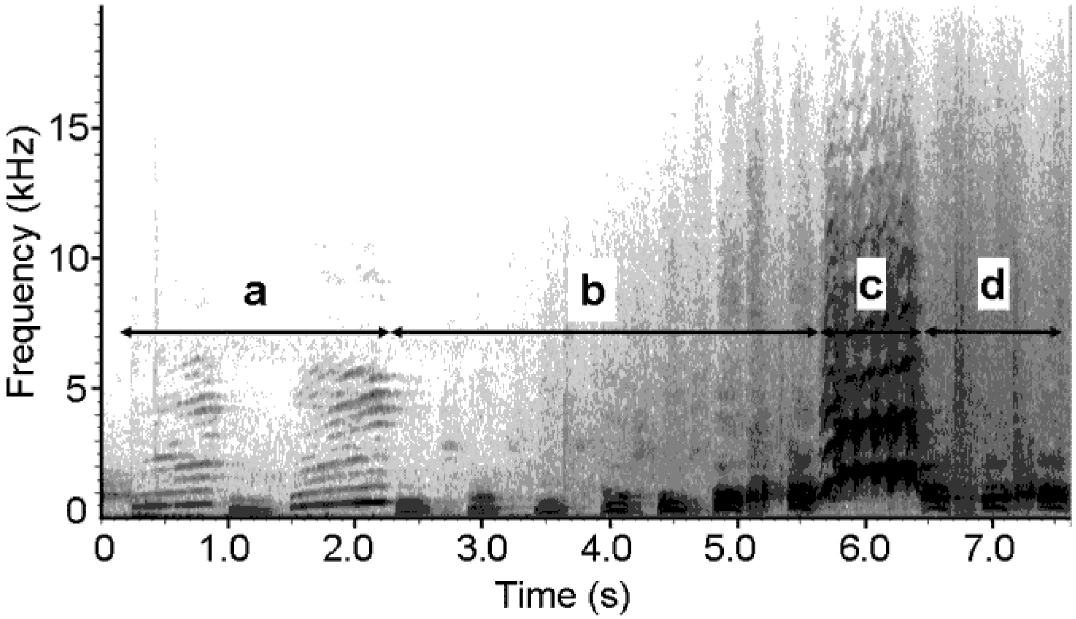

Figure 2. 1: A spectrogram showing the four phases of a pant hoot. A = introduction, B = build-up, C = climax, D = let down [From Slocombe & Zuberbühler (2010)].

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). I divided the context of pant-hooting into four categories:

Travel: caller travelling;

Feeding: caller feeding or arriving at a feeding site;

Resting: caller resting – neither travelling nor feeding;

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).

Focal pant hoot rates were calculated by dividing the total number of pant hoots produced by the focal on a given day by the time of focal observation 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 5-minute scans in which the focal was observed travelling by the total number of 5-minute scans.

Social rank

Each male was assigned an ordinal linear rank (1-11; Table 2.1). The amount of data on pant grunts was insufficient to establish a linear hierarchy for the males. Therefore, following Muller and Wrangham (2004) the obtained linear hierarchy was based on the outcomes of win-lose interactions combining both pant grunt and agonistic interactions [i.e., physical attack, chase, charge, displacements, etc (Goodall 1986; Bygott 1989; Muller and Wrangham 2004)] recorded during the study period using focal animal sampling. The analysis was carried out using the Matman Software Package (version 1.1, Noldus Information Technology; de Vries 1993) and all males dominance hierarchies were significantly linear using a two-step randomization procedure with 10,000 iterations (de Vries 1993, 1995; Appendix A).

Food type and availability

If during the 5-minute scan the focal male was observed feeding, the species and type of food consumed were recorded. I divided the food consumed into three categories: (i) ripe non-fig fruits, (ii) ripe fig fruits and (iii) piths and leaves, which were the three most common food types consumed by the Kanyawara chimpanzees. For the Kanyawara chimpanzees, like other chimpanzee populations (Chapter 1), ripe fruits are preferred foods and in seasons of high fruit availability these primates consume mostly this type of food at the expense of other food types (Conklin-Brittain et al. 1998). In contrast, piths and leaves of terrestrial vegetation or tree leaves are regarded as fallback foods and chimpanzees consume this type of food mostly on days of fruit shortage (Wrangham et al. 1991; Wrangham et al. 1993). In addition, within the fruit category chimpanzees prefer to feed on non-fig or drupe fruits than on fig fruits (Emery Thompson et al. 2009). Studies on nutritional values of particular food types showed that leaves and piths contain low quantities of proteins (piths) and sugars (piths and leaves) and are fibre-rich (Wrangham et al. 1991) whereas ripe fruits, especially non-fig fruits, are fibre-low and carbohydrate-rich (Conklin-Brittain et al. 1998). Consequently, ripe fruits, especially non-fig fruits, are regarded as high-quality food whereas piths and leaves as low-quality foods (Conklin-Brittain et al. 1998).

Based on the approach of Emery Thompson et al (2009), days of data collection were divided into three categories in terms of the type of food consumed by the focal. If more than 50% of focal's feeding time was spent consuming piths and leaves, the day was labelled as '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 labelled 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 focal's feeding time within the fruit category.

The presence of an oestrous female

In chimpanzees a female is considered in oestrous when her sexual swelling is maximally swollen and males tend to mate only with these females. The tumescence of the sexual skin was evaluated using a three-grade scale (e.g. Muller and Wrangham 2004): 1) No swelling: the sexual skin is completely flat; 2) Partial swelling: the sexual skin is not fully swollen and droopy; 3) Maximal swelling: the sexual skin is maximally expanded. For each day of data collection I recorded whether (*N*=61) or not (*N*=107) a parous female (*N*=12) in oestrous was present (i.e., during at least one 5-minute scan) in the focal male's party.

Fusion-fission rates

Focal's fission-fusion rates with males and females were based on the number of changes in terms of the presence of males and females in the focal's party and as recorded in 5-minute scans over one day of data collection. For example, if during a 5-minute scan there was a change in terms of the composition of males in the focal's party compared to the composition recorded in a previous scan, it was coded as one change in the composition of males in the party. The total number of changes in the composition of males and females 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 fission-fusion rates with male or female party members.

Party size

Average number of males and females in the focal’s party on a given day was calculated by averaging the numbers of males or females in a party recorded during 5-minute scans on that day.

Statistical analysis

Generalised Linear Mixed Models (GLMM) with a Gaussian error structure were the main statistical tools used in the analyses. Using GLMM for hypothesis testing is a very effective approach because it permits the examination of the effects of several independent variables (fixed factors) on a continuous or categorical variable (Pinheiro and Bates 2000). This facilitates effective testing of alternative hypotheses. Importantly, GLMM deals effectively with the problem of pseudo-replication (or non-independence of data) by incorporating into the model data on entities from which repeated measurements were taken as ‘random effects’ (i.e. variables that influence the variance). GLMM therefore permits both fixed factors and random effects to be included in the model (Antonio and Beirlant 2007). Thus in these analyses Focal ID was inserted into all the models as a random effect. Before running GLMMs I checked whether independent variables were co-linear. There was no co-linearity 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.

Models created

I first created an initial GLMM with the rate of pant hoots given by the focal male in one day of data collection (i.e., pant hoots/hour) as the continuous dependent variable. I entered the following variables into the model as independent variables: (i) the rank of the focal male (1-11), (ii) the average number of males in focal’s party (iii) the average number of females in focal’s party (iv) focal’s fission-fusion rates with males (v) focal’s fission-fusion rates with females (vi) the presence of a parous female in oestrous (0/1), (vii) food availability (i.e. non-fig fruits, fig fruits and piths/leaves), and (viii) proportion of time spent travelling. I then selected an optimal model using the Akaike Information Criterion (AIC) method which measures the goodness of fit and model complexity (Zuur et al. 2009; Burnham et al. 2011). This approach of model selection is conducted by removing one by one (i.e., backwards selection) the most non-significant independent variable from the model to produce the most optimal model, which means a model with the lowest AIC value possible (Zuur et al. 2009; Symonds and Moussalli 2011). This procedure allowed the selection of the optimal model of male pant-hooting by including the variables that explained most of the variance of this behaviour (e.g. Zuur et al. 2009).

In situations where multiple post-hoc tests were conducted on the same dataset, the α-level for significance was corrected using Sidak's (1967) adjustment equation to control for family-wise error.

RESULTS

The general context of pant-hooting

Pant hoots were most likely to be given in the travelling context (50.30%) than in the feeding (25.45%), resting (16.60%), or displaying (7.65%) contexts.

The initial and optimal model of male pant hoot rates

When all the investigated factors were inserted into the model, only the proportion of time spent travelling, focal's fission-fusion rates with males and food availability, were significant (Table 2.2).

Table 2.2: The relationship between pant hoot rates and the investigated (independent) variables – the initial model [GLMM; ****P*≤0.001, ***P*≤0.01, **P*≤0.05; Dependent variable: pant hoot rates; All independent variables included; Random effect: Focal ID; AIC=358.35; significant results are in bold].

Independent variables	Coef.	Std. Err.	z	[95% Conf.	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 oestrus female	0.26	0.14	1.87	-0.01	0.52
Food availability	**0.17**	**0.07**	**2.43 ***	**0.03**	**0.31**

After the removal of variables that made the weakest contribution to the model, the optimal model with the lowest AIC also revealed that rank and the presence of parous females in oestrous, also substantially contributed to the model (Table 2.3). Variables such as the average number of males and females in focal's party were not significant in either model.

Table 2.3: The relationship between pant hoot rates and the investigated (independent) variables – the optimal model [GLMM; ****P*≤0.001, ***P*≤0.01, **P*≤0.05; Dependent variable: Pant hoot rates; Random effect: Focal ID; AIC=353.44; significant results are in bold].

Independent variables	Coef.	Std. Err.	z	[95% Conf.	Interval]
Rank	-0.05	0.03	-1.86	-0.10	0.00
Time travel	**0.02**	**0.01**	**2.74 ****	**0.00**	**0.04**
Fission-fusion rates with males	**0.72**	**0.13**	**5.40 *****	**0.46**	**0.98**
Presence of oestrus female	**0.32**	**0.10**	**3.06 ****	**0.11**	**0.53**
Food availability	**0.17**	**0.07**	**2.40 ***	**0.03**	**0.31**

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 females (Table 2.2). The rate of fission and fusion with other males was also the most significant correlate out of all the variables investigated.

Time spent travelling

Males pant hooted more on days when they travelled more (Table 2.2).

Rank

Although the variable 'rank' was above the level of significance (*P*=0.060), there was a pattern of high-ranking males calling more often than low-ranking ones. This variable, also contributed considerably to the optimal model of male pant-hooting rates (Table 2.3).

The presence of a female in oestrous

Males also pant hooted more often on days when a parous female in oestrous was available (Fig. 2.2).

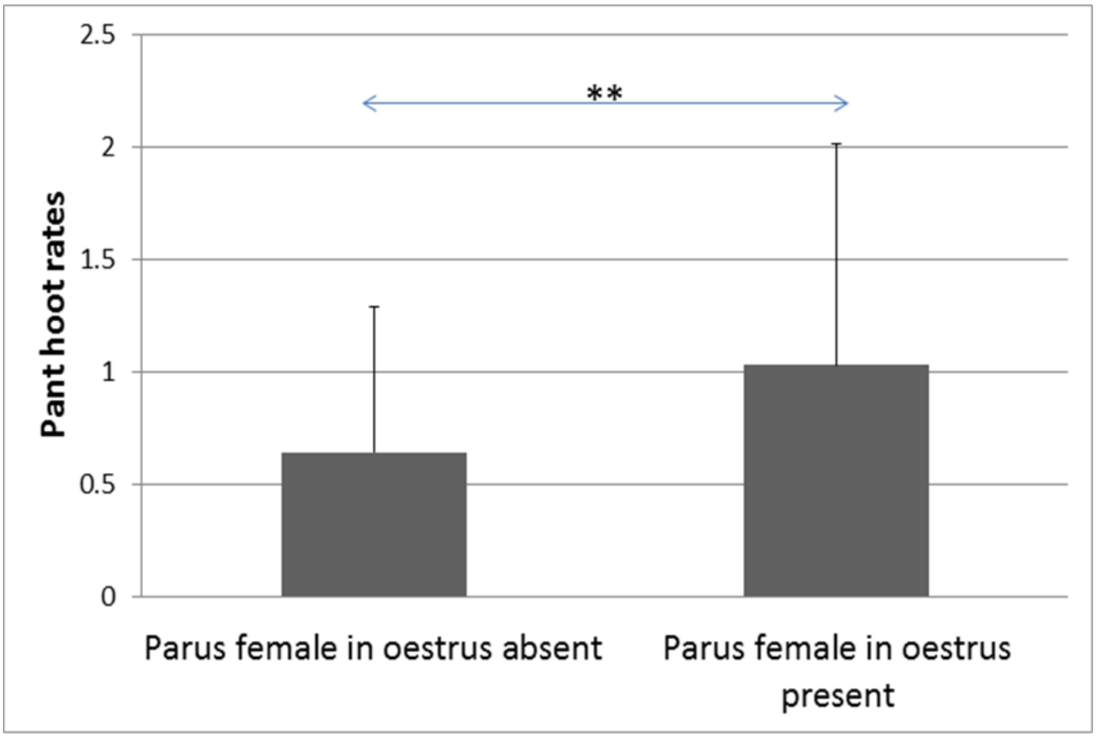

Figure 2.2: Mean pant hoot rates (number of pant hoots per hour) depending on whether an oestrous female was present during a focal day [*P*≤0.01; Random effect: Focal ID; Error bars represent 1 SD].**

Food availability

Another strong predictor of male pant-hooting was the type of food available (Table 2.3). Figure 2.3 and post-hoc analyses showed that males pant hooted more often on days when they consumed mostly non-fig fruits rather than fig fruits (β±SE=0.852±0.13, z=4.07, *P*<0.001) or, although not significantly, piths/leaves (β±SE=-0.40±0.19, z=-2.09, P=0.036; Sidak—corrected α-level for significance *P*=0.025).

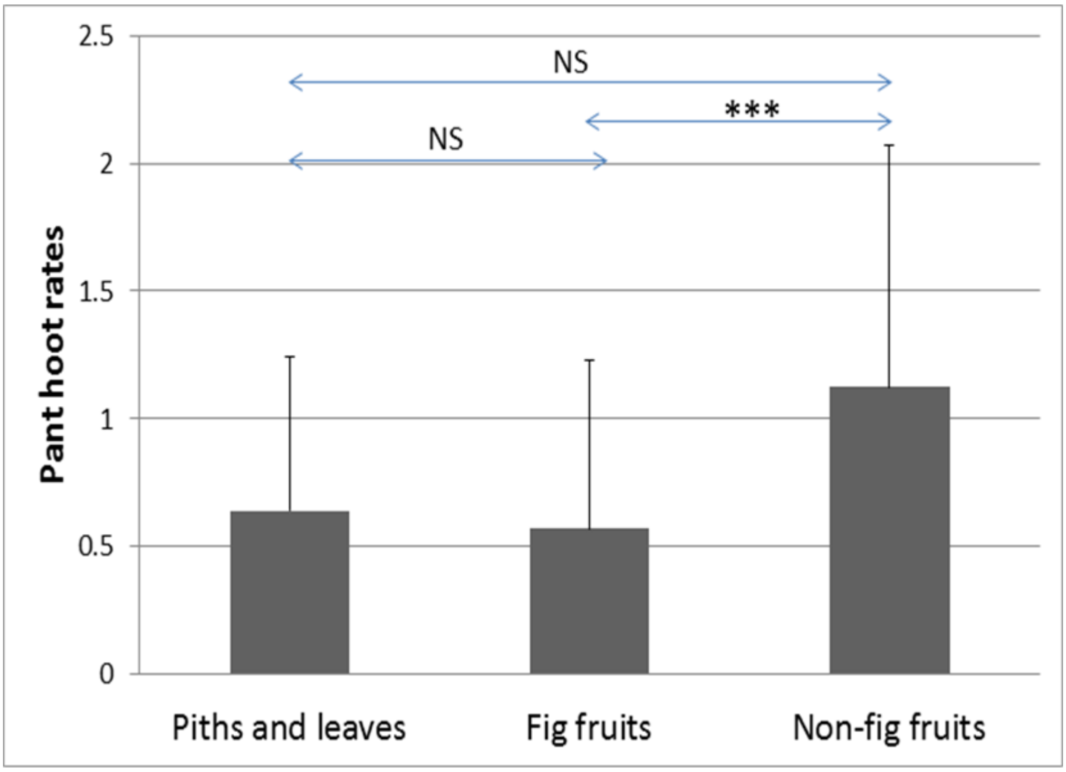

Figure 2.3: Mean pant hoot rates (the number of pant hoots per hour) as a function of the type of food that the focal male spent most of his feeding time consuming on a given day [GLMM; ******P*≤0.001, NS=not significant; Random effect: Focal ID; Error bars represent 1 SD].

This pattern might be however confounded by the possibility that males were more likely to pant hoot when arriving at feeding trees containing non-fig fruits rather than other food types. However, a similar pattern emerged when pant hoots produced in feeding contexts were excluded in the post-hoc analyses: males produced more pant hoots on days when their diet was dominated by non-fig fruits than by figs (β±SE=3.87±1.13, z=3.44, *P*=0.001) or, although again not significantly, piths and leaves (β±SE=-3.41±1.71, z=-2.00, *P*=0.046; Sidak—corrected α-level for significance *P*=0.025). Hence, the type of food available seems to correlate with pant hoot rates regardless of the context in which these calls are given.

DISCUSSION

My study shows that there are several social and ecological factors that strongly correlate with male chimpanzee pant-hooting. Social factors that correlated with this behaviour were male fission-fusion rates with other males, the presence of an oestrous female as well as the social rank of a focal male. Ecological factors that predicted male pant hoot rates were time spent travelling and the availability of particular food types.

As predicted, my results show that pant hoot rates produced by a male are highly associated with the rate of fusion-fission on that day. An obvious interpretation of this result is that pant-hooting mediates grouping dynamics by either facilitating location of community members or by attracting them to the caller’s own party. A similar interpretation might be applied to the result showing that males travelled more on days when they gave more pant hoots since I would expect that a male is more likely to fusion or fission with other community members when travelling rather than resting. It is important to note, however, that in this study I focused on fusion-fission rates rather than solely on fusion rates, which might be important to test more directly the hypothesis that pant hoots facilitate fusion with males in other parties. This is an aspect that might be worth investigating in the future.

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 indicates that male pant hoots are directed to other males rather than females. This result is therefore in line with the fact that male chimpanzees tend to form stronger social bonds with males than with females (Chapter 1), and therefore signals facilitating grouping decisions such as pant hoots should be more likely to be 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 (Chapter 5). Compared to other examined factors, the rate of fission and fusion with other males was the most significant predictor of male’s pant-hooting rates. Overall, these results are consistent with a general opinion that chimpanzee pant-hooting play a pivotal role in coordinating grouping patterns, especially amongst socially important individuals, in these primates (Goodall 1986).

However, another interpretation, but not mutually exclusive with the above one, might also be applied to the positive relationship between fusion-fission rates and pant hoot production. It has been shown that aggression between individuals in chimpanzees, and other primates living in fission-fusion societies such as spider monkeys, is more likely to occur after a reunion between community members (Nishida et al. 1999; Muller 2002; Aureli and Schaffner 2007). Therefore, on days when the rates of fusion and fission are high the uncertainty with regard to the occurrence of aggression between party members is high (Aureli and Schaffner 2007). Forming temporary social bonds or coalitions with other males might be a potentially effective strategy minimising the costs of potential male-male aggressive interactions on days when grouping patterns are unstable. Pant hoot choruses, which are produced by the Kanyawara chimpanzees more often than solo pant hoots, might be signals mediating temporary social bonds between males (Chapter 3). For example, males are more likely to support each other in agonistic interactions on days when they pant hoot together than on days when they do not (Chapter 3). Moreover, males often pant hoot in choruses immediately prior to the fusion with other community members but after the party with which they fusion has been located (P.Fedurek, pers. obs.). Therefore, one future direction would be examining whether a male is more likely to pant hoot when in the company of other males (so as to initiate a chorus) than when alone (and therefore able to produce only a solo pant hoot) immediately prior to fusion with a party that has been already located by this male. It is possible that solo and chorus pant hoots differ in this respect, with choruses as potential bonding signals being more likely to be produced in this particular situation. More systematic studies are however needed to examine this aspect thoroughly.

The outcome of my study supports a previous study on male chimpanzee pant-hooting showing that there is no relationship between the number of other males in the focal's party and the rates of pant hoots (Mitani and Nishida 1993). My study also shows that there was no relationship between male pant-hooting rates and the average number of females in focal's party. Therefore, the hypothesis that pant-hooting coordinates the maintenance of large male or female parties in chimpanzees is unlikely to be valid.

My study provides support for 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, fusion-fission rates or the type of food consumed, this variable contributed substantially to the optimum model explaining variation in male pant-hooting. This result is therefore in line with the claim that this vocalisation serves as a signal of a high social status (Mitani and Nishida 1993; Clark and Wrangham 1994). Alternatively, the obtained rank effect might be a consequence of the fact that in chimpanzees high-ranking males are usually more social and have more male alliances than low-ranking males (Duffy 2006). In line with this, high-ranking males might use signals that facilitate location of other males or/and signals that mediate social bonds between males (in the case of chorusing) more often than low-ranking males.

Another factor that was not considered in previous studies on chimpanzee pant-hooting and that strongly predicted male pant hoot production in my study, was the type of food consumed. For example, males were more likely to give a pant hoot on days when the majority of food consumed consisted of non-fig fruits rather than fig fruits or piths/leaves. Furthermore, the same pattern emerged after excluding from the analysis calls produced in feeding contexts, suggesting that the type of food consumed correlates with pant hoot production in general rather than being due to chimpanzees being more likely to pant hoot when arriving or feeding on trees with non-fig fruits than on other food sources. 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 more often than during days in which the diet is dominated by less 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-hooting as potentially a signal of both high social status and a tool for mediating social bonds between males might enhance male effectiveness in competing for these valuable food sources.

