VOCAL COMMUNICATION IN BONOBOS (PAN PANISCUS): STUDIES IN THE CONTEXTS OF FEEDING AND SEX

Zanna Clay

**A Thesis Submitted for the Degree of PhD
at the
University of St Andrews**

2011

**Please use this identifier to cite or link to this item:
http://hdl.handle.net/10023/1842**

Vocal communication in bonobos (*Pan paniscus*): studies in the contexts of feeding and sex

Zanna Clay

Dissertation submitted to the University of
St Andrews for the Degree of Doctor in
Philosophy

December 2010

Declarations

1. Candidate's declarations:

I, Zanna Clay,hereby certify that this thesis, which is approximately 59 000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in anyprevious application for a higher degree.

I was admitted as a research student in November, 2007 and as a candidate for the degree of Doctor in Philosophy in November, 2008; the higher study for which this is a record was carried out in the University of St Andrews between 2007 and 2010

Date ……….….Signature of candidate ……………………..

2. Supervisor's declaration:

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

Date ……………Signature of supervisor……………………………

3. Permission for electronic publication:

In submitting this thesis to the University of St Andrews I understand that I am giving permission for it to be made available for use in accordance with the regulations of the University Library for the time being in force, subject to any copyright vested in the work not being affected thereby. I also understand that the title and the abstract will be published, and that a copy of the work may be made and supplied to any bona fide library or research worker, that my thesis will be electronically accessible for personal or research use unless exempt by award of an embargo as requested below, and that the library has the right to migrate my thesis into new electronic forms as required to ensure continued access to the thesis. I have obtained any third-party copyright permissions that may be required in order to allow such access and migration.

The following is an agreed request by candidate and supervisor regarding the electronic publication of this thesis:

Embargo on both all of printed copy and electronic copy for the same fixed period of two years on the following ground(s): publication would preclude future publication

Date ……….. Signature of candidate ……………….Signature of supervisor ………

Acknowledgments

I am extremely grateful to all those who have helped me with this thesis. First and foremost, I thank my supervisor, Klaus Zuberbühler, for all his guidance, encouragement and wisdom. Klaus has been a great source of support throughout my studies and his continuous enthusiasm towards my explorations of the frequently puzzling, but fascinating behaviour of bonobos, will be always fondly remembered.

I thank the Leverhulme Trust, the Lucie Burgers Foundation for Comparative Behaviour Research and the University of St Andrews School of Psychology for their generous financial support of my research.

I have had some amazing experiences during my studies and I am very grateful to all those who have helped me at my various study sites. I am especially thankful to Claudine Andre and all the staff at Lola Ya Bonobo Sanctuary, DR Congo. Lola Ya Bonobo translates as ‘paradise for bonobos’ in Lingala, and that it is. Lola was a wonderful place to work, not only because it provided me with intimate access to the daily lives of bonobos, but also because of the incredible team that manage it. I am truly inspired by the work that Claudine and her team do in their efforts towards education and conservation of bonobos. In particular, I thank Papas Stanny, Phillipe, Jean-Claude and Claude for all their invaluable help, as well as to Papa Jean and Didier for their huge quantities of delicious crepes and potage. I also thank Fanny Mehl, Valery Dhanani, Dominique Morel and Suzy Kwetuenda for their support (and for being such a formidable female team!). I am also very grateful to Brian Hare and his research team for their support of my work at Lola Ya Bonobo. Brian has shown great enthusiasm towards my work with the bonobos and has gone out of his way to help me on my way with my PhD. Brian is a true ambassador to the bonobos and his help has been invaluable.

I greatly thank all the staff at San Diego Zoo and Wild Animal Park for their support. In particular, I thank the Zoo head-keeper, Mike Bates; his love for the bonobos, country music and extremely strong margaritas will always be remembered. I also wish to thank Donna Lundy at the Park, for all her kindness and help, as well as Kim Livingstone and Michele Stancer for coordinating my research.

I would also like thank the staff at Twycross Zoo for all their help. In particular, I thank the research coordinator, Jackie Hooley, for her help and guidance with my project. I am also very thankful to the great team of bonobo keepers: Donna Smithson, Liz Cubberley and Emma Swaddle, for all their support during my playback study.

Many people at St Andrews have been hugely supportive during my studies. I especially thank Mike Oram for his generous support with statistics, and to Dick Byrne and Andy Whiten for their help, guidance and wisdom. I am very grateful to Katie Slocombe and Simon Townsend, as well as to Jeroen Stevens, for all their help and advice. Thanks also to Kate Arnold; her passion towards the field of primate vocal communication is an inspiration. I thank Eric Bowman and Cristie Marr for statistical help, as well as Peter Slater and the BDG folk for those wonderful evenings of great food, for both mind and body. Thanks also to all of those in 'Team Wolfson', I have had some really great moments in that office: Cris, Guill, Nuri, Katie, Emily, Jessica, Verena, Marion and Cat, to name but a few. Thanks to Lisa for her insightful proof-reading and a huge thanks to Thibaud for all his help. Thibaud and I have had some great times and his help with my studies has been invaluable.

I am hugely thankful to my family: Julia, Charles, Felix, Joe and Zelda, for all their love, encouragement and support. Mum has been especially amazing, always being there at the end of the phone to provide love and guidance, as well as for taking time to proof-read my entire thesis. All my love and thanks to Gid, for being such a great source of support, comfort and laughs. I also thank my housemates, Oli and Rakshi, as well as my friends from far and wide, for all their enthusiasm towards my work.

All the 90 plus bonobos I have come to know during my studies have never failed to delight and inspire me. I feel so privileged to have had this opportunity to gain an insight into their fascinating worlds. In particular, I will always fondly remember: Semendwa, Manono, Kasongo, Nioki, Lukaya (who made it to the wild), Mimi, Kikwit, Loretta, Lana and Kichele and Diatou.

Finally, I dedicate this thesis to my dearest friend Emma, whose love for the natural world continues to be a great source of inspiration.

Contents

List of tables

List of figures

List of appendices

Abstract

Despite having being discovered nearly 80 years ago, bonobos (*Pan paniscus*) are still one of the least well understood of the great apes, largely remaining in the shadow of their better known cousins, the chimpanzees (*Pan troglodytes*). This is especially evident in the domain of communication, with bonobo vocal behaviour still a neglected field of study, especially compared to that of chimpanzees. In this thesis, I address this issue by exploring the natural vocal communication of bonobos and its underlying cognition, focusing on the role that vocalisations play during two key contexts, food discovery and sex. In the context of food-discovery, I combine observational and experimental techniques to examine whether bonobos produce and understand vocalisations that convey meaningful information about the quality of food encountered by the caller. Results indicate that bonobos produce an array of vocalisations when finding food, and combine different food-associated calls together into sequences in a way that relates to perceived food quality. In a subsequent playback study, it was demonstrated that receivers are able to extract meaning about perceived food quality by attending to these calls and integrating information across call sequences. In the context of sexual interactions, I examine the acoustic structure of female copulation calls, as well as patterns in call usage, to explore how these signals are used by individuals. My results show that females emit copulation calls in similar ways with both male and female partners, suggesting that these signals have become partly divorced from a function in reproduction, to assume a greater social role. Overall, my results highlight the relevance of studying primate vocalisations to investigate the underlying cognition and suggest that vocalisations are important behavioural tools for bonobos to navigate their social and physical worlds.

Chapter one: Vocal communication in primates and other animals

Summary

In this chapter, I review a number of more general theoretical points relating to animal vocal communication, focusing particularly on the non-human primates. First, I examine the notion that, due to the intimate link between cognition and communication, vocalisations provide a good opportunity to investigate the psychological processes underlying the behaviour of non-human animals. From here, I introduce the question of language origins and its link to the vocal communication of our closest relatives, the non-human primates. Although there are clear distinctions between human and non-human primate communication, a growing body of evidence indicates that foundations of language lie rooted within the primate lineage. Here, I introduce three key topics which are considered to be precursors to language: functionally referential communication, call combinations and audience effects. Finally, I examine two key topics which shall form the essential focus of this thesis: the contexts of food discovery and sex. Food discovery and sex represent two of the most important biological challenges that any animal must face, and thus provide ideal arenas for investigating the interaction between cognition and communication in animals. Whilst there is still much left to be learned about bonobo behaviour, I argue that vocalisations provide a useful window for investigating the cognitive mechanisms underlying the behaviour of this ape species.

Vocal communication as a window into cognition

The task of exploring animal minds represents a long-standing challenge of biological science. In the absence of language, non-human animals lack the necessary communicative and cognitive skills required to externalise their mental processes in the way that humans can. One approach to investigating underlying social cognition is to study how animals communicate with one another. This follows the logic that in any social animal, communication and cognition are intimately linked (Seyfarth & Cheney, 2003a). Therefore, by studying how animals communicate with one another, one may gain a useful window through which their minds and social awareness can be explored. This approach has proved especially fruitful in the study of non-human primates, with studies of their vocal communication revealing intricate information about how primates see the world and navigate their social landscapes (e.g. Cheney & Seyfarth, 1990; Seyfarth et al., 2010).

Signallers and receivers

Before moving further into the question of vocal communication and cognition, it is important to establish the conceptual framework of signallers and receivers. There are some important differences in the communicatory roles of signallers and receivers and, as a consequence, it has often proved best to approach, or at least acknowledge, them separately (Seyfarth & Cheney, 2003a). From an evolutionary perspective, natural selection favours signallers whose calls influence recipient behaviour in a way that provides the signaller with benefits. Likewise, natural selection favours receivers who are able to acquire information from the signaller that is of use to them (e.g. Dawkins & Krebs, 1978; Seyfarth & Cheney, 2003a). In many contexts, communication is co-operative and the signaller and receiver overlap in their evolutionary interests. An example of this is the production and comprehension of predator-specific alarm calls in a group of conspecifics (e.g. Zuberbühler, 2009). In the alarm context, calling is costly to the signaller as it may attract the attention of predators, to both themselves and their kin group (Zuberbühler et al., 1997). However, for alarm calling to evolve, the benefits of calling must be greater than the costs incurred. This includes decreasing the risk of predation of kin, either by alerting them to the danger, or signalling to the predator that it has been detected (Sherman, 1977; Zuberbühler et al., 1999). In high-risk contexts, evolution favours signal systems which are both simple to produce as well as to decode (Seyfarth & Cheney, 2003a).

Whilst communication is an essentially social phenomenon and the evolutionary strategies of signallers and receivers often converge, there are also cases where signallers and receivers compete in their evolutionary interests (Marler, 1961). For instance, some predators are able to exploit the alarm and social calls of their prey as a means to aid their successful hunting strategies. In the Tungara frog (*Physalaemus pustulocus),* males give 'chuck' and 'whine' calls, which have evolved to both maximise the information communicated to conspecifics (to attract females and repel rivals) whilst simultaneously minimising the information transmitted to 'eavesdropping' predators (Ryan et al., 1982). Whilst the frequency range of the chuck call falls within the hearing frequencies of conspecifics (Capranica, 1978), their principal predators, bats, have also evolved super-sensitive hearing, enabling them to easily identify these prey calls. In their evolutionary arms race with bats, Tungara frogs have also evolved the strategy of adding the acoustically noisy whine calls to their chuck calls, a vocalisation which appears to have been favoured by natural selection because it makes the frogs more difficult to locate by bats (Ryan et al., 1982).

In addition to fundamental differences in their evolutionary interests, the cognitive mechanisms underlying call perception and production may also differ for signallers and receivers within the same species. In general, signal production in animals appears to be closely related to their underlying motivational states (e.g. Bickerton, 1990; Marler et al., 1992). In this way, it is thought that individuals may have little cognitive control over call production, with calling largely being a reflexive response to a particular stimulus (e.g. Rendall et al., 2009). Nevertheless, even if signallers are influenced by their underlying motivational states, evidence of audience effects, flexible vocal production and tactical vocal signalling in some species suggest that signallers may also be able to control call production in some cases (e.g. Zuberbühler, 2005, 2008). For instance, subordinate tufted capuchins (*Cebus apella nigritus*) have been shown to give false alarm calls which usurp food from conspecifics, a behaviour which is indicative of tactical deception (Wheeler, 2009). False alarm calls have also been demonstrated in a number of birds that kleptoparasitise other foraging species by stealing their food when they run for cover (Munn, 1986). For example, the fork-tailed drongo (*Dicrurus adsimilis)* produces false alarm calls when co-foraging with pied babblers (*Turdoides bicolour*) (Ridley & Raihani, 2007). Recent research has indicated that the drongo is able to mimic the alarm calls of the different species it kleptoparasites (e.g pied babblers and meerkats, *Suricata suricata*) as a strategy to ensure that their deception continues to be effective (Flower, *in press*). Whether or not such acts reflect a hard-wired behavioural strategy or indicate any level of intentionality in the signaller requires further investigation.

Compared to vocal production, the cognitive mechanisms underlying call comprehension appear to be considerably more complex (Seyfarth & Cheney, 2003a). Rather than simply passively responding to ‘arousing’ stimuli, results from a growing body of literature have revealed that receiver responses can be flexible and dynamic (Seyfarth & Cheney, 2003a; Seyfarth et al., 2010). By attending to vocalisations, receivers may be able to form mental representations about the meaning of the call in reference to the external world. This is particularly the case for calls which are tightly linked to their eliciting stimulus (Marler, 1977). Although tapping into internal representations is challenging, the development of experimental techniques, such as playback studies, has demonstrated that the information extracted by listeners can be studied scientifically (Seyfarth et al., 2010). For instance, such studies have revealed that receivers can respond differently to acoustically similar calls as well as respond similarly to acoustically different calls (Seyfarth et al., 2010).

Primate communication: Vocalisations and gestures

Primate vocalisations have often been disregarded as being cognitively uninteresting, (e.g. Tomasello, 2008). This follows the prevailing view that most primate vocalisations are genetically hardwired, involuntary expressions of emotions (Lancaster, 1975; Lieberman, 1968; 1998), which lack flexibility, are based on almost no learning and are broadcast indiscriminately without an intended audience (Tomasello, 2008). This is normally contrasted with the more flexible and ‘language-like’ gestural signals. Gestures in primates, especially those of apes, have been shown to exhibit three characteristics considered to be essential features of human communication: learning, flexibility and attention (Call & Tomasello, 2007; Genty et al., 2009). For example, many ape gestures are used in a range of different social contexts, may be learned from others or even invented, and can be used intentionally towards specific recipients, with signallers taking into account their attentional state (e.g. Call & Tomasello, 2007). In this sense, it has often been suggested that gestures, rather than vocalisations, provide the evolutionary foundations of language (Arbib et al., 2008; Corballis, 2003).

Whilst the communicative complexity of ape gestures is indeed impressive and arguments for language origins are persuasive, a growing body of research indicates that the assumption of vocal communication being cognitively uninteresting is rather inaccurate. Studies of vocal communication from the signaller's and particularly the receiver's perspective have indicated considerably greater levels of sophistication than have been previously assumed (e.g. Seyfarth et al., 2010). Nevertheless, the debate is ongoing and this is partly because it is still unclear what psychological mechanisms underlie vocal communication.

The role that arousal appears to play in vocal production is often used as a basis for the argument against underlying cognitive sophistication. For example, Owren and Rendall (2001) argue that vocalisations are essentially motivational signals that have evolved to induce 'nervous system-induced responses' in the receiver. They particularly argue this hypothesis for calls with evolutionary-urgent functions, such as alarm or distress (Rendall et al., 2009). For example, they argue that primate screams exhibit acoustic properties, such as sharp onsets and large fluctuations in frequency and amplitude, which are likely to have strong effects on a receiver's nervous system. However, whilst such vocalisations may indeed contain arousing or aversive acoustic properties, empirical studies have also demonstrated that listeners can extract considerable information from these calls and are not simply passive recipients, swept away in a wave of emotions. For example, primate screams have been shown to convey information to receivers about different types of aggression (Gouzoules et al., 1984; Slocombe & Zuberbühler, 2007), the social role of the caller (Slocombe & Zuberbühler, 2005a; Slocombe et al., 2010a) and the caller's identity (Hammerschmidt & Fischer, 1998). Furthermore, primate screams can also be modified by the presence of some audiences (Slocombe & Zuberbühler, 2007). The range of information transmitted by primate screams is further highlighted by evidence from playback experiments, showing that individuals respond differently to the same screams, depending on its acoustic variant or accompanying context (Fischer, 2004; Gouzoules et al., 1984; Palombit et al., 1997; Slocombe et al., 2009). Thus, whilst arousal clearly plays a key role in animal vocal communication (e.g. Bickerton, 1990), arousal does not, by itself, explain animal vocal complexity, from neither the signallers' nor the receivers' perspectives (Seyfarth et al., 2010).

Referential communication

Referential communication is said to be a key milestone in the evolution of semantic communication, one of the core properties of human language. The term 'reference' is borrowed from linguistics (O'Grady' et al., 1997) and is used to describe signals which come to refer to an object or event in the external world. Kripke (1977) distinguished two main forms of reference: that of 'speaker' reference and 'semantic' reference. Semantic reference is defined as 'what the speaker's words meant, on a given occasion' and speaker reference being 'what the speaker actually meant, on that particular occasion' (Kripke, 1977, following Grice, 1969). Kripke (1977) illustrates the differences between semantic and speaker reference in the following imaginary scenario: at the end of a burglary, one burglar says to his accomplice: "The cops are around the corner". In terms of semantic reference, these words mean that the police were around the corner. However, in terms of speaker reference, the speaker may well have actually meant: 'We can't wait around anymore collecting more goods, we need to go!'. One major difference between these two forms of reference is the level of communicative intention instilled in the signal. Signals with semantic reference do not require communicative intention and can serve to provide context-independent, unambiguous facts or information about something in the external world. In contrast to semantic reference, speaker reference is context-dependent and potentially ambiguous, requiring the signaller to instil their communicative intentions into the receiver, on a particular occasion (Grice, 1961, 1969; Kripke, 1977). The intentional act of communicating in order to change the mental states of the receiver is thought to be one of the major dividing factors between human and animal communication, above all, in the vocal domain (Tomasello, 1999; 2008; Tomasello & Rakoczy, 2003).

The notion of intentional signalling also forms an integral part of reference within the domain of gestural communication (Tomasello, 2008). Referential gestures fall within the concept of 'speaker reference' (Kripke, 1977) and represent a common feature of human communication (McNeill, 1992). Referential gestures are used as a means to either refer the attention of the receiver to an object or place in their environment (deictically), or refer their imagination to something that typically is not in their immediate environment, by a behaviour simulating an action, relation, or object (Kendon, 2004; Tomasello, 2008). One of the first developmental milestones in human communication is considered to be the emergence of the 'point' in human infants (Tomasello et al., 2007). From a cognitive perspective, the developmental onset of referential gestures is significant as it indicates that children are motivated to establish common-ground with others, share their thoughts and intentions, as well as attribute mental states (Liszkowski, 2005, Liszkowski et al., 2006; Tomasello et al., 2005, 2007).

Among non-human primates, referential gestures have been identified in captive chimpanzees (*Pan troglodytes*) during their interactions with human experimenters (Leavens et al., 2004), as well as in individuals of all four species of great apes that have been language-trained or raised in human environments (Gardner & Gardner, 1969; Miles, 1990; Patterson, 1978; Savage-Rumbaugh & Lewin, 1994). Evidence for referential gestures in wild chimpanzees has been demonstrated by Pika and Mitani (2006) in their work on the 'directed scratch'. The 'directed scratch' is used by the groomee to direct the attention of their groomer to the site they desire to be groomed.