If male pant-hooting was related to male-male competition I would also expect that males are more likely to pant hoot on days when a parous female is in oestrous. Previous studies showed that the level of male-male aggression is especially elevated when a parous (but not nulli-parous) female in oestrous is available because males aggressively compete to gain sexual access to these females (Muller and Wrangham 2004; Muller et al. 2006). Indeed, my data provide support for this hypothesis showing that the presence of a parous female in oestrus was a strong predictor of the rates with which males pant hooted. Therefore, similarly as in the case of food availability, male pant-hooting might contribute positively to male effectiveness in competing for a valued resource. My results thus do not support a previous study on chimpanzee pant hoots reporting that the presence of an oestrous female is not a major correlate of male pant-hooting behaviour (Mitani and Nishida 1993). However, it is important to note that the study by Mitani and Nishida (1993) did not distinguish between parous and nulli-parous females in oestrus. As mentioned earlier, chimpanzee males compete more vigorously for the access to parous than nulli-parous females in oestrous (Muller et al. 2006), which might also correlate with male pant-hooting. Therefore, the fact that the previous study did not distinguish between these two classes of females might be the reason for the inconsistency between the results of my study and that of Mitani and Nishida (1993).

Taken together, the above results suggest that pant-hooting is a behaviour that plays several social functions. The variable which correlated most with the pant-hooting behaviour, however, was the rate of fusion-fission. This result is consistent with the view that a pant hoot is a long-distance call that most probably evolved for the purpose of maintaining contact with other parties (see Chapter 6). However, the fact that pant hoots were more likely to be given when high quality food or a female in oestrous was present, suggests that there are also other important social functions fulfilled by this behaviour. This function might be, for example, signalling social bonds between chorusing males (Chapter 3) on days when competition for valuable resources is high. Therefore, while maintaining contact with community members might be the original function of pant-hooting, in the course of evolution this behaviour may have acquired other important social functions such as mediating social bonds between males (which is a topic discussed more thoroughly in Chapters 3 and 6).

CHAPTER 3: Pant hoot chorusing and social bonds in male chimpanzees

ABSTRACT

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 investigated the effectiveness of vocalisations as bonding signals in comparison to other affiliative behaviours. In this study I test the hypothesis that in male chimpanzee pant hoot chorusing, a common behaviour in these primates, is a reliable but also flexible signal of affiliative relationships. The results of the study, conducted on the Kanyawara community of chimpanzees in Uganda, show that a male was more likely to join in another male's pant hoot if a well affiliated male was calling. This supports the hypothesis that this behaviour is a good indicator of strong or long-term social bonds between male chimpanzees. However, my 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 displays and coalitions, on days when they chorused together, compared to days when they did not. This pattern applied to both preferred and neutral long-term social partners. Moreover, on a short-term basis chorusing was a better indicator of other affiliative behaviours than grooming. I suggest that in male chimpanzees pant hoot choruses are efficient signals of short-term affiliative relationships. I 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.

INTRODUCTION

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 in many pair living birds (Hall 2004). As discussed in Chapter 1, 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 (Harcourt and Stewart 1996), rhesus macaques (Hauser and Marler 1993a), squirrel monkeys (Biben 1993; Soltis et al. 2002), spider monkeys (Ramos-Fernandez 2005), ring-tailed lemurs (Oda 1996), and gibbons (Geissmann and Orgeldinger 2000; Geissmann 2002)]. It has been suggested that, in primates, vocal interactions play a similar bonding role to grooming, which is a well-established bonding behaviour in primates (Chapter 1). 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, which is one of the aims of this study.

As discussed in Chapter 1, male chimpanzees 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 opportunities. Interactions such as grooming and support in agonistic interactions are commonly recognised as well established indicators of social bonds in this species (Chapter 1). In Chapter 1 I also proposed that because of the costs associated with the well-established indicators of social bonds in chimpanzees, chimpanzees might also use vocal interactions as flexible (i.e., employed often by both long-term preferred and neutral social partners) bonding signals. I also suggested that calls as potentially flexible bonding behaviours might be especially beneficial in unstable chimpanzee societies where grouping patterns are often unpredictable (Chapter 1). In this study I investigated the relationship between male chimpanzee pant hoot chorusing and social bonds.

As discussed in detail in Chapter 2, pant hoots are species-specific long-distance calls which probably fulfil complex and multiple social functions. However, most of the studies on pant-hooting have not incorporated the chorusing aspect of pant-hooting when investigating the function of this call. As mentioned in Chapter 1, pant hoot chorusing or joint pant hooting is a common behaviour in chimpanzees (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 (Chapter 4). A previous study showed that bonded males, who associate and support each other in conflicts, pant hoot in choruses more often than those who do not (Mitani and Gros-Louis 1998). Males also can actively adjust acoustics of their calls to the partner's one (Mitani and Brandt 1994; Mitani and Gros-Louis 1998). These studies suggest that pant hoot chorusing plays a role in social bonding between male chimpanzees (Mitani and Brandt 1994).

I built on previous studies of pant hoot chorusing and examined in detail whether pant hoot chorusing is a reliable indicator of strong long-term social bonds amongst male chimpanzees (Mitani and Gros-Louis 1998). To test this bonding hypothesis, I investigated whether a male was more likely to join a pant hoot produced by another male if the calling individual was a long-term preferred social partner for him.

I also tested the hypothesis that joint pant-hooting reflects short-term affiliations between males. As mentioned above, call interactions are relatively low-cost behaviours, making it possible that these behaviours are flexible (i.e., employed often by both long-term preferred and neutral social partners) but on a short-term basis effective bonding signals. Such low-cost bonding behaviours operating on a short-term basis would be especially beneficial in a chimpanzee fission-fusion society where valuable long-term preferred social partners are not always in the same party (Chapter 1). I tested this hypothesis by investigating whether dyad partners were more likely to be involved in interactions that are generally regarded as markers for strong social bonds in this species, such as reciprocated grooming, support in agonistic interaction and joint non-vocal displays (Chapter 1), on days when they chorused together than on days when they did not. I then investigated whether these short-term correlates differed between long-term preferred and 'neutral' social partners. Secondly, I compared joint pant-hooting to 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 should expect that on a short-term basis chorusing is 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 (see Chapter 2).

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 minutes of direct focal observation per day and 16.81 [SD=5.60] focal follow days of data collection/male). Table 3.1 provides a summary of data collected on the focal males.

In order to test the hypothesis that males are more likely to join in a call when an affiliated male is calling, all-occurrence sampling was used to record pant-hooting behaviour of all males in the party that were visible to the researcher. In contrast, to test the hypothesis that pant hoot chorusing reflects short-term social bonds, continuous sampling was used to record all vocal behaviour of the focal, including all pant hoot interactions between the focal and other party members. The context of the vocalisation (travelling, resting and feeding), the identities of the individuals involved in a pant hoot chorus, the identities of all visible individuals and the identity of the individual who started the bout, were noted. It is important to note that although pant hoots are long-range calls, I concentrated on whether or not particular male dyads within the same party join in each other’s pant hoots so as to produce a chorus, rather than the response of distant individuals in other parties or communities.

Table 3.1: Summary of the data collected on the focal males. Focal days: number of focal follow days (only days in which the focal was followed for at least 6 hours [*N*=169] are included); Chorus days: number of days in which the focal was involved in a pant hoot chorus with another male; Grooming days: number of days in which the focal was involved in reciprocated grooming with another male; Coalition days: number of days in which the focal formed a coalition with another male; Display days: number of days in which the focal performed a joint non-vocal display with another males; Co-feeding days: number of days in which the focal was involved in tolerated co-feeding with another male.

Male ID	Focal days	Chorus days	Grooming days	Coalition days	Display days	Co-feeding days
AJ	20	12	17	6	9	19
BB	18	7	16	2	1	16
ES	14	12	7	2	4	13
KK	19	17	19	5	4	19
LK	22	19	20	5	7	18
PB	13	7	9	1	3	10
PG	15	10	12	1	6	12
ST	18	15	15	7	2	18
TJ	12	7	6	0	1	12
TU	3	2	3	1	0	3
YB	15	9	11	1	2	10

Each male was assigned an ordinal linear rank (1-11) (see Chapter 2)

All focal grooming interactions were recorded and details such as duration, direction and grooming reciprocity (i.e., whether or not grooming was reciprocated within grooming bouts) were recorded. All agonistic interactions in which the focal was involved were recorded to obtain data on coalitions.

In order to establish the identity of preferred social partners for each focal animal the following additional data were collected. First, 5 min scans were conducted to record the behaviour of the focal (resting, travelling, grooming and feeding), the identity of the nearest neighbour of the focal, and the identities and behaviour of individuals present within 5, 10, 15 and 30m of the focal, as well as to record information on party composition (i.e., identities of all individuals in the party). Party composition was defined as a collection of individuals that are separated from other community members by at least 50m. An individual that has not been seen within the party in the last 15 min was excluded from the party (see Clark and Wrangham 1994).

Definitions

Dyadic association measures

Long-term preferred social partners were determined in two different manners to test the two main hypotheses. Firstly, I identified mutual preferred social partners (mutual-PSPs) to test aspects of the short-term hypothesis. Secondly, I identified unidirectional preferred social partners (Uni-PSPs) to test the hypothesis that a male is more likely to join another male's pant hoot if the calling individual is a long-term preferred social partner for him. I established both mutual PSPs and uni-PSPs separately for two six-month periods within the whole study period: October 2010-March 2011; April 2011-September 2011. Six month periods provided sufficient data for meaningful analyses, but also captured important changes in social relationships that occurred over the whole study period.

Preferred social partners (PSP) were established on the basis of three different dyadic association measures. The first measure, Simple Ratio Index (SRI), reflects the total proportion of scans in which both individuals were together in the same party (Cairns and Schwager 1987), or:

$$\mathrm{SRI}_{\mathrm{AB}} = \frac{P_{\mathrm{AB}}}{P_{\mathrm{A}} + P_{\mathrm{B}} - P_{\mathrm{AB}}}$$

Where P_{AB} = the number of parties containing both A and B, P_A = the number of parties containing A, P_B = the number of parties containing B.

The second dyadic association measure is the ‘5 metre association index’ (5M) (Gilby and Wrangham 2008) which measures the frequency with which a dyad was observed within 5m of one another, given that one of the individuals was present in the party and another one was a focal:

$$5\mathrm{M}_{\mathrm{AB}} = \frac{A_{\mathrm{f}}(B_5) + B_{\mathrm{f}}(A_5)}{A_{\mathrm{f}}(B_{\mathrm{p}}) + B_{\mathrm{f}}(A_{\mathrm{p}})}$$

Where $A_f(B_5)$= the number of instances in which A was the focal animal and B was within 5m of A, $B_f(A_5)$= the number of instances in which B was the focal animal and A was within 5m, $A_f(B_p)$= the number of instances A was the focal and B was in the same party, $B_f(A_p)$= B was the focal and A was in the same party.

The third employed dyadic association measure is the ‘nearest neighbour association index’ (NN) (Gilby and Wrangham 2008), which reflects the frequency with which two individuals were observed as nearest neighbours, provided that one was the focal and the other was within 5m, or:

$$\mathrm{NN}_{\mathrm{AB}} = \frac{A_{\mathrm{f}}(B_{\mathrm{nn}}) + B_{\mathrm{f}}(A_{\mathrm{nn}})}{A_{\mathrm{f}}(B_5) + B_{\mathrm{f}}(A_5)}$$

Where $A_f(B_{nn})$= the number of instances A was the focal and B was the nearest neighbour and $B_f(A_{nn})$= the number of instances B was the focal and A was the nearest neighbour.

Mutual preferred social partners

To investigate the difference in terms of probabilities of occurrence of such behaviours as grooming, coalitions and joint non-vocal displays between ‘chorus’ and ‘non-chorus’ days, I divided male dyads into ‘mutual preferred social partners’ and ‘neutral social partners’. For a given index (SRI, 5M and NN) individuals A and B were classified as ‘mutual associates’ if the value was one-third standard deviation larger that the averages of both A and B. I classified a dyad as mutual preferred social partners (mutual PSP) if they were mutual associates for at least two of the three different indices (Gilby and Wrangham 2008). Using this procedure I identified 10 dyads for the period between October 2010 and March 2011 (mean=1.82/focal individual, SD=1.25, range=0-4), and 12 dyads for the period between April 2011 and September 2011 (mean=2.40/focal individual, SD=1.07, range=1-4) that met the criteria of mutual PSP. The remaining dyads (43 for the period between October 2010 and March 2011 and 41 for the period between April 2011 and September 2011) were classified as neutral social partners (non-PSPs).

Unidirectional preferred social partners

In order to test the long-term bond hypothesis and the extent to which PSP join in each other’ pant hoots, I identified ‘unidirectional preferred social partners’ (Uni-PSPs) and ‘unidirectional neutral social partners’ (Uni-Non-PSPs). This is because chimpanzee associations can be one-sided (i.e., within a dyad, A might be a preferred social partner for B, B however might not be a preferred social partner for A), and joining in other male’s pant hoots is likely only to be affected by the joining individual’s relation to the initiator. In other words, if A starts a pant hoot in the presence of B, it is the type and strength of the relation of B to A that may mediate B’s decision to join in; a mutual bond is not necessarily required.

To calculate uni-PSPs for a given focal male, I first examined each index (SRI, 5M and NN) to identify any individuals for whom the index value was one-third standard deviation larger than the mean for this focal male (labeled an associate). Hence, male A was a uni-PSP for male B if male A was categorised as an associate of male B on at least two of the three indexes. I identified 33 uni-PSP dyads for the period between October 2010 and March 2011 (mean=3.00/focal individual, SD=1.00, range=2-5), and

31 uni-PSP dyads for the period between April 2011 and September 2011 (mean=3.10/focal individual, SD=1.20, range=1-5) across the eleven focal chimpanzees (mean=3.45/focal individual, SD=0.82, range=2-5). All remaining possible dyads (77 for the period between October 2010 and March 2011 and 79 for the period between April 2011 and September 2011) were labelled as unidirectional neutral social partners (Uni-Non-PSP).

Pant hoot chorusing

Males were involved in a pant hoot chorus (or a joint pant hoot) when two or more males performed a pant hoot at the same time (Mitani and Brandt 1994). If there was no time overlap between the occurrences of the pant hoots, the call was not recorded as a pant hoot chorus. In addition, a male was involved in a pant hoot chorus only when he gave a pant hoot with a climax. In total, I recorded 872 bouts of pant hoot choruses.

Reciprocated grooming bouts

A grooming bout was reciprocated if both partners were involved in providing grooming to the partner at any stage of the grooming bout [*N*=417]. When the same dyad resumed grooming within one minute I recorded this as the same grooming bout.

Coalitions

The term coalition refers to an event where two males jointly directed an aggressive behaviour (such as charge, chase or physical attack) towards another individual [*N*=50] (Mitani and Gros-Louis 1998).

Tolerated co-feeding

Two males were involved in tolerated co-feeding (feeding tolerance) if they were observed within 5m from each other when feeding during a 5 min scan [*N*=1968 scans of co-feeding].

Joint non-vocal display

The term joint non-vocal display refers to a situation when at least two males were observed performing a non-vocal display at the same time [*N*=76]. A non-vocal display takes place when a male runs (sometimes bipedal) pilo-erect, and may include shaking vegetation, slapping the ground or making buttress drums (Goodall 1986). Such displays might be performed in the presence of a female who usually reacts submissively to the performing male (Nishida 2012). However, if during the display the displaying males jointly charged or attacked another individual, this behaviour was recorded as a coalition. Similarly, if during a non-vocal display one of the males pant hooted, this behaviour was not recorded as a joint non-vocal display. In addition, males sometimes chorus shortly before or after a joint non-vocal display. Therefore, to avoid the problem of non-independence of these two sets of data, I only recorded a joint non-vocal display if the displaying males had not chorused together 5 min before and after the display.

Outline of the study design

Hypothesis 1: Chorusing and long-term social bonds

To test the hypothesis that chorusing reflects long-term social bonds, I compared the likelihood of the nearby male joining in the caller's pant hoot so as to produce a chorus depending on whether or not the male starting the call was a uni-PSP or uni-non-PSP for him. In this analysis all occurrence data were used and any adult male in the party that was visible to the observer and who started the call was labelled as the 'caller' whereas any adult male who was present within a visible distance (from the observer's point of view) was labelled as a 'potential partner'. For this analysis a single data-point was a caller-potential partner dyad (N=1639) and I coded if the potential partner joined in with a pant hoot to form a chorus and if the caller was a preferred social partner. Therefore, if during a call there were 5 males within a visible distance, this resulted in 5 caller-potential partner dyads whose behaviour and relationships were coded.

Hypothesis 2: Chorusing and short-term social bonds

To test the hypothesis that joint pant-hooting reflects social bonds on a short-term basis, continuous focal data were used and I compared data on affiliative interactions from a given dyad (containing the focal) collected during days in which they produced a chorus pant hoot with the data collected during days in which they did not. All males who were together in the party with the focal for at least six hours were considered dyad partners of the focal, thus one day of focal data could generate multiple dyads for analysis. In addition, I incorporated in the analyses only these focal-other male dyads (*N*=41; including both mutual PSP and Non-PSP dyads) which spent at least one day in the same party when they chorused together and one day when they did not (Total *N*=402 days). While making these between-day comparisons I looked at the relationship between the occurrence of chorusing and the presence of such behaviours as reciprocated grooming bouts, coalitions, feeding tolerance and joint non-vocal displays during ‘chorus’ and ‘non-chorus’ days. I then compared this pattern between mutual PSP and non-PSP dyads.

To investigate whether chorusing was a better indicator of short-term social bonds than reciprocated grooming, I first compared the occurrence of such behaviours as coalitions, feeding tolerance and joint non-vocal displays between days on which a dyad was involved in reciprocated grooming and days in which they were not. Similarly as in the case of the chorus data, to conduct these analyses I incorporated only these dyads (*N*=35; both mutual PSP and Non-PSP dyads) which spent at least one day in the same party (i.e., at least 6 hours per one day of data collection) when they groomed together and one day when they did not (Total *N*=369 days). I then compared whether grooming was a better predictor of these three affiliative interactions than chorusing.

Statistical analysis

Generalised Linear Mixed Models (GLMM) with a binomial error structure were the main statistical tools used in the analyses (see Chapter 2). In all analyses Focal ID and Partner ID were inserted into all the models as random effects. All variables within a data-point had a binomial distribution and therefore indicated whether the investigated behaviours, such as chorusing, reciprocated grooming, support in agonistic interactions, joint non-vocal displays, and tolerated co-feeding, occurred or not (0/1) during particular days. All statistical analyses have been carried out using STATA 12.0 software.

Models created

I created a GLMM to investigate whether a potential partner was more likely to join in a caller's pant hoot to produce a chorus depending on whether the caller was a uni-PSP for the potential partner. In this model as the dependent variable I put whether or not (0/1) the potential partner joined in a pant hoot produced by the caller, whereas as the independent variable I put whether or not (0/1) the caller was a uni-PSP for the potential partner. The relative social status of the caller might be a factor that influences the probability with which the potential partner joins in the call produced by the caller (e.g. Mitani and Gros-Louis 1998). Therefore, to control for this possibility I put another independent variable into the model which was whether or not (0/1) the caller was a higher-ranking male than the potential partner. Caller ID, potential partner ID and call ID were set as random effect variables.

To test the hypothesis that joint pant-hooting reflects short-term affiliations, I created three GLMMs in which I put as the dependent variable whether or not (0/1) the dyad was involved in (i) reciprocated grooming or (ii) coalitions or (iii) joint non-vocal displays when being in the same party for a minimum of 6 hours, whereas as independent variables I put whether or not (0/1) the dyad produced a joint pant hoot on that day. In this model I also put as another independent variable whether or not (0/1) the dyad partners were mutual PSPs to examine if the affiliation level between the males affects the relationship between chorusing and the three affiliative behaviours. In these analyses one day of data collection for a given dyad was treated as one data-point (*N*=402). On a finer level, to investigate whether these models predict different outcomes for mutual preferred and neutral social partners, I created further models and reran these analyses separately for mutual PSPs (*N*=142 data-points) and non-PSPs (*N*=260 data-points).

To investigate whether chorusing had similar short-term correlates as reciprocated grooming, I created three GLMMs in which I put as the dependent variable whether or not (0/1) a dyad was involved in (i) tolerated co-feeding or (ii) coalitions or (iii) joint non-vocal displays on a given day, whereas as the independent variable I put the information whether or not (0/1) a dyad was involved in reciprocated grooming on that day. All dyads (i.e., both mutual PSP and non-PSP) were included in the analysis. To allow comparisons between grooming and chorusing, I did parallel analyses for chorusing and created three additional GLMMs. In these models as the dependent variable I put whether or not (0/1) given dyad partners were involved in (i) tolerated co-feeding or (ii) coalitions or (iii) joint non-vocal displays on a given day, whereas the information whether or not (0/1) a dyad chorused on a that day I put as the independent variable.

In addition, Wilcoxon Signed Ranks Test was used to examine how often males pant hooted jointly in comparison to solo pant-hooting.

RESULTS

Solo and joint pant hoots

Males produced pant hoots jointly with others (62.96% of all pant hoots [*N*=1385] given by focal males throughout the study period) considerably more often than alone (Wilcoxon Signed Ranks Test z=-2.13, *N*=11, *P*=0.033). The difference was even more pronounced when only the subset of data were analysed, where at least one male was present in proximity to the focal male, providing the opportunity for a joint pant hoot to occur (31.34% [*N*=398] and 68.66% [*N*=872], solo pant hoots and joint pant hoots respectively; Wilcoxon Signed Ranks Test z=-2.67, *N*=11, *P*=0.008).

Reciprocated grooming, coalitions and joint non-vocal displays as markers of long-term social bonds

When in the same party, mutual PSPs were more likely than non-PSPs to be involved in reciprocated grooming bouts (β±SE=1.28±0.37, z=3.47, *P*=0.001), coalitions (β±SE=1.30±0.42, z=3.04, *P*=0.002) and joint non-vocal displays (β±SE=1.07±0.42, z=2.56, *P*=0.010). These results indicate that these three interactions reliably reflect long-term social bonds between males in this community.

Pant hoot chorusing and long-term social bonding

A male was more likely to join in another male's pant hoot to produce a chorus, when the caller was a uni-PSP for him: 42% of pant hoots given by males were joined by uni-non-PSPs, compared to 50% joined by Uni-PSPs (β±SE=0.41±0.16, z=2.59, *P*=0.010). In addition, a male was equally likely to join in the caller's pant hoot regardless of whether or not the caller was a higher or lower ranking male than him (β±SE=-0.15±0.24, z=-0.64, *P*=0.525).

Short-term correlates of pant hoot chorusing

When all dyads (mutual-PSP and non-PSPs) were included in analyses, the results show that dyad partners groomed each other reciprocally (β±SE=1.16±0.28, z=3.80, *P*<0.001), performed joint non-vocal displays (β±SE=1.51±0.43, z=3.46, *P*=0.001) and supported each other in agonistic interactions (β±SE=1.95±0.44, z=4.48, *P*<0.001) more often on days when they chorused than on day when they did not (Fig. 3.1).

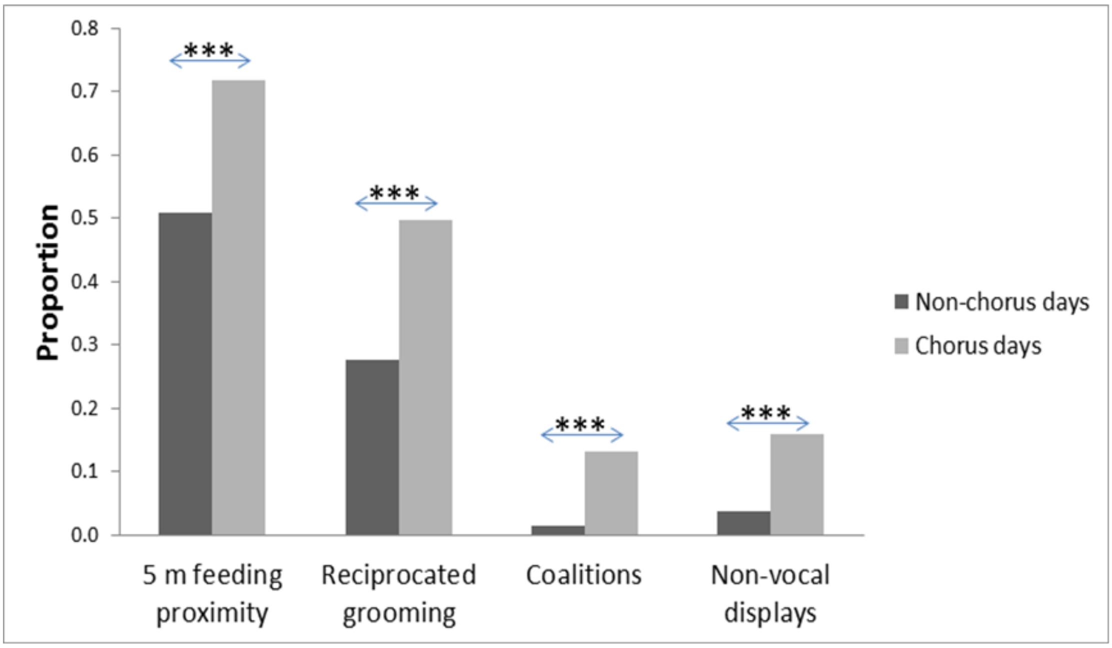

Figure 3.1: The proportion of days in which dyad partners were involved in feeding tolerance, reciprocated grooming, coalitions and joint non-vocal displays as a function of whether or not a dyad produced a joint pant hoot on these days [GLMM; ******P*≤0.001; random effects: Focal ID and Partner ID].

As expected, the long term affiliation level between dyad partners also affected their behaviour, with mutual PSPs showing significantly higher levels of affiliative behaviour than non-PSP, in terms of reciprocated grooming (β±SE=0.86±0.37, z=2.30, *P*=0.022) and coalitions (β±SE=0.90±0.43, z=2.09, *P*=0.037) but not joint non-vocal displays (β±SE=0.43±0.41, z=1.08, *P*=0.280). In order to examine if chorusing correlated with the behaviour of mutual PSP and non-PSPs in the same way, these models were then run separately for mutual PSP and non-PSP dyads: both non-PSPs and mutual PSPs were more likely to groom each other (Non-PSPs: β±SE=0.94±0.38, z=2.29, *P*=0.013; Mutual PSPs: β±SE=1.15±0.40, z=2.82, *P*=0.005), support each other in conflicts (non-PSPs: β±SE=1.76±0.82, z=2.15, *P*=0.031; mutual PSPs: β±SE=2.81±1.06, z=2.63, *P*=0.008) and perform non-vocal displays (non-PSPs: β±SE=1.43±0.63, z=2.28, p=0.022; mutual PSPs: β±SE=1.61±0.67, z=2.42, *P*=0.016), on days when they pant hooted together.

Comparison between short-term correlates of joint pant-hooting and grooming

Considering mutual PSPs and non-PSPs together, while individuals were more likely to feed in close proximity on days when they groomed each other (β±SE=0.77±0.24, z=3.19, *P*=0.001), they were equally likely to perform a joint non-vocal display (β±SE=0.04±0.43, z=0.09, *P*=0.930) or support each other in agonistic interactions (Fig. 3.2; β±SE=-0.09±0.45, z=-0.21, *P*=0.834) on grooming and non-grooming days. In contrast, males were more likely to feed in close proximity (β±SE=0.95±0.23, z=4.09, *P*<0.001) as well as to perform joint non-vocal displays and support each other in agonistic interactions (Fig. 3.1) on days when they chorused than on days when they did not.

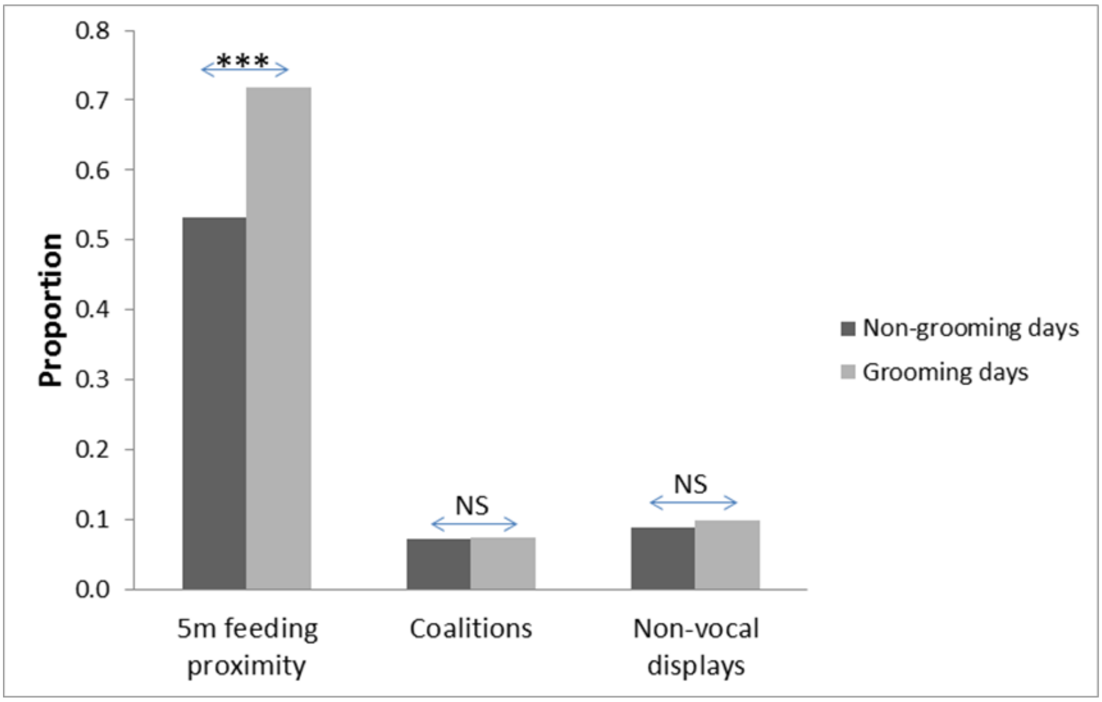

Figure 3.2: The proportion of days in which dyad partners were involved in feeding tolerance, coalitions and joint non-vocal displays as a function of whether or not a dyad was involved in reciprocated grooming on these days [GLMM; ******P*≤0.001; NS=not significant; random effects: Focal ID and Partner ID].

DISCUSSION

The results of my study show that pant hoot chorusing is indeed a very common behaviour among male chimpanzees. For example, males pant hooted jointly with others significantly more often than alone. Overall, my results support previous studies suggesting that pant hoot chorusing might reflect strong social bonds between male chimpanzees (Mitani and Brandt 1994; Mitani and Gros-Louis 1998). For example, a male was more likely to join in another male's pant hoot, if the calling individual was a long-term preferred social partner for him. However, males also often joined pant hoots produced by long-term neutral social partners, suggesting that in terms of partner choice chorusing is a flexible bonding behaviour that is often employed by males who are not necessarily affiliated on a long-term basis.

Indeed, I found considerable support for the hypothesis that this behaviour reflects social bonds on a short-term basis. For example, males were more likely to be involved in reciprocated grooming, coalitionary support and joint non-vocal displays, on days when they chorused than on days when they did not. It is possible, therefore, that a joint pant hoot is a mutual signal for the individuals involved in the call that the calling partner is likely to participate in other affiliative activities. Such signals that allow prediction of each other's behaviours or attitudes might be highly beneficial in male chimpanzees where social status is a function of both male-male competition and cooperation (Muller and Mitani 2005). It is important to note, however, that in this study I only examined the co-occurrence of chorusing with other affiliative interactions rather than investigating cause-effect relationships between these behaviours. Therefore, the question of whether chorusing indeed precedes other affiliative interactions remains to be examined in future studies.

Nonetheless, the fact that on a short-term basis chorusing correlated with other affiliative behaviours for both long-term preferred and neutral social partners is consistent with the view that vocal interactions might be flexible bonding signals. One would imagine, for instance, that when males are in potentially risky close physical proximity, the need to signal short-term affiliations towards each other is vital regardless of the overall (long-term) bond between them. This might especially apply to animals such as chimpanzees, which, as discussed in Chapter 1, form highly fluid and flexible societies in which party size and composition change on both seasonal and daily bases. Therefore, in this species grouping patterns are often unpredictable and valuable long-term social partners are not always available (Chapter 1). Furthermore, although long-term social bonds predict the occurrence of interactions such as coalitions, in chimpanzees, males are also often opportunistic in this respect and can frequently switch between coalition partners across interactions (Nishida and Hosaka 1996; Newton-Fisher 2002; Muller and Mitani 2005), which might be another reason why forming flexible short-term affiliations between males might be advantageous. Vocal interactions such as joint pant hoots, as potentially low-cost bonding behaviours, might be especially efficient signals of such short-term affiliations between individuals who are not necessarily strongly affiliated. Indeed, my data show that while on a short-term basis both grooming and chorusing were good predictors of feeding proximity, coalitions and joint non-vocal displays were more reliably predicted by the occurrence of joint pant-hooting than reciprocated grooming. Hence, while grooming might more reliably reflect long-term social bonds (Mitani 2009b), chorusing might be more effectively employed as an indicator of temporary affiliations. This is in line with the fact that chorusing is an interaction that is less time-consuming and brings about fewer opportunity costs than grooming. My results are therefore in line with Dunbar’s (1993) hypothesis positing that, in primates, vocalisations are less costly bonding behaviours than grooming (see also McComb and Semple 2005; Greeno and Semple 2009). Nevertheless, I again emphasise that the correlational design of this study limits my conclusions and more detailed studies are needed to determine the relative values of chorusing and grooming to a chimpanzee male.

Another interpretation of joint pant-hooting is that this behaviour is a signal of a bond between the chorusing males, which is directed not to the chorusing partner but to other males. For example, if the fact that within dyads chorusing correlates with frequencies of coalitions is informative to the audience (i.e., that the chorusing males are likely to support each other in conflicts), a chorus might be a powerful signal for its recipients. It is also possible that pant hoot chorusing is a territorial display fulfilling an important role in inter-community signalling (e.g., Wilson et al. 2007). For instance, by chorusing, males might advertise to neighbouring communities social bonds between them and/or the number of males constituting their community (and therefore its territorial strength). This interpretation is consistent with the fact that pant hoots are loud long-distance vocalisations. Although the hypothesis that chorusing is a signal that allows males testing each others' affiliations and the hypothesis that this behaviour is a signal of a bond directed to other males or communities are not necessarily mutually exclusive, more studies are needed to test each of these interpretations.

In conclusion, my data support the hypothesis that joint pant-hooting is a good indicator of strong social bonds in male chimpanzees. My results also suggest that joint pant-hooting is a flexible affilative behaviour reflecting short-term bonds between both neutral and preferred long-term social partners. I conclude that vocal interactions such as pant hoot choruses might be effective and flexible bonding signals in complex fission-fusion societies that characterise this species.

CHAPTER 4: The acoustic structure of chimpanzee pant-hooting facilitates chorusing

ABSTRACT

Duetting or chorusing behaviour occurs in a wide variety of animals and is posited to fulfil various important functions including territory defence and social bonding. The structure of calls produced in choruses might be shaped in a way that facilitates such joint vocal displays. In this study I test the hypothesis that flexibility in terms of the temporal structure of chimpanzee pant hoots, a vocalisation often given jointly with other individuals, facilitates chorusing. The results of this study, which was conducted on two wild communities of chimpanzees in Uganda, support this hypothesis. First, the duration of the build-up phase of the call correlated with the latency with which the partner joined in the call, suggesting that males prolong the duration of the build-up to allow others to join in the call and to increase the likelihood of a chorus occurring. Second, the loud climax phases were significantly longer when produced in choruses than alone, which suggests that males prolong this part of the call when calling in choruses. Within chorus pant hoots, there was a positive relationship between the number of climax elements given by calling partners, suggesting that males adjust the temporal structure of their call to mirror their partner's call. I conclude that the basic acoustic structure of chimpanzee pant hoots and the flexibility with which males adjust the duration of the constituent phases promotes chorusing and that the temporal structure of this rather stereotyped vocalisation is sensitive to fine details of the vocal responses of the audience.

INTRODUCTION

Joint vocal displays, such as duetting or chorusing, are common phenomena in the animal kingdom and can be observed in species ranging from insects to mammals (Gerhardt et al. 2000; Geissmann 2002; Bailey 2003; Hall 2004; Greenfield and Schul 2008; Schulz et al. 2008). There have been a substantial number of studies, particularly focussed on pair bonded birds and primates, which have examined social and developmental correlates of this behaviour (Wickler and Seibt 1980; Geissmann 1999). As I discussed in Chapter 1, the ultimate function of joint vocal displays has also received a lot of attention. For example, in many animals coordinated vocal displays have been suggested to play a vital role in social bonding, territorial defence, mate-guarding as well as coordinating activities between individuals (Geissmann 2002; Hall 2004; Mendez-Cardenas and Zimmermann 2009). It has been argued that examining the acoustic structure of animal calls and investigating factors that influence their production can be an effective method of deciphering their functions and the selective pressures that may have influenced their evolution (Wiley and Richards 1978; Waser and Brown 1986). For example, the efficacy of calls, including those produced in choruses, in propagating through the environment to reach and influence receivers, depends in part on how suitable their acoustic characteristics are to conditions of the physical and social environment (Waser and Waser 1977; Greenfield et al. 1997; Brown and Handford 2003). However, few studies have specifically addressed the question of whether the acoustics of calls or songs that tend to be produced in choruses are shaped in a way that facilitates a partner’s reply and consequently a joint vocal display. The aim of this study is to investigate whether flexibility in the temporal structure of chimpanzee pant-hooting facilitates chorusing.

Pant hoots are common long-distance vocalisations in chimpanzees and these calls appear to fulfil a complex social function (Chapter 2). Males often produce pant hoots in choruses and such joint pant-hooting might play an important role as an affiliative signal (Chapter 3). A pant hoot has a specific acoustic pattern (Fig. 4.1).

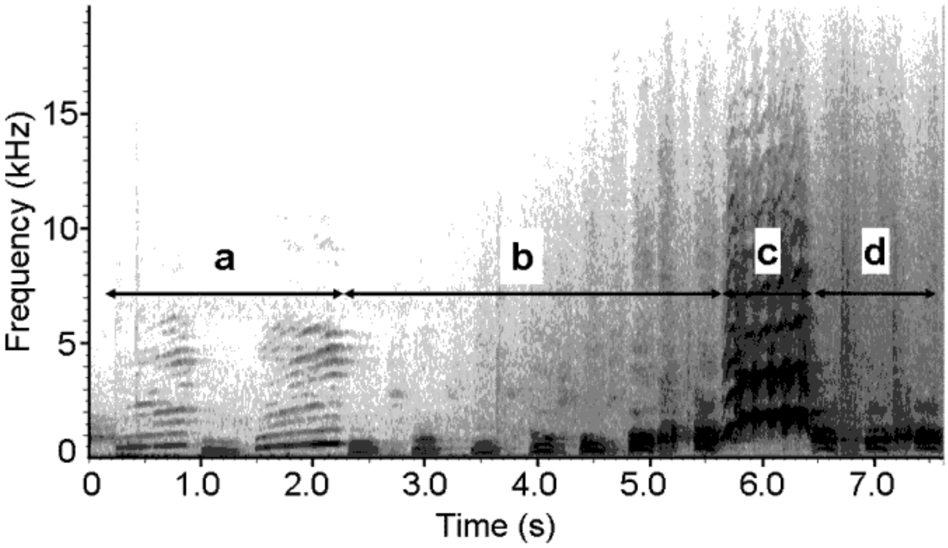

Figure 4.1: A spectrogram showing the four phases of a pant hoot. A = introduction, B = build-up, C = climax, D = let down. From Slocombe & Zuberbühler (2010)

This call typically consists of four distinctive parts: introduction, build-up, climax and let down (Marler and Tenaza 1977). Pant-hooting usually begins with a short introduction consisting of low frequency and low amplitude elements (Mitani and Gros-Louis 1998). The introduction grades into a build-up phase comprising a series of short inhalations and exhalations. Build-up in turn grades into the climax, which is the loudest part of the call that can include one or several 'screams' given in succession (so called 'climax elements'). The call might be finalised with a short let down phase that has similar acoustic features to the ones characterising a build-up phase (Mitani and Gros-Louis 1998). Although a pant hoot is a highly stereotyped call, the acoustic structure of the overall call and its different phases have been shown to correlate with the behavioural context of the caller. For example, males are more likely to produce a pant hoot with a let down phase upon arriving at feeding trees compared to other contexts (Clark and Wrangham 1993). Another study showed that the acoustics of the build-up and climax phases of pant hoots given in travelling contexts prior to a fusion with other community members differ substantially from the acoustics of pant hoots given in other contexts (Notman and Rendall 2005).

The acoustic structure of a pant hoot seems not only dependent on the behavioural context of the caller but also on the acoustics of calls given by other males that are involved in a chorus. When chorusing, males can actively adjust spectral aspects of the individually distinctive acoustic structure of their calls to match the calls of the partner (Mitani and Brandt 1994; Mitani and Gros-Louis 1998). For example, the frequencies of climax elements of pant hoots within a chorus produced by a single dyad were more similar to each other than to those of pant hoots produced by either of these individuals alone or given in a chorus with a different individual (Mitani and Gros-Louis 1998). These studies suggest that although chimpanzees [(like other primates (Hammerschmidt and Fischer 2008)] lack the highly flexible vocal control characteristic for humans, these animals actively modify some acoustic features of their calls. Recent studies also show that primates have control over aspects of call production such as its timing and length (Egnor et al. 2007; Roy et al. 2011). It is possible, therefore, that if selection pressures were to favour chimpanzees who produced pant hoots that facilitate acoustic convergence, this might be achieved by favouring individuals that modify the timing of call production and/or the duration of the call. Considering the above, I aimed to investigate whether the flexibility to modify the duration of specific phases of the call such as the build-up and the climax, facilitates chorusing. To test this hypothesis I make comparisons between pant hoots given within duets as well as between solo pant hoots and duet pant hoots, and generate the following predictions.

The build-up phase is the part of the call that precedes the culmination of the call – the climax. Therefore, this phase of the call might function to allow nearby males to join in the call before it grades into the climax. If this is the case, the duration of the build-up should depend on the latency with which the chorusing partner joins in the call. Hence, I expect that the individual starting the call prolongs this phase of the call if the partner is late joining in the call. Accordingly, I predict that, within duet pant hoots, the build-up phase of the initiator’s call of the duet is shorter when the partner joins the call during the introduction rather than the build-up phase of the call.

Importantly, on a finer level, I predict that in duets where the partner joins in the call after the initiator has finished the introduction phase of his call, there is a positive relationship between the duration of the build-up of the initiator's pant hoot and the latency with which the partner joins in the call.

As mentioned in Chapter 1, coordinating or synchronising a vocal display with a social partner might make it an effective test of the bond between them (Smith 1994). Mirroring the temporal structure of each other's calls could be a way to achieve such a synchronised vocal display. Since the climax phase of a pant hoot is the loudest part of the call that can consist of one or several climax elements given in succession, chorusing males might mirror the temporal structure of each other's climax elements so as to prolong and synchronise their chorus and therefore make it a more effective bonding signal. Thus, the number of climax elements given by the chorusing males might be adjusted in accordance with the partner's contribution to the call so as to optimise the display in terms of it acoustic symmetry. Therefore, I predict that there is a positive relationship between the number of climax elements given by the initiator of the chorus and the partner.