Within the vocal domain, observational and experimental studies of numerous primate species have revealed that certain calls can function as referential labels for external objects or events in the environment (e.g. Hauser, 1998; Seyfarth et al., 1980; Slocombe & Zuberbühler, 2005b; Zuberbühler, 2000; Zuberbühler et al., 1999b). However, in contrast to the notion of reference as an 'intentional act' in human communication and ape referential gestures, referential vocalisations do not, for the most part, appear to be produced intentionally, as a means to inform the receiver, and may be by-products of other processes (Seyfarth & Cheney, 2003a). In this sense, referential vocal communication in animals represents a form of Kripke's (1977) 'semantic reference'.

In order to account for the differences between referential communication in non-human animals and the notion of 'reference' in the human, linguistic sense, Macedonia and Evans (1993) developed the term 'functionally referential communication'. Functionally referential signals are defined as signals that refer to an object or event in the external world, to the extent that the production of the signal elicits the same adaptive response in the receiver as if they had actually experienced the original eliciting stimuli themselves (Evans, 1997; Macedonia & Evans, 1993). The term 'functional' deals with the fact that although animals may produce calls which appear to function to refer to objects or events in the external world, the psychological processes which underlie call production in animals are still poorly understood. Functionally referential vocalisations have aroused considerable interest and debate owing to their implications for the evolution of symbolic communication and language (e.g. Scarantino, 2010), as well as for the indication that some aspects of animal communication may be conceptually-driven (Cheney & Seyfarth, 1990; Zuberbühler et al., 1999b).

In order to be classified as referential, Macedonia and Evans (1993) provided three production and perception criteria that must be demonstrated. First, the signal must possess a discrete acoustic structure. Second, the signal must elicit the appropriate receiver response, independent of context. Third, there must be production specificity, that is to say, a tight relationship between signal production and eliciting stimuli. In this sense, signal X may functionally refer to Y when (1) X is reliably elicited by Y (production criterion) and (2) the production of X reliably results in responses in the receiver specifically adapted for dealing with Y (perception criterion) (Evans 1997; Marler et al., 1992; Seyfarth et al., 1980).

Following this definition, functionally referential vocalisations have been identified in numerous primate species (e.g. Zuberbühler, 2003, 2009), although they have also been demonstrated in other animal and bird species, such as chickens (*Gallus gallus*, Evans & Evans, 1999; Evans & Marler, 1994), ravens (*Corvus crovax,* Bugnyar et al., 2001), chickadees (*Poecile atricapillus,* Templeton et al., 2005) and meerkats (*Suricatta suricatta*, Manser et al., 2001). Many functionally referential vocalisations have been described in the alarm context (see Zuberbühler, 2003, 2009) although they have also been reported in other contexts, such as food discovery (e.g. Bugnyar et al., 2001; Di Bitetti, 2003; Evans & Evans, 1999; Kitzmann & Caine, 2009) and in social situations (Gouzoules et al., 1984; Gouzoules et al., 1998; Slocombe & Zuberbühler, 2005a). For example, the food-associated calls of domestic chickens fulfil the three criteria for functional reference (Evans & Evans, 1999, 2007). Chicken food calls are produced specifically within the feeding context, have an acoustically distinct structure, and playback experiments have demonstrated that they elicit specific feeding behaviours in receivers in the absence of other stimuli.

The seminal example of functionally referential communication is the alarm-calling system of vervet monkeys, *Cercopithecus aethiops* (Seyfarth et al., 1980; Struhsaker, 1967). Vervet monkeys produce acoustically distinct calls to their three principal predators: raptors, large mammalian carnivores and snakes (Struhsaker, 1967). Upon sounding these calls, vervets quickly make the evasive action that appropriately counters the hunting tactics of the predator (e.g. receivers of calls to eagles run out of trees, receivers of calls to leopards run up trees and receivers of snake calls stand up tall). A playback study demonstrated that recipients of alarm-calls receive enough information from the calls to respond with the appropriate predator avoidance behaviour, in the absence of the actual predator (Seyfarth et al., 1980). Since this discovery, referential alarm call systems have been identified in a number of primate species (e.g. Diana monkeys, *Cercopithecus diana*, Zuberbühler et al., 1999b, Zuberbühler, 2000; Campbell's monkeys *Cercopithecus campbelli*, Zuberbühler, 2001; ring-tailed lemurs, *Lemur catta*; Macedonia, 1990; Pereira & Macedonia, 1991) as well as in other mammals, including ground squirrels, *Spermophilius richardsonii*, (Hare, 1998; Sloan et al., 2005; Warkentin et al., 2001), marmots, *Marmota flaviventris* (Blumstein, 1995) and meerkats (Manser et al., 2001).

One question relating to the production of functionally referential signals is whether receivers are attending to the meaning of the call or just its acoustic properties. This question was investigated by Zuberbühler and colleagues (1999b) with Diana monkeys. Diana monkeys produce acoustically distinct alarm calls to their two main predators, eagles and leopards (Zuberbühler et al., 1997). In the experiment, subjects heard sequences of typical calls of leopards (*Panthera pardus*) or eagles (*Stephanoaetus coronatus*) followed by the alarm calls of male Diana monkeys responding to either of these predators. In each trial, subjects heard two calls, a ‘prime’ followed by a ‘probe’, which were separated by five minutes of silence. The two calls either shared the same acoustic and semantic features (e.g. eagle shriek followed by eagle shriek) or only shared semantic features (i.e. monkey alarm call to an eagle followed by eagle shriek). Results indicated that the semantic features, rather than the acoustic features of the ‘prime’ stimuli alone, explained the receivers’ responses to the probe stimuli, suggesting that receivers attended to the call’s meaning rather than its acoustic properties alone (Zuberbühler et al., 1999b).

Among the apes, functionally referential vocalisations have thus far only been demonstrated in chimpanzees. The work of Slocombe and colleagues has demonstrated the presence of referentially specific vocalisations in the contexts of food discovery (Slocombe & Zuberbühler 2005b, 2006), as well as during agonistic interactions (Slocombe & Zuberbühler, 2005a, 2007). During agonistic encounters, victims and aggressors produce screams which are acoustically distinct from one another, with victim screams also coding information concerning the level of intensity of the attack. Subsequent playback studies have demonstrated that listeners not only acquire information about the level of attack (Slocombe et al., 2009) but also about the social role that the screamer has taken (Slocombe et al., 2010a).

Call combinations

Beyond the individual call unit, more recent studies have highlighted the role that call combinations play in primate vocalisations. These studies have revealed that several primate species are able to modify the structure of call sequences in a way that alters the information conveyed to receivers (e.g. Campbell’s monkeys, *Cercopithecus campbelli*, Ouattara et al., 2009a, b; putty-nosed monkeys, *Cercopithecus nictitans*, Arnold & Zuberbühler 2006a, b, 2008; gibbons, *Hylobates lar*, Clarke et al., 2006). For instance, male putty-nosed monkeys produce two acoustically distinct alarm call types (‘pyows’ and ‘hacks’) mainly in response to leopards and eagles respectively

(Arnold & Zuberbühler, 2006a). As well as producing these calls singly or in homogeneous call sequences, males also regularly combine these two calls together into ‘pyow-hack’ sequences. Subsequent playback experiments have demonstrated that hearing pyow-hack sequences triggers group movement in the receivers, indicating that combining the two calls together changes the information conveyed to receivers. In Campbell’s monkeys, Ouattara and colleagues (2009a) have shown that males regularly combine different call types into at least nine context-specific call sequences. In the alarm calling context alone, males were shown to produce four different stereo-typed call sequences to crowned eagles and three to leopards, depending on how the caller learned about the predator’s presence.

Whilst changing the composition of call sequences may represent one means to alter what information is conveyed, other primates appear to have evolved more probabilistic calling systems, where modifying the relative quantities of a call type changes the semantic content of the longer sequence. For example, in two species of Colobus monkey (*Colobus polykomos* and *C. guereza*), individuals produce two different alarm call types in response to both leopards and eagles (Schel et al., 2009). However, although both call types are produced in both predator contexts, changes in call numerosity and the structure of call phrases has been shown to relate to a range of information about the event, such as predator type, response-urgency, or the caller’s imminent behaviour (Schel et al., 2009). Subsequent playback experiments have confirmed that changes in the probabilistic structure of Colobus alarm calls provide meaningful information to listeners (Schel et al., 2010)

Currently, evidence for the use of call combinations in apes is relatively weak. In a study of gibbon song, Clarke and colleagues (2006) compared predator-induced and normal songs, and found that predator-induced songs contained the same repertoire as normal songs, but that there were reliable differences in the way call notes were combined together within songs. Although relevant playbacks still need to be conducted, observations of the responses of neighbouring individuals have indicated that these call sequences may be meaningful to them as they often responded with their own matching song type (Clarke et al., 2006). In wild chimpanzees, Crockford and Boesch (2005) demonstrated the prolific use of call combinations across a multitude of different contexts. In this analysis, the authors investigated the types of combinations, the contexts they were produced in, and their possible functions in comparison to single calls. They found that almost half of all calls were produced in combination with others, documenting a total of 88 different call combination types. Furthermore, the contexts eliciting call combinations differed in five different ways relative to those eliciting the component calls. For example, some calls appeared to have an additive function, enabling more than one piece of information to be conveyed simultaneously. In another manner, combining calls together appeared to create a new meaning beyond that of its component calls. Whilst more research is needed, this study highlighted the considerable potential for vocal complexity in the use of call combinations in apes. Ultimately, playback experiments are required to demonstrate that the way calls are combined together is meaningful to receivers.

Vocal communication and audience effects

Recent advances in our understanding of audience effects in animal communication have started to challenge the notion that vocalisations are hard-wired, motivational responses that lack production flexibility (e.g. Tomasello, 2008). The term 'audience effect' refers to the manner in which signaller's output is modified by the presence of other individuals in the audience (Zuberbühler, 2008). Audience effects are interesting because they indicate that, at some level, signallers are sensitive to the presence of others. Furthermore, they can also indicate that signallers may be capable of directing their vocalisations at others, potentially altering the behaviour of receivers in strategic ways. In the domestic chicken, the production of food-associated calls by males is strongly influenced by the presence and composition of their audience. In a series of studies, it was demonstrated that males preferentially produce food-associated calls in the presence of females, but not males, even sometimes in the absence of food (Evans & Marler, 1994; Marler et al., 1986). The production of food-associated calls was interpreted as a strategic courtship display, produced specifically to attract potential mates, one of the first examples of tactical deception documented in animal communication (Hauser, 1997).

Audience effects have been demonstrated in a range of animals and birds, including primate species. Male Thomas langurs (*Presbytis thomasi)* show an exceptional level of audience awareness by continuing to produce alarm calls to a model tiger until every single individual in the entire group has replied with at least one alarm call (Wich & de Vries, 2006). In chimpanzees, victims of agonistic attacks exaggerate recruitment screams when potential allies are in the audience (Slocombe & Zuberbühler, 2007). This result suggested that chimpanzees may be strategically modifying their vocal production to maximise chances of eliciting support. Whether such calls are actually intentional is a matter of considerable debate and certainly requires further empirical attention.

Food-associated calls

Numerous bird and mammal species produce distinct vocalisations upon the discovery of food. Typically, these calls attract other group members to the food source and thus appear to play a role in social recruitment (Wilkinson & Boughman, 1998). The production of food-associated calls is especially common in social species that aggregate together at common nesting and feeding sites. Among bird species, socially flocking house sparrows (*Passer domesticus*) and ravens (*Corvus corax*) produce food-associated calls that attract conspecifics to the food source (Elgar, 1986b; Heinrich & Marzluff, 1991). Socially foraging cliff swallows (*Hirundo pyrrhonota*) produce an acoustically distinct ‘squeak’ call that is only used when food is discovered and serves to recruit conspecifics to the food source (Brown et al., 1991). In Carolina chickadees (*Poecile carolinensis*), individuals vary the acoustic structure of their food-associated calls depending on whether a conspecific has joined them to feed. Subsequent playbacks revealed that their food-associated calls attract more foragers than other types of calls given by individuals joining the caller (Mahurin & Freeberg, 2009).

The production of food-associated calls is particularly widespread in primates. Food-associated calls have been described in numerous species of capuchins (e.g. white-faced capuchins, *Cebus capucinus*, Boinski & Campbell, 1996; tufted capuchins, *Cebus apella nigritus*, Di Bitetti 2003), macaques (e.g. Toque macaques, *Macaca sinica*, Dittus, 1984; rhesus macaques, *Macaca mulatta,* Hauser et al., 1993a, b), tamarins (e.g. golden-lion tamarins, *Leontopithecus rosalia*, Benz et al., 1992), as well as spider monkeys (*Ateles geoffroyi*, Chapman & Lefebvre, 1990), marmosets (*Callithrix geoffroyi*, Kitzmann & Caine, 2009) and chimpanzees (Slocombe & Zuberbühler, 2005b).

In terms of function, the production of a signal that attracts potential foraging competitors to the caller's feeding site seems somewhat paradoxical. However, for a signal to evolve, especially one apparently so prevalent in the animal kingdom, the benefits to call production must ultimately outweigh the costs. Indeed, results from studies on a range of different species have indicated that there may be various benefits to attracting foraging conspecifics. In terms of direct foraging benefits, recruiting conspecifics to the feeding source may serve to decrease risks of predation, either by dilution or increased vigilance (Caine et al., 1995; Elgar 1986b; Newman & Caraco 1989). This appears to be especially important for socially foraging birds, which are particularly vulnerable to predation. Attracting conspecifics may also benefit the forager in terms of manipulation of the food patch. For example, in colonially nesting cliff swallows (*Hirundo pyrrhonota)*, that feed on insect swarms, attracting more foragers may increase the chance of the insects' movements being tracked (Brown et al., 1991). As a consequence, the signaller may accrue the benefit of being able to exploit the same insect swarm for longer than if they were foraging alone. In other species, callers may receive foraging benefits by recruiting foragers who can assist in the cooperative defence of resources (Heinrich & Marzluff, 1991; Marzluff & Heinrich, 1991; Wilkinson & Boughman, 1998).

In addition to foraging benefits, signallers may receive other social and reproductive rewards by attracting conspecifics to the food source. As described, male chickens call more in the presence of females, something thought to be part of a courtship display to attract potential mates (Evans & Marler 1994; Marler et al., 1986). Likewise, in bonobos (*Pan paniscus*), the production of food-associated calls by males has been shown to attract females to the food source, who subsequently engage in copulations with them (van Krunkelsven et al., 1996). Reproductive benefits may also work at the level of maintaining an association with long-term mating partners. For instance, Pinyon jays (*Gymnorhinus cyanocephalus*) are sensitive to the presence of an audience and call more when their long-term mate is present compared to non-mates (Dahlin et al., 2005).

As well as gaining direct reproductive benefits, signallers may also receive indirect benefits, through kin selection, by alerting kin to a food patch (Hauser & Marler, 1993a; Judd & Sherman, 1996). In brown capuchins (*Cebus apella*), for example, individuals call more for larger audiences containing kin compared to non-kin (Pollick et al., 2005). However, audience effects are not always solely restricted to the presence of kin members or mating partners. In wild tufted capuchins, individuals vary the latency to call as a function of the proximity of other group members (Di Bitetti, 2005). In a recent study of wild male chimpanzees (Slocombe et al., 2010b), males were shown to be sensitive to the composition of their audience, calling more and recommencing calling upon the arrival of their long-term allies. It was suggested that the enhanced production of food-calls in the presence of long-term allies may strengthen affiliative ties with coalition partners.

Whilst attracting conspecifics appears to be the main function of food-associated calls, there may be other factors underlying call production. For example, it was shown that rhesus macaques are less likely to receive aggression from higher-ranked individuals if they announce their food discovery, rather than remaining silent (Hauser & Marler, 1993b). It was concluded that these calls may therefore announce food ownership as a means to reduce threats of punishment from higher-ranked individuals (Hauser, 1992; Hauser & Marler 1993b). In white-faced capuchins, the production of food-associated calls regulates spacing between foragers, thereby decreasing foraging competition (Boinksi & Campbell, 1996). In addition, a subsequent study of the same species, involving naturalistic observations and food placement experiments (Gros-Louis, 2004a), revealed that callers were less likely to be approached or receive aggression than non-callers, suggesting that calls may also serve to announce ownership and thus to decrease aggression from other individuals.

Informational content of food-associated calls

Beyond their functional significance, food-associated calls represent promising candidates for investigating the information conveyed in animal signals. As shown previously, research across a variety of species has revealed that food-associated calls provide different kinds of information about the food encountered by the caller. This may be in terms of food presence (Kitzmann & Caine, 2009), quality (Benz et al., 1992; Elowson et al., 1991; Gros-Louis, 2004b; Roush & Snowdon, 2000), divisibility (Hauser et al., 1993a) and quantity (Caine et al., 1995). In some studies, hearing food calls attracts conspecifics to the food or playback source, indicating that these calls are meaningful to them. Tufted capuchins approach a speaker more rapidly and directly when food-associated calls are played compared to when played a control stimulus (Di Bitetti, 2005). Cotton-top tamarins (*Saguinus oedipus*), that are not given food themselves, vocalise in response to food calls of their feeding mate, irrespective of whether the food or mate is itself visible (Roush & Snowdon, 2000). Furthermore, in marmosets, playing back food calls elicits an increase in foraging and feeding, indicating that these calls provide information about food presence itself (Kitzmann & Caine, 2009).

In several monkey species, individuals have been shown to vary the rates of food-associated vocalisations in a way that provides information about the quality and quantity of food (e.g. golden lion tamarins, Benz et al., 1992; Benz, 1993; cotton-top tamarins, Roush & Snowdon, 2000; Elowson et al., 1991; white-faced capuchins, Gros-Louis, 2004a, b and red-bellied tamarins, *Saguinus labiatus*, Caine et al., 1995).

Variation at the level of the calls' acoustic morphology may also code information regarding the food encountered by the signaller. This has so far been demonstrated in the food calls of rhesus macaques (Hauser & Marler, 1993a) and chimpanzees (Slocombe & Zuberbühler, 2006). Systematic analysis has revealed that chimpanzee 'rough grunts' provide semantic information about the signaller's preference for the food (Slocombe & Zuberbühler, 2006). In a naturalistic playback experiment, a focal chimpanzee was shown to use information provided in the food-associated 'rough grunts' of other group members to successfully locate the food item associated with their calls (Slocombe & Zuberbühler, 2005b).

Copulation calls

Another promising topic for investigating animal vocal complexity is the study of vocalisations produced during mating events. Numerous birds and mammals produce vocalisations in association with this context. In some species, females emit vocalisations known as ‘oestrous calls’. Oestrous calls may be produced across a female’s phase of sexual receptivity, in a range of contexts, rather than being tied to the copulation event specifically (e.g. woolly spider monkeys, *Brachyteles arachnoids*, Milton, 1985; lion-tailed macaques, *Macaca silenus*, Lindburg 1990; gelada baboons, *Theropithecus gelada*, Moos-Heilen & Sossinka 1990; see Montgomerie & Thornhill, 1989, for other mammals and birds). For example, in a study of pig-tailed macaques (*Macaca nemestrina*) only 19% of female oestrous calls were produced during copulations, and although 26% were produced within 30 seconds of the copulation, 55% were produced in other contexts (Gouzoules et al., 1998).