In comparing solo and duet pant hoots, I examine whether the duration of different call phases differed. If the temporal structure of pant hoots plays a role in facilitating or/and prolonging a chorus, I would expect that phases such as the climax are longer on average in duet than in solo pant hoots. In addition, if climax elements function to prolong a chorus with the partner, I predict that the number of climax elements within duet pant hoots is greater than in solo pant hoots. Prolonging the duration of this phase of the call might prolong the chorus making it a more effective display. With regard to the duration of the build-up, I predict that the duration of this phase is modified depending on the behaviour of other males: if no one has joined in the pant hoot yet, the build-up should be longer than in solo pant hoots to increase the chances for other individuals to join in the call. Conversely, if another male has already joined in, males might shorten the build-up and therefore this part of the call should be shorter than in solo pant hoots.

METHODS

Study subjects

I studied two Ugandan communities of wild chimpanzees, the Kanyawara community in the Kibale National Park (Chapter 2) and the Sonso community in the Budongo Forest Reserve. The Sonso community contained 75 individuals (including 9 adult males and 22 adult females) and had a home range of around 15 km^2 at the onset of the study in August 2009. The Sonso community has been studied regularly since 1990 and is well habituated. In both communities the study subjects were adult and sub-adult males (*N*=10 and *N*=11, Kanyawara and Budongo populations respectively).

Data collection

At Kanyawara, 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 minutes of direct focal observation per day). At Budongo, the focal was followed from 0700 until 1630. Fieldwork was conducted between August 2009 and June 2012 and resulted in 309 days of observations (Mean= 228 minutes of direct focal observation per day).

At both field sites continuous sampling was used to record all pant hoots by the focal individual, including any vocal interactions between the focal and other party members. The context of the vocalisation (i.e., resting, travelling and feeding), the identities of the individuals involved in a vocal bout, and the identity of the individual who started the bout, were noted. Vocalisations were recorded using Marantz Professional solid state recorder PMD661 and a Seinnheiser ME67 directional microphone.

The selection of call recordings

Prior to conducting acoustic analyses, I selected pant hoot recordings for analysis that met several criteria. Firstly, to control for the context of the call [which has been shown to correlate with the acoustics of pant hoots (Notman and Rendall 2005)] I included in the analyses only those pant hoots that were given in a travelling (rather than feeding or resting) context. To control for the number of individuals involved in a chorus I incorporated in the analyses only duet pant hoots, and therefore all chorus pant hoots which involved more than two males were excluded. A duet took place when there was a time overlap between the pant hoots given by two partners. I analysed only these duets in which I could establish the time at which the partner joined in the call. In addition, only the duet pant hoots in which the number of elements and duration of build-up and climax phases given by the individual starting the call could be established, were analysed. Detailed measurements of the introduction phase of the calls were not taken, as in contrast to the other three call phases, it was not always possible to establish with certainty whether a given recording contained a complete introduction phase. The soft introductory hoo calls could be difficult to detect and often there was a delay between detecting the onset of an introductory phase and starting the sound recording. In total, I analysed 249 calls (Mean=17.00 [SD=13.50] and Mean=7.09 [SD=4.32] calls per individual, Kanyawara and Budongo communities respectively), including 120 solo pant hoots (N=64 and N=56, Kanyawara and Budongo communities respectively) as well as 129 duet pant hoots (N=106 and N=23, Kanyawara and Budongo communities respectively). All acoustic measurements were conducted using Praat software (Version 5.2.19).

Measurements of temporal structure

I extracted up to 5 measurements from the pant hoots that met the selection criteria. I took measurements from solo pant hoots (given by a single individual), initiator's/starting duet pant hoots (given by the individual who started the duet) and the partner's duet pant hoot (given by the individual who joined in the call), as detailed in Table 4.1.

Table 4.1: Measurements of the temporal structure taken from the pant hoot calls.

Measure	Definition	Type of pant hoot the measure was extracted from
Build-up duration	Time from the start of the first exhalation to the end of the last exhalation	Solo pant hoot, Initiator’s duet
Number of build-up exhalations	Number of exhalations (i.e., rapid ‘hoos’ produced is succession)	Solo pant hoot, Initiator’s duet
Climax duration	Time from the start of the first element to the end of the last element	Solo pant hoot, Initiator’s duet
Number of climax elements	Number of climax elements (i.e., ‘screams’ given in succession)	Solo pant hoot, Initiator’s duet, partner’s duet
Let down duration	Time from the end of the last climax element to the end of the last let down exhalation	Solo pant hoot, Initiator’s duet

Comparing pant hoots given in duets and solos

For duets, I compared the duration of build-up, climax and let down phases, and the number of build-up exhalations of initiator pant hoots, in relation to variation in the latency with which the partner joined in the call. In this respect, I divided the duets into those in which the partner joined in the call when the male initiating the chorus was at the introduction (labelled as *introduction duets*, N=72), build-up (labelled as *build-up duets*, N=37), climax (N=14) or let down (N=1) stage of his call. I used only the initiator’s pant hoots in comparisons of duet and solo calls.

Statistical analysis

Generalized Linear Mixed Models (GLMM) were the main statistical tools used in the analyses (Chapter2). Depending on the nature of the distribution of the dependent variable, I used two types of GLMMs. For a continuous dependent variable (e.g., duration [sec]) I used GLMM with a Gaussian error structure (labeled here as Gaussian GLMM). If the dependent variable was entered as count data (e.g., number of climax elements), I used GLMM with a Poisson error structure (labeled as Poisson GLMM).

In models comparing the structure of duet pant hoots the variable Community (i.e., Kanyawara or Budongo) as well as IDs of both individuals involved in a call (i.e., the entities from which repeated samples were taken) were inserted as 'random effects'. In models comparing solo to duet pant hoots the variables Community, the ID of the individual that gave a solo pant hoot or who initiated the duet, were set as random effects.

In situations where multiple post-hoc tests were conducted on the same dataset, the α-level for significance was corrected using Sidak's (1967) adjustment equation to control for family-wise error.

I used Stata 12.0 software (StataCorp LP) for all statistical analyses and the specific variables entered into each GLMM in order to test my hypotheses are outlined below.

Models created

Comparisons between Kanyawara and Budongo pant hoots

To investigate whether the duration of particular phases of solo pant hoots differed between the two populations, I created three Gaussian GLMMs in which I put the duration (in seconds) of the (i) build-up or (ii) climax or (iii) let down phase as the dependent variable and "Community" as the independent variable.

To check whether the duration of particular phases of initiator duets differed between the two populations, I created another Gaussian GLMM in which I put the duration of the (i) build-up or (ii) climax or (iii) let down phase of the initiator's pant hoot as the dependent variable whereas " Community" as the independent variable.

For the remainder of GLMM analyses I merged data from both communities and I present the results accordingly. However, to show that there was a similar pattern observed in both communities in terms of the key investigated patterns, I also provide descriptive statistics (i.e., Mean and SD) for both Kanyawara and Budongo populations in Appendix B.

Comparisons between solo and duet pant hoots

To investigate whether particular pant hoot phases differed between solo and duet pant hoots, I created three Gaussian GLMMs in which as the dependent variable I put the duration of the (i) build-up or (ii) climax or (iii) let down, and as the independent variable the information whether the call was a solo pant hoot (0) or the initiator's pant hoot within a duet pant hoot (1). I created additional GLMMs to run the same comparisons separately for introduction duets and build-up duets.

Comparisons between pant hoots given in duets

To test the prediction that the build-up phase of the initiator's pant hoot depends on the latency with which the partner joins in the call, I created three Gaussian GLMMs in which as the dependent variable I put the duration of the (i) build-up or (ii) climax or (iii) let down phase, whereas the information as to whether the partner joined in the call during the introduction (0) or the build-up (1) phase of the initiator's call, as the independent variable. In another GLMM with Poisson distribution, I kept the same independent variable and as the dependent variable I put the number of build-up exhalations of the initiator's pant hoot. I created another Gaussian GLMM in which I used only duets where the partner joined in the call when the initiator has already finished the introduction phase of his call (*N*=52). In this GLMM I put the duration of the build-up phase as the dependent variable and the latency from the start of the build-up with which the partner joined in the call as the independent variable.

Finally, to test the prediction that there is a positive relationship between the numbers of climax elements given by the two partners in a duet, I created a Poisson GLMM. In this model I inserted the number of climax elements given by the individual initiating the duet as the dependent variable and the number of climax elements given by the partner as the independent variable. I created two further models with the same variables to conduct this analysis separately for introduction duets and build-up duets.

RESULTS

Comparisons between Kanyawara and Budongo pant hoot durations

The temporal structures of the pant hoots recorded from Kanyawara and Budongo communities were not significantly different (Table 4.2). Thus, in subsequent analyses data are merged.

Table 4.2: Descriptive and inferential statistics comparing the overall temporal structure of solo and initiator duet pant hoots from the two study communities.

	Community		**Results from GLMM**		
	Kanyawara	Budongo	β±SE	z	*P*
Solo pant hoots					
Build-up duration	*N*=64 calls, Mean=3.65s, SD=1.71s	*N*=56 calls, Mean=3.66s, SD=2.07s	0.08±0.48	0.18	0.860
Climax duration	*N*=64 calls, Mean=1.33s, SD=0.89s	*N*=56 calls, Mean=1.30s, SD=0.59s	-0.03±0.17	-0.21	0.832
Let down duration	*N*=64 calls, Mean=1.54s, SD=1.33s	*N*=56 calls, Mean=1.35s, SD=0.98s	-0.19±0.21	-0.91	0.365
Initiator duets					
Build-up duration	*N*=106 calls, Mean=3.20s, SD=1.49s	*N*=23 calls, Mean=2.64s, SD=1.53s	-0.32±0.48	-0.68	0.499
Climax duration	*N*=106 calls, Mean=2.43s, SD=1.50s	*N*=23 calls, Mean=1.84s, SD=1.03s	-0.72±0.41	-0.78	0.075
Let down duration	*N*=106 calls, Mean=2.15s, SD=1.12s	*N*=23 calls, Mean=2.34s, SD=2.41s	0.31±0.38	0.80	0.421

Comparisons between pant hoots given in duets

The duration of the build-up phase of the call was significantly longer when the partner joined later in the pant hoot, i.e. at the build-up rather than the introduction phase (Fig. 4.2; β±SE=1.49±0.24, z=6.17, *P*<0.001).

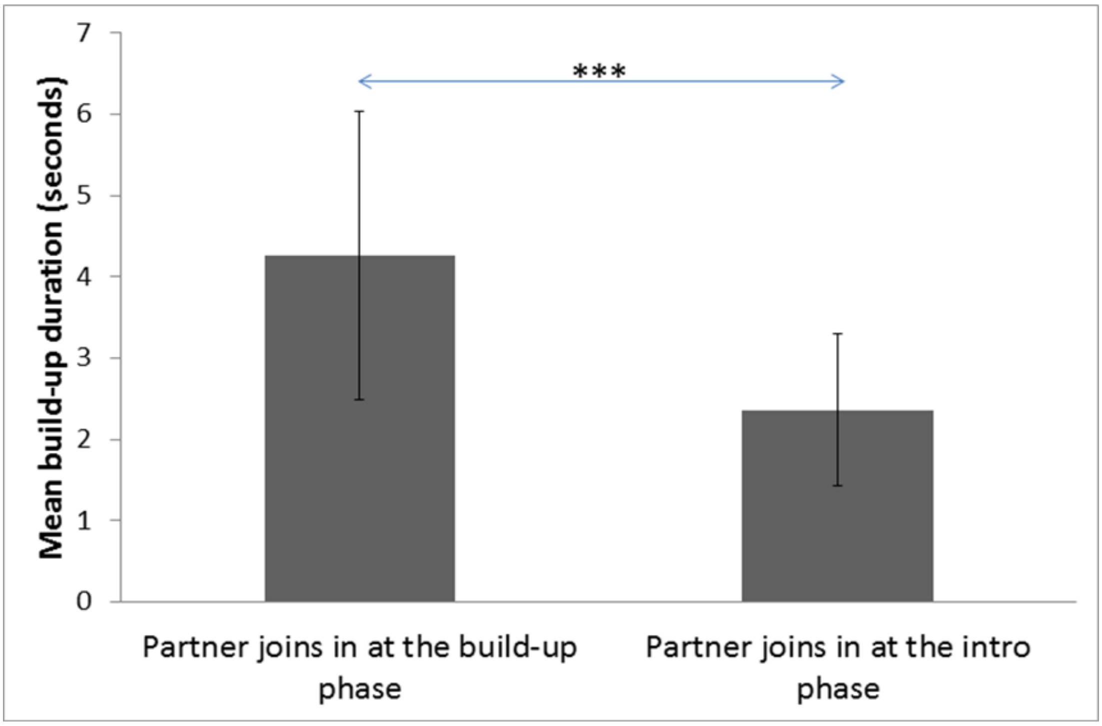

Figure 4.2: The duration (Mean±SD) of the build-up phase of the pant hoot starting the duet depending on whether the partner joined in the call at the introduction or the build-up phase of the call (GLMM; * *P*≤0.001; random effects: Community, Focal ID and Partner ID; data from both populations included; error bars represent 1SD)**

Similarly, the build-up duet pant hoots were composed of a significantly larger (Fig. 4.3; β±SE=3.20±0.59, z=5.43, *P*<0.001) number of build-up exhalations than the introduction duets. There was no significant relationship between the phase in which the partner joined the call and the duration of the climax (β±SE=-0.04±0.23, z=-0.17, *P*=0.886) or the let down (β±SE=-0.04±0.23, z=-0.18, *P*=0.861).

Crucially, in duets where the partner joined in the call after the build-up phase had started, the longer the latency (from the onset of the initiator's build-up) with which the partners joined in the call, the longer the build-up phase of the initiator's pant hoot lasted (β±SE=0.39±0.15, z=2.66, *P*=0.008).

Finally, there was a positive relationship between the number of climax elements given by chorusing males during duets in which the partner joined in at the introduction (β±SE=0.11±0.04, z=2.67, *P*=0.008) but not the build-up (β±SE=-0.02±0.09, z=-0.24, *P*=0.812) phase of the initiator's call.

Comparisons between solo and duet pant hoots

Overall, when all initiator's duet calls are considered together, solo pant hoots had significantly longer build-up phases (Mean=3.65s, SD=1.88s) than initiator's duet pant hoots (Mean=3.13s, SD=1.51s; β±SE=-0.59±0.21, z=-2.83, *P*=0.005). However, the build-up phases of solo pant hoots (Mean=3.65s, SD=1.88s) were significantly longer than those of the introduction duet pant hoots (Mean=2.36s, SD=0.93s; β±SE=-1.29±0.24, z=-5.46, *P*<0.001), but shorter, although not significantly, than those of the build-up duet pant hoots (Mean=4.26s, SD=1.78s; β±SE=0.46±0.34, z=1.36, *P*=0.175). Similarly, build-up phases of solo pant hoots tended to contain fewer build-up exhalations than build-up phases of build-up duet pant hoots did (β±SE=1.59±0.78, z=2.04, *P*=0.041; Sidak—corrected α-level for significance *P*=0.025) but more than introduction duet pant hoots (Fig. 4.3; β±SE=-1.92±0.55, z=-3.49, *P*<0.001).

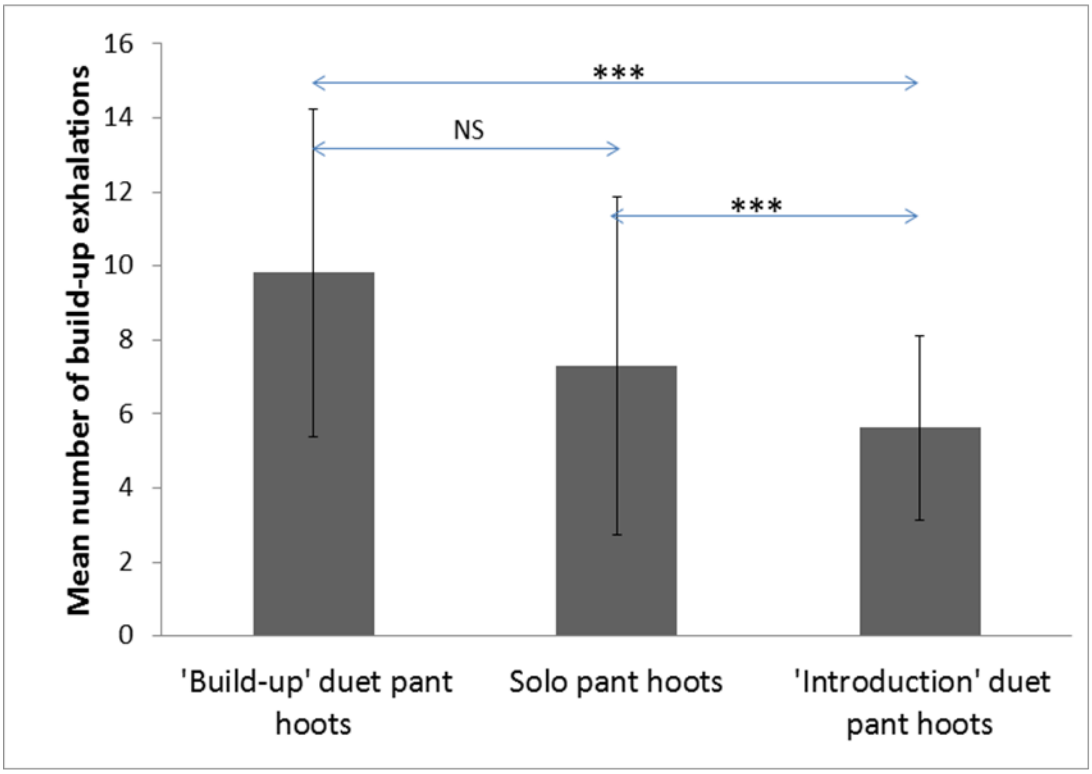

Figure 4.3: Mean number of build-up exhalations in solo, build-up duet and introduction duet pant hoots (GLMM, * *P*≤0.001, NS=not significant; random effects: Community, Focal ID and Partner ID; data from both study populations included; error bars represent 1SD).**

Initiator's duet pant hoots had longer climax (Duets: Mean=2.33s, SD=1.44s; Solos: Mean=1.32s, SD=0.76s; β±SE=1.03±0.14, z=7.20, *P*<0.001) and let down (Duets:

Mean=2.18s, SD=1.41s; Solos: Mean=1.45s, SD=1.18s; β±SE=0.73±0.17, z=4.34, *P*<0.001) phases than solo pant hoots.

In addition, initiator's duet pant hoots contained significantly more (Mean=3.36, SD=2.25) climax elements than solo pant hoots (Mean=1.96, SD=1.00; β±SE=1.39±0.21, z=6.70, *P*<0.001).

DISCUSSION

The results of my study support the hypothesis that flexibility in call production facilitates chorusing. Within duets, the duration of the build-up phase of the initiator's call correlated with the latency with which the partner joined in to produce a chorus. If the partner joined in the call at a relatively early stage of the initiator's pant hoot, such as the introduction, the build-up phase of this call was significantly shorter than in the case when the partner joined at a later stage of the call (e.g., in the build-up stage). Conversely, there was no relationship between the duration of other phases of initiator's pant hoots, such as the climax and the let down phases, and the latency with which the partner joined in the initiator's pant hoot. Similarly, the number of exhalations in the build-up part of the call in solo pant hoots was smaller than in the initiator's calls of the duets in which the partner joined relatively late in the call (i.e., at the build-up phase) but greater than in duets where the partner joined in the call at an early stage (i.e., at the introduction stage). This suggests that the build-up phase of a solo pant hoot might be characterised by a 'default' duration or number of exhalation elements which are flexibly modulated in accordance with the latency with which the partner joins in the call. My study suggests therefore that the build-up phase has an important function with regard to chorusing, because the individual starting the chorus seems to adjust its duration to facilitate chorusing. More specifically, my results suggest that if the nearby individual did not join the initiator's call at its introductory stage, prolonging the build-up phase of the call increases the probability with which he joins in the call to produce a chorus.

Although within duets only the build-up phase (i.e., the duration and the number of exhalations) correlated with the latency with which the partner joined in the call, comparisons between solo and duet pant hoots suggest that the duration of other elements of the call also depends on whether the call is performed jointly with others. For example, the durations of the climax and let down were on average longer in initiator's duet than solo pant hoots. My interpretation of this result is that within choruses, prolonging phases of the call such as the climax (which on a proximate level might be mediated by an elevated arousal of the caller as a result of calling in a chorus with another male) might induce a similar response in the chorusing partner, and consequently result in a longer and therefore more effective joint display. Indeed, my data seem to support this hypothesis. For example, there was a positive correlation between the number of climax elements between the initiator and the partner pant hoots in those duets in which the partner joined in the call at an earlier stage, i.e. at the introduction phase of the initiator's call. However, there was no correlation in those duets in which the partner joined in the call during the build-up phase of the starting call. It seems therefore that the earlier the partner joins in the call, the more likely he is to mirror the structure of the pant hoot of the initiator of the chorus. This effect may be influenced by the reduced time available to a partner who joins the call late for coordinating his pant hoot behaviour with the partner's one. Nevertheless, both the latency with which the partner joins in the call and the extent to which he mirrors the call of the initiator of the chorus might reliably reflect the degree to which he contributes to the chorus.