In contrast to oestrous calls, some species produce distinct vocalisations, known as ‘copulation calls’, which are restricted purely to the mating event itself (e.g. African elephants, *Loxodonta africana*, Poole et al., 1988; lions, *Panthera leo*, Schaller, 1972; elephant seals, *Mirounga angustirostris*, Cox & LeBouef, 1977). Copulation calls may occur at onset, during and immediately after copulation, although they most typically occur during the latter stage of the copulation (Gouzoules et al., 1998; Hamilton & Arrowood 1978; Hohmann & Herzog 1985; O’Connell & Cowlishaw 1994). In some species, copulation calls are produced by the male, that may call alone or be accompanied by the female (e.g. rhesus macaques, *Macaca mulatta*, Hauser, 1993; little brown bat, *Myotis lucifugus*, Barclay et al., 1979), although in most species, it is more commonly the female that calls.

Female copulation calls are especially prevalent amongst Old-World primates (Pradhan et al., 2006, see table 1.1), particularly for species with multi-male and multi-female groups, where females are promiscuous and advertise receptivity with pronounced sexual swellings (Dixson, 1998). Although generally loud and conspicuous, there is considerable variation in the acoustic structure of copulation calls across species. For example, in baboon (*Papio* sp.) and macaque (*Macaca* sp.) species, copulation calls tend to be low-pitched ‘grunt-like’ vocalisations, whereas in chimpanzees (*Pan troglodytes*) and talapoin monkeys (*Miopithecus talapoin*), copulation calls tend to be high-pitched series of screams and squeaks (e.g. Dixson, 1998).

Table 1.1. Review of primate species in which copulation calls have been described.

Species	Common name	Calling sex	Reference
1. *Miopithecus talapoin*	Talapoin monkey	Both	Gautier (1974)
2. *Cheirogaleus medius*	Fat-tailed dwarf lemur	Female	van Schaik et al. (1999)
3. *Tarsius bancanus*	Bornean tarsier	Female	van Schaik et al. (1999)
4. *Cercopithecus mona*	Mona monkey	Female	Glenn et al. (2004)
5. *Cercopithecus solatus*	Sun-tailed monkey	Unsure	Gautier (1988)
6 *Cebus apella*	Brown capuchin	Female	van Schaik et al. (1999)
7. *Chirpotes spp*	Bearded saki	Female	van Schaik et al. (1999)
8. *Macaca sylvanus*	Barbary macaque	Female	Paul (1989)
9. *Macaca fascicularis*	Long-tailed macaque	Both	Deputte & Goustard (1980)
10. *Macaca nemestrina*	Pig-tailed macaque	Female	Gouzoules et al.(1998)
11. *Macaca mulatta*	Rhesus macaque	Male	Hauser (1993)
12. *Macaca tonkeana*	Tonkean macaque	Female	Aujard et al. (1998)
13. *Macaca radiata*	Bonnet macaque	Both	Hohmann (1989)
14. *Macaca silenus*	Lion-tailed macaque	Female	Hohmann & Herzog (1985)
15. *Macaca cyclopsis*	Formosoan macaque	Both	Hsu et al. (2002)
16. *Macaca thibetana*	Tibetan macaque	Both	Zhao (1993)
17. *Colobus badius*	Red Colobus	Female	van Schaik et al. (1999)
18. *Cercocebus atys*	Sooty mangabey	Female	Gouzoules et al. (1998)
19. *Cercocebus albigena*	Grey-cheeked mangabey	Female	Chalmers (1968)
20. *Cercocebus torquatus*	Collared mangabey	Female	van Schaik et al. (1999)
21. *Cercocebus galeritus*	Tana river mangabey	Female	Dixson (1983)
22. *Cercocebus sanjei*	Sanje mangabey	Female	Mwende & Dixson (unpub.)
23. *Papio cynocephalus*	Yellow baboon	Female	Semple (2001)
24. *Papio hamadryas ursinus*	Chacma baboon	Both	Hall & DeVore (1965)
25. *Papio anubis*	Olive baboon	Female	Hall & DeVore (1965)
26. *Papio papio*	Guinea baboon	Female	Maestripieri et al. (2005)
27. *Hylobates hoolock*	Gibbon	Both	Hamilton & Arrowood (1978)
28. *Gorilla g. berengei*	Gorilla	Both	Byrne & Whiten (1990)
29. *Pan troglodytes*	Chimpanzee	Female	Hauser (1990)
30. *Pan paniscus*	Bonobo	Female	Thompson-Handler et al. (1984).

Functionally, copulation calls may promote the caller's reproductive success via a number of different mechanisms (table 1.2). Principally, copulation calls appear to advertise the reproductive state or sexual receptivity of the female caller (Aich et al., 1990; Engelhardt et al., 2004; Gust et al., 1990, Semple & McComb, 2000). For example, in long-tailed macaques (*Macaca fascicularis*), playback experiments have indicated that in addition to sexual swellings and pheromones, copulation calls represent useful cues for males to assess female reproductive status (Engelhardt et al., 2004). Hohmann & Herzog (1985) proposed that females use copulation calls to advertise receptivity to other females, as a means to inhibit breeding synchrony. This followed from evidence that in their study group of long-tailed macaques, only one female came into oestrous and copulated at any one time. However, most studies of other species have indicated that multiple females can be sexually receptive and produce copulation calls simultaneously (Pradhan et al., 2006). Thus, for most primates, it is more likely that copulation calls advertise receptivity to potential mates (Semple, 1998). By attracting the attention of potential mating partners, a female may accrue both direct and indirect benefits of mate choice. In this way, copulation calls may incite male-male competition, either directly, via physical competition between males (Cox & LeBoeuf, 1977), or indirectly, through sperm competition (Harcourt et al., 1981; O'Connell & Cowlishaw, 1994). By promoting sperm competition, a female may achieve reproductive benefits by increasing the probability of being fertilised by the best sperm or the most compatible genotype (O'Connell & Cowlishaw, 1994).

Table 1.2. Current hypotheses concerning the functional significance of primate copulation calls (adapted from Maestripieri & Roney, 2005 and Pradhan et al., 2006).

Hypothesis	Theme	Functional significance	Ref’
1	Non-adaptive	Non-adaptive by-product of sexual stimulation	1
2		Non-adaptive behaviour, under phylogenetic inertia	2
3	Stimulates ovulation/ orgasm	Self-stimulation of female ovulation	3-4
4		Facilitates synchronised male & female orgasm	1
5		Strengthening pair bond	1
6	Female-directed advertisement of reproductive state /receptivity	Advertise to other females to inhibit breeding synchrony	5-6
7		Advertise to other females to promote breeding synchrony	4
8		Advertises male presence to reduce female harassment	7
9	Male-directed advertisement: sperm competition, parental investment & protection from infanticide	Incites male-male competition (direct)	8
10		Honest advertisement of female reproductive status	9
11		Honest advertisement of receptivity by low-rank females	10
12		Incites sperm competition for sons to inherit ‘best’ sperm	7
13		Incites sperm competition to promote paternity uncertainty & protection from infanticide	7
14		Promotes paternity certainty to promote mate guarding & protection from infanticide	11
15		Promotes paternity certainty to promote parental investment	2

[1] Hamilton & Arrowood, 1978; [2] Henzi, 1996; [3] Cheng, 1992; [4] Semple, 1998; [5] Viljoen, 1977; [6] Hohmann & Herzog, 1985; [7] O’Connell & Cowlishaw, 1994; [8] Cox & LeBoeuf, 1977; [9] Aich et al., 1990; [10] Gouzoules et al., 1998; [11] Todt et al., 1995

Producing copulation calls to promote sperm competition and polyandrous mating may also serve as a behavioural counter-strategy to minimise risks of infanticide (Pradhan et al., 2006). This may be achieved both by promoting paternity uncertainty amongst potentially infanticidal males, or by enhancing mate guarding in the consort male (O’Connell & Cowlishaw 1994). Promoting mate guarding in the consort male is consistent with the common finding that females are more likely to call with dominant males, the most likely perpetrators as well as defenders against infanticides by other males (e.g. Tuomi et al., 1997). Risk of infanticide is a significant threat for females of many species and appears to be an especially relevant selective force in the evolution of female behavioural strategies in primates (Steenbeeck et al., 1999; Sterck et al., 2005; van Schaik, 2000). In chimpanzees, females are vulnerable to infanticide by both males (e.g. Goodall, 1986; Muller et al., 2007) and females (Pusey et al., 2008; Townsend et al., 2007). Therefore, by confusing paternity through copulation calling, a female may increase her chances of gaining support from a male, especially during agonistic and infanticidal encounters.

Informational content of copulation calls

Research on several primate species has indicated that copulation calls have the potential to convey a considerable amount of information to listeners. Furthermore, there is evidence that this information can influence their subsequent mating decisions and social behaviour. In Barbary macaques (*Macaca sylvanus*), female copulation calls have been shown to convey reliable information about caller identity (Deputte & Goustard, 1980). The encoding of caller identity has also been demonstrated in yellow baboon copulation calls (*Papio cynocephalus*), where it was also subsequently confirmed by playback experiments (Semple, 2001). By alerting males to her presence, a female may attract potential mates, which may serve to incite male-male competition and promote indirect mate choice (i.e. by increasing the quality or quantity of partners). This could be an especially useful strategy for species where more than one female is cycling simultaneously (Altmann et al., 1996). In addition to female identity, Semple and colleagues (2002) showed that the acoustic structure of yellow baboon copulation calls co-varied with the rank of their male partner, as well as the size of her sexual swelling (an approximate cue to her fertility status, e.g. Nunn, 1999). Similar effects of identity and partner rank have also been demonstrated in chimpanzees, although more precise hormonal analysis revealed that copulation calls were not a reliable indicator of ovulation (Townsend, 2009; Townsend et al., 2008).

Likewise, although the acoustic structure of Barbary macaque copulation has been shown to provide cues to sexual swelling size (Semple & McComb, 2000), accompanying hormonal analyses using faecal and urine samples (Deschner et al., 2003; 2004; Heistermann et al., 2008) have revealed that these calls do not reliably indicate the point of ovulation (Pfefferle et al., 2008a). However, the acoustic structure of copulation calls was shown to co-vary with the occurrence of ejaculation (Pfefferle et al., 2008a). This was confirmed in playback experiments, which demonstrated that male subjects discriminated ejaculatory from non-ejaculatory matings and adjusted their subsequent decisions to approach the female to mate (Pfefferle et al., 2008b). By providing information about the success of the last copulation as well as the rank of the male partner, potential mates may be able to acquire useful information that influences and promotes a more successful mating strategy (Semple et al., 2002).

Like their close relatives, the chimpanzees, bonobo females also produce copulation calls (Kano, 1992; Thompson-Handler et al., 1984). In bonobos, copulation calls consist of a single or succession of high-frequency squeaks and screams that usually begin during the copulation (Kano, 1992; Thompson-Handler et al., 1984). Bonobo copulation calls are described as distinctive and conspicuously loud, two features which suggest that these calls are advertising a female’s sexual receptivity to bystanders other than just the male in question. In addition to the standard reproductive context of male copulation, bonobo females also produce vocalisations with female partners (Hohmann & Fruth, 2000; Kano, 1992; Thompson-Handler et al., 1984). The production of copulation calls in purely social contexts is not well explained by current hypotheses, which solely focus on their reproductive significance. Whilst bonobos therefore represent an interesting species for studying copulation calling, there are unfortunately no studies exploring the reproductive and behavioural patterns associated with these calls, nor the possible variations in acoustic structure. This provides a key motivation for two of the studies presented in this thesis.

In conclusion, a growing body of evidence from a breadth of studies highlights the considerable complexity possible within animal vocal systems, especially among primates. In particular, the presence of functionally referential communication, call combinations and audience effects indicates sophisticated levels of underlying cognition. Thus, although primate vocal communication is certainly different to human language, evidence of rudimentary forms of semanticity, as well as other capacities, such as syntax and audience sensitivity, may highlight the evolutionary foundations of human communication within the primate lineage.

Chapter two: Introduction to the study species - the bonobo

Summary

In this chapter, I introduce my study species, the bonobo (*Pan paniscus*). This chapter provides a backdrop to my research on their vocal behaviour, the main topic of my thesis. For many, bonobos represent one of the least well understood of the great apes, thus I provide a comprehensive review about what is currently known about their ecology, social system and behaviour. I examine their socio-sexual behaviour in some detail, as this represents one of the defining features of bonobo social behaviour and also forms the foundation for the scientific rationale for my studies of bonobo copulation calls. I explore what is currently known about bonobo vocal communication, from both a gestural and vocal perspective. I also examine what has been learned about the representational and communicative skills of bonobos based on studies of language-trained individuals. To conclude, I argue that although considerable progress has been made investigating bonobo ecology and social behaviour, current knowledge is still very limited concerning their natural use of communicative signals, particularly in the vocal domain.

Morphology, demographics and socio-ecology

Bonobos (*Pan paniscus*) are a species of great ape, endemic to the equatorial forests of the Democratic Republic of Congo. Bonobos are part of the genus *Pan*, which is composed of the bonobo and three genetically distinct subspecies of chimpanzee: the central (*Pan troglodytes troglodytes*), eastern (*Pan t. schweinfurthii*) and western (*Pan t. verus*) chimpanzees (Becquet et al., 2007; Groves, 2001; Hill, 1969). Chimpanzees and bonobos represent our closest living relatives, sharing approximately 99.4% of their genetic makeup with humans (Wildman et al., 2003). Whilst more attention has been typically focused on the cognitive and communicative capacities of the chimpanzee, an understanding of both *Pan* species is needed in order to construct a balanced model of human evolution (e.g. de Waal, 1997).

Bonobos are morphologically similar to chimpanzees and to the untrained eye, it is often difficult to tell them apart. Although of similar height to some subspecies of chimpanzee (73-80cm), bonobos are considerably more slender (Wrangham, 1985) and tend to have blacker hair and faces, as well as paler coloured lips (de Waal, 1997). Like chimpanzees, sexual dimorphism is low in bonobos, with captive males weighing an average of 43.0 kg and females 37.0 kg (Parish, 1994). Due to their superficial morphological similarities, bonobos were considered to be a sub-species of chimpanzee for many years. However, following more extensive anatomical analyses by Coolidge in 1933, bonobos were eventually granted the status of being a distinct species in their own right. Subsequent morphological, behavioural and genetic analyses have confirmed this view, with current estimations of the split between bonobos and chimpanzees occurring more recently than was previously assumed, at around 0.9 million years ago (Won & Hey, 2005). Recent genetic analyses, using micro-satellite techniques, have again strongly supported the genetic subdivision of bonobos from other species of chimpanzee, as well as highlighting clear genetic differences between the three chimpanzee subspecies (Becquet et al., 2007).

Bonobos occupy the Cuvette Centrale region of northern DR Congo, an area bordered by four rivers: the Congo, Lualuba, Kasai and Sankuru Rivers (Audenaerde, 1984; Thompson-Handler et al., 1995, see fig. 2.1). This area, occupying approximately 800 000 km^2, is classified as primary and secondary lowland tropical forest and is composed of four principal types of vegetation: rainforest, dry forest, swamp forest and disturbed forest (Hashimoto et al., 1998). Although bonobos are principally thought to inhabit these dense tropical forest habitats, recent studies in the Lukuru region, in the Southern part of their range area, have revealed that bonobos also occupy forest mosaics and savannah lands (Myers-Thompson, 2002). In these areas, Myers-Thompson reported numerous behavioural differences, such as an increase in bipedalism (Myers-Thompson, 2002). Such studies highlight the behavioural and ecological flexibility that bonobos, like chimpanzees, possess (Boesch et al., 2002).

Figure 2.1 Map illustrating the bonobo range within the DR Congo, Africa (created by Christopher Auger for Bonobo Conservation Initiative©, with permission).

Aside from these drier forest mosaic habitats in the South, the dense forest habitat of bonobos is known to be highly abundant in fruit and herbaceous food resources, as well as having relatively low seasonality (Kano, 1992; Kano & Mulawa, 1984; Malenky et al., 1994; White & Wrangham, 1988). Such features appear to have had considerable impact on their social structure, as I come to discuss. The principal diet of wild bonobos consists of ripe fruits, leaves, flowers and terrestrial herbaceous vegetation. In addition, bonobos have been observed to consume a range of other food types, including animal proteins, honey and mushrooms (e.g. Badrian & Malenky 1984; Bermejo et al., 1995; Kano & Mulawa, 1984). A stream of more recent studies has revealed that hunting and the consumption of other primate species and small mammals is also fairly common, particularly in the region of Lui Kotale, in the Salonga Forest, DR Congo[1] (Fruth & Hohmann, 2002; Hohmann & Fruth 1993; Surbeck & Hohmann, 2008; Surbeck et al., 2009). Chimpanzees are known to be active hunters, especially in some communities (e.g. Boesch, 1999; Gilby, 2006; Pruetz & Bertolani, 2007; Stanford et al. 1994). The finding that hunting in bonobos is frequent in some populations but not in others (e.g. as well as in Salonga, hunting has been observed regularly in the region of Wamba, Ihobe, 1992; but infrequently in the Lomako forest, Badrian & Badrian, 1984) supports the argument put forward by Stanford (1998), that some of the reported differences in the diet and behaviour of bonobos compared to chimpanzees may be an artefact of the fewer number of bonobo study populations.

Social structure

In a similar way to chimpanzees, bonobos live in fission-fusion societies, within ‘communities’ of up to fifty males, females and their dependent offspring. They inhabit loose home ranges of approximately 15-50 km^2. Their social structure is characterised by male philopatry and female migration (Furuichi et al., 1998; Gerloff et al., 1999; Kano, 1992), a pattern observed in a minority of other primates (Sterck et al., 1997; Sterck & Korstjens, 2000; Moore, 1984). In bonobos, females typically emigrate from their natal groups as they approach sexual maturity. Before immigration, young nulliparous females go through a ‘wandering stage’, where they have weak bonding attachments with other group members and opportunistically join any party and community (Kano, 1992). After spending several years wandering between other non-natal groups, females eventually settle and integrate into a community, typically composed of individuals unrelated to them (Gerloff et al., 1999; Hashimoto et al., 1996; Hohmann et al., 1999). In contrast, whilst males have been known to occasionally disperse (Gerloff et al., 1999 but see Furuichi, 1989), they generally remain within their natal groups, staying proximate to their mothers, with whom they form strong and enduring relationships (Furuichi, 1989).

---

[1] All field sites for studies of wild bonobos are based within the DR Congo, so I will henceforth omit adding the country name when field sites are mentioned.

For species displaying male philopatry, inclusive fitness theory predicts that males, who are the most closely related to one another, should form the strongest affiliations and cooperate (Hamilton, 1963). This is indeed the pattern observed in chimpanzees (Goodall, 1986; Wrangham, 1986). Chimpanzee males are highly sociable; they form strong affiliations with one another, develop alliances and travel in male-biased parties (Goodall, 1986, Mitani et al., 2000; Reynolds, 2005; Watts, 2002). Female chimpanzees, on the other hand, who emigrate from their natal groups at adolescence (Bygott, 1979), do not generally affiliate with one another and except during oestrus, tend to avoid travelling in mixed parties with males, in order to reduce aggression and increase foraging efficiency (Williams et al., 2002). In general, most wild female chimpanzees remain semi-solitary for most of their lives, keeping with their dependent offspring within overlapping core areas (Halperin, 1979; Wrangham, 1979; although see Langergraber et al., 2009; Lehmann & Boesch, 2009).

Compared to chimpanzees and other male philopatric species, bonobos show some truly striking differences. Females are highly gregarious and form strong affiliations with other group members, despite being only distantly related to them (Badrian & Badrian, 1984; Furuichi, 1987, 1989, 2009; Hohmann et al., 1999; Kano, 1982; Kitamura, 1983; Kuroda, 1980; White, 1988, 1989; White & Burgman, 1990). In contrast to close female-female associations, male-male relationships are generally weak (Hohmann et al., 1999; Kano, 1992; Palagi et al., 2004; Parish, 1994; White, 1996; although see Furuichi & Ihobe, 1994). However, male bonobos do form close associations and alliances with females (Furuichi, 1989, 1997; Hohmann & Fruth, 2003a). In particular, adult males maintain especially close and enduring relationships with their mothers, something which has been shown to positively influence their dominance rank (Furuichi, 1989, 1997).

Dominance styles

For most of the year, female bonobos aggregate together and forage in large, mixed parties (Kuroda, 1984), sharing food as well as supporting each other in food defence against males (Hohmann & Fruth, 1993; Hohmann et al., 1999). The tendency for bonobo females to aggregate and form affiliations with one another, in the absence of genetic ties, is thought to underlie their generally enhanced dominance status, compared to female chimpanzees (e.g. Furuichi, 2009). The raised status of females is further facilitated by the virtual absence of alliances among males (de Waal, 1997; Paoli et al., 2006a; Parish, 1994; White, 1996) as well as the apparent lack of interest of males in high status positions (Paoli et al., 2006a). Unlike other great ape species, the bonobo social system is described as female-biased and egalitarian (de Waal, 1995). Furthermore, although individuals may sometimes dominate others aggressively (Hohmann & Fruth, 2003a), aggression is relatively low in bonobos, especially compared to chimpanzees, and their conflicts are often settled in non-agonistic ways (de Waal, 1987, 1995; Furuichi & Ihobe, 1994).

Whilst females regularly exhibit enhanced status and a female typically occupies the alpha position in a group, patterns of female dominance are dynamic and flexible (Paoli & Palagi, 2008; Stevens et al., 2008; Vervaecke et al., 2000a). In captivity, linear hierarchies have been demonstrated for several different groups (e.g. Franz, 1999; Paoli et al., 2006a; Stevens et al., 2005a, 2007; Vervaecke et al., 2000a). However, the steepness and linearity of dominance hierarchies have also been shown to vary considerably amongst populations (e.g. Stevens et al., 2007). In general, rather than being absolutely dominant over males, female dominance appears to depend upon both context and the formation of alliances, especially with high-ranked females (Paoli et al., 2006a; Vervaecke et al., 2000a, b; White & Wood, 2007).

The flexible nature of female dominance appears to be especially true in the wild. Individually, females in wild communities are most commonly shown to be equal to males in terms of social status (Hohmann & Fruth, 2003a; Furuichi, 1989; White, 1996). However, they acquire considerable power within the context of foraging and following the formation of alliances (White & Wood, 2007). In the feeding context, individuals can displace males to secure priority access to the best feeding patches, something which also extends to meat eating following hunting (Hohmann & Fruth, 2008; White & Wood, 2007). Female dominance is often reported to be much more pronounced in captivity than in the wild (Stevens et al., 2007, 2008). It has been suggested that raised levels of female dominance in captive settings may be attributed to more frequent occurrence of competitive interactions over food, the context in which female dominance is at its strongest (Furuichi, personal communication).

The formation of alliances strongly facilitates the enhanced status of female bonobos in both the wild and in captivity (Vervaecke et al., 2000b; White & Wood, 2007). By joining together in coalitions, female bonobos are able to dominate males and execute considerable power within their groups (Hohmann & Fruth, 2003a; Parish, 1996; Vervaecke et al., 2000b; White & Wood, 2007). Although female-female coalitions are particularly common, females may also join together with males in order to dominate other males (e.g. Hohmann & Fruth, 2003a; Vervaecke et al., 2000b). The formation of coalitions is exhibited in a variety of contexts, from securing feeding priority, instigating group travel and to provide support during conflicts (Furuichi, 1997; Parish, 1996; Vervaecke et al., 2000a; White & Wood, 2007). Forming alliances with established females appears especially important for newly immigrating females joining the group. This is demonstrated by their overt efforts to affiliate with high-ranked females, especially during the period of integration (Idani, 1991). Upon arrival, newly immigrating females focus their affiliative behaviours toward this female and in the case of party fission, will generally remain proximate to her, presumably so as not to lose this potential ally (Idani, 1991). Against the possibility that these targeted females are in fact relatives of female immigrants (i.e. previously immigrating sisters), genetic analyses have consistently supported the assertion that affiliative relations amongst females are not based upon kinship (e.g. Gerloff et al, 1999; Hashimoto et al. 1996; Hohmann et al., 1999).

Influences on bonobo sociality

Feeding ecology is also thought to play a pivotal role in the increased sociality of female bonobos, as well as for the reduced levels of aggression within and between groups (Furuichi, 2009; White, 1996, 1998; White & Wood, 2007). As mentioned earlier, the equatorial forests of the Congo Basin are characterised by a high abundance of large, dense food patches, with low seasonality (e.g. White, 1988; White & Wood, 2007). As a result of a year-round abundance of food, bonobos experience considerable reductions in both foraging competition and travel time between patches as compared to chimpanzees (Furuichi, 2009; Furuichi et al., 1998; White & Wrangham, 1988). The current opinion is that these two ecological factors may promote the formation of female aggregations within large, mixed foraging parties, which are generally more stable than for chimpanzees (Furuichi, 1997, 2009; Nishida & Haraiwa-Hasegawa, 1987; White, 1998; White & Lanjouw, 1992; White & Wrangham, 1988). For example, a study of the seasonal feeding ecology of wild bonobos in the Lomako forest revealed that, although there was some seasonal variation in fruit abundance, there was no period of food shortage in which large foraging parties and female sociality were not feasible (White, 1998).

Whilst evidence is lacking concerning the ecological features of the forests in which bonobos first evolved, the current hypothesis of relaxed feeding competition and ecological predictability appears to fit most consistently with patterns in their social behaviour. For example, bonobos are more socially tolerant (Hare et al., 2007), they value future food pay-offs less than chimpanzees (Rosati et al., 2007), are willing to share food (Hare & Kwetuenda, 2010, although see Jaeggi et al., 2010) and have enhanced female sociality (e.g. Wrangham, 1993). Nevertheless, although providing a useful evolutionary framework, the socio-ecological approach does not fully explain why comparative shifts towards more pro-social patterns of sociality have not been observed in other chimpanzee communities living in forests that are also characterised by super-abundance. For example, the Budongo forest, Uganda, is also known to have highly abundant food resources (Reynolds, 2005). Nevertheless, females chimpanzees living in communities within this forest remain socially isolated and both male-led and female-led infanticides are not infrequent (e.g. Townsend et al., 2007).

Whilst testing these socio-ecological hypotheses indeed remains challenging, patterns in the current socio-ecological behaviour of bonobos appears to have considerable explanatory power when examining their behavioural and ranging strategies. For example, the notion put forward by van Hooff and van Schaik (1994), that male ranging patterns are influenced by female distribution and patterns of oestrous, appears to be consistent with male bonobos. Van Hooff and van Schaik (1994) suggested that for species with females living in large or loose aggregations, monopolisation of females by males would be impossible or meaningless. In bonobos, males range more independently and although they join mixed-sex parties, they often remain at the periphery and are not able to monopolise females (Furuichi et al., 1998; White, 1988). In comparison to males, bonobo females are more gregarious and tend to join mixed-sex parties more readily (Furuichi, 1987; Kano, 1982; White, 1988;

White & Wrangham, 1988). Cohesive female ranging strategies appear to favour the more flexible, and often solitary, ranging strategies in males (White & Lanjouw, 1992). For example, long term observations of male and female ranging patterns in the Lomako forest have revealed that during party travel, males frequently travel alone, in front of the main female-biased party (White, 1998). Upon discovery of feeding sites, males may compete amongst themselves to gain priority access before the females arrive. Consequently, the male who has successfully retained his position at the feeding site is able to both copulate with females arriving at the feeding site, as well as gain improved foraging opportunities.

Reproductive factors relating to female physiology and behaviour may also promote the enhanced status of females in bonobo society. For example, bonobo females exhibit an especially prolonged period of oestrous compared to other primates, both in terms of extended swelling cycles (Dahl, 1986; Furuichi, 1987) as well as in the duration of the peak swelling phase (Blount, 1990; Dahl, 1986; Furuichi, 1987; Thompson-Handler et al., 1984). A consequence of this prolonged perineal tumescence appears to be extended female attractivity (Furuichi & Hashimoto, 2004) and a presumably heightened sexuality (Wrangham, 1993). With prolonged attractivity, females may experience extended mate choice, which consequently promotes an elevation of their social status (Wrangham, 1993). In this way, prolonged oestrous is thought to underlie the formation of more stable and mixed foraging parties (Furuichi, 2009). In addition, the fact that females conceal ovulation and mate promiscuously (Paoli et al., 2006b) may also account for an apparent lack of interest that male bonobos have in high status positions. If males are not able to dominate females during oestrous periods, there may be less adaptive benefits for males to be aggressive and compete for the high-ranked position (Wrangham, 1999).

Females also appear to gain additional social power through the formation of strong and enduring bonds with their adult sons (Furuichi, 1989; 1997; Furuichi & Ihobe, 1994; Hohmann et al., 1999). For example, results from long-term studies of the wild bonobos at Wamba revealed a close link between the dominant males and females within each group, with alpha females often being the mothers of the alpha males (Furuichi, 1989). For both mothers and sons, there seem to be a number of social and reproductive benefits to remaining affiliated (Furuichi, 1989). For example, mothers and sons may receive benefits of gaining coalitionary support. In terms of reproductive benefits, a recent study of wild bonobos in the Salonga forest demonstrated that the presence of the mother increased her son's mating success (Surbeck et al., 2010). Behavioural observations indicated that mothers achieved this either by intervening into the matings of other males, or by increasing their son's access to oestrous females by themselves remaining proximate to them (Surbeck et al., 2010). Such a strategy not only promotes the direct reproductive success of the son, but also provides indirect reproductive benefits to the mother, via her son's mating success.

Cognition and social tolerance

From a cognitive perspective, most of what is known about bonobos is based on comparisons with chimpanzees (Hare, 2009). Generally, bonobos and chimpanzees have been shown to perform comparably in a range of cognitive tasks, especially for those dealing with the physical world (Herrmann et al., 2010). They show competency in tasks concerning spatial memory, object permanence, spatial transposition and discriminating quantities, as well as problems of physical causality (Herrmann et al., 2010). In the domain of tool use, experimental tests have shown that chimpanzees are more competent tool-users than bonobos (Herrmann et al., 2010), although observations in captivity have indicated their abilities are actually comparable (Gruber et al., 2010). However, in contrast to chimpanzees, who have been shown to be sophisticated tool users in a number of communities in the wild (e.g. Whiten et al., 1999), there have only been reports of very limited tool use in wild bonobos (Hohmann & Fruth, 2003b; Ingmanson, 1996). Currently, it is still unclear whether the relative absence of tool use in wild bonobos highlights a fundamental difference between the two *Pan* species, or rather inadequate sampling of different bonobo communities occupying a range of ecological habitats (e.g. Hohmann & Fruth, 2003b).

Whilst bonobos and chimpanzees appear to demonstrate comparable abilities in regards to social learning (Herrmann et al., 2010), there appear to be some striking differences in other aspects of their social cognition. In experimental tasks, bonobos have been shown to be more socially tolerant compared to chimpanzees, something which appears to facilitate their greater performance in co-operative tasks (Hare et al., 2007). Hare and Kwetuenda (2010) also found that bonobos are surprisingly motivated to share food with one another, even at the cost of losing food themselves (although see Jaeggi et al., 2010). Bonobos have also been shown to have greater capacities in some social and theory of mind related tasks, something that is thought to relate to evidence of more cautious/nervous temperaments compared to chimpanzees (Herrmann et al., 2010). Unlike chimpanzees, that have been shown to become increasingly less tolerant as they grow into adulthood, bonobos appear to retain juvenile levels of social tolerance as adults (Wobber et al., 20l0). This is also reflected in their tendency to engage in particularly high levels of play, a behavioural trait which tends to be maintained into adulthood (Palagi & Paoli, 2007). Enhanced levels of social tolerance as well as increased levels of play are also thought to contribute to their apparently dampened levels of aggression, with social tolerance promoting cooperation, food sharing and a more peaceful co-existence between group members (de Waal, 1995; Hare & Kwetuenda, 2010).

Sexual behaviour

Enhanced social tolerance and reduced levels of aggression are thought to relate to the frequent performance of socio-sexual behaviours by bonobos (e.g. de Waal, 1987). Bonobos exhibit an exceptionally rich and heightened socio-sexuality, with sex frequently divorced from biological reproduction to be used socially (de Waal, 1987, 1989, 1995; Furuichi, 1989; Hashimoto, 1997; Hohmann & Fruth, 2000; Idani, 1991; Kano, 1989; Thompson-Handler et al., 1984; White, 1996). Sex is freely incorporated into the daily lives of bonobos, with individuals frequently engaging in sexual interactions in all age and sex combinations. Bonobo females remain sexually active across their sexual cycles and, unlike most other primates, often engage in sexual interactions in which they face their partner ventro-ventrally (e.g. Kano, 1992; Paoli et al., 2006b; Thompson-Handler et al., 1984). Socio-sexual behaviour appears to serve as a kind of ‘social grease’ that alleviates tension and facilitates peaceful co-existence and affiliation between group members, who generally lack close genetic ties (Fruth & Hohmann, 2006).

Whilst other species of apes and monkeys also engage in homosexual genital contacts (e.g. chimpanzees, *Pan troglodytes,* Anestis, 2004; gorillas, *Gorilla gorilla*, Fischer & Nadler, 1978; orangutans, *Pongo pygmaeus*, van Schaik et al., 2003; capuchins, *Cebus capucinus*, Manson et al., 1997), bonobos are the only primate species that performs socio-sexual behaviours habitually, both in the wild and in captivity. (e.g. Blount, 1990; de Waal, 1987; Kano, 1980, 1989, 1992; Kuroda, 1980; Mori, 1983; Parish, 1994; Thompson-Handler et al., 1984). Sexual interactions between females are known as ‘genital contacts’, whereby two individuals embrace one another ventro-ventrally, whilst swinging their hips laterally, keeping their vulvae in contact (Hohmann & Fruth, 2000; Kuroda, 1980; see fig 2.2). The majority of genital contacts occur within the feeding context, although they are also performed during periods of social tension/conflict, inter-group interactions and during play (de Waal, 1987; Fruth & Hohmann, 2006; Hohmann & Fruth, 2000).

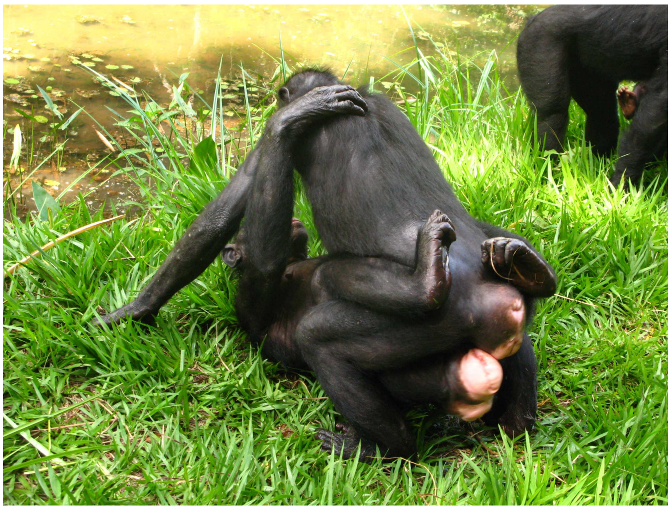


Figure 2.2. Photograph showing a homosexual genital contact between two female bonobos, taken at Lola Ya Bonobo Sanctuary, D R Congo (photograph by Z. Clay).

There appear to be numerous social and communicative functions to genital contacts in female bonobos (de Waal, 1987; Hohmann & Fruth, 2000; Wrangham, 1993). Regulation of social tension is one of the most commonly ascribed functions (e.g. de Waal, 1987; Hohmann & Fruth, 2000; Kano, 1989). This follows Hanby’s (1977) more general prediction that socio-sexual behaviours in non-human primates are used to regulate social stress (see also Vasey, 1995). In both the wild and in captivity, studies have shown that rates of genital contacts increase significantly during periods of social instability and tension, occurring most commonly during feeding, but also after conflict and during inter-group encounters (de Waal, 1987; Furuichi, 1989; Hohmann & Fruth, 2000; Kano, 1989; Parish, 1994; Manson et al., 1997).

One obvious, but nevertheless, difficult question concerns why a behaviour that appears to alleviate social stress, has become firmly entrenched in the behavioural repertoire of bonobos but not so in other primates. Part of the answer may lie in the fact that bonobo societies are composed of aggregations of closely affiliated females and males who, aside from mothers and sons, are mostly unrelated to one another (Gerloff et al., 1999; Hohmann et al., 1999). These loose genetic ties presumably enhance the potential for social stress between group members and consequently, a need to employ additional mechanisms to alleviate it (de Waal, 1987). Thus, in addition to grooming, the classic behavioural mechanism for reducing stress in social animals, bonobos appear to use socio-sexual interactions as another avenue to lubricate their social relations and facilitate their peaceful co-existence with other group members (Fruth & Hohmann, 2006).

Whilst the stress-regulation hypothesis appears most consistent with observational evidence, results from a recent hormonal study have indicated that the relationship between socio-sexual behaviours and stress regulation may not be as direct as has been previously assumed. Hohmann and colleagues (2009) tested the stress regulation hypothesis by examining levels of salivary cortisol, a hormonal marker of stress, during tense social situations. In this captive study, rates of female genital contacts and accompanying cortisol levels were compared for baseline data and matched samples in contexts where food access was restricted. Whilst they found a temporal relationship between genital contacts and cortisol levels, particularly during the anticipation of food, the authors found no clear relationship between higher genital contact rates and a greater decline in cortisol levels. Thus, although the authors did not discount the physiological link between genital contacts and stress reduction, their results suggested that the causal relationship may not be as strong as has been previously assumed. This study did however suffer from technical limitations, both in small sample size and collection techniques, indicating that further work is needed.

It has also been suggested that genital contacts may help to increase social tolerance between individuals, which serves to facilitate food sharing and access to preferred food patches. For example, studies in both the wild (Kuroda, 1980, 1984) and in captivity (Manson et al., 1997; Parish, 1994) have demonstrated that females are more likely to co-feed in desirable food patches and gain food from other individuals after engaging in genital contacts with them. In food-sharing and social tolerance studies, Hare and colleagues reported that bonobo subjects frequently engaged in sexual behaviours during testing (Hare et al., 2007; Hare & Kwetuenda, 2010).