Overall, the results of this study suggest that there are two aspects of the temporal structure of chimpanzee pant-hooting that facilitate and coordinate chorusing. Firstly, the duration of pant hoot phases, especially the gradual build-up, seems to be actively regulated in line with the vocal response of the audience so as to facilitate a chorus. For example, males seemed to shorten the duration of the build-up when the partner joined in the call at an early stage and to prolong this phase if the partner had not yet joined the call. Secondly, once the partner has joined in the call, the initiator seemed to adjust the duration of call phases such as the climax to prolong the display. This is reflected, for instance, by the fact that climax phases are longer in duet calls than solo calls. In addition, individuals sometimes match the number of climax elements given by the partner, suggesting that the duration of this part of the call is adjusted in accordance with the vocal contribution of the partner. Therefore, the flexibility with which individuals alter the duration of particular call phases seems to both facilitate and coordinate chorusing. In this respect, my results are consistent with findings of previous studies showing that, within pant hoot choruses, males actively adjust the spectral acoustic features of their pant hoots to the partner's one (Mitani and Gros-Louis 1998). For example, in the M unit-group of chimpanzees in the Mahale National Park in Tanzania the average frequency of climax elements of pant hoots produced in duets with a specific partner were more similar to each other than those produced either in solos or in duets with other males. The results of my study suggest that the temporal structures of particular phases within a pant hoot are also objects of such active vocal accommodation. In chimpanzees the need to adjust the structure of a pant hoot to match that of a partner's, in order to produce a coordinated vocal display, might be important, especially considering that the acoustic structure of pant hoots varies considerably across individuals (Marler and Hobbet 1975; Herbinger et al. 2009).

An alternative interpretation of my results could be that the reaction of potential partners to specific acoustic features, rather than the flexibility over the temporal structure by the caller, facilitates chorusing. The acoustic pattern of particular call phases may vary between individuals, and some acoustics features are more likely than others to elicit a vocal response from nearby individuals. However, this alternative hypothesis is not likely to explain the fact that, in duets where the partner joined in the call after the start of the build-up, there was a positive relationship between the duration of the build-up phase of the initiator's pant hoot and the latency with which the partner joined in the call. Similarly, this alternative hypothesis cannot explain the positive relationship between the numbers of climax elements produced by chorusing partners. My hypothesis concerning flexibility in the production of pant hoots seems to explain more of the data I present here than the alternative hypothesis concerning receiver preference for responding to pant hoots with certain acoustic features.

As discussed in Chapter 3, chimpanzee pant hoot chorusing might play an important role in social bonding in these primates. Chorusing or duetting has also been suggested to play a vital role in social bonding in many monogamous birds and some monogamous primates such as gibbons (Chapter 1). However, little is known about proximate mechanisms underpinning a bonding function of this vocal phenomenon. As mentioned in Chapter 1, by coordinated responding to each other’s calls animals might test the partner’s attention to its actions and therefore the level of a social bond between them (Smith 1994; see also Zahavi and Zahavi 1997). Following Smith’s (1994) suggestion, one interpretation of my results is that the latency with which the partner joins in another male’s call reflects his attention to the call which in turn reflects his level of affiliation to the pant-hooting individual. The degree with which his call matches the call of the individual starting the chorus might also reflect the level of involvement of the joining individual into the display and therefore the level of affiliation between the calling males. This may especially apply to the climax, which is the loudest part of the call and likely requires more energy to produce it compared to other call phases. In animal communication the effectiveness of a given signal, especially if its role is to test social bonds, is often a function of the level of investments needed to produce it (Zahavi and Zahavi 1997). Therefore, mirroring and prolonging this part of the call might be an honest signal of a good relationship between the callers.

Considering the proposed ultimate benefits of a coordinated vocal display such as facilitating social bonds, territorial defence or mate guarding (Geissmann and Orgeldinger 2000; Hall and Magrath 2007; Hall 2009; Koloff and Mennill 2011; Templeton et al. 2011; Weng et al. 2012) it is likely that the acoustic structure of calls of other duetting or chorusing animals has been shaped through evolution in a way that facilitates joint vocal displays. Several studies suggest that this might be the case in at least some species of duetting birds (Hall 2009). For example, some acoustic variants of songs of black-bellied wren are more likely than other to elicit a reply in a partner (Logue 2006; Logue 2007). Some birds also prolong a vocal display when calling in a duet with a partner (Hall 2009). Virtually no studies have been conducted to investigate this issue in primates. However, it is possible that the gradual onset of duet songs in gibbons (termed as 'introduction'; Geissmann 2002) facilitates joint vocal displays in a similar way as the build-up phase of chimpanzee pant hoots. However, in orang-utans, a species phylogenetically more closely related to chimpanzees, males, who range alone and do not vocalise jointly with other individuals, also produce long-distance calls which typically begin with an introductory phase (so called ‘bubbling’) leading to a loud climax (Mitani 1985; Ross and Geissmann 2007). It is possible therefore that the characteristic acoustic structure of a chimpanzee pant hoot did not originally evolve for the purpose of chorusing,

It is worth noting that overall the durations of particular phases in both solo and duet pant hoots did not differ significantly between calls from Kanyawara and Budongo communities. Several earlier studies on chimpanzee pant hoots showed that there are considerable inter-population differences in terms of the occurrence and acoustic features such as the frequency and rate of particular phases of the call including the build-up (Mitani et al. 1992; Clark Arcadi 1996; Crockford et al. 2004). Although the purpose of this study was not to look in detail at inter-population differences in terms of acoustic structures of pant hoots or to consider reasons behind potential differences in this respect, it is possible that durations of particular pant hoot phases might be less population-specific than other acoustic features of this call.

In conclusion, the results of my study support the hypothesis that flexibility in terms of the temporal structure of chimpanzee pant-hoots facilitates chorusing. The build-up phase of the call seems to be especially important in this respect because males appear to adjust its duration in accordance with the latency with which other individuals join in the call to produce a chorus. My study therefore supports the view that the acoustic structure of pant hoots, which are acoustically rather stereotyped calls, is highly sensitive to the vocal response of the audience. I conclude that the basic acoustic structure of a pant hoot and the flexibility with which the duration of particular phases of the call is regulated might function to promote chorusing.

CHAPTER 5: The social function of food-associated calls in male chimpanzees

ABSTRACT

There is an on-going debate about the adaptive function of chimpanzee food-associated calls. In this study I tested a new hypothesis, that food-associated calls in male chimpanzees function to signal that the calling individual is likely to initiate or prolong feeding. I propose that the signal functions to coordinate activities between individuals and that its ultimate function is to retain the nearby individuals in proximity. To test this hypothesis I collected data on social and ecological correlates of food-associated calls in male chimpanzees. The results of this study, which was conducted on the Kanyawara community in the Kibale National Park, Uganda, show that males fed for significantly longer after giving food-associated calls upon initiating feeding than after remaining silent. The type of audience had a significant effect on food calling, with males producing food-associated calls more often when males rather than females and preferred rather than neutral male social partners were in close proximity. However, the total party or male party size did not correlate with food calling behaviours, suggesting that the signal targets those in close proximity. Finally, a male feeding partner was more likely to remain with the focal until the end of a feeding bout after the focal gave a food-associated call at the beginning of the feeding bout than when he was silent. These results support my hypotheses and suggest that one of the functions of food calling in chimpanzees might be signalling that the caller is likely to initiate and prolong a feeding bout. This information might be used by receivers to make the decision whether to stay with the calling individual on a feeding patch or leave him (fission). The study suggests therefore that ultimately the function of food calling is to coordinate feeding behaviours between males.

INTRODUCTION

Food-associated calls are defined as calls produced specifically in the foraging context (Elowson et al. 1991). These vocalizations have been recognized in a wide array of animals ranging from avian species to primates [e.g., domestic chickens (Marler et al. 1986), cliff swallows (Brown et al. 1991), spear-nosed bats (Boughman and Wilkinson 1998), Toque macaque (Dittus 1984), Geoffroyi marmosets (Kitzmann and Caine 2009), tufted capuchins (Di Bitetti 2005), spider monkeys (Teixidor and Byrne 1999), and cotton top tamarins (Cleveland and Snowdon 1982)].

Because food calling is such a common behaviour in many animal species a number of hypotheses have been proposed to explain the adaptive function of these vocalizations (see review by Clay et al. 2012). One of the most popular ultimate hypotheses posits that the main function of these vocalizations is to attract conspecifics to food (Dittus 1984; Di Bitetti 2003; Gros-Louis 2003). Attracting others to a food source brings about a larger concentration of individuals feeding on a food patch and therefore has obvious costs in terms of increased competition (Chapman 1988; Janson 1988). In order to be an evolutionarily stable strategy attracting others to food must also bring about clear benefits overriding these costs. Researchers have suggested such benefits may include improving anti-predator vigilance (Elgar 1986; Caine et al. 1995; Sridhar et al. 2009), defending food source from other groups or species (Heinrich and Marzluff 1991), exploiting food sources more effectively (Chapman and Lefebvre 1990; Boinski and Campbell 1996) and kin-selection (Hauser and Marler 1993a; Hauser and Marler 1993b; Pollick et al. 2005). Another hypothesis posits that these vocalizations are ‘repelling’ signals that function to promote spacing between individuals feeding on high-quality and clumped food sites such as fruit trees (Boinski and Campbell 1996).

It has been shown that in many animal species the production of food-associated calls correlates with food quantity (Hauser et al. 1993; Di Bitetti 2005) or even food quality (Elowson et al. 1991; Benz 1993; Caine et al. 1995; Roush and Snowdon 2000). Social factors, such as the composition of audience, have also been shown to correlate with aspects of food calling behaviour (Dahlin et al. 2005; Di Bitetti 2005; Pollick et al. 2005). However, despite identifying these social and ecological correlates of food-associated calls in primates as well as suggesting their potential roles, the ultimate function of these vocalizations is still a topic of an ongoing debate (Clay et al. 2012).

As mentioned in Chapter 1, chimpanzees produce two kinds of calls when arriving on food patches: long-distance pant hoots and short-distance food-associated calls [labelled by some researchers as rough grunts (Marler and Tenaza 1977; Slocombe and Zuberbuhler 2006)]. Because pant hoots are often given by males upon arriving at feeding trees some researchers labelled these calls as 'food-calls' (Wrangham 1977a). It has been suggested that pant hoots given in this context function to either inform ignorant individuals from other parties about the presence of food (Reynolds and Reynolds 1965) or to inform individuals who are already aware of the presence of the feeding tree, that the resource is being exploited (Wrangham 1977a).

In contrast to the long-distance pant-hoot calls, rough grunts are lower amplitude calls and are unlikely to be audible to individuals beyond the same party (Marler and Tenaza 1977; Slocombe et al. 2010) and it is these calls that are the focus of this study. These food-associated calls are common vocalizations in chimpanzees and they are produced mainly when approaching food and feeding (Reynolds and Reynolds 1965; Goodall 1986). There is considerable acoustic variation within food-associated calls and these vocalizations can grade from low-pitched food grunts to high-pitched food barks (Goodall 1986). These calls are produced more frequently by males than females (Marler and Tenaza 1977). It has been recently shown that food-associated calls in captive chimpanzees are functionally referential. Slocombe and Zuberbuhler (2006) were able to show that chimpanzees produce acoustically different food calls when consuming food of different quality. Moreover, they were able to show that these acoustic differences are meaningful to the listeners as they adjust their foraging behaviour in accordance to the calls they hear (Slocombe and Zuberbuhler 2005b).

A more recent study suggests that food-associated calls in male chimpanzees have substantial audience correlates. For example, males are more likely to produce a food-associated call when valuable social partners are present in the party (Slocombe et al. 2010). This suggests that these calls are involved in social bonding. However, as mentioned in Chapter 1, despite identifying these bonding correlates of food-associated calls in male chimpanzees, it remains unclear why this behaviour may benefit affiliated males (both producers and receivers of the signal). Given the short-range nature of these calls, it is unlikely that they inform ignorant receivers about the presence of food (individuals who can hear the calls are highly likely to be able to see the food patch themselves). One possibility is that in chimpanzees food-associated calls ultimately function to provide valuable social partners with information about the quality of food, which would allow them to make advantageous foraging decisions (Slocombe et al. 2010). The fact that acoustically different types of food-associated calls are produced when feeding on different types of food (Slocombe and Zuberbuhler 2006) makes this possibility reasonable and there are potential benefits to the receiver from obtaining reliable information about food quality from others' calls (Slocombe et al. 2010).

However, the suitability of this 'food information sharing' hypothesis as an ultimate explanation for these calls is problematic as the benefits to the signaller from sharing information about food quality are difficult to identify. In addition, observations of chimpanzees in the wild suggest that informing others about food quality do not accrue sufficient benefits to the receivers for this to be the ultimate function of these calls. For example, food-associated calls are frequently given when entering food patches already familiar to all animals in the foraging group (such as when entering ripe fruit trees visited by animals on a daily basis, P.Fedurek, pers. obs.). Food calls are also often given on large patches of food with low homogeneous value (such as elephant grass *Pennisetum purpureum*) that are visible to all party members.

The specific hypothesis tested here is that food-associated calls in male chimpanzees function to signal to nearby individuals that the calling individual is likely to initiate and/or prolong feeding. Unlike the food information hypothesis, this hypothesis identifies clear benefits for both signallers and receivers. For example, signalling the likelihood of the caller to initiate or prolong feeding might facilitate coordination of feeding decisions between callers and listeners and ultimately facilitate them remaining in proximity or/and the same party. As highlighted in Chapter 1, chimpanzees live in highly fluid fission-fusion societies in which individuals leave and join subgroups frequently even within a single day. It might be expected that in such societies the need to anticipate and consequently coordinate behaviours, especially amongst affiliated individuals, would be beneficial. Indeed, in the Kanyawara community of chimpanzees on average 31.9% males leave a feeding tree before the focal male does (P.Fedurek, unpublished data) suggesting that a signal coordinating feeding behaviours in this species would be adaptive. Food calling in chimpanzees may fulfil this coordination function. For instance, if food calling behaviour reliably correlated with feeding durations of callers, listeners could make the decision whether to join the calling individual on the food patch or to leave him (which usually leads to fission). The specific predictions that arise from this hypothesis are outlined below.

One of the main predictions of the hypothesis is that individuals feed for longer after giving a food-associated call as only in this situation would the signal be effective (i.e., informative for the listeners). An individual's decision to feed or prolong feeding might be mediated by the decisions of others. For example, on the basis of other individuals' calling behaviour an individual can predict others' decisions to feed or prolong feeding, and thus adjust its own feeding decision and signalling behaviour accordingly. Therefore, if food calling facilitates feeding coordination between males I predict that the correlation between food call instances and feeding duration of an individual is stronger when other party members also call with the focal. If this was the case, a synchronized calling behaviour might be a reliable signal of coordinated feeding decisions, and therefore an indicator of a prolonged feeing.

If food calling plays a role in coordinating foraging behaviour and maintaining group cohesion, I expect that these signals target individuals whom are most valuable for the signaller to retain in proximity. As discussed in Chapter 1, in chimpanzees males form stronger social bonds with other males than with females and these bonds tend to be formed preferentially with some males (i.e., preferred social partner) and not others. Hence, signals allowing prediction of each others' behaviours that in turn facilitates remaining in proximity or the same party might be especially beneficial for affiliated males. I therefore also predict that food-associated calls correlate more with the number of males present rather than females and they are more likely to be given when preferred male social partners are present, a pattern that has been previously shown in another chimpanzee community (Slocombe et al. 2010). In addition, since affiliated males tend to be in close proximity when they are in the same party (Gilby and Wrangham 2008), I predict that food calling frequencies are more strongly correlated with the number of males in close proximity rather than with the total male party size.

The possibilities that males feed longer after producing a food-associated call and that they tend to food call in the presence of preferred social partners only indirectly test the proposed coordination hypothesis. In order to test the hypothesis more directly one needs to investigate whether food calling correlates with the subsequent behaviour of the receiver. According to the proposed hypothesis by giving food-associated calls males can influence the decisions of others whether or not to stay with the calling individual on a feeding site. Hence, I predict that a male feeding partner is more likely to remain with the focal in proximity until the end of a feeding bout after the focal gave a food call at the beginning of the feeding bout.

In addition, an individual should be more likely to food call when starting feeding after travelling than resting. This is because the probability of being separated from a group and therefore the need to coordinate action with others is stronger while travelling rather than resting. An alternative explanation for this possibility, suggested by the logic of the food information sharing model, might be that travel, rather than resting, is more likely associated with food discovery and therefore calling in the arrival feeding bout functions to inform others about the food source. To control for this alternative explanation (i.e., that the function of food calling is to inform others about newly discovered food rather than to coordinate feeding decisions with others) I exclude arrival feeding bouts, and focus instead on subsequent feeding bouts within the same food patch (i.e., non-arrival feeding bouts). As the vast majority of non-arrival feeding bouts in fruiting trees tend to be preceded by resting, I focus on feeding events where terrestrial herbivorous vegetation (THV) is being consumed. THV tends to be evenly distributed across spatially large areas and is regarded as food of relatively poor quality (Wrangham et al. 1991) and chimpanzees consuming THV, commonly move within these large patches between feeding bouts. Thus, looking at non-arrival feeding bouts within THV food patches provide a clear test of whether calls are more likely to occur at the start of a feeding bout preceded by travelling than resting.

METHODS

The study was conducted on the Kanyawara community in the Kibale National Park in western Uganda (Chapter 2). The study subjects were 11 males including 9 adults and 2 sub-adults.

Data collection

Focal animal sampling (Altmann 1974) was the main data collection method used and randomly chosen individuals were followed for whole days ('nest to nest' focal follows usually between 7 am and 6:30 pm). Data were collected between 11 February and 30 October 2011 and resulted in 111 days of focal observations (Mean=546.39 [SD=152.62] minutes of direct focal observation per day and 9.91 [SD=3.20] focal follow days of data collection/male). Whenever a focal individual started feeding a number of different variables were recorded:

Definitions

Presence and absence of food-associated calls

The presence or absence of calls was recorded for the period when the focal was entering a food patch (see definition below) or/and during the first 5 seconds of the feeding bout. Three types of acoustically distinct calls given in the feeding context have been distinguished: food barks (*N*=111), food grunts (*N*=314) and soft grunts (or 'hoos'; *N*=140). Although these three types of calls grade from one to another (Marler and Tenaza 1977) they all have distinguishable acoustic characteristics:

Food barks (also described as 'loud food aaa call', Goodall 1986), are loud, high-pitched vocalizations or 'squeaks', with a clear harmonic structure, usually given in bouts that contain many calls.

Food grunts (also described as 'soft food grunts'; Goodall 1986) are soft, low-pitched calls, that are less tonal and noisier in their structure, usually given in bouts that contain many calls.

Soft grunts (Goodall 1986) are quiet, low-pitched vocalizations that are typically produced as single calls.

The presence and absence of each of these three types of call during the first 5 seconds of a feeding bout was recorded. When both food barks and food grunts (or soft grunts) were produced during the first 5 seconds of feeding, the feeding bout was classified as a ‘food bark’ bout. During the first 5 second of a feeding bout I also recorded whether or not other visible individuals gave food-associated calls.

Feeding bouts

When a chimpanzee fed on a food source, I identified feeding bouts within the feeding event. A feeding bout started as the focal started to consume food and ended if his feeding stopped for more than 2 minutes, or if he consumed a new food type or species, or when the focal moved to another food patch (see definition below). An exception to one of these rules was made when the focal was feeding on THV (see definition below). THV food patches contain many herbaceous species and chimpanzees often switch from one species to another too frequently to label these events as separate feeding bouts. Thus, when the focal started feeding on a new species within the same food patch containing THV, I did not recognize this as the start of a new feeding bout. In total 1529 feeding bouts were recorded.

Food calling might be affected by whether or not an individual arrives on a new feeding patch or resumes feeding on the same feeding patch. Therefore, I defined *arrival feeding bout as* the first feeding bout on a particular feeding patch (*N*=1346).

Food species and type

The species of plant being eaten was noted along with the type of food. Food type categories that were recorded are in Table 5.1.

Table 5.1: Types of food consumed by focal chimpanzees.

Ripe fruits	Tree and shrub ripe fruit pulp
Unripe fruits	Tree and shrub unripe fruit pulp
Seeds	Seeds
Mature leaves	Mature tree and shrub leaves
Young leaves	Young tree and shrub leaves
Flowers	Flowers
Animal prey	Monkey meat, insect prey
Honey	Honey
Dead wood	Dead wood
Soil	Soil
THV	Pith and leaves of terrestrial herbaceous vegetation
Other	Other

As discussed in Chapter 2, ripe fruits are preferred over other food types and in seasons of fruit abundance chimpanzees consume mainly this type of food. In contrast, THV, especially piths, is generally regarded as low quality food (Chapter 2). Nevertheless, this food type is an important component of chimpanzee diet and functions as fall-back food during seasons when tree fruit is scarce (Wrangham et al. 1991). THV densities in the Kibale forest can vary from isolated plants to high density mono-specific large 'fields' (Wrangham et al. 1991).

Food Patch

Chimpanzees often resume feeding on the same *food patch* so it is important to control for this while conducting analyses so as to avoid the problem of non-independence of data points. Although it was not always unproblematic to define a food patch, the food patch definition employed in this study is simple and conservative. The situation was straightforward when the focal animal fed on a single tree or shrub, which constituted single separate food patches. If the focal travelled directly from one tree or shrub to another one of the same species, he remained within the same food patch. Defining a food patch constituting of THV was usually more challenging as it was often not possible to distinguish where a food patch starts and ends. In this situation a new food patch was recorded when two THV feeding events were separated by a feeding event with a different food type.

Behaviour preceding feeding

Behaviour preceding feeding refers to the behavioural state of the focal that immediately preceded a feeding bout. Only two categories of behaviour preceding feeding were distinguished: travelling and resting.

Audience composition

At the beginning and end of every feeding bout the identities of all individuals within 5 meters from the focal animal as well as the IDs of any visible individuals were recorded. 5 min scans were conducted to obtain data on party composition (see Chapter 2 for definition).

Preferred social partners

Preferred social partners (PSP) for each focal chimpanzee were established on the basis of three independent dyadic association measures, which were Simple Ratio, 5-metre and Nearest Neighbour association indexes (see Chapter 3).