Bonobos habitually engage in homosexual genital contacts following conflict, something that suggests that genital contacts may play a role in reconciliation (de Waal, 1987, 1995; Hohmann & Fruth, 2000). For example, in a captive group, de Waal (1995) found an overall increase in socio-sexual behaviours following agonistic interactions. In a study of wild bonobos in Lomako forest, Hohmann and Fruth (2000) compared rates of genital contacts before and after conflict, and found a threefold-increase in genital contacts after conflicts than prior to them. Nevertheless, whilst genital contacts may facilitate reconciliation, the vast majority of genital contacts actually occur independently of agonistic encounters (Hohmann & Fruth, 2000; Kano, 1980), suggesting that reconciliation is unlikely to be a primary function of this behaviour.

Sexual interactions also appear to be important in establishing and maintaining social relations between females (Furuichi, 1989; Hohmann & Fruth, 2000; Kano, 1980; Kuroda, 1980, 1984; Parish, 1994; White & Lanjouw, 1992). In particular, the performance of genital contacts appears to be important for the integration of newly immigrating females. During the immigration period, immigrating females frequently engage in sexual interactions with other group members, particularly focusing their sexual behaviours onto a particularly established female within the group (Idani, 1991). The performance of genital contacts in this context may not only serve to facilitate affiliation between unknown group members, but also to alleviate presumably high levels of social stress provoked by the arrival of a new, nulliparous female into the group. However, whilst genital contacts may bring affiliative benefits to subordinates, this hypothesis does still not explain why established, high-ranking females also participate in this behaviour. More work exploring the rank-related social benefits of genital contacts is required to further understand inter-individual motivation.

Rank-related asymmetries in the performance of genital contacts have also indicated that genital contacts may be a means for individuals to communicate social relations and express social status (de Waal, 1995; Hohmann & Fruth, 2000; Wrangham, 1993). Genital contacts most frequently occur between partners of different social status: they are initiated mostly by subordinates, who frequently target dominant females (Hohmann & Fruth, 2000; Parish, 1994, 1996). Furthermore, during the performance of the genital contact, the higher-status female typically takes the 'mounter' position on top of the other female (bonobos: de Waal, 1987; Hohmann & Fruth, 2000, although see Paoli et al., 2006b; stump-tailed macaques, *Macaca arctoides*: Goldfoot et al., 1980). For high-ranking females, accepting and performing genital contacts may serve as a low-cost means to advertise their superior status.

Reproductive behaviour versus socio-sexual behaviour

Due to their heightened levels of socio-sexuality, bonobos have acquired the reputation of being extremely sexually active in comparison to chimpanzees. However, in terms of viable reproductive events, analyses of their copulation rates and oestrous cycles indicate that bonobos do not actually have offspring more frequently than chimpanzees, nor do they copulate more frequently during oestrous (Furuichi & Hashimoto, 2002, 2004; Takahata, 1996). These differences in copulatory rates can be accounted for by the fact that, although female bonobos copulate more across the swelling cycle than chimpanzees, they also copulate more during the non-swelling phase (e.g. Dahl, 1986; Furuichi, 1987; Thompson-Handler et al., 1984). In contrast, chimpanzees exhibit a sharper increase in copulations during the peri-ovulation period (Wrangham, 2002). Furuichi and Hashimoto (2002) suggest that the relatively lower copulation rate of bonobos during the oestrous period may reflect differences in their oestrous cycles during inter-birth intervals compared to chimpanzees. Bonobo females spend a greater proportion of time in oestrous during inter-birth intervals in comparison to chimpanzees (Furuichi & Hashimoto, 2002; Paoli et al., 2006b). They also have longer swelling cycles and periods of peak swelling (Blount, 1990; Dahl, 1986; Furuichi, 1987). Female bonobos may be therefore less eager to copulate during oestrous periods than chimpanzees, as their time window available for conception is less limited (Furuichi & Hashimoto, 2002, 2004).

Bonobo communication

Although there has been considerable progress in understanding the evolutionary roots and patterns of bonobo ecology and behaviour, much less is known about how bonobos communicate with one another. Whilst the number of studies is relatively low, especially compared to chimpanzees, the next section outlines what is currently known about gestural and vocal communication in bonobos.

Gestural communication

Compared to facial expressions and vocalisations, which are considerably more fixed and under less volitional control, gestures are thought to be used more flexibly and therefore have potential for communicative complexity (e.g. Arbib et al., 2008). They may be used intentionally, with meaning emerging from a dynamic interaction between context and signal (Pollick et al., 2008). Furthermore, combined use of gestures with vocalisations and facial expressions has the potential to further enhance the level of communicative complexity (Pollick & de Waal, 2007).

Bonobos have been shown to use a considerable array of gestures to communicate with others in flexible and dynamic ways (Pollick & de Waal, 2007; Pika et al., 2005). Whilst numerous gestures have been documented in studies of wild populations (e.g. Badrian & Badrian, 1984; Ingmanson, 1996; Kano, 1980; Kuroda, 1980), the most extensive studies of bonobo gestural communication have been conducted in captive settings (Pika et al., 2005; Pollick & de Waal, 2007; Savage & Bakeman, 1978; Savage-Rumbaugh et al., 1977).

De Waal (1988) provided the first ethogram describing the gestural as well as vocal repertoire of bonobos, based on a captive group housed at San Diego Zoo. De Waal described 15 distinct gestures, many of which were linked to specific contexts. The majority of these gestures were classed as imperative, meaning that they were used to get another individual to change its behaviour (i.e. to help attain a goal; Bates, 1976). For example, the arm-waving gesture (stretch arm high into air and wave, with concave back) is used by males as a sexual initiation signal to females (de Waal, 1988).

More recent studies, using a tighter definition of the term ‘gesture’, have since extended the repertoire and have highlighted the considerable flexibility and communicative complexity of bonobo gestures (Pika et al., 2005; Pollick & de Waal, 2007). For example, Pika and colleagues (2005) documented a total of 20 different distinct gesture types which occurred in three different modalities, across a range of contexts. A study on gestural communication during play revealed that bonobos use gestures to communicate intention (Pika & Zuberbühler, 2008). In this study, juvenile bonobos interacted in a social game with human caregivers. During this interaction, the caregiver unexpectedly paused the game and it was found that bonobos used gestures to communicate their intention to continue and remain engaged with their play-partner.

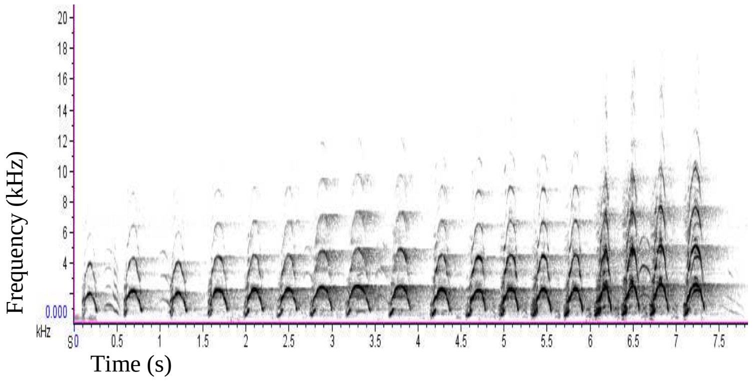
Vocal communication: A graded vocal system

As with gestures, de Waal (1988) was the first to extensively describe the vocal system of bonobos, comparing it to the vocal system previously reported for chimpanzees (Marler & Tenaza, 1977; van Hooff, 1973). De Waal described the bonobo vocal system as highly graded, with similarities to the graded vocal system of chimpanzees. The graded nature of an animal vocal system refers to the scaling of acoustic similarity between call types. A graded vocal system lies at one end of a continuum, with discretely organised call types at the other. For example, capuchin monkeys (*Cebus capucinus*) have a discrete system of vocal communication with acoustically distinct call types, such as a ‘trill-like’ greeting signal (Boinksi & Campbell, 1995). Graded vocal systems have been described in numerous primates, including chimpanzees (Marler, 1976; Marler & Tenaza, 1977; van Hooff, 1973), baboons (*Papio cynocephalus ursinus*, Fischer et al., 2001) and red colobus monkeys (*Procolobus badius*; Marler, 1970). Though considerably more difficult to describe systematically, the acoustic variation present in graded signals has the potential for considerable communicative complexity. This is especially so if a tight relationship exists between context production and signal grading (Marler, 1977), and if receivers are able to perceive graded signals categorically (Hauser, 1998).

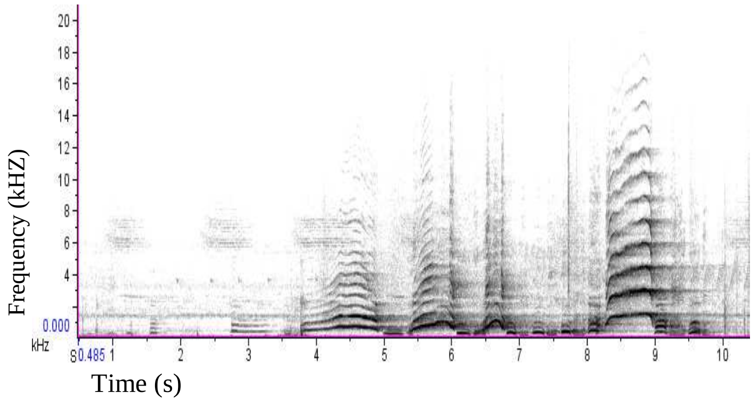
Compared to chimpanzees, bonobos produce vocalisations that are generally much higher in pitch (de Waal, 1988; Mitani & Gros-louis, 1995). A number of anatomical and social differences, related to the presence of neotenous characteristics, are thought to explain the raised pitch of bonobo vocalisations. As well as being smaller in body size, bonobos show juvenilised features in their craniomorphology (Cramer, 1977) and in regions surrounding the basicranium (Laitman & Heimbuch, 1984). Size differences, particularly in the area of the cranium, are likely to give rise to related variations in laryngeal mechanisms and vocal tract length (Mitani & Gros-Louis, 1995). In addition to anatomy, social difference in party cohesion may also influence the evolution of vocal pitch in bonobos compared to chimpanzees. For example, bonobos typically travel in more stable and cohesive groups compared to chimpanzees (e.g. Nishida & Hiraiwa- Hasegawa, 1987). Considering that higher frequency sounds attenuate more rapidly than lower frequency sounds (Wiley & Richards, 1978), enhanced levels of social dispersion in chimpanzee foraging parties may have acted on the selection of low-pitched vocalisations in chimpanzees due to their more efficient long-distance transmission (Mitani & Gros-Louis 1995). Likewise, in another species of great ape, the orangutan (*Pongo pygmaeus*), solitary males range over large distances and emit low-pitched loud calls for communication with other orangutans. The emission of low-pitched vocalisations is required for effective sound transmission over long-distances, thus enabling males to be identifiable to both females and other males (Delgado, 2007; Setia & van Schaik, 2007).

Vocal Repertoire

The bonobo repertoire, as described by de Waal (1988), is composed of 12 main vocal types. These include three hoots, (‘high hoot’, ‘contest hoot’, ‘low hoot’), three peeps (‘food peep’, ‘alarm peep’, ‘peep-yelp’), two barks (‘wieew bark’, ‘whistle bark’) as well as grunts, pant laughs, pout moans and screams (see table 2.1). It is likely, and was suggested by de Waal, that much greater variation exists within each of these broader call categories than was actually documented. Although bonobo vocalisations are generally higher in pitch than chimpanzees’ (Mitani & Gros-Louis 1995), there are numerous parallels in both the acoustic form and contextual usage (table 2.1). This is perhaps unsurprising considering the very recent phylogenetic divergence of bonobos from chimpanzees (Won & Hey, 2005). For example, pant laughs, pout moans, low hoots, and wieew barks showed considerable overlap in both their acoustic structure as well as their contextual usage with those of chimpanzees (although the bonobo wieew bark is known as a ‘woaow bark’ in chimpanzees: van Hooff, 1973). In terms of long-distance communication, the bonobo high hoot call shows most contextual similarity with the chimpanzee ‘pant hoot’. Bonobos, like chimpanzees, use these vocalisations during long-distance communication between unseen individuals, as well as in response to food discovery and other relevant events or disturbances (de Waal, 1988; Marler & Tenaza, 1977; van Hooff, 1973). Structurally, however, there are numerous differences (fig. 2.3). In chimpanzees, the pant hoot is a composite vocalisation, composed of four distinct phases: the introduction, build-up, climax and downward phase. The homologous call in bonobos, the high hoot, is a ‘whooping’ call that has either a staccato (brief and sharp) or legato form (longer and less sharp). Generally, bonobo high hoot sequences contain a rapid sequence of legato hoots, which may increase in speed and crescendo but do not possess the phrase-like form of a pant-hoot sequence. In another difference, bonobos often produce these calls in choruses, where the high hoots of different individuals are tightly synchronised with those of other group members (Hohmann & Fruth, 1994).



a. Bonobo high hoot



b. Chimpanzee pant hoot

Figure 2.3. Time-frequency spectrograms illustrating a bonobo high hoot and a chimpanzee pant hoot (high hoot given by adult male bonobo, MN, on arrival to the feeding site at Lola Ya Bonobo Sanctuary, DR Congo; pant hoot given by an adult male chimpanzee, NK, upon arrival at a feeding tree in Budongo Forest, Uganda).

Despite numerous parallels between the vocal repertoires of bonobos and chimpanzees, several vocalisations described in the bonobo repertoire have not been described for chimpanzees (de Waal, 1988). These include the staccato hoots, contest hoots, food peeps and alarm peeps. For example, whilst chimpanzees tend to produce their most impressive displays in the visual domain, bonobo males appear to intimidate their rivals using contest hoots during agonistic confrontations. Typically, contest hoot displays involve rapid vocal dialogue between two hooting individuals (typically males), which represents an agonistic vocal behaviour not observed in chimpanzees (de Waal, 1988).

The vocal repertoire proposed by de Waal (1988) was re-evaluated by Bermejo and Omedes (1999) in a study of wild bonobos in Lilungu, DR Congo. As with de Waal's study, this study was purely descriptive and although the authors provided spectrographic examples, no quantitative analyses of acoustic structure or call usage were performed. The repertoire described in this study largely confirmed de Waal's findings, although the authors added three more vocal units to the repertoire: whistle, hiccup and croak (table 2.1). Furthermore, the authors also stressed the graded nature of the vocal units as well as the role that combinatorial vocal sequences appear to play in bonobo vocal communication. Overall, 19 different vocal sequences were identified, although the authors emphasised this analysis was only preliminary and that further investigation may reveal more. The vocal sequences were shown to be used in a range of contexts, and within a given behaviour there was a broad array of sequences each with considerable variation. For example, one sequence, labelled as the 'soft mixed series', contained a variable number (approx. 10-57 units) of peeps, peep-yelps and barks (fig. 2.4). This sequence was observed in a range of contexts, including feeding on trees, feeding on the ground, during agonistic interactions and during displays.

Whilst both lacking quantitative analyses of acoustic structure and call usage, these two studies together provide a promising and detailed description of the vocal repertoire of bonobos in both wild and captive settings. In particular, both studies highlight the graded nature of the bonobo vocal repertoire, something which creates significant possibilities for subtle but relevant variation within these signals. Furthermore, the flexible use of heterogeneous vocal sequences highlights a further potential for the calls to be combined in different ways to provide different meanings.

Table 2.1. Bonobo vocal repertoire (adapted from Bermejo & Omedes, 1999 and de Waal, 1988) compared to the chimpanzee vocal repertoire (adapted from Marler & Tenaza, 1977 and van Hooff, 1973).

Call type	Context and use	Homologous chimpanzee vocalisation
Low hoot	Environmental changes/disturbances	Low hoot
High hoot	*Staccato* and *legato* types: for inter-party communication, response to discovery (e.g. food)	Legato hoot akin to chimpanzee pant hoot. Staccato hoot distinct to bonobos
Wieew bark	Alarm/hostility, response to disturbances	Woaow bark
Contest hoot	Conspicuous warning of charge, vocal contest/agonistic confrontation	Unlike chimpanzee vocalisation (most similar to pre-display hoot)
Greeting grunt	Submissive greeting, up hierarchy	Pant grunt
Pant laugh	Play/wrestling	Pant laugh
Pout moan	Appeasement	Pout moan
Whistle bark	Offensive agonistic signal, agonistic recruitment	Bared-teeth bark
Food peep	Feeding (various call variants: *soft barks*, *whistles*, *peeps*, *grunts*, *peep yelps*)	Rough grunts
Alarm peep	Unknown/surprising objects & disturbances	Hoo call
Peep-yelp	Food, victim aggression, appeasement	Bared-teeth yelp/squeak
Scream	Agonistic interactions, stressful situations *(peep scream, rasp scream, bark scream, full scream, sex scream)*	Scream
Whistle	Feeding, social excitement, inter-party communication	Bark-screams and hoots
Hiccup	Grooming, feeding, play, inter-party communication	Unclear
Croak	Play, spontaneous	Laughter

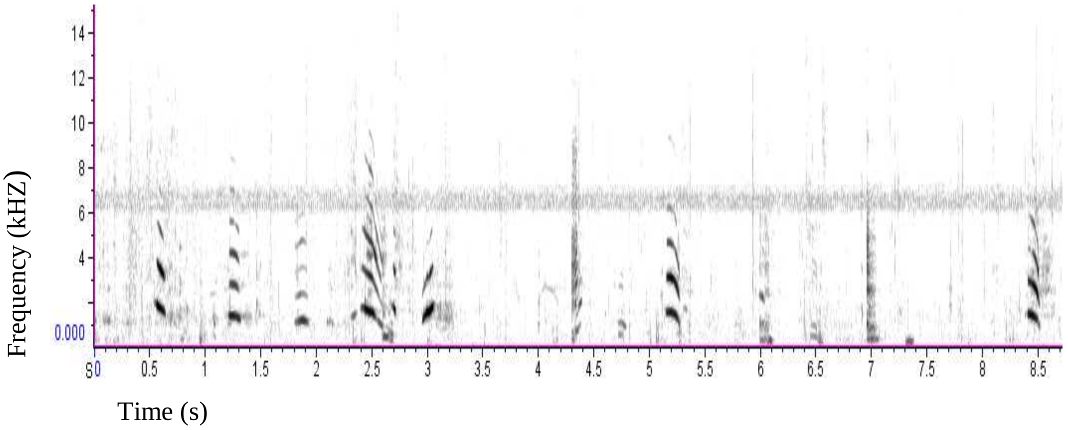


Figure 2.4. Time-frequency spectrogram illustrating a mixed vocal series composed of peeps, peep-yelps, yelps and grunts, produced by female KS, feeding on papaya.

<u>Vocal production</u>

Hohmann and Fruth (1994) examined the use and acoustic structure of high hoot vocalisations during long-distance communication between wild bonobos in the Lomako forest. Although spectrographic analyses revealed high acoustic variability, results indicated a high degree of behavioural synchronisation between signallers, with individuals producing high hoots in distinct alternating sequences with other group members that were out of sight, but in close proximity. Furthermore, acoustic analysis revealed that individuals adjusted the structural characteristics of their vocalisations, by shifting the frequency of the high hoots to correspond with those of group members. This surprising degree of vocal flexibility and synchronisation with vocal partners suggested that bonobos might be able to control and modify their vocalisations in response to certain social situations. Unfortunately, this study was somewhat limited owing to problems with individual identification and habituation. Nevertheless, results indicate that long-distance communication in wild bonobos is a promising area that requires further attention.

Using data collected from bonobos from the Eyengo community in Wamba, Mitani and Gros-Louis (1995) compared the acoustic structure of bonobo screams with those of wild chimpanzees, recorded in the Mahale Mountains, Tanzania. As previously mentioned, bonobos were shown to produce considerably higher pitched scream vocalisations in comparison to chimpanzees. For example, the mean frequency of chimpanzee screams was 1275 Hz compared to 2846 Hz for bonobos. In addition, acoustic differences between males and females were reported for both bonobos as well as chimpanzees.

In the feeding context, results from a study of captive individuals indicated that bonobos may be able to strategically control the production of food-associated calls, as a means to decrease feeding competition and promote reproductive strategies (van Krunkelsven et al., 1996). In this study, conducted at Planckendael Zoo, Belgium, high-preference food items of two differing quantities were first hidden in the enclosure and then individuals were subsequently released to forage, either alone or with others. Whilst neither the quantity of food, nor the sex or identity of the subject were shown to influence call production, individuals called significantly more when feeding alone than when others were present (98% in the non-social condition versus 44% in the social condition). Although the dominance status of the signaller was not measured, the authors concluded that the bonobos were able to strategically suppress vocalisations in the presence of potential food competitors. However, analyses of male behaviour revealed that the production of food-associated calls by males often resulted in the approach of females, who frequently copulated with them. This result, although somewhat contradictory to the main finding, suggested that whilst males might experience a cost in attracting feeding competitors, there might be a sex-specific trade-off, where males call to exchange food for sex. Corresponding data were unfortunately lacking for females, although it was suggested that females may accrue benefits by calling to attract coalition partners, who will ultimately enhance their status and enable them to monopolise feeding over males. A replication of this study, testing the hypothesis of strategic production and inhibition, would be helpful in addressing these intriguing but mixed results.

Studies of language-trained bonobos

Sue Savage-Rumbaugh’s long-term research on the linguistic capabilities of a group of language-trained apes has indicated that bonobos might possess some of the cognitive capacities required for human language (Savage-Rumbaugh & Lewin, 1994). In particular, Savage-Rumbaugh’s work on one bonobo, a male named Kanzi, has highlighted his remarkable capacity in a range of communicative and representational tasks. Raised from birth in a human environment, Kanzi has successfully learned an artificial language based on lexigrams, learning the referents of 256 symbols (Savage-Rumbaugh & Lewin, 1994). Although his grasp of human language is still a matter of considerable debate (see Shanker et al., 1999), Kanzi shows undeniably impressive levels of linguistic competence, particularly in the domain of understanding human speech. Kanzi has been shown to differentiate and attach communicative intent to hundreds of speech sounds, as well as to link them to events and referents in the external world (Savage-Rumbaugh, 1986; Savage-Rumbaugh et al., 1986; Sevcik & Savage-Rumbaugh, 1994). For example, when Kanzi hears the word 'ball', he is able to not only retrieve a ball, but can also select a picture of a ball, select an arbitrary symbol previously learned to be associated with ball, as well as respond to simple sentences in which the word 'ball' is embedded (Savage-Rumbaugh, 1987).

In addition to Kanzi, his younger sister, Panbanisha, has also shown capabilities in acquiring an artificial language system and comprehending spoken language. For example, 483 unique sentences spoken by care-givers to Panbanisha (then aged 3 years) were extracted from records of daily interactions. Subsequent tests of Panbanisha's comprehension of these sentences revealed that she responded appropriately to 93% of the sentences spoken to her, despite the majority being context-independent. It was suggested that, like Kanzi, Panbanisha is able to extract information from spoken sentences by attending to their syntactic structure (Brakke & Savage-Rumbaugh, 1995). Whilst such studies indicate considerable linguistic capacity, it may be desirable to replicate these findings in more controlled environments by experimenters blind to the hypotheses.

In terms of vocal production, Kanzi's capability is considerably more limited, although nevertheless impressive. Two studies investigating Kanzi's vocal production have indicated high levels of flexibility and vocal control (Hopkins & Savage-Rumbaugh, 1991; Taglialatela et al., 2003). For example, Kanzi has been shown to use four structurally unique vocalisations not heard among non-language-trained subjects (Hopkins & Savage-Rumbaugh, 1991). The authors concluded that Kanzi acquired a greater capacity for vocal learning and flexibility as a consequence of his unique rearing experience. Furthermore, when communicating with humans about food, Kanzi has been shown to modify the species-typical ‘food peep’ vocalisation into four unique variants, which he uses to label four specific contexts (Taglialatela et al., 2003). These include the terms ‘banana’, ‘grape’, ‘juice’ and ‘yes’.

Although such results are striking and impressive, language-trained studies still severely lack ecological relevance and external validity, owing to the unique training, unnatural environment and human-orientated upbringing that Kanzi and the other bonobos have received. Nevertheless, with further empirical work, these findings may indicate that bonobos are able to flexibly produce referential labels and modify their vocal signals to communicate with a specified audience.

Summary and outlook

In these two introductory chapters, I reviewed some of the main themes that have been investigated in the field of primate vocal communication and introduced the behaviour and socio-ecology of my study species, the bonobo. Throughout this thesis, I take a cognitive perspective to vocal communication, and thereby explore how this approach has been used in previous research on vocal communication in primates and other animals. Against the assumption that vocalisations are purely hard-wired and cognitively uninteresting, a growing body of research has highlighted the considerable complexity and flexibility present in the communication systems of primates and other animals. This was demonstrated in my reviews of the current evidence for functionally referential communication, call combinations and audience effects in animal vocal communication systems.

Using the framework established in previous studies, I aim to conduct a systematic investigation of the vocal behaviour of one of our closest living relatives, the bonobo. Due to their close phylogenetic relatedness to chimpanzees, late discovery and their remote and isolated habitat, bonobos have long been left in the shadow of chimpanzees. That is not to say that all aspects of bonobo behaviour have been neglected, as my review of the rich literature concerning their socio-ecology and behaviour has demonstrated. In this thesis, I aim to take a focused look at patterns in bonobo vocal communication, in order to examine whether some of the features and vocal complexity demonstrated in other primates are also present in their vocal communication system. In the first two empirical chapters that follow, I combine observational and experimental techniques to examine whether bonobos are able to both produce and understand vocalisations that convey meaningful information about an object or event in the external world. To do this, I explore vocal communication from both the caller's (chapter four) and the receiver's perspective (chapter five), during food discovery. In the next two empirical chapters, I investigate some of the more social aspects of bonobo vocal behaviour, examining how females use vocalisations during their sexual interactions with males and other females. In chapter six, I conduct acoustic and behavioural analyses to explore how females use copulation calls in the traditional context of the heterosexual copulation in comparison to the social context of homosexual genital contacts. I build on these findings in my next chapter (chapter seven), conducting finer-scaled analyses of the social use of vocalisations during female-female sexual interactions. Overall, I use insights from studies of bonobo behaviour and socio-ecology to explore the role social life has played in shaping the vocal communication of this species.

Chapter three: General methods

Study sites

In total, I collected data from four study sites. For my studies of bonobo food-associated calls (chapters four and five), I collected data at three facilities: San Diego Zoo, USA; San Diego Wild Animal Park, USA; and Twycross Zoo, UK. For my studies of copulation calls (chapters six and seven), I collected data at one study site: Lola Ya Bonobo Sanctuary, DR Congo. This chapter provides an overview of these facilities, the study groups, details of feeding and enrichment routines. Although the set-up at different facilities required some methodological adjustments, my main protocols for collecting and recording vocalisations remained essentially the same, which are described here. Specific methodological details for each study are provided in subsequent chapters.

San Diego Zoo and San Diego Wild Animal Park

Study period

At these two captive facilities in San Diego, USA, I conducted an empirical study on bonobo food-associated calls. I received full ethical approval from the San Diego Zoo Research and Welfare Committee to conduct research. I collected data for three months from January until April 2008. During this time, I was assisted by another observer (TG), who independently collected data at the group that I was not working with on a given day. San Diego Zoo (henceforth Zoo) and San Diego Wild Animal Park (henceforth Park) provide some of the best opportunities for collecting outdoor vocal recordings of large groups of bonobos in captivity (N =16 individuals in total). The close spatial proximity of the two facilities in San Diego and the similar management programme meant that it was possible to collect data during the same study period, resulting in a larger data set of subjects with comparable management routines.

San Diego Zoo, USA

Group composition and facility set-up

The Zoo group was composed of eight individuals, which included three adult females, two adult males, one sub-adult female, one juvenile male and one juvenile female (age range: 4-29 years; age-classes described by Kano, 1992, see table 3.1)[2]. The facility consisted of an outdoor enclosure (560m^2) connected to heated indoor rooms (one larger room, 136m^2, and four smaller rooms, each 55m^2) via a hydraulic door and a wire tunnel. During the daytime, the group was housed in the outdoor enclosure and at night, all individuals slept in the heated indoor rooms. Group composition was managed to simulate a fission-fusion social system, so in the mornings, one or two individuals typically remained in the indoor sleeping rooms for several hours, before being switched with other individuals into the outdoor enclosures. The keepers managed individual movements, so that individuals were unable to pass independently between enclosures during the day. The outdoor enclosure consisted of multi-layered artificial mounds and grass areas, with a flowing water feature in the centre, an artificial termite mound and numerous climbing structures, that were connected with rope swings.

Diet and enrichment

Individuals were fed together, three to four times per day, in both their indoor and outdoor enclosures. Food was scattered by a care-giver, ensuring that all individuals received food, something which resulted in minimal competition. The diet consisted of 9% ape biscuits and cereals, 35% vegetables, 26% green leaf vegetables, and 29% fruits. Individuals were fed a selection of approximately 25 different types of food per week and each feed was typically composed of a mixture of two or more food types. Water was freely available via water feeders in their outdoor and indoor enclosures. The artificial termite mound in the outdoor enclosure was filled each day with honey and human baby food. Previously, the bonobos had been trained how to use dipping sticks, which were provided for them when the termite mound was filled. The bonobos were also given separate supplementary enrichment feeds (such as ice lollies, popcorn and seeds), several times per week. In their indoor rooms, the bonobos were

---

[2] Additionally, any bonobo known to parent offspring was classed as an adult

provided with additional enrichment materials, such as clothing, boxes and newspaper. Music and television were also provided to the bonobos, with devices placed next to their indoor enclosures.

San Diego Wild Animal Park, USA

Group composition and facility set-up

The Park group consisted of eight individuals, which included three adult females, three adult males, one sub-adult female and one juvenile female (age range 3-34 years, table 3.1). The group spent all observation time together as a group. During the daytime, the group was housed in a large outdoor enclosure (approximately 3,000m^2), which was interconnected to heated, indoor housing facilities (one larger room, 47m^2, and three smaller rooms, each 40m^2). The outdoor enclosure consisted of a large open grass ‘island’ with trees and climbing structures, surrounded by a moat border. The outdoor enclosure at the Park provided particularly good opportunities for collecting high-quality recordings of vocalisations, because as well as having an open-air moat, the facility was closed to visitors.

Diet and enrichment

The diet consisted of 17% ape biscuits and cereals, 20% vegetables, 24% green leaf vegetables and 39% fruits. Similarly to the zoo, individuals were fed a selection of approximately 25 different types of food per week and individual feeds were composed of two or more food types. Individuals were given separate supplementary enrichment feeds (such as ice lollies, popcorn and seeds), several times per week. Clothes, boxes and newspaper were provided to the bonobos in both their indoor and outdoor enclosures.

Table 3.1. Group composition of the two bonobo study groups at San Diego Zoo and San Diego Wild Animal Park, USA.

Study group	Identity code	Name	Sex	Date of birth
San Diego Zoo	LN	Lana	F	03.04.79
	YN	Yenge	M	25.12.82
	LL	Lolita	F	20.07.89
	IK	Ikela	F	20.07.89
	JU	Junior	M	14.01.95
	MB	Mchumba	F	15.08.04
	MK	Makasi	M	22.04.00
	KS	Kesi	F	20.12.00
San Diego Wild Animal Park	LT	Loretta	F	22.01.74
	LO	Lori	F	04.11.87
	AK	Akili	M	07.02.80
	LR	Lenore	F	03.02.82
	EN	Erin	M	23.12.91
	JJ	Jumanji	M	05.05.96
	KL	Kalli	F	14.03.05
	MD	Mhude	F	15.04.01

Twycross Zoo, UK

Study period

At Twycross Zoo, UK, I conducted a naturalistic playback study on bonobo food-associated calls (chapter four). I conducted the research over four months, from April until July 2009. I received full ethical approval to conduct my research from the Twycross Zoo Research Committee and worked in compliance with the ethical guidelines set out by the British and Irish Association of Zoos and Aquariums (BIAZA).

Group composition and facility set-up

During the study period, the bonobo group was permanently separated into two subgroups (subgroups A and B). The two subgroups occupied separate indoor facilities but shared the same outdoor enclosure, via two separate doors. Subgroup A consisted of five individuals, which included two adult males, two adult females and one juvenile female (age range: 6-29 years). Subgroup B consisted of six individuals, which included one adult male, three adult females, one juvenile male and one juvenile female (age range 4-32 years, see table 3.2).

The two subgroups were housed within one large ‘bonobo house’, that was subdivided to have identical facilities on each side (see figure 5.1 in chapter five). Each subgroup was housed in one of two separated heated indoor halls ($62m^2$), with additional sleeping areas ($22m^2$, divided into three connected wire cages). A solid wall partitioned the two subgroup indoor rooms, which meant that no visual contact and only very minimal vocal contact was possible. Both facilities were separately connected to an outdoor enclosure ($588m^2$), via hydraulic doors. There was no visual contact between indoor and outdoor enclosures, although vocalizations produced outside could be heard indoors. In the mornings, subgroup A had access to the outdoor enclosure as well as their indoor enclosure. In the afternoons, subgroup A was brought inside and subgroup B was then provided access to both the outdoor enclosure and their indoor enclosure.

The outdoor enclosure consisted of an open grass mound with one large and two small climbing structures, which included a protective shelter. The top area of the grass mound was flat, but all edges were steep slopes, which descended as far as a concrete moat that encircled the perimeter of the enclosure. At the farthest end from the indoor facility was a water pool and flowing water feature. Surrounding the enclosure was a wall (1.8m from observer position) made of reinforced glass.

Diet and enrichment

The diet consisted of approximately 57% fruits, 35% vegetables, and 8% biscuits and cereals. Both subgroups were fed a range of fruits and vegetables (12-14 different types, twice per day) in scatter feeds in their indoor and outdoor enclosures. Water was freely available at dispensers and from the outdoor water pool. The bonobos were provided with regular enrichment feeds (such as seeds, grapes, raisin or frozen juice), as well as edible branches. Once per week, the bonobos were provided supplements, including yogurt, egg, cheese and bread.

A diverse array of enrichment materials were provided on a daily basis. These ranged from cardboard/paper, shoes, clothing, rubber tubes (often lined with seeds and honey), balls and plastic containers, in which enrichment foods could be extracted.

Table 3.2. Composition of the two bonobo subgroups at Twycross Zoo, UK.

Group	Identity code	Name	Sex	Date of birth
subgroup A	KT	Kakowet	M	07.06.1980
	BY	Banya	F	16.02.1990
	KK	Keke	M	02.01.1994
	MR	Maringa	F	05.05.1998
	BK	Bokela	F	14.10.2003
subgroup B	DT	Diatou	F	21.10.1977
	JS	Jasongo	M	02.08.1980
	KH	Kichele	F	19.04.1989
	CK	Cheka	F	18.03.1996
	LU	Luo	M	01.12.2002
	GM	Gemena	F	07.11.2005

Lola Ya Bonobo Sanctuary, DR Congo

Study period

I conducted my research on copulation calls at Lola Ya Bonobo Sanctuary, DR Congo over two periods, for a total of seven months. I collected data between September and November in 2008, and between August and November in 2009. I received ethical approval from the Scientific Coordinator and Scientific Committee of ‘Les Amis des Bonobos du Congo’ (www.friendsofbonobos.org) for all aspects of this study. For one month in September 2008, I was assisted by another observer (T.G.), who collected independent focal data on the same group. In 2008, I collected data from the bonobos in enclosure one, henceforth ‘group 1a’. In 2009, I collected data from bonobos in both enclosure one and two, henceforth ‘group 1b’ and ‘group 2’, respectively. During this second period, the group composition in enclosure 1 had changed considerably. This was largely due to the transferral of individuals between groups during the period between study sessions. In addition, ten individuals left the sanctuary to be released into the wild and six others had died.

Group composition and facility set-up

Lola Ya Bonobo Sanctuary is situated in the Bas-Congo region of DR Congo, 30 km from Kinshasa. The tropical climate features a lengthy rainy season, which spans from October through May, with a relatively short dry season between June and September. Founded in 1996, Lola Ya Bonobo Sanctuary is the largest bonobo facility in the world (75 acres/30 ha) providing sanctuary for approximately 60-65 bonobos at any one time. Most individuals arrive as wild-caught infant or juvenile orphans, typically victims of the bush-meat and pet trades. Individuals spend their first few years rehabilitating within a nursery ‘cohort group’, where each bonobo is assigned a subsitute human mother. Following the nursery phase, individuals are then fully integrated into large, mixed social groups. Owing to the apparent tolerance and willingness of bonobos to integrate with new group members (Z. Clay, personal observation), bonobos at Lola Ya Bonobo Sanctuary are managed in a fluid and flexible manner, with individuals being regularly transferred between groups, in order to equilibrate group dynamics.

During the daylight hours, individuals roamed freely outdoors in one of three naturalistic forest enclosures (ranging from 5-15 ha), which comprised of primary natural rainforest, lake, swamp, streams and open grass areas (fig. 3.1). As a result of living in these forest microcosms, the bonobos at Lola Ya Bonobo were able to exhibit a full range of naturally occuring behaviours observed in wild bonobos (Andre et al., 2008). At night, individuals slept together inside dormitories (approx 75m^2, divided into open sub-rooms). Each enclosure had its own separate dormitory facilty connected to it.

During the period of study, group 1a was composed of 22 individuals, which included seven adult females, two sub-adult females, three adult males, two sub-adult males, four juvenile males and four infants (age classes as defined by Kano, 1992). Group 1b was composed of 20 individuals, which included six adult females, one sub-adult female, two adult males, four sub-adult males, three juvenile males and four infants.

Group 2 was composed of 19 individuals, which included four adult females, one juvenile female, three adult males, four sub-adult males, four juvenile males and three infants. Further information is provided in table 3.3.