To calculate PSPs for each focal chimpanzee, I first examined each index (SRI, 5M and NN) to identify any individuals for whom the index value was ¼ standard deviation larger than the focal's average (labelled an associate). Because preferred social partners were established using data coming from a longer study period than the period used in Chapter 3 (i.e., approximately eight and half months in contrast to two six-month periods), the index values obtained in this chapter were smaller than in Chapter 3. Therefore, the value of 1/4 rather than 1/3 of standard deviation was used to establish associates equivalent to the ones obtained in Chapter 3. In order to be classified as a preferred social partner, individuals had to be categorized as an associate on at least two of the three indexes. I identified 38 preferred social partners across the eleven focal chimpanzees (mean=3.45/focal individual, SD=0.82, range=2-5). All remaining possible male social partners for each focal were labelled as neutral social partners (non-PSPs). It is important to note that I calculated uni-directional rather than mutual PSPs. Therefore, within a dyad A might be a preferred social partner for B, B however might not be a preferred social partner for A (Chapter 3).

Social rank

Each male was assigned a linear ordinal rank (1-11) [see Chapter 2].

Statistical analysis

Generalized Linear Mixed Models (GLMM) were the main statistical tools used in the analyses (Chapter 1). In my analyses Focal ID and Food patch ID (i.e., two entities from which repeated samples were taken) were inserted into all the models as 'random effects'. In addition, in situations where multiple post-hoc tests were conducted on the same dataset, the α-level for significance was corrected using Sidak's (1967) adjustment equation to control for family-wise error.

Models created

To investigate the relationship between food calling and variables such as food type, behaviour preceding feeding and the composition of audience, I created four separate GLMMs with binary error structures for each variable, with either (i) Call (i.e. all food-associated calls included), (ii) Food bark, (iii) Food Grunt or (iv) Soft Grunt, each with binary distribution (0/1), as the dependent variable. The full list of variables that were used in these GLMMs is shown in Table 5.2.

Table 5.2: List of variables included in four GLMMs

Dependent variable
Food-associated call (0/1) or food bark (0/1) or food grunt (0/1) or soft grunt (0/1)

Independent variables
Behaviour preceding feeding (0-rest, 1-travel)
Food type
Number of males within 5 m
Number of females within 5 m
Total number of males in the party (minus the focal)
Total number of females in the party

Random effects
Focal ID
Food patch ID

Before running GLMMs I checked whether independent variables were co-linear. There was no co-linearity between any independent variables (Variance Inflation Factor [VIF] of the independent variables were considerably below the value of 10 [mean=1.39]) allowing for the inclusion of all the independent variables in the same model. All statistical analyses have been carried out using STATA 12.0 software.

Type of food and dominance

To investigate the relationship between the probability of food-associated calls being produced when arriving at new food patches and the type of food being consumed, I created a GLMM with a binomial error structure (hereafter, binomial GLMM) in which I put the variable Call (i.e., all types of food-associated calls included; 0/1) as the dependent variable and as the independent variable I put Food Type. I then created three additional models with the same independent variable and with (i) Food Bark or (ii) Food Grunt or (iii) Soft Grunt as dependent variables, each with binary distribution (0/1).

To investigate whether there were rank differences between the males in terms of the probability with which they produced food-associated calls at the beginning of a feeding bout, I created another binomial GLMM in which I put as the dependent variable Call (0/1) and as the independent variable the rank of the focal male (from 1 to 11). Focal ID and Food Patch ID were set as random effects.

Food-associated calls and feeding duration

Four separate GLMMs with a Gaussian error structure (hereafter, Gaussian GLMM) were run to test the hypothesis that after giving a food-associated call males feed longer than after remaining silent at the start of a feeding bout. As the dependent variable I put the duration of feeding bouts (seconds) whereas either Call (0/1) or Food Bark (0/1) or Food Grunt (0/1) or Soft Grunt (0/1) were inserted into the models as independent variables. In all four models Food Type was put as another independent variable. Focal ID and Food patch ID were set as random effects.

Feeding duration of the focal depending on whether or not others food call with the focal

To test the prediction that the focal feeds longer after party members also gave food-associated calls at the start of the focal's feeding bout (i.e., during first 5 seconds of the bout), I included in the analyses only these feeding bouts in which a focal produced food-associated calls (*N*=560). I then created a new Gaussian GLMM and put into the model feeding duration of the focal as the dependent variable and the variable 'others call or not' (0/1) as the independent variable.

Similarly, to investigate whether the focal fed for longer in feeding events when other individuals in the party, but not the focal, gave food-associated calls compared to feeding events when others were silent, I included in the analyses only these feeding bouts where the focal did not give a call (*N*=943). I then put into a Gaussian GLMM feeding duration of the focal as the dependent variable and the variable 'others call or not' as the independent variable. In both models Focal ID and Food patch ID were included as random effects.

Food calling and the presence and absence of preferred social partners

Separate binomial GLMMs were run to test the hypothesis that male food calling is more likely when preferred social partners are in close proximity. These analyses were run separately from the main model, because PSP values were only available for males, not females, so this factor could not be entered into the overall model. I created three additional GLMMs with Food-associated Call (i.e., all types of food-associated calls included [0/1]), Food Bark (0/1) or Food Grunts (0/1) as dependent variables. In each of these three models I put two independent variables which were the presence or absence (0/1) of PSP and neutral social partners within 5 m from the focal. Focal ID and Food patch ID were set as random effect variables.

<u>Male feeding partner presence</u>

To test the prediction that a male feeding partner was more likely to remain with the focal on a feeding patch until the end of a feeding bout after the focal gave a food-associated call, I ran another binomial GLMM. As the dependent variable I put the presence or absence (0/1) of feeding partner within a visible distance (from the observer's perspective) at the end of the feeding bout whereas the independent variable was the presence or absence of a food-associated call given by the focal at the start of the feeding bout (0/1). Only situations in which no more than one male feeding partner was present at the start of a feeding bout (*N*=267) were included in the analysis because otherwise it is very difficult to interpret the results (i.e., with more than one feeding partner present it is impossible to know which individuals affected the calling). With regard to food type only THV and young leaves were included in the analyses. The 'ripe fruit' category was not inserted into the model as usually there were more than two individuals feeding on a feeding tree which, as mentioned above, makes it difficult to interpret the data. When running this particular GLMM three variables were set as random effects, which were Focal ID, Partner ID and Food patch ID.

RESULTS

General results: type of food and dominance rank

Focal chimpanzees produced food-associated calls at the beginning of only 37.72% of all feeding bouts (45.13% when only the arrival feeding bouts were examined). Ripe fruit (*N*=696 out of 1529 feeding bouts), THV (*N*=449) and young leaves (*N*=258) were the most common food types consumed by the focal chimpanzees. Food type was one of the factors correlated with food calling (Table 5.3).

Table 5.3: The relationship between food calling and the investigated (independent) variables. Dependent variable: Call [0/1]; random effects: Focal ID, Food Patch ID (GLMM; ******P*≤0.001; significant results in bold; all feeding bouts included).

Independent variables	Coef.	Std.Err.	z	[95% Conf.	Interval]
Preceding Behaviour	**1.92**	**0.28**	**6.76 *****	**1.36**	**2.48**
Food Type	**-0.30**	**0.07**	**-4.28 *****	**-0.44**	**-0.16**
Number of Males 5m	**0.73**	**0.14**	**5.05 *****	**0.45**	**1.01**
Number of Females 5m	-0.41	0.27	-1.46	-0.95	0.14
Total Male Party	-0.00	0.04	-0.01	-0.08	0.07
Total Female Party	-0.06	0.04	-1.37	-0.14	0.02

Analysis of arrival feeding bouts on the three most common food types, revealed calls were most likely to be produced when arriving at feeding patches containing ripe fruits and young leaves and less frequently when arriving at THV feeding patches (ripe fruit=48.96%, young leaves=44.48% and THV=28.51%; β±SE=-0.41±0.08, z=-5.12, *P*<0.001).

Food barks were predominantly given when arriving at food patches with ripe fruits (87.73 %) compared with both young leaves (8.50%) and THV (3.77%; β±SE=-0.-15±0.23, z=-6.46, *P*<0.001), whereas the frequencies of food grunts (ripe fruit=51.31%, young leaves=28.09% and THV=20.60%; β±SE=-0.21±0.09, z=-2.35, *P*=0.019) and soft grunts (ripe fruit=53.00%, young leaves=29.00% and THV=18.00%; β±SE=-0.10±0.13, z=-0.80, *P*=0.422) were more balanced across the three main food types.

Whilst there was a trend for more dominant individuals to be more likely to produce food-associated calls, this pattern was not significant (β±SE=-0.10±0.05, z=-1.92, *P*=0.054).

Food-associated calls and feeding duration

Focal males fed for significantly longer after giving a food-associated call at the beginning of a feeding bout than after remaining silent (β±SE=611.58±59.03, z=10.36, *P*<0.001, Fig. 5.1).

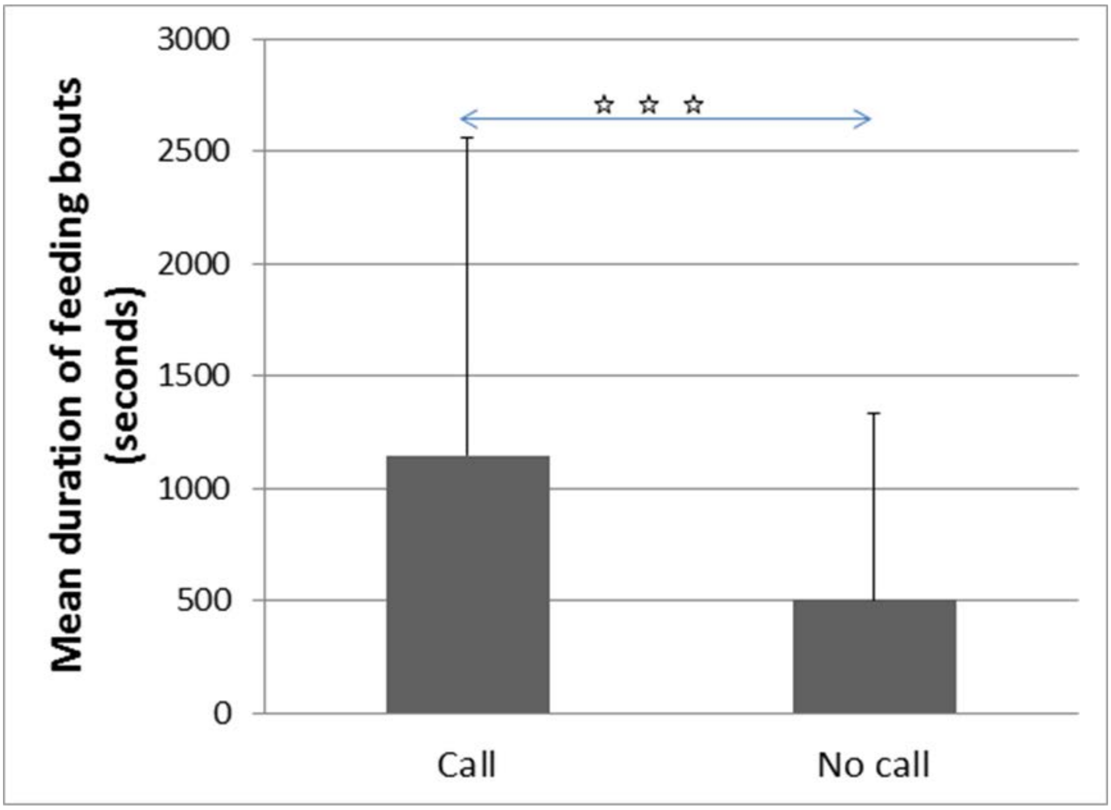

Figure 5.1: The duration (Mean±SD) of feeding bouts in relation to the absence or presence of food-associated calls (GLMM; * *P*≤0.001; error bars represent 1 SD; all food types included).**

There was the same pattern when only the arrival feeding bouts were analyzed (β±SE=655.57±70.00, z=9.38, *P*<0.001). Food type also correlated with feeding durations, with males feeding longer on ripe fruits (mean=1220.02s, SD=1547.18s) than on young leaves (mean=445.72s, SD=582.07s) and THV (mean=494.71s, SD=731.98s; β±SE=-118.80±18.60, z=-6.39, *P*<0.001). However, the relationship between food calling and feeding bout durations held after controlling for food type (ripe fruits: calling mean=1608.92s, SD=1732.52s and not calling mean=753.08s, SD=1055.93s; β±SE=868.10±108.54, z=8.00, *P*<0.001; young leaves: calling mean=629.75s, SD=677.86s and not calling mean=246.96s, SD=300.45s; β±SE=385.03±62.70, z=6.14, *P*<0.001; THV: calling mean=705.00s, SD=750.00s and not calling mean=371.68s, SD=629.68s; β±SE=335.26±68.54, z=4.89, *P*<0.001).

A food calling focal male fed for longer after other individuals in the party also gave a food-associated call (mean=1507.73s; SD=1912.62s) than when others did not call (mean=681.81s; SD=913.03s; β±SE=845.40±115.05, z=7.35, *P*<0.001). Similarly, when only feeding bouts in which the focal did not give a food-associated call were analyzed, focal males fed for longer (mean=836.59s; SD=924.23s) when other individuals food called at the start of a feeding bout than when they did not (mean=489.84s, SD=822.20s; β±SE=333.09±135.31, z=2.46, *P*=0.014).

Figure 5.2 shows that food barks preceded longer feeding bouts than food grunts (β±SE=-1050.37±156.7, z=-6.70, *P*<0.001) and food grunts in turn preceded longer feeding bouts than soft grunts (β±SE=-394.24±112.60, z=-3.50, *P*<0.001). In contrast, soft grunts were not reliable predictors of feeding duration (Fig. 5.2).

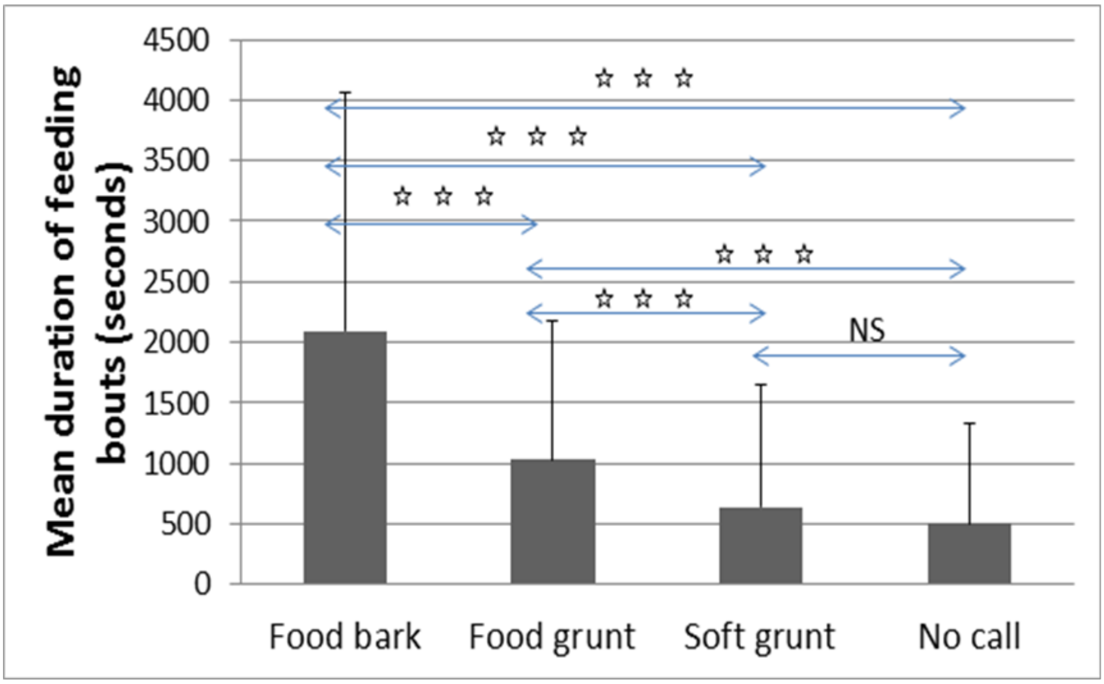

Figure 5.2: The duration (Mean±SD) of feeding bouts in relation to particular types of food-associated calls (* *P*≤0.001; GLMM; error bars represent 1 SD; all food types included).**

Food-associated calls and audience effects

Food-associated calls, especially food barks and food grunts, were rarely produced when the focal fed alone (*N*=119; food barks: 2.54%, food grunts: 9.48%, soft grunts: 12.82%). The number of males but not females within 5 m from the focal correlated with the likelihood of males producing food-associated calls (Table 5.3, Fig. 5.3). However, both the total number of males and females in the party were not good predictors of the focal male food calling (Table 5.3, Fig. 5.4).

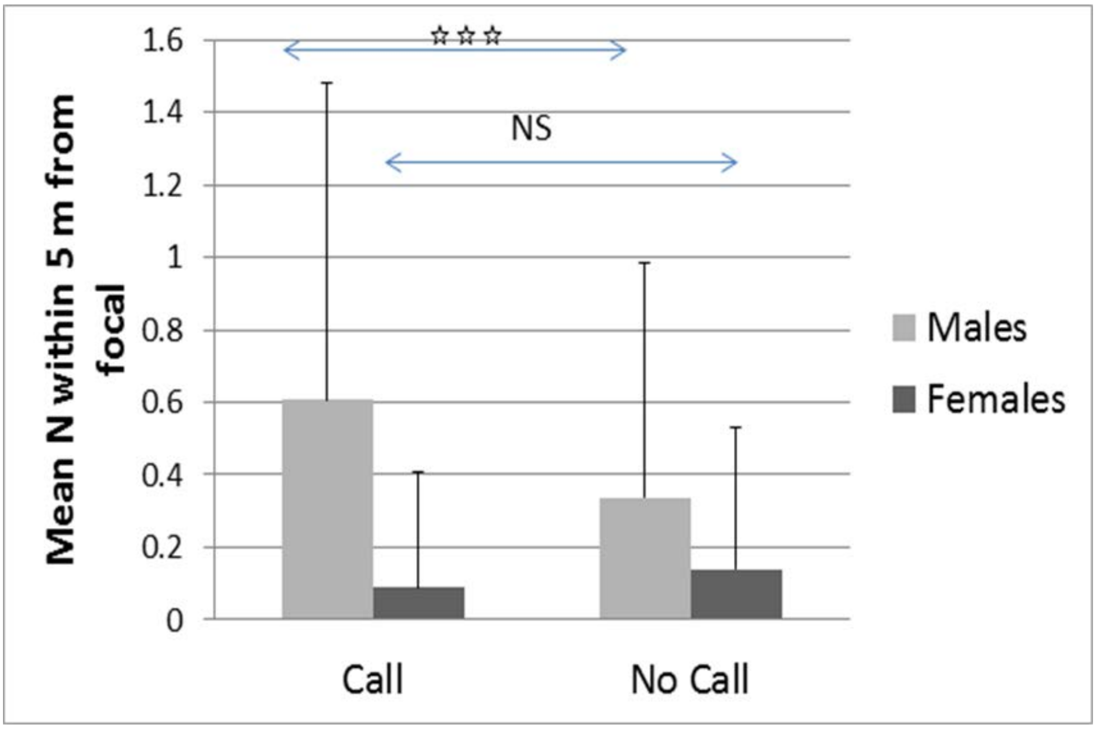

Figure 5.3: The relationship between food calling (0/1) and the number of males and females within 5 m from the focal (GLMM; * *P*≤0.001, NS=not significant; error bars represent 1 SD).**

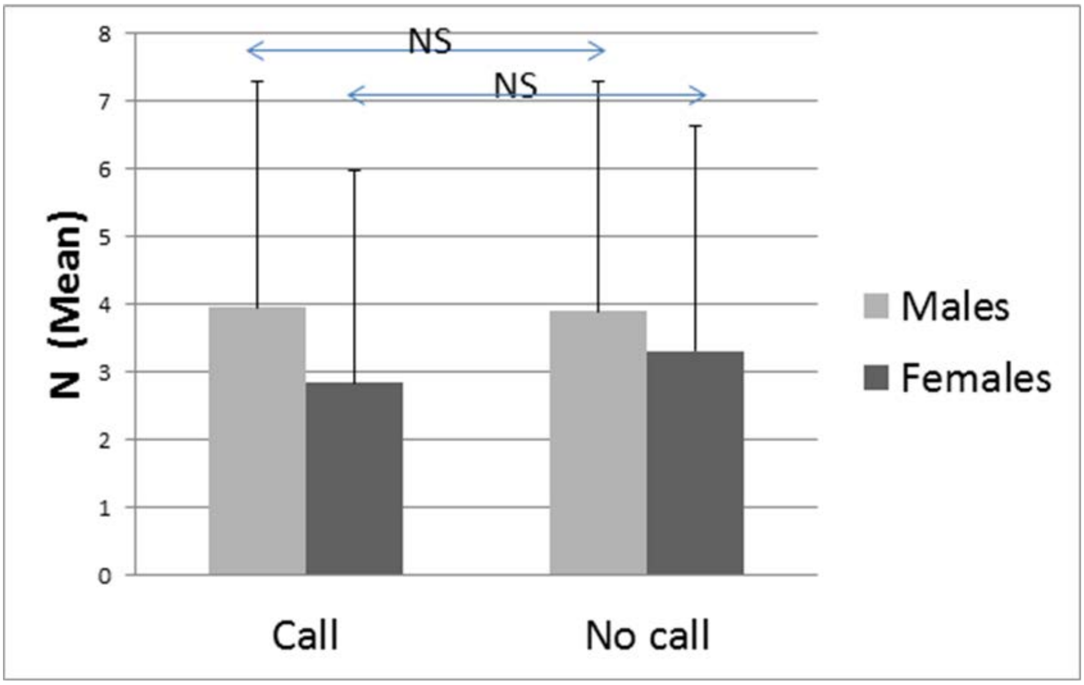

Figure 5.4: The relationship between male and female party size and food calling (0/1) [GLMM; NS=not significant; error bars represent 1 SD].