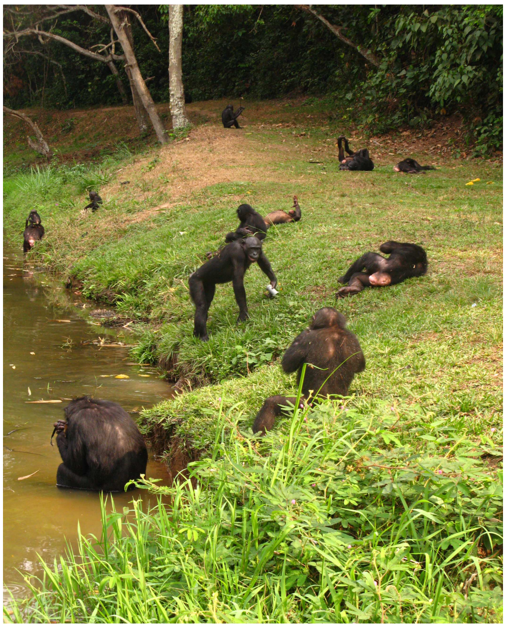


Figure 3.1. Photograph illustrating the study site at Lola Ya Bonobo Sanctuary, D R Congo. Photograph by Z. Clay.

<u>Diet and enrichment</u>

In addition to foraging themselves for wild fruits, leaves and herbaceous vegetation, the bonobos were provisioned with a wide variety of seasonal fruits and vegetables (typically 2-4 types of fruits and 6-9 types of vegetables per day) by caregivers, 3-4 times per day. The food was provided in a scatter feed, with each individual receiving approximately 6kg per day. Typically, fruits were provided in the mornings and vegetables in the afternoons. Sojamilk, supplemented with honey, maize and nutrients, was provided once per day to each individual. The bonobos were also provided with daily supplement feeds comprising of seasonal fruits and nuts. Water was freely available in lakes, ponds and streams within their enclosures. The consumption of vertebrates/invertebrates and the hunting of small mammals was never observed during the period of study.

Table 3.3. Composition of the three study groups at Lola Ya Bonobo Sanctuary, DR Congo. Individuals arrived as wild juveniles/infants, so age ranges are estimations, based on veterinary assessment. Dependent infants are indicated in super-script. Methods to assess dominance rank are indicated in subsequent sections of general methods.

Females				Males			
ID Code	Name	Age (years)	Rank	ID Code	Name	Age (years)	Rank
Group 1a							
MM	Mimi	26	High	MN	Manono	14	High
OP^{+1}	Opala$^{+\text{ Pole (m)}}$	13	High	TT	Tatango	14	High
SW^{+1}	Semendwa$^{+\text{ Elikia (f)}}$	12	High	KW	Kikwit	11	High
BD^{+1}	Bandundu$^{+\text{ Wongolo (m)}}$	11	High	BN	Beni	10	High
KL^{+1}	Kalina$^{+\text{ Malaika (f)}}$	11	Low	MA	Matadi	7	Low
IS	Isiro	11	Low	MX	Mixa	10	Low
SL	Salonga	11	Low	KD	Kindu	7	Low
NO	Nioki	10	Low	KG	Kasongo	6	Low
LK	Lukaya	8	Low	IB	Ilebo	7	Low
Group 1b							
MY^{+1}	Maya$^{+\text{ Bisengo (m)}}$	16	High	MN	Manono	15	High
OP^{+1}	Opala$^{+\text{ Pole}}$	14	High	KW	Kikwit	12	Low
BD^{+1}	Bandundu$^{+\text{ Wongolo}}$	12	High	MA	Matadi	8	Low
KS	Kisantu	11	Low	MD	Mbandaka	8	Low
SL^{+1}	Salonga$^{+\text{ Kimia (f)}}$	12	Low	BO	Boende	9	Low
NO	Nioki	11	Low	DL	Dilolo	8	Low
LI	Likasi	8	Low	LZ	Kasongo	7	Low
				KG	Luozi	6	Low
				VG	Vanga	5	Low
Group 2							
TL^{+1}	Tchilomba$^{+\text{ Moyi (m)}}$	24	High	MK	Makali	25	High
SW^{+1}	Semendwa$^{+\text{ Elikia}}$	13	High	KZ	Keza	19	High
KL^{+1}	Kalina$^{+\text{ Malaika}}$	12	Low	TB	Tembo	12	Low
IS	Isiro	12	Low	LM	Lomami	10	Low
MU	Muanda	6	Low	FZ	Fizi	9	High
				AP	Api	9	Low
				BL	Bili	8	Low
				MB	Mabali	8	Low
				IB	Ilebo	8	Low
				YL	Yolo	6	Low
				BY	Boyoma	5	Low

General protocols for data collection

Recording vocalisations

At all facilities, I collected audio recordings of bonobo vocalisations using similar methodology and equipment. Although the focus of my observations differed, the methodological protocol remained largely the same. At the first three facilities described (San Diego Zoo, San Diego Wild Animal Park and Twycross Zoo), I recorded food-associated vocalisations of bonobos during feeding events, which I then used either in further acoustic analysis (chapter four), or to construct playback stimuli (chapter five). At Lola Ya Bonobo Sanctuary, I recorded copulation calls from all sexually mature females or those approaching sexual maturity (with visible sexual swellings) during their sexual interactions with males and females.

In all facilities, I recorded vocalisations from a distance of 2-15m using a SENNHEISER MKH816T directional microphone and MARANTZ PMD660 solid-state recorder (sampling rate = 44.1 kHz, 16 bits accuracy). In order to identify the vocaliser or describe behavioural details, I provided additional verbal comments, which were later transcribed. Audio recordings were recorded as WAV files, which I digitally transferred onto a TOSHIBA EQUIUM laptop computer. I conducted file editing and quantitative acoustic analyses using PRAAT Sound Analyis Software version 4.3.37 (www.praat.org), including a pitch analysis script written by M. Owren (personal communication). All additional sampling methods are provided in subsequent chapters.

Food preference tests (chapters four and five)

An important aspect of my studies on food-associated calling behaviour (chapters four and five) was conducting tests of food preference. Using results from these food preference tests, I was able to explore the relationship between food-associated calls and the perceived quality of different food types. Whilst exact methods needed to be adjusted for each facility, the essential protocol and analyses remained the same.

Following the protocol designed by Slocombe and Zuberbühler (2006), all food preference tests consisted of a series of pair-wise tests. In each test, an individual was provided with two different types of foods and their first food choice was recorded. In order to determine the more preferred food within a given pair of foods, I repeated the pair-wise food test a minimum of two times, on two separate occasions. To calculate a preference score for each individual, I counted the number of times each food type was chosen over the other food types. I then converted these ‘first choice’ scores into percentages (high-preference foods = 67-100%, medium-preference = 34-66%, low-preference = 0-33%). Generally, vegetables consistently ranked as low preference foods in all study groups. Sweet and exotic fruits such as mangoes, bananas and kiwis ranked as highly preferred foods.

At San Diego Zoo, subjects chose between two food items of similar size and shape that were presented to them on a tray by a caregiver. Each individual was presented with the same array on at least two separate occasions, with item location counterbalanced. At San Diego Wild Animal Park, food preferences were established during regular lunchtime feeds, whereby subjects were individually provided with two different food items at least twice on two separate occasions. At Twycross Zoo, equal sized piles of two foods were placed next to each other on the ground and the first choice was recorded for each individual, repeated across four days, once per day.

Assessing social dominance (chapters six and seven)

Dominance data

An important aspect of my studies of copulation calls in bonobos was assessing the dominance status of female callers and their partners. Although pant-grunting has been shown to be a reliable indicator of dominance relations in chimpanzees (Noë et al., 1980), bonobos do not use pant-grunting as a reliable indicator of subordination (Furuichi & Ihobe, 1994; Stevens et al., 2005). Therefore, I created dominance hierarchies based upon the outcome of agonistic interactions between individuals (e.g. Stevens et al., 2007). I used ‘fleeing upon aggression’ as a behavioural marker for dominance, following previous work showing this to be a reliable measure of dominance in bonobos (e.g. Stevens et al., 2005a, 2007; Vervaecke et al., 2000a). I excluded any instances of agonistic interactions in which there was no fleeing behaviour (i.e. no reaction to the attempted aggression). I collected all-occurrence data on agonistic interactions during focal sampling periods as well as collecting additional data on an ad-libitum basis (Altmann, 1974).

Dominance analysis

I used the Matman matrix analysis program (by Noldus, version 1.1) in order to examine dominance relationships and to investigate linearity amongst the individuals in the three groups separately. I calculated the significance of the adjusted linearity index h' to investigate the linearity of the dominance relationships. This measure is corrected for the number of unknown relationships. Using Matman, I was able to test whether the adjusted linearity index differed significantly from the expected value for random dominance relations (de Vries, 1998; de Vries et al., 2006).

If there was significant linearity in a set of dominance relations, the dominance matrix was reorganized into a linear rank order. This rank order was consistent with the "I&SI" method, which involves minimizing the number of inconsistencies (I) and therefore the overall strength of the inconsistencies (SI) (de Vries, 1998). I also calculated the directional consistency index (DCI), which provides a measure for assessing how frequently a behavior occurred in its more frequent direction relative to the total number of times it occurred (van Hooff & Wensing, 1987). DCI is calculated using the equation DCI = (H - L)/(H + L), where H is the total number of times the behaviour occurred in the direction of the higher frequency, and L is the number of times in the less frequent direction. This index ranges from 0 (completely equal exchange) to 1 (complete undirectionality).

Demonstrating significantly linear dominance hierarchies influenced subsequent analyses of individual dominance ranks. If a linear hierarchy was demonstrated, I went on to investigate cardinal rank scores for each individual within the hierarchy.

To calculate cardinal dominance rank scores, I calculated David's Scores. David's scores (DS) are a type of cardinal rank measure, which use dyadic dominance proportions to provide a dominance score for a given individual (David, 1987). DS are based upon the individual's proportions of wins and losses in agonistic encounters, taking into account the relative strengths of each of their opponents (David, 1987; de Vries, 1998; de Vries et al., 2006). DS has been shown to be a more appropriate measure to calculate dominance ranks of individuals than the index derived by

Clutton-Brock et al. (1979), because it takes the relative strength of the opponents into account. Thus, in DS, an individual's dominance score is calculated by weighting each dyadic success measure by the un-weighted estimate of the individual's overall success: $w + w_2 - l - l_2$, where w is the number of wins of individual i over j, w_2 is the number of wins of their opponent j over i, and l being their respective losses. The overall DS is based upon the summation of individual i's dyadic interactions with each of their opponents (each termed individual j). Therefore the overall w_2 and l_2 scores are based upon also a summation of the outcome of each of their opponents' interactions with all of their own opponents). Further explanation of this method, accompanied by worked examples, is provided by de Vries et al. (2006).

In order to control for differences in the number of interactions, as well as group size, I calculated the normalized DS based upon the dyadic dominance index, corrected for chance (de Vries et al., 2006; Stevens et al., 2007). The dyadic dominance index calculates the degree in which individual i dominates individual j, relative to the total number of interactions between individuals i and j. This is calculated with $D_{ij} = s_{ij} / n_{ij}$, where s represents the proportions of wins of individual i over individual j, and n being the total number of dominance interactions between individuals i and j. To correct for chance, I used the assumption that the n + 1 possible outcomes of s and n are equally likely, leaving the normalized dyadic dominance index corrected for chance to be: $D_{ij} = (s_{ij} + 0.5)/(n_{ij} + 1)$ (de Vries et al., 2006). Replacing the normal proportions of winning and losing a conflict with the dyadic dominance index scores enabled me to assess dominance scores independent of group size or variation in number of dyadic interactions. Thus, using this correction for chances of winning, I calculated $DS = w + w_2 - l - l_2$, where w is the sum of i's D_{ij} values and l the sum of i's D_{ji} values. Similarly, w_2 and l_2 represent the summed w and l values of those individuals with which individual i interacted (de Vries et al., 2006; Stevens et al., 2007). Thus, the DS is based upon the summated values of interactions for which individual i and each of their opponents (individual j) were involved.

Finally, I normalized the DS (becoming NDS) based on my calculations for the dyadic dominance index (DDI), corrected for chance using: $NDS - DDI = [DS + (N (N - 1)/2)/N]$ where N is a group of N individuals. From this, I then plotted a regression line of these values organised in rank order (x-axis) against their respective

NDS – DDI values (y-axis) (using formulae created by J. Stevens, personal communication). I then performed an ordinary least squares linear regression on these NDS - DDI values to calculate the absolute value of the regression line slope, which gives the measure of the steepness of the dominance hierarchy.

It was especially important to gain accurate cardinal scores for female dominance as this formed a key aspect of my analyses of the influence of dyadic dominance relationships on female-female copulation calls (chapter seven). Fortunately, I found that female-based hierarchies were shown to be highly linear, which meant I was able to go on to calculate accurate cardinal rank scores for females (see appendix I). However, due to finding a large number of unknown relationships between males, I found that matrices that both combined males and females together, as well as male-only matrices, did not yield significantly linear hierarchies. Thus, in order to retain the accurate dominance scores that could be calculated for females, I refrained from combing the hierarchies and developed an alternative way to analyse male dominance that did not require cardinal rank scores, as I will explain.

For both females and males, I divided the individuals into either high or low rank classes. For females, I created these classes based on the regression line which plotted their cardinal rank scores (appendix I). I divided the female hierarchy into high- and low-ranked classes at the place where there was the clearest divide in dominance scores (appendix I: fig.1). These rank classes reflected intuitions about the social relations of the females during observations. For instance, the high-ranked females occupied the central positions in the groups, had priority access to food, elicited submissive behaviour in males and rarely behaved submissively. Results are shown in appendix I.

Amongst males, the absence of significant linearity was most likely due to the high-number of unknown relationships, something attributable to a large number of sub-adult males in the groups that had not yet organised themselves into stable hierarchies (discussed in appendix I). Whilst an absence of linearity meant it was therefore inappropriate to assign individual dominance scores, or place the individuals on a linear hierarchy, it was clear during observations that there were several high-ranking males in each group, who consistently elicited submission from others. In order to account for this dominance distinction, I therefore took a more simplistic approach of assigning males to a ‘high’ and ‘low’ rank category, based upon the number of agonistic interactions in which the male dominated their partner (other male fled). I assigned ‘high-rank’ status to any male who dominated at least 50% of the other males in the group. The results of dominance analyses are indicated in appendix I (see appendix I: table 1).

Chapter four: Food-associated calling sequences in bonobos

Summary

When encountering food, chimpanzees and some other primates produce specific food-associated vocalisations, whose acoustic structure co-varies with the caller's food preference. In chimpanzees, individuals produce the acoustically graded 'rough grunt' in response to food, and there is evidence that variation in the acoustic structure of this call type is meaningful to receivers. In comparison to chimpanzees, there has been no empirical investigation of the acoustic structure of food-associated calls in bonobos. In the current study, I addressed this by exploring the vocal behaviour of two groups of captive bonobos in response to food. Results indicated that bonobos produce five acoustically distinct calls types during interactions with food, with only one call type, the 'grunt', being acoustically similar to the chimpanzee 'rough grunt'. Furthermore, rather than given singly, I found that individuals frequently mixed these different call types together into longer, heterogeneous call sequences. I established the food preference hierarchies for ten different individuals, housed at two different facilities. I found that the composition of call sequences produced by these individuals was not random, but related to the type of food encountered by the caller. Significant variation in call composition was explained by taking into account the caller's individual food preferences, suggesting that bonobo food-associated calling sequences may convey meaningful information to other group members.

Results from this study have been published in:

Clay, Z., & Zuberbühler, K. (2009). Food-associated calling sequences in bonobos, *Pan paniscus*. *Animal Behaviour*, 77 (6), 1387- 1396.

Introduction

Upon the discovery of food, numerous mammals and birds produce specific vocalisations that frequently attract other group members to the food source (e.g. Chapman & Lefebvre, 1990; Dittus, 1984; Elgar, 1986a, b; Hauser & Marler, 1993a, b; Henrich & Marzluff, 1991; Roush and Snowdon, 2000; but see Gros-Louis, 2004b). Since food is often patchily distributed and seasonally dispersed, calls indicating food discovery can provide listeners with a useful means to access foraging patches more effectively. A number of suggestions have been put forward to explain the potential fitness benefits of these calls. For example, food-associated calls may serve to decrease predation risk by increasing group size, resulting in increased vigilance (Elgar, 1986b) or dilution (Newman & Caraco, 1989; Pulliam & Caraco, 1984; Ruxton, 1995). In rhesus macaques (*Macaca mulatta)*, food-associated calls have been suggested to announce ownership, in order to decrease risk of punishment from dominant conspecifics (Hauser & Marler, 1993b). In white-faced capuchins (*Cebus capucinus*), food-associated calls are thought to announce ownership as a means to decrease foraging competition from other conspecifics (Gros-Louis, 2004b). In some primates, food-associated calls may provide a number of other social benefits, including attracting mates (Marler et al., 1986b; Stokes & Williams, 1971; van Krunkelsven et al., 1996) or coalition partners (Caine et al., 1995; Slocombe et al., 2010b; van Krunkelsven et al., 1996).

The proximate mechanisms and cognitive sophistication underlying the production of food-associated calls have been subject to considerable debate. In particular, it remains elusive as to whether these calls are simply inflexible and hardwired responses primarily driven by the arousal state of the signaller, or serve as more communicative acts that inform others about feeding events (e.g. Marler et al., 1992). Whatever governs call production, various primate and bird studies have demonstrated that receivers can interpret food-associated calls in terms of the event experienced by the caller, at least by having their attention referred to the event (e.g. toque macaques, *Macaca sinica*, Dittus, 1984; cotton-topped tamarins, *Saguinus oedipus*, Roush and Snowdon, 2000; tufted capuchins, *Cebus apella*, Di Bitetti, 2005). In some primates, call production has been shown to be associated with food quantity or divisibility (e.g. chimpanzees, *Pan troglodytes*, Hauser & Wrangham, 1987; spider monkeys, *Ateles geoffroyi*, Chapman & Lefebvre, 1990; rhesus macaques, Hauser & Marler, 1993a). In other species, features of the acoustic signal itself appear to convey information about food quality, mainly in terms of changes in call rates (domestic chickens, *Gallus domesticus*, Marler et al., 1986; Gyger & Marler, 1988; cotton-top tamarins, Elowson et al, 1991; Roush & Snowdon, 2000; red-bellied tamarins, *Saguinus labiatus*, Caine et al., 1995; white-faced capuchins, Boinski & Campbell, 1996; Gros-Louis, 2004a,b), but also in terms of changes in call structure (e.g. golden lion tamarins, *Leontopithecus rosalia*, Benz, 1993; Benz et al., 1992).

One of the more complex systems of primate food-associated calls so far described is in rhesus macaques. These primates have been shown to produce five acoustically distinct calls and production varies with the perceived food quality, although some call types are also produced in non-food contexts (Hauser & Marler, 1993a, b). In a habituation-dishabituation experiment, listeners were found to distinguish these food-associated calls on the basis of their functional referents rather than acoustic structure (Hauser, 1998), supporting the argument that such calls convey meaningful information about external objects to receivers.

In comparison to monkeys, relatively less is known about how apes communicate about food. Chimpanzees, in contrast to rhesus monkeys, have been shown to produce one main graded call type in response to food, the ‘rough grunt’ (Goodall, 1965, 1968, 1986; Marler & Tenaza, 1977). In a comparative study of wild and captive chimpanzees, Slocombe & Zuberbühler (2006) found that the acoustic structure of this grunt vocalisation co-varied with perceived food quality. Furthermore, a playback experiment demonstrated that a receiver’s foraging strategy was influenced by hearing different acoustic variants of this call, suggesting these calls can provide meaningful information to receivers (Slocombe & Zuberbühler, 2005b).