When two additional GLMMs were created with food bark (0/1) or food grunt (0/1) as dependent variables the same independent variables were significant (Table 5.4 and 5.5).

Table 5.4: The relationship between food barking and the investigated (independent) variables. Dependent variable: Food Bark [0/1]; random effects: Focal ID, Food Patch ID (GLMM; *****P*≤0.01, ******P*≤0.001; significant results in bold; all feeding bouts included).

Independent variables	Coef.	Std.Err.	z	[95% Conf.	Interval]
Preceding Behaviour	**2.39**	**0.75**	**3.18 *****	**0.92**	**3.87**
Food Type	**-1.16**	**0.37**	**-3.13 ****	**-1.89**	**-0.43**
Number of Males 5m	**1.34**	**0.47**	**2.84 ****	**0.42**	**2.27**
Number of Females 5m	-0.27	0.64	-0.43	-1.53	0.98
Total Male Party	0 .04	0.08	0.63	-0.12	0.20
Total Female Party	-0.09	0.09	-1.05	-0.27	0.08

Table 5.5: The relationship between food grunting and the investigated (independent) variables Dependent variable: Food Grunt [0/1]; random effects: Focal ID, Food Patch ID (GLMM; ******P*≤0.001; significant results in bold; all feeding bouts included).

Independent variables	Coef.	Std.Err.	z	[95% Conf.	Interval]
Preceding Behaviour	**2.44**	**0.38**	**6.44 *****	**1.70**	**3.19**
Food Type	**-0.30**	**0.09**	**-3.41*****	**-0.47**	**-0.13**
Number of Males 5m	**0.85**	**0.18**	**4.79 *****	**0.50**	**1.20**
Number of Females 5m	-0.14	0.33	-0.41	-0.79	0.52
Total Male Party	-0.05	0.05	-1.11	-0.15	0.04
Total Female Party	-0.04	0.05	-0.77	-0.14	0.06

Males were also more likely to call when preferred (β±SE=0.81±0.17, z=4.64, *P*<0.001) rather than neutral (β±SE=0.33±0.16, z=1.61, *P*=0.108) social partners were within 5 m (Fig. 5.5).

This pattern also applied to food grunt data (preferred social partners: β±SE=1.01±0.20, z=5.07, *P*<0.001: neutral social partners: β±SE=0.26±0.23, z=1.13, *P*=0.260). Although the focal males were significantly more likely to give food barks when either preferred or neutral social partners were present, the correlation was stronger for preferred social partners (preferred social partners: β±SE=3.87±1.19, z=3.25, *P*=0.001: neutral social partners: β±SE=2.30±1.00, z=2.29, *P*=0.022).

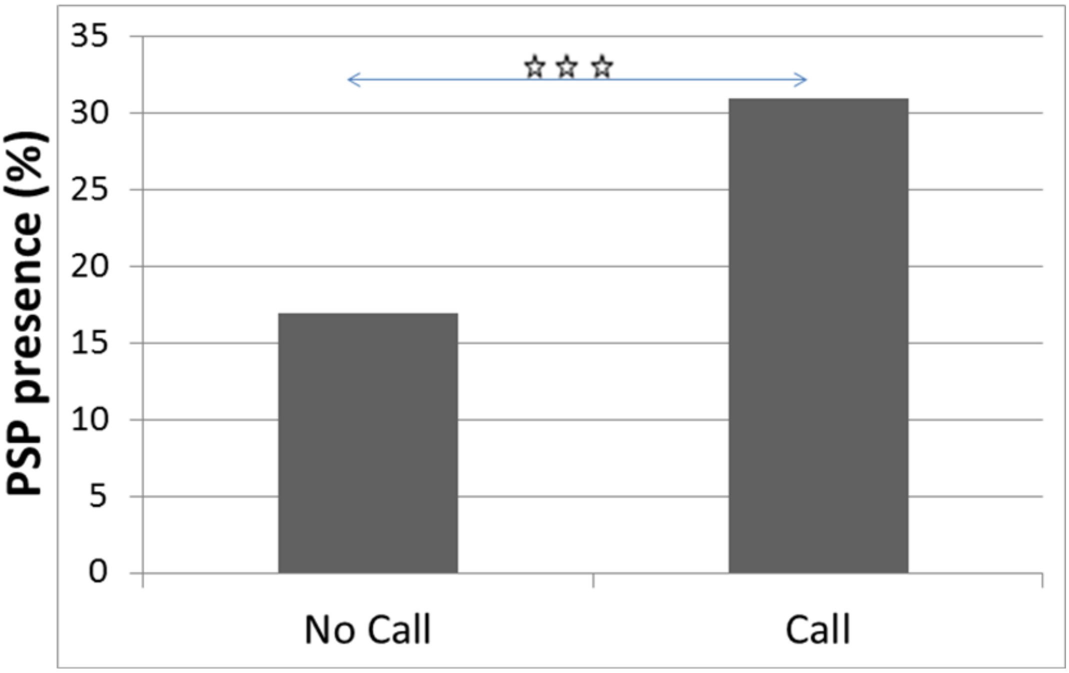

Figure 5.5: The relationship between food calling (all calls) and the percentage of instances when a preferred social partner was within 5 m of the focal at the start of the feeding bout (GLMM; * *P*≤0.001).**

Finally, a male feeding partner was more likely to be within a visible distance from the focal until the end of a feeding bout after the focal gave a food-associated call at the beginning of the feeding bout (β±SE=0.93±0.37, z=2.49, *P*=0.013; Fig. 5.6).

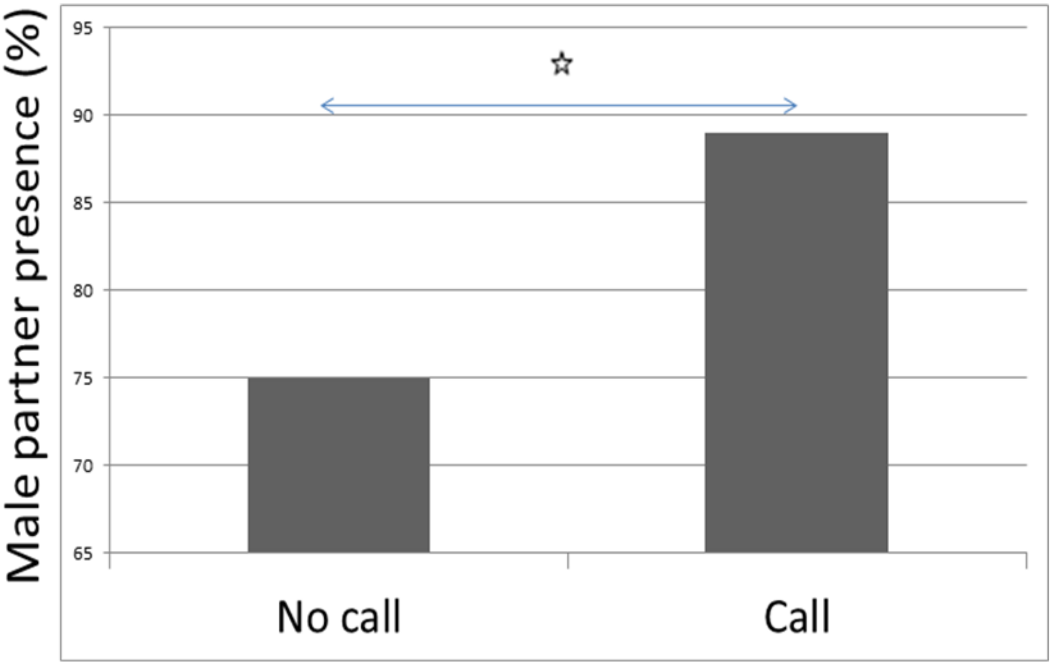

Figure 5.6: The percentage of feeding bouts in which a male feeding partner remained within visible distance of the focal until the end of the bout, illustrated as a function of whether or not the focal gave a food-associated call at the beginning of the feeding bout (GLMM; *$P \leq 0.05$)

This result, however, might be confounded by the relationship quality of the dyads considered: it may be that preferred social dyads were more likely to have called and stayed in close proximity and neutral dyads were less likely to have both called and stayed in close proximity. In order to control for this possibility I analyzed only the subset of feeding bouts (N=142) in which the dyad partners were preferred social partners. Importantly, preferred social partners were significantly more likely to be retained to the end of a feeding bout when a call was given by the focal (β±SE=1.64±0.63, z=2.55, P=0.011).

Food calls and behaviour preceding feeding

Focal chimpanzees were more likely to give a food-associated call after travelling than after resting when initiating a feeding bout (Table 5.3). The same pattern emerged after including in the analysis only THV non-arrival feeding bouts (*N*=162; β±SE=2.34±0.82, z=2.84, *P*=0.004).

DISCUSSION

The results of this study support my hypothesis that one of the functions of chimpanzee food calling might be to signal to the audience that the caller is likely to initiate or/and prolong feeding. Males fed for longer after giving a food-associated call at the start of a feeding bout regardless of the type of food being consumed. These kinds of signals allowing anticipation of each other behaviours might be beneficial for coordinating grouping decisions in species living in highly fluid and flexible societies such as chimpanzees where grouping patterns are often unpredictable. My data suggest that food-associated calls are more likely to be given when starting to feed after travelling rather than resting, when the need to coordinate group decisions is highest. Importantly, I show that food-associated calls facilitate the retention of a feeding partner. For example, a male feeding partner was more likely to remain with the focal until the end of the feeding bout after the focal gave a food call at the beginning of this feeding bout (even though animals tended to feed significantly longer after giving a call providing more opportunity for fissions). These results suggest that the function of food calling in male chimpanzees is to deter other males from leaving the food patch, and consequently retain them in the party. Therefore, the ultimate function of the signal might be promoting coordination of the grouping decision between that caller and the listener. This seems to be supported by the fact that after giving a call, males fed for longer when others also food called. It is possible that on the basis of whether or not feeding partners produce food-associated calls, the caller predicts more accurately whether there is a conflict of interest regarding feeding decisions between him and other party members. In this respect, food-associated calls in chimpanzees might have a similar function in promoting group coordination as grunt vocalizations in mountain gorillas. For example, it has been suggested that in mountain gorillas an increased production of grunts preceding a group movement reflects ‘readiness’ of the group members to move (Stewart and Harcourt 1994; Pyritz et al. 2011). Food calling in chimpanzees might therefore in a similar way promote collective decision making in feeding contexts.

My data show that these calls correlate most with the presence of other male chimpanzees in close proximity and preferred social partners in particular. This supports my hypothesis as given the importance and strength of male-male bonds in chimpanzees, I would expect that males use signals that allow anticipation of each others' behaviours more often with socially important individuals (e.g., males and PSP) rather than females and neutral male partners. Chimpanzees tend to stay in close proximity to socially important individuals (Gilby and Wrangham 2008) and thus it is the composition of the audience in close proximity to them, rather than the whole party, that seems to mediate call production. These results therefore support the 'bonding' hypothesis of chimpanzee food-associated calls (Slocombe et al. 2010) and suggest that coordinating feeding/grouping decisions among affiliated males is the mechanism underpinning this function.

My results do not support an alternative hypothesis for the bonding function of food-associated calls in male chimpanzees, which posits that the function of these calls is to inform affiliated party members about food quality (or quantity), allowing listeners to adjust their foraging decisions (Slocombe et al. 2010). For example, the results of this study, which investigated audience effects on male food calling on a finer (within-party) level than previous studies, show that the likelihood of food calling correlates most with the number of males who are in very close proximity to the caller (i.e., less than 5 meters). This makes it likely that the 'targeted' receivers of the signal are already on the feeding patch and therefore aware of not only the presence of food but also about specific characteristics of the food such as its quantity and quality. These results suggest therefore that the food information sharing hypothesis is unlikely to be applicable to the ultimate function of food calling in male chimpanzees because this signal seems to target those in close proximity. This is not to say that individuals who are further from the caller do not use food-associated calls to be guided to food [which is a likely possibility as demonstrated by Slocombe and Zuberbuhler (2005)]. My data suggest, however, that the presence of individuals beyond close proximity from the caller (i.e., individuals potentially unaware of the food) was probably not the selecting factor driving the evolution of food calling in male chimpanzees. In other words, the possibility of using others' food-associated calls to locate food is likely to be an evolutionary by-product rather than the main ultimate function of these calls.

The proposed hypothesis can explain why food-associated calls are frequently produced when feeding on food of low quality [the need for the signal is less relevant to food quality], a fact that has been difficult to explain by the food information sharing model (Clay and Zuberbuhler 2009). Furthermore, in contrast to the models suggesting that the function of food calling is to inform about food presence or quality (a model which explains well benefits for the receiver but not the signaller), the proposed hypothesis implies that benefits of food calling are rather balanced between the producers and receivers of the signal. For example, the signaller benefits by increasing the chances of retaining valuable social partners in close proximity and the receiver benefits by being able to more accurately predict the behaviour of the caller.

My study suggests that food type is an important correlate of chimpanzee food calling. For example, food barks were significantly more frequently produced when initiating feeding on ripe fruits than on young leaves or THV. This result supports previous studies on food-associated calls in other chimpanzee populations as well as in bonobos where high-pitched calls also correlated with high-quality food (Slocombe and Zuberbuhler 2006; Clay and Zuberbuhler 2009). In light of the proposed 'coordination' hypothesis high food bark frequencies on food patches with ripe fruits might be explained by the fact that the variation in feeding time in the fruit context is much larger than in the case of any other food types. Therefore, the need for a more reliable signal is stronger when initiating feeding on fruits, where there is greater uncertainty as to how long an individual will feed, than on other food types. Food barks might be examples of such reliable signals of a prolonged feeding bout. This is because food barks are louder and higher pitched vocalizations than food grunts and especially soft grunts that probably also require more energy to produce them. This view is in line with studies on animal communication which show that the reliability of a signal, including a vocal signal, is often a function of the level of investment needed to produce it (Zahavi 1975; Zahavi 1979; Bradbury and Vehrencamp 2011). This might explain why food barks are a more reliable indicator of prolonged feeding than food grunts (and food grunts are in turn more reliable indicators of feeding duration than soft grunts). In this respect, particular types of food-associated calls might make these vocalizations more informative signals regarding feeding durations of the caller.

In a similar vein, the coordination hypothesis can offer an explanation for previous findings that food-associated calls are more commonly produced on larger food patches (Slocombe et al. 2010). I argue that variations in feeding duration are greatest on large food patches, and therefore the need for the signal may be considerably greater than on small food patches. Animals are unlikely to stay for a long period of time on small patches of food and therefore the need for the signal is less urgent. Nevertheless, this prediction remains to be tested.

An alternative explanation for a high frequency of food barks produced in the ripe fruit contexts might be that food barks function to signal to the audience the presence of high-quality food (i.e., ripe fruits). However, as mentioned above, results on audience effects of food calling shown in this study suggest that this is unlikely. For example, the fact that food bark instances correlated more with the number of males in close proximity than with the total (male) party size suggests that the signal is directed to those who most probably are already aware of the food patch and its quality.

Another ultimate level alternative explanation for high frequency of food barks produced in the ripe fruit context is offered by the ‘spacing’ hypothesis (Boinski and Campbell 1996; Gros-Louis 2003). However, promoting feeding space (or repelling others) seems unlikely to be the main function of food calling in male chimpanzees as this hypothesis predicts opposite results to the ones obtained in this study. For example, if the function of food-associated calls were to repel others, we would expect that males are less likely to retain a feeding partner in proximity until the end of a feeding bout after they gave a food-associated call at the onset of this feeding bout than after remaining silent. My data however show an opposite pattern.

Nevertheless, it is important to note that the spacing hypothesis has not been thoroughly tested in this study.

Since food barks are loud and high-pitched vocalizations, these calls probably reflect an elevated arousal of the calling individual arriving at a high-quality feeding site (e.g., Owren and Rendall 2001). However, the purpose of this study is not to investigate the proximate mechanisms (such as hunger or excitement) driving food call production but rather to explore the ultimate (evolutionary) functions of these calls. Proximate mechanisms of food calling can explain how organisms produce these calls in response to certain stimuli (such as high-quality or abundant food) but they are not able to explain why food calling is such a common behaviour in this species (and therefore why it might have been favoured by natural selection). Moreover, proximate and ultimate functions of a given behaviour are not mutually exclusive (Seyfarth and Cheney 2003). For example, on a proximate level food barks might reflect an elevated arousal level or hunger of the caller and at the same time their ultimate function may be to signal the relative feeding duration of the individual producing the call that consequently facilitates behavioural coordination.

Although my data show that the relationship between food calling and the social rank of the caller was not significant, there was a trend for high-ranking males to produce these calls more often than low-ranking males. This trend is probably an effect of the fact that high-ranking males have a higher number of preferred social partners than low-ranking males (Duffy 2006), and therefore are more likely to have an appropriate audience for calling when arriving at food patches.

In conclusion, my results support the bonding hypothesis of food-associated calls in male chimpanzees. My study also suggests a mechanism underpinning the bonding role of food calling: food-associated calls allow anticipation of group member's feeding decisions that in turn facilitate the retention of valuable social partners in proximity. These calls therefore might be important mechanisms regulating the coordination of grouping decisions in this species.

CHAPTER 6: General discussion

Chimpanzee calls as bonding signals in a fission-fusion society

The results of my study support previous studies on chimpanzee calls suggesting that vocal behaviour play an important role in social bonding in these primates (Chapter 1). For example, the potential role of both pant-hooting and food calling in male chimpanzee social bonding has been suggested before (Mitani and Nishida 1993; Slocombe et al. 2010). The results of my study, however, have the potential to explain why vocalisations might be especially adaptive as bonding signals in the type of society formed by chimpanzees. As discussed in Chapter 1, chimpanzees live in unstable fission-fusion societies where party composition can change frequently even within a single day. It has been suggested that animals living in such societies face more complex social challenges than animals forming more stable societies (Amici et al. 2008; Aureli et al. 2008; Lehmann and Dunbar 2009). For instance, the fluid nature of this sociality means that party composition is often unpredictable and therefore preferred long-term social partners are not always available (Chapter 1). Therefore, for a male chimpanzee the choice of with whom he interacts on a given day is often limited. Thus, flexibly forming affiliative partnerships with other males, who are in the same party but who are not necessarily affiliated with this male on a long term basis, might be an effective strategy of mitigating the costs of living in a fluid chimpanzee society. Such short-term affiliative partnerships might, for example, facilitate other affiliative interactions between males such as grooming, tolerated co-feeding, or mutual support in agonistic interactions against other males. It has been argued here that vocal interactions might be especially suitable as signals facilitating the formation of such short-term affiliations, and pant hoot chorusing might play precisely such a role (Chapter 3). Pant hoot chorusing, for example, was often employed between both preferred and neutral social partners. Males, irrespective of the long-term affiliation status between them, were also more likely to be involved in grooming or form coalitions on days when they chorused together. Moreover, for a given male dyad on a given day, chorusing interactions were more reliable indicators of other affiliative interactions than grooming. Therefore, on a short-term basis chorusing might be a more effective affiliative signal than grooming, which is an interaction traditionally regarded as a good marker for long-term social bonds in male chimpanzees (Mitani 2009b). In addition, since males were more likely to stay in close proximity on days when they chorused than on days when they did not, it is likely that such vocal displays also increase the likelihood of staying together longer in the same party.

Vocal behaviour might also facilitate affiliated males to remain in proximity or the same party by enabling them to more reliably predict each other's subsequent activity. Food-associated calls might play exactly such a role in feeding contexts. For example, on the basis of food calling behaviour males can predict each other feeding durations more accurately, which in turn might facilitate them remaining in close proximity or the same party (Chapter 5). Critically, a male feeding partner was more likely to remain with the focal until the end of a feeding bout if the focal food called at the onset of this bout. Since an individual's feeding duration was also dependent of food calling behaviour of party members, these vocalisations might mediate collective decision making in foraging contexts. Although it remains to be empirically tested, it is possible that food-associated calls facilitate coordination of feeding decisions through similar signalling mechanisms in other animals living in fission-fusion societies. Overall, this study suggests that vocalisations might be important signals mediating grouping patterns in unstable chimpanzee societies.

The complex function of pant-hooting

While this study indicates an important bonding role of pant-hooting, it is also important to note that signalling social bonds is by no means the sole function of this behaviour. Pant hoots are long-distance calls that most probably originally evolved for the purpose of maintaining contact with other parties that in turn facilitates an individual's grouping decisions. The results of this study support the view that pant hoots might play a pivotal role in modulating grouping decisions in this species. For example, males pant hooted more frequently on days when rates of fusion and fission where high (Chapter 2). The role of pant-hooting as a bonding signal most probably has been acquired later in the course of evolution of this vocalisation. In this respect, pant-hooting might be similar to social grooming in primates. For example, although there is a general opinion that the original function of grooming was to remove dirt and parasites from the fur of the grooming partner (Hutchins and Barash 1976; Barton 1985), it is also widely acknowledged that this behaviour plays an important bonding role. This bonding function, however, was most probably acquired later in the evolutionary time than the original hygienic function of this behaviour (McKenna 1978; Dunbar 1991). In fact, group-living primates (at least Old World primates) groom considerably more often than it is required by the hygienic function of this behaviour (Dunbar 1991). Nevertheless, grooming retained the initial hygienic function, which is supported by studies showing that primates tend to groom these body parts that are affected by a high parasite load (Zamma 2002) or those that are not possible to groom by means of self-grooming (Barton 1985). Although there has been considerable debate on the relative importance of the hygienic and the social function of grooming (Hutchins and Barash 1976; Boccia 1983; Dunbar 1991) it is difficult to determine which one is more important (Grueter et al. 2013).

In a similar vein, although pant-hooting seems to be crucial in maintaining contact between different parties, this (Chapter 2) and previous (Mitani and Nishida 1993; Mitani and Gros-Louis 1998) studies suggest that chimpanzee pant-hooting, especially chorusing, might be an important bonding signal. This view seems to be also supported by the result of my study showing that males pant hooted jointly with other males considerably more often than alone (Chapter 3). It is therefore very possible that males, when being in company with other males, pant hoot substantially more frequently than is required by the original function of this behaviour (i.e., maintaining contact with individuals in other parties).

The view that pant-hooting might play more than one evolutionary function is consistent with the current view on the evolution of animal signalling. For example, a signalling behaviour often arises through the course of evolution, as a result of gradual elaboration (or ritualisation) of a behaviour, that originally served a different role (Cullen 1972). This probably was the case during the evolution of the social function of grooming in primates (Hutchins and Barash 1976). Pant-hooting behaviour might have been shaped by a similar process. For example, considering the specific acoustic structure of a pant hoot and the fact that when chorusing males produce longer pant hoots with more climax elements than when calling alone, this behaviour might have also been shaped in accordance with the process of ritualisation. It is very possible, therefore, that if the function of a pant hoot was solely to locate other parties or to signal the caller's location, the basic acoustic structure of this call would be different (Chapter 4). Nevertheless, as in the case of grooming and other behaviours serving multiple functions (e.g., Bradbury and Vehrencamp 2011), it is challenging to establish which particular function of pant-hooting is the most important one.

Pant-hooting and acoustic flexibility

The results of this study suggest that male chimpanzees flexibly modify the temporal structure of their calls when chorusing (Chapter 4). For example, the duration of the build-up phase of the initiator's call correlated positively with the latency with which the partner joined in the call. Similarly, there was a positive relationship between the numbers of climax element given by the chorusing males. Males thus seem to adjust durations of phases of a pant hoot such as the build-up and the climax to both facilitate the occurrence and prolong a chorus (Chapter 4). It is possible therefore that both the basic acoustic structure of a pant hoot and the flexibility to modify the durations of its constituent phases might have evolved to promote chorusing. My results also are in line with the claim that even though the basic acoustic structure of chimpanzee pant-hooting seems to be under a strict genetic constraint, chimpanzees actively modify finer acoustic features of their calls when calling in choruses. In this respect, my study is consistent with a previous study on chimpanzee pant-hooting, where it was shown that males actively accommodate some features of partners' calls, such as climax frequencies, when pant-hooting in choruses (Mitani and Gros-Louis 1998).

It is possible that such mechanisms of adjusting the temporal structure of a call in accordance with the partner's vocal response also exist in other chorusing or duetting animals. Whereas this might be the case in some duetting birds (Hall 2009), virtually no studies of this kind have been conducted on duetting primates (Chapter 4). More studies are therefore needed to determine whether the mechanism identified in this study also applies to other primates. In a more general perspective, the results of this study is consistent with a large body of literature showing that primate calls, although genetically constrained by a limited repertoire (Hammerschmidt and Fischer 2008), are endowed with some degree of acoustic flexibility within the existing repertoire (Snowdon 2009). On a finer level, this study supports the findings of previous studies showing that primates are able to actively modify the acoustic features of their calls to match the partner's one (Sugiura 1993; Mitani and Gros-Louis 1998; Sugiura 1998).

Audience effects of calling

This study shows that chimpanzee callers are very sensitive to fine details of the audience. Audience effects (i.e., modulations of signalling behaviour as a function of the presence and/or composition of audience) in primates have been often interpreted as support for the claim that primate vocal production is characterised by a high degree of flexibility (Fedurek and Slocombe 2011). In primates, the type of audience correlates with both the frequency with which animals call (Chapman and Lefebvre 1990; Caine et al. 1995; Roush and Snowdon 2000; Di Bitetti 2005; Slocombe et al. 2010) or with the acoustic structure of calls (Pollick et al. 2005; Slocombe and Zuberbuhler 2007).

Previous studies showed that chimpanzee vocal behaviour is highly sensitive to the presence and type of audience. For example, the composition of audience correlates highly with the probability with which males pant hoot (Clark 1991; Mitani and Nishida 1993) and food call (Slocombe et al. 2010). My study supports these findings. For example, males pant hooted considerably more often with other males than alone, suggesting that male audience might be an important factor facilitating male chimpanzee pant-hooting (Chapter 3). Males were also more likely to join in another male's pant hoot when a well affiliated male was calling. These specific audience effects of pant-hooting are therefore similar to the ones identified in previous studies on chimpanzee pant-hooting (Mitani and Nishida 1993; Mitani and Gros-Louis 1998). As far as food-associated calls are concerned, males were considerably more likely to produce these calls when feeding in close proximity to other males rather than females or when feeding alone (Chapter 5). Males were also more likely to produce these calls when feeding in spatial proximity to preferred male social partners. These results are therefore in line with a previous study on chimpanzee food-associated calls showing that males are more likely to food call when affiliated males were in the same party (Slocombe et al. 2010). In contrast to previous studies on chimpanzee food calling, however, my results suggest that it is composition of the audience in close proximity to the caller, rather than that of the whole party, that mediates the production of these calls. In sum, the audience effects identified in my study of both pant-hooting and food calling are consistent with previous studies suggesting that the production of these two types of vocalisations are highly sensitive to details of the audience. The specific audience effects found in my study also support the view that these calls are involved in male social bonding.

Potential proximate correlates of chimpanzee vocal communication

Audience effects have generated considerable debate in the field of animal communication. One of the reasons for this interest is that the apparent behavioural complexity of these effects might indicate that elaborated cognitive mechanisms, such as intentional signalling, underpin them (Zuberbuhler 2008). For example, studies showed that male langur monkeys alarm call until all group members call (Wich and de Vries 2006) and blue monkeys are more likely to give an alarm call when other group members are exposed to danger (Papworth et al. 2008). A more recent study suggests that complex audience effects occur also in chimpanzees. Crockford et al (2012) in an experimental study were able to show that after encountering a snake model, individuals were more likely to call in the presence of individuals who had just joined the caller’s party (and therefore potentially unaware of the presence of a ‘snake’) than in the presence of individuals who had been already aware of the danger. This result has been interpreted as indicative that chimpanzees might take into account the knowledge of others while alarm calling, and therefore intentionally inform ignorant individuals about the danger (Crockford et al. 2012). However, the fact that audience effects are found in animals such as fish and domestic chickens suggests that the involvement of such intricate cognitive processes is not required for a basic audience effect to take place (Marler et al. 1986; Plath et al. 2008). For example, in a fish species males who won a contest with a rival spend less time displaying towards females who witnessed the context than towards the ones who were absent during the context (Herb et al. 2003). The audience effects recognised by Herb et al (2003) in fish do not differ qualitatively from the ones identified by Crockford's et al (2012) in chimpanzees, and therefore the proximate underpinnings involved in both these situations might be similar.

Likewise, the fact that the production of food-associated calls in chimpanzees is sensitive to the composition of audience also does not necessarily mean that on a proximate level these calls are given intentionally. A more parsimonious explanation of this phenomenon is that the presence of certain individuals (such as preferred social partners) upon encountering food is just another external stimulus that makes males more aroused and consequently more likely to produce these calls (e.g., Fedurek & Slocombe 2011). It might be therefore unjustified to claim that if on a proximate level the production of a call is driven by arousal, this call cannot function as a signal targeted at specific receivers [as suggested by Zuberbuhler (2008)].

Similarly, the identified process of adjusting the temporal structure of a pant hoot when chorusing with a partner might be also simple on a proximate level. For example, this process might be mediated by elevated arousal levels of the pant-hooting individuals as a result of being involved in a chorus with another male (or males). This would explain why particular phases of a pant hoot, such as the climax, were longer in duets than solo pant hoots (Chapter 4). Similarly, adjusting the duration of the build-up stage of the initiator's pant hoot in accordance with the latency with which the partner joins in, might also be mediated by arousal with initiators possibly being more aroused and therefore more likely to proceed to the climax earlier if the partner has joined in the call at its early stage.

However, the possibility that more elaborated proximate mechanisms, such as intentionality, mediate the production of these calls cannot be excluded. One might also argue that this possibility might especially apply to chimpanzees and other great apes since these primates apparently have advanced social cognition in comparison to monkeys (Byrne 1995). This ape-monkey distinction in terms of social cognition has, however, been recently challenged (Call and Santos 2012). Nevertheless, until convincing evidence to the contrary is obtained, it is more conservative to explain the immediate mechanisms governing the investigated behaviours in a more parsimonious way (e.g., Morgan 1903). One of the reasons for this is that simple mechanisms, if effective, will always be favoured be natural selection at the expense of more elaborated ones (e.g., Williams 1966). On a physiological level, for example, the investigated vocal interactions might be mediated hormonally to a considerable extent (see below).

Although the observational nature of my study does not allow me to make conclusions with regard to the proximate underpinnings of the examined call interactions, literature on proximate correlates of other bonding behaviours in primates might provide a clue to these underpinnings. It has been shown here that vocal interactions such as pant hoot chorusing have similar social correlates as grooming. It is possible, therefore, that on a proximate level these two kinds of interactions have also similar physiological correlates. As mentioned in Chapter 1, there is substantial evidence that social grooming in primates is linked to an elevated production of certain chemicals in the body of grooming individuals, such as oxytocin and certain types of endorphins (Keverne et al. 1989; Snowdon et al. 2010). Since oxytocin has been also linked to social bonding in animals (Insel and Shapiro 1992; Curley and Keverne 2005; Schneiderman et al. 2012), on a proximate level the bonding function of grooming might be linked to this hormone. A recent study on chimpanzees indicates that also in this species oxytocin levels correlate with grooming behaviour, with well affiliated individuals having an elevated urinary level of this hormone after grooming each other (Crockford et al. 2013). The authors concluded that on a proximate level oxytocin might be an important molecule mediating social bonding in these primates (Crockford et al. 2013). This raises the question of whether, on a physiological level, vocal interactions such as pant hoot choruses also have similar correlates. However, virtually no studies have been carried out to investigate this issue in non-human animals. In humans, however, active performance in music production, including singing, might trigger endorphin release (Dunbar et al. 2012). The bonding role of human singing, like primate grooming, might be therefore linked to endorphins (Dunbar et al. 2012). Considering the bonding correlates of chimpanzee chorusing found in this and previous studies, it is likely that this behaviour is also endorphin-mediated. Nevertheless, the question of whether or not chimpanzee chorusing has similar physiological correlates as grooming should be determined in future studies. Following Crockford et al (2012), examining urinary levels of oxytocin in the context of chorusing behaviour would potentially address this aspect as far as this hormone is concerned. Controlling for potential confounds such as grooming activity, however, would be vital to obtain meaningful results.

Recent studies also identified neural underpinnings that might be important in facilitating coordinated vocal displays in animals. For example, in songbirds a certain group of brain neurons, termed as mirror neurons, activate upon singing or hearing a similar song to its own produced by another individual (Prather et al. 2008). Hence, on a proximate level the involvement of mirror neurons might be vital in performing coordinated vocal displays in which partners match the acoustic features of each others' calls (Prather et al. 2008). It is possible therefore that mirror neurons are also involved in chimpanzee chorusing behaviour. The function of mirror neurons has been intensely studied in monkeys (Ferrari et al. 2003). It was shown, for example, that these neurons fire both when performing an action such as grasping or holding and when observing these actions performed by others (Buccino et al. 2001; Iacoboni et al. 2005). It has been suggested that in group-living primates imitating behaviour of conspecifics might promote affiliation between group members, which in turn might facilitate tolerance and ensure behavioural synchrony in vital activities such as foraging and travelling (Paukner et al. 2009). A similar interpretation might be attributed to the function of chimpanzee chorusing (Chapter 3). Considering that when pant-hooting in a duet, males seem to match some acoustic features of the partner's call (Chapter 4), it is a possibility that on a neural basis this behaviour has similar underpinnings.

Chimpanzee vocalisations and the aspect of honest signalling

Although in this study I argued that the investigated vocal interactions are flexible bonding signals, certain costs should apply to these behaviours so as to make them effective signals of affiliation (e.g., Zahavi 1977b). There is however an ongoing debate whether the model of honest signalling (Zahavi 1975; Zahavi 1977a) can apply to animal vocalisations, and a great deal of this debate concerns vocal displays in birds (Searcy and Nowicki 2005). Several types of costs of avian singing have been proposed. For example, the developmental stress model suggests that learning songs from others might be energetically too costly when an animal is exposed to physiological stress at a certain stage of its ontogenetic development (Catchpole and Slater 2008). Since learning is not very important in the development of a chimpanzee vocal repertoire, this model is unlikely to be applicable to this species. Another type of cost related to vocal production might be associated with opportunity costs imposed by calling. In other words, singing requires time which otherwise could be allocated to more urgent activities such as foraging (Reid 1987). Again, while this model finds support in avian species, it is rather unlikely to be applied to chimpanzees as vocal bouts in this species are usually not as time consuming as bird songs.

The third type of cost of vocalising is associated with physiological costs of vocal production. The aspect of whether or not animal or avian vocal output incurs any direct costs on the caller has been highly debated. For example, some researchers argued that direct costs of singing are too negligible to limit vocal displays (Searcy and Nowicki 2005). However, other studies showed that bird singing might incur substantial physiological costs on its producer, measured by oxygen consumption, basic metabolic rate or body mass loss (Thomas 2002; Ward et al. 2003) and that these costs might be larger for individuals with limited energy balance (Ward et al. 2003). Moreover, it has been proposed that even if the direct costs of vocal production are negligible on a short-term basis, its intensity or duration might make vocal output physiologically costly (Leech and Leonard 1996; Bachman and Chappell 1998).

However, it has also been put forward that vocal signals might be both ‘cheap’ and at the same time reliable provided that there is no conflict of interest between the signaller and the receiver [and therefore both the signaller and the receiver do not benefit by cheating each other (Johnstone and Grafen 1992)]. Alarm calls in many animals are often given as examples of such signals (Zuberbuehler 2012). At the same time, however, to avoid deceitful signalling direct or indirect costs of cheating must apply to all signals and the only situation in which the signaller does not ‘require’ a signal to be honest is when it produces it for itself (e.g., echolocation in bats) (Bradbury and Vehrencamp 2011).

The question is whether any type of costs mentioned above can be recognized in the chimpanzee vocalisations investigated in this study. One way to answer this question is to examine whether there is a potential conflict of interests between the signaller and receiver in situations in which these calls are produced. As far as food calling is concerned, it has been argued here that these calls function to signal to the receiver that the caller is likely to initiate or/and prolong a feeding bout and that the signal might influence the receiver's decision with regard to whether or not to leave the food patch (Chapter 5). Therefore, a conflict of interest in light of the proposed function of these calls is highly plausible. For example, individuals within a party might have different feeding requirements, and therefore the between-individual conflict with regard to when leave the feeding patch might occur. This might be especially relevant in a chimpanzee society, where its fission-fusion nature makes it highly possible that individuals within a party have different feeding histories. To avoid fission, therefore, it is in the interest of the sender to reliably signal to the receiver about his feeding decision. While the direct costs of food calling output are unlikely to be very high, the graded nature of these calls ranging from quiet food grunts to loud and high-pitched food barks probably correlates with the amount of energy needed to produce these call types, potentially making some types of food-associated calls more reliable signals (Chapter 5). It is also possible that food calling interferes with the process of food consumption, in which case this would be another type of cost associated with these calls. Comparing an individual's food intake rates in calling and non-calling situations would be a way to test this hypothesis. The question of whether and how food calling is costly to the producer, therefore, needs to be answered empirically.

As far as pant hoot chorusing is concerned, there might be two types of costs potentially associated with this behaviour. One of these costs might be a physiological cost generated by call production. If there are any such direct costs of pant-hooting, they are most likely associated with the climax phase, which is the loudest part of the call (Chapter 4). These costs might be more pronounced when a male produces several climax elements within a single call. Although a single pant hoot call is generally a much shorter call than songs produced by birds or gibbons, pant hoots can be produced in succession in bouts comprising several calls within a minute, and this happens especially when calling in a chorus with other individuals (P.Fedurek unpublished data). Therefore, while costs of a single pant hoot might be negligible, calls given in succession and containing multiple climax elements might bring about some direct physiological costs. Moreover, pant hoots are most commonly produced in the travelling context (Chapter 2) and often when running and/or buttress drumming (P.Fedurek unpublished data), which might generate additional physiological burden on the caller.

Provided that the above costs apply to chorusing, by calling together males can test the strength of a bond between them. This is because males who are in a good relationship (at least during the time of calling) would be more likely to invest energy to produce a call, or to join in the partner's call, than less affiliated individuals. The fact that pant hoot choruses contained on average more climax elements than solo pant hoots (Chapter 4) might be interpreted as support this view, since this result suggests that males are more likely to produce more climax elements when calling with a partner. Nevertheless, as in the case of food calling, the aspect of whether pant-hooting brings about direct physiological costs needs to be examined empirically.

Another potential cost of chorusing which might be linked to social bonding is related to the aspect of attention to the partner's call (Chapter 1). The rationale for this hypothesis is that coordinated actions such as joint vocal displays are possible only if the partners are attentive to each other's actions (e.g., Smith 1994). As shown in Chapter 4, the latency with which males join in each other's' pant hoots varies considerably. Hence, it is possible that the degree of this latency is a signal of a bond, at least temporary, between the calling individuals. Indeed, males who joined in a call earlier usually produced more climax elements than those who joined later (P.Fedurek, unpublished data), suggesting that the latency of joining in is correlated with the motivation of the joining individual to contribute to the call. However, the aspect of how reliably the joining latency reflects social bonds needs to be investigated in future studies. Examining the relationship between the type of a chorus (i.e., in terms of the latency with which the partner joins in) and the degree of affiliative interactions between the callers immediately following the call, would be one way to address this issue.

Relevance to human evolution

In a more general perspective, this study might contribute to our understanding of the evolution of human communication, especially the ultimate function of language. Both chimpanzees and humans are characterised by a fission-fusion structure of their societies, which makes it likely that the common ancestor of these two species formed similar societies. However, most studies dealing with the factors influencing grouping strategies in fission-fusion societies have been mainly focused on ecological factors, such as the distribution of food sources and predation risk (Dunbar 1988; Strier 1992; Chapman et al. 1995). In contrast, few studies have addressed behavioural and social factors in this respect (Aureli et al. 2008). It has been established, however, that the level of affiliative relationships is one of the major factors mediating the decisions regarding association patterns of animals living in such societies [at least among chimpanzees and humans (Dunbar and Spoors 1995; Mitani and Amsler 2003; Gilby and Wrangham 2008)]. At the same time, however, the unstable and unpredictable nature of a fission-fusion society means that valuable social partners are not always available, in which situation flexible bonding signals might be favoured. In chimpanzees, pant hoot chorusing might be an example of such flexible but effective bonding behaviour operating mainly on a short-term basis. Humans, like chimpanzees, also form flexible societies where individuals fission and fusion frequently on a daily basis. In contrast to chimpanzees, however, humans, especially in their most recent evolutionary history, often interact with individuals with whom they have interacted very rarely in the past or with whom they have never interacted before. To be effective in such fluid societies, an individual often needs to form temporary relationships with unfamiliar individuals. I suggest that human vocal communication, such as language, might be a behaviour that facilitates the formation of such short-term relationships and that the bases for the bonding role of human language are rooted in human evolutionary history (e.g., Dunbar

1993). It remains a great scientific challenge to identify the other selection pressures that have driven human communication to become the complex system we see in modern human language. Nevertheless, both human language and chimpanzee pant hoot chorusing might be examples of flexible vocal interactions that effectively mediate social bonds in fission-fusion societies formed by these two species of primates.

Final conclusion

To conclude, the key results of my study suggest that vocalisations in male chimpanzees play important roles as bonding signals. My study also shows that the examined calls might be especially suitable as affiliative interactions in unstable fission-fusion societies formed by these primates. Pant hoot chorusing, for example, might be a flexible signal facilitating the occurrence of other affiliative interactions between individuals who are not necessarily long-term preferred social partners. Such signals might be especially important in chimpanzee societies where valuable social partners are not always available. Food-associated calls, on the other hand, might be signals facilitating anticipation of each feeding decisions which in turn facilitates individuals remaining in proximity or the same party. Both these types of vocalisations, therefore, might mitigate the costs of living in unpredictable and unstable societies formed by this species.

APPENDIX A

Linearity measure results

Matrix total		**275**
Landau's linearity index (h)		**0.713636**
Linearity index h' (corrected for unknown relationships)		**0.772727**
Expected value of h or h'		**0.25**
Maximum number of circular triads		**55**
Expected number of circular triads		**41.25**
Actual number of circular triads		**15.75**
Kendall's coefficient of linearity (K)		**0.713636**
Chi-square value (degrees of freedom)	**49.91837**	**20.20408**
Directional consistency index		**0.992727**
Number and % of unknown relationships	**13**	**23.64%**
Number and % of one-way relationships	**41**	**74.55%**
Number and % of two-way relationships	**1**	**1.82%**
Total number of relationships	**55**	**100%**
Number and % of tied relationships	**0**	**0.00%**

Improved Linearity Test using h' Index

Number of Randomizations	**10000**
Right tailed probability	**0.0004**
Left tailed probability	**0.9998**

APPENDIX B

Descriptive data for each community for the main effects described in the results section with the merged data set. Similar patterns are seen across the two communities, with both communities showing (i) a longer build-up duration in ‘Build-up duets’ (where partner joins in the build-up) than the ‘Introduction duets’ (where partner joins in the introduction) (ii) a higher number of build-up exhalations in the ‘Build-up duets’ (where partner joins in the build-up) than the ‘Introduction duets’ (where partner joins in the introduction)

	Community	
	Kanyawara	**Budongo**
Introduction duets		
Build-up duration	*N*=59, Mean=2.51s, SD=0.93s	*N*=13, Mean=1.66s, SD=0.62s
Number of build-up exhalations	*N*=59, Mean=6.13, SD=2.38	*N*=13, Mean=3.31, SD=1.44
Build-up duets		
Build-up duration	*N*=30, Mean=4.33s, SD=1.85s	*N*=7, Mean=3.96s, SD=1.58s
Number of build-up exhalations	*N*=30, Mean=10.43, SD=4.47	*N*=7, Mean=7.14, SD=3.23

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