As outlined in chapter two, relatively little is known about how bonobos communicate about food as compared to chimpanzees. Preliminary observations in wild and captive settings have suggested that bonobos produce a range of call types when encountering food (Bermejo & Omedes, 1999; de Waal, 1988). Furthermore, individuals have been shown to regularly combine calls together into longer vocal sequences that frequently attract other group members (Bermejo & Omedes, 1999; de Waal, 1988; Z. Clay, personal observation). The variable use of vocal sequences suggests the potential for calls to be combined in different ways to provide different meanings.

In the current study, I systematically examined the food-associated vocal behaviour of two groups of bonobos housed in San Diego, USA. The main aims were to describe their food calling behaviour and to examine whether patterns were related to the callers' food preferences, and as such, provide referential information to listening conspecifics.

Methods

Study sites

I collected data from two groups of captive bonobos at San Diego Zoo and San Diego Wild Animal Park (both $N = 8$ individuals), between January and April 2008. Further information describing the group composition, diet and facility set-up is provided in chapter three.

Food preferences

I determined the food preferences of ten adult individuals, five from each group. I excluded the juveniles and sub-adults ($N = 2$ juveniles and $N = 1$ sub-adults at both the Zoo and the Park) as their extremely low rates of food-associated call production prevented their inclusion as study subjects. Using the methods described in chapter three, I conducted pair-wise comparison tests for twelve different food types at the Zoo and eleven at the Park. These foods are indicated in table 4.1.

Recording vocal behaviour

As outlined in chapter three, I recorded vocalisations given by individuals interacting with one type of food. I conducted my observations and collected recordings during routine feeds provided by the caregiver. I excluded calls produced by individuals interacting with more than one type of food, or when caller identity was uncertain. I recorded vocalisations from a range of locations throughout the enclosures, from a distance of 2-15m. To control for hunger levels, novelty and other environmental and social factors, I only conducted subsequent analyses on calls produced during first main feeds. I recorded a minimum of 30 seconds of food-associated calling behaviour for a given focal animal in order to conduct acoustic analyses of sequence composition.

Call selection

I recorded a total of 448 calling sequences from the ten most vocally active adult individuals (Zoo females: LN, IK, LL; Zoo males: YN, JU; Park females: LT, LR; Park males: EN, JJ, AK). The youngest individuals (KS, MK, MB, MD) rarely vocalised during feeding events and so I was unable to include them in analysis. The beginning of a call sequence was defined as the point at which an individual made physical contact with a food item. To maximise the quality of the data set, I excluded any recordings that suffered from extensive background noise or other interference. I then randomly selected, for each individual, three calling sequences from the high, medium and low preference classes ($N = 90$). Within each preference class, calls were selected randomly with regard to food type. Because sequences varied considerably in the number of calls produced (approx range 1- 40 calls per uninterrupted sequence), I only conducted acoustic analyses on the calls within the first three calls of a sequence of at least three calls ($N = 270$ calls).

Acoustic analyses

I carried out quantitative analyses of the acoustic structure of the different vocalisations, using PRAAT 4.3.17 Sound Analysis Program (www.Praat.org). Except for one call type, the ‘grunts’, the other food-associated call types lay on a graded continuum and thus could be analysed using the same selection of acoustic parameters (fig. 4.1). However, the grunts showed a fundamentally different acoustic structure compared to the other vocalisations, which required a different set of acoustic parameters. Grunts were typically unvoiced, much noisier, low-pitched and exhibited strong formant bands (fig. 4.2). For grunts, I used the following settings: analysis window length 0.025s, dynamic range 30dB, and spectrogram window length 0.005s. For all other calls, I used the following settings: pitch range: 500-2500Hz, optimised for voice analysis; spectrogram view range: 0–20kHz (to determine the number of harmonics) and 0-5kHz (window length 0.01s, dynamic range 70dB) to measure fundamental frequency. I performed pitch analyses using a script written by M. Owren (personal communication), and I verified the generated values using a harmonic cursor. All further spectral measurements were taken from the fundamental frequency (F_0). I conducted my acoustic analyses based on the following parameters (fig 4.1):

(1) mean fundamental frequency (Hz): average F_0 across the entire call

(2) transition onset (ΔHz): frequency of maximum energy at call onset, minus frequency of maximum energy at call middle

(3) transition offset (ΔHz): frequency of maximum energy at call middle minus frequency of maximum energy at call offset

(4) overall transition (ΔHz): frequency of maximum energy at call end minus frequency of maximum energy at call beginning

(5) maximum fundamental frequency (Hz): maximum frequency of F_0

(6) minimum fundamental frequency (Hz): minimum frequency of F_0

(7) peak time: location in the temporal domain where maximum acoustic energy occurs, expressed as a proportion of the call duration

(8) number of harmonics: number of harmonic bands visible

(9) call duration (s)

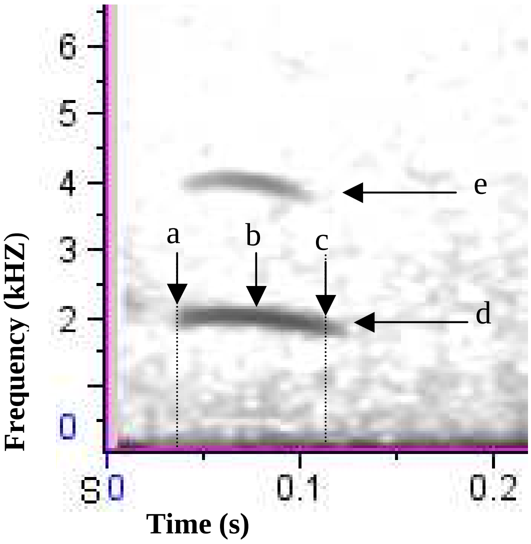


Figure 4.1. Example of some of the temporal and structural parameters measured on food-associated calls: call duration (s) = c-a; fundamental frequency, F_0 (Hz) = d; *N* harmonics (*N* = 1 in this call) = e; transition onset (ΔHz) = frequency of maximum energy at call onset (a) - frequency of max energy at call middle (b); transition offset

(Δ Hz) = frequency of maximum energy at call middle (b) – frequency of maximum energy at call offset; overall transition (ΔHz) = frequency of maximum energy at call end (c) – frequency of maximum energy at call onset (a). Depicted is a time-frequency spectrogram of a peep vocalisation made by adult female LR.

As grunts were mainly unvoiced, they did not possess an F_0 produced by oscillations of the vocal folds. Thus, to calculate the F_0 for grunts, I counted the number of oscillations visible in the spectrogram produced by other filtering mechanisms within the vocal tract, divided by the duration of the call (fig. 4.2).

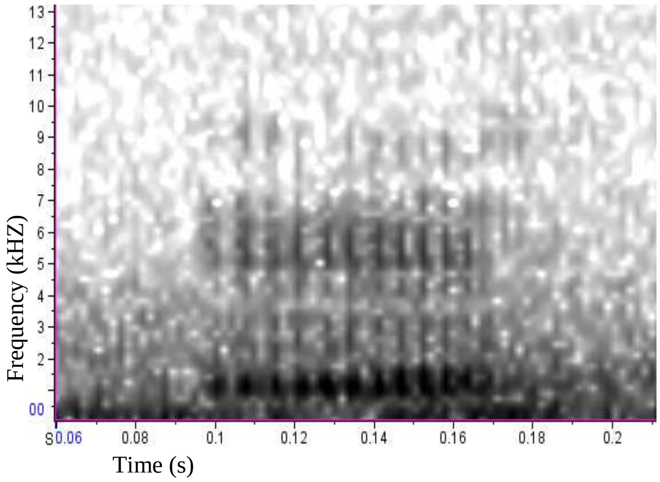


Figure 4.2. Time-frequency spectrogram illustrating a grunt vocalisation produced by LT, an adult female, whilst feeding on apples.

Before continuing, I first screened the data for outliers in any of the acoustic parameters by producing standardised Z scores. I rejected calls with a Z score greater than 3.29 (+/-) in one or more parameters, as recommended by Tabachnick & Fidell (2001). I then screened for multi-colinearity and singularity amongst parameters by regressing all parameters and removing any parameters with a variance inflation factor greater than 10.0. Variance inflation factors measure the degree to which the variance of one parameter is inflated by the existence of linear and higher order correlation amongst other parameters in the model. They are therefore a sensitive measure of co-linearity and highlight potential problems of instability in a model.

Following these checks, I conducted a Discriminant Function Analysis (DFA) to assess whether each of the uncorrelated acoustic variables, when combined in one model, could discriminate between the four graded call types. Discriminant Function Analysis can be sensitive to unbalanced datasets and thus to account for this, each of the 10 individuals equally contributed five randomly selected calls for each of the four vocalisations (*N* = 200 calls, excluding grunts). Therefore, 50 calls were entered for each vocalisation. In the DFA, I used the leave-one-out classification procedure in order to cross-validate the discriminant functions that were generated. In this cross-validation procedure, each call is classified by the functions derived from all calls other than that one. Since the acoustic data for food-associated calls were two-factorial (caller identity; call type), it has been argued that conventional DFA does not allow for an entirely valid estimation of the overall significance of discriminability (Mundry & Sommer, 2007). Therefore, to control for caller identity and repeated contributions, I conducted an additional permutated Discriminant Function Analysis (pDFA), using a macro written by R. Mundry and C. Sommer (Mundry & Sommer, 2007). The pDFA estimated the significance of the number of correctly classified calls (cross-validated).

After checking that the data fulfilled the parametric assumptions, I also ran one-way, related samples analysis of variance tests (ANOVAs) to examine whether each of the individual acoustic parameters varied statistically with each call type. In this parameter-based analysis, I was able to include grunts in the analyses of call duration and mean fundamental frequency. Each individual (*N* = 10) contributed a mean value per call type per parameter, which was derived from 5 calls per call type category (*N* = 250 raw calls). I conducted post-hoc, pairwise comparisons, with a Sidak correction, to examine whether any of the acoustic parameters could discriminate between the call types.

In addition to the statistical analyses, I wanted to test whether human observers could reliably discriminate call types. To do this, I carried out inter-observer reliability tests for the classification of call types using two naïve observers. After completing a training set of pre-classified calls (randomly selected 10%, of original call set), the naïve observers independently classified 10% of the original call set (*N* = 30 calls). The test set comprised of an equal selection of each of the 5 call types, all randomly selected. With their scores, I calculated Cohen’s Kappa coefficients to determine whether the levels of observer agreement reached the standard accepted level (Cohen's κ = 0.80).

Structure of call sequences

The focus of the second major analysis concerned the structure and composition of call sequences. In total, I analysed N = 236 raw call sequences produced by 10 individuals. Each individual contributed at least two call sequences per food type (range of 2-5 call sequences for high, medium and low preference food classes). I then calculated the means of the raw call sequences for three randomly selected different food types for each of the three preference categories. Because call number and sequence length were variable, I measured the sequence composition in the first 30 seconds. I measured (i) the absolute number of each call type (first 30s per sequence) and (ii) the relative proportion of different call types (first 30s per sequence), (iii) the inter-call interval (first three calls only) and (iv) the call rate (N calls within first 30s per sequence). Due to my considerable experience with the calls, I was able to assign the call types in this analysis by visual and audio inspection. This was validated by results indicating statistically significant call type categorisation in the acoustic analysis as well as reliable classification in inter-observer reliability tests (see results section).

In order to examine whether sequence composition varied as a function of food preference, I calculated the mean number and relative proportion of each call type produced in sequences to high, medium and low preference foods. The absolute number provided information as to the distribution of each call type across preference classes, whereas the proportions data provided information as to the relative contributions each call type made to the overall sequence. One overall mean per combination of individual and food preference category was entered. For each individual, the overall mean was calculated from the means of three randomly selected food types for each of the three food preference levels. For both analyses, I used a matched pairs design using Friedman and Wilcoxon-signed ranks tests (exact, two-tailed) and a Sidak’s correction to minimise the risk of family-wise errors.

To analyse the inter-call intervals, the data were shown to fulfil parametric assumptions and thus I was able to conduct univariate ANOVAs, with food preference entered as the fixed factor (high, medium, low) and caller identity as the random factor. Data were analysed from all ten individuals, with inter-call intervals taken from three randomly selected food types for each of the three preference categories (N = 90 sequences). I calculated the median of the first three inter-call intervals within each sequence.

To analyse call rate within the sequence, I calculated the mean number of calls produced within the first 30 seconds of a sequence. Each individual contributed a mean call rate per preference class, taken from the means of three randomly selected food types. As the call rate data were not normally distributed, I conducted non-parametric Friedman and Wilcoxon signed ranks tests (exact, two-tailed).

I conducted all statistical tests using SPSS version 17.0 except for the permuted Discriminant Function Analysis, which was conducted using R 2.8.1. (R core development team) using a script written by R. Mundry & C. Sommer (personal communication). All tests were two-tailed and alpha levels were set at 0.05, unless stated as being corrected.

Results

Food preferences

I conducted pair-wise choice tests for all possible combinations of twelve food types at the Zoo and eleven food types at the Park. Whilst I found some consistency of food preferences across individuals, particularly for the most preferred foods, I also found some minor individual differences (table 4.1). Sweet fruits, such as figs, raisins and bananas rated highly, whereas vegetables rated as low preference. As described in chapter three, I used results from the food preference tests to assign the foods into three preference classes for each individual, based on the preference scores: high (67-100% first choices), medium: (34-66% first choices), low: (0-33% first choices).

Table 4.1. Results of food preference tests conducted at the San Diego Zoo and Wild Animal Park. Italicised font indicates high preference foods, bold font indicates medium preference food and normal font represents low preference foods. Dashes indicate foods that were not provided.

	Zoo individuals					Park individuals				
	LN	LL	IK	YN	JU	LT	LR	EN	AK	JJ
Food	Individual's food preference (%)									
Fig	-	-	-	-	-	*100*	*100*	*100*	*100*	*100*
Raisin	*100*	*100*	*100*	*95*	*91*	*90*	*90*	*90*	*90*	*90*
Grape	*91*	*91*	*91*	*95*	*91*	*70*	*75*	*80*	*75*	*80*
Banana	*77*	*77*	*73*	*82*	*91*	-	-	-	-	-
Popcorn	*73*	*73*	**55**	**60**	**60**	-	-	-	-	-
Apple	**55**	**64**	**59**	**59**	**55**	**60**	**60**	**65**	*70*	*70*
Orange	**65**	**55**	**66**	**64**	**64**	**50**	**50**	**50**	**45**	**50**
Biscuit	**46**	**36**	32	32	**36**	**65**	**65**	**65**	**60**	**60**
Celery	-	-	-	-	-	25	**40**	**40**	**40**	**40**
Melon	27	**34**	14	**36**	41	-	-	-	-	-
Lettuce	18	18	14	18	18	25	30	25	30	30
Yam	9	18	18	18	9	8	20	10	10	10
Pepper	9	31	9	27	18	10	0	0	0	0

Acoustic analyses

My preliminary observations suggested that bonobos produced five perceptually distinct call types in response to food: barks, peeps, peep-yelps, yelps and grunts (fig. 4.3).

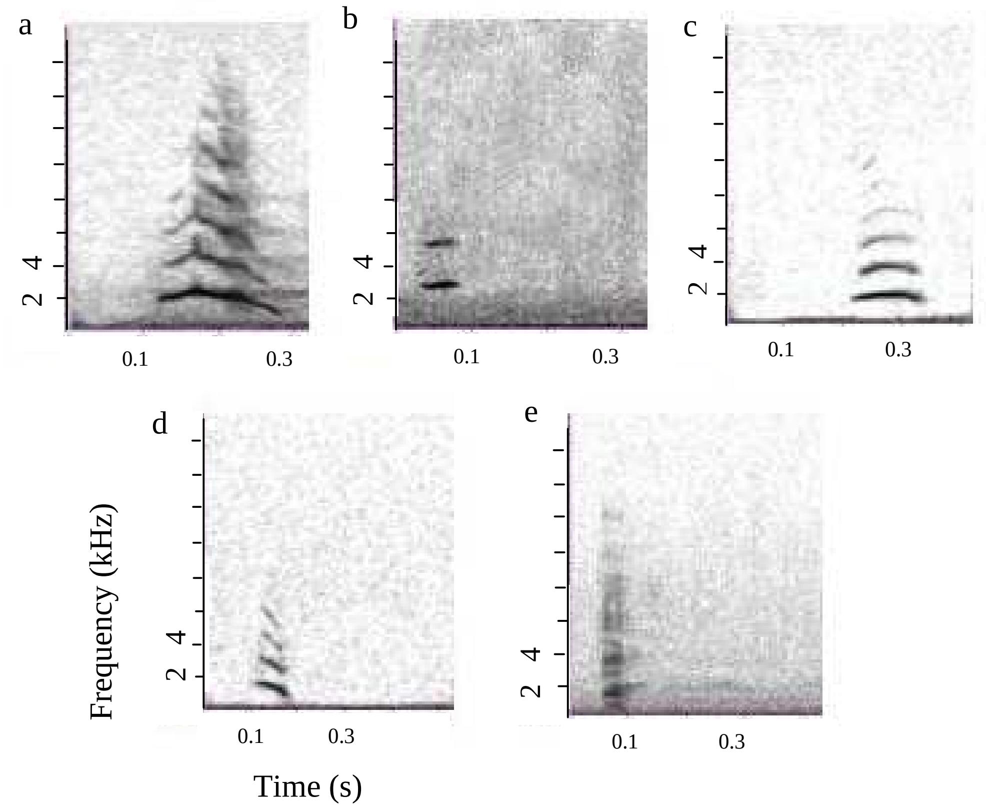


Figure 4.3. Examples of time-frequency spectrograms illustrating five different types of food-associated calls, produced by EN, an adult male bonobo: (a) = bark, (b) = peep, (c) = peep-yelp, (d) = yelp, (e) = grunt.

After checks for multi-colinearity and singularity, I was able to enter seven uncorrelated acoustic parameters, out of the original nine, for further analyses (N = 200 calls, excluding grunts): call duration, peak time, mean fundamental frequency, number of harmonics, transition onset, transition offset, and overall transition. Using these uncorrelated variables, I conducted a Discriminant Function Analysis (DFA), derived from all seven acoustic variables, in order to assess how well each of the acoustic variables could discriminate between the four graded call types (bark, peep, peep-yelp and yelp). Of the three functions used in the DFA, two functions significantly discriminated between the call types (see fig. 4.4). The functions explained a significant amount of the variation in the acoustic structure of the call types (Wilks' lambda = .089, $\chi^2 = 468.718$, df = 21, $P < .001$). In a cross-validated analysis, the functions successfully classified 86% (172/200) of the calls according to call type, a level of accuracy that was significantly higher than expected by chance (binomial test (0.25): $P < .001$). The success rate of classification of call types was highest for barks and peeps, followed by yelps and then peep-yelps (correct classification for barks = 96%, peeps = 94%, yelps = 80%, peep-yelps = 74%). I then used a permutated DFA (pDFA; Mundry & Sommer, 2007) to estimate the significance of the number of correctly classified calls (cross-validated, $N = 1000$ permutations). Results from the pDFA indicated a highly significant level of discrimination when caller identity was controlled for ($P = .001$).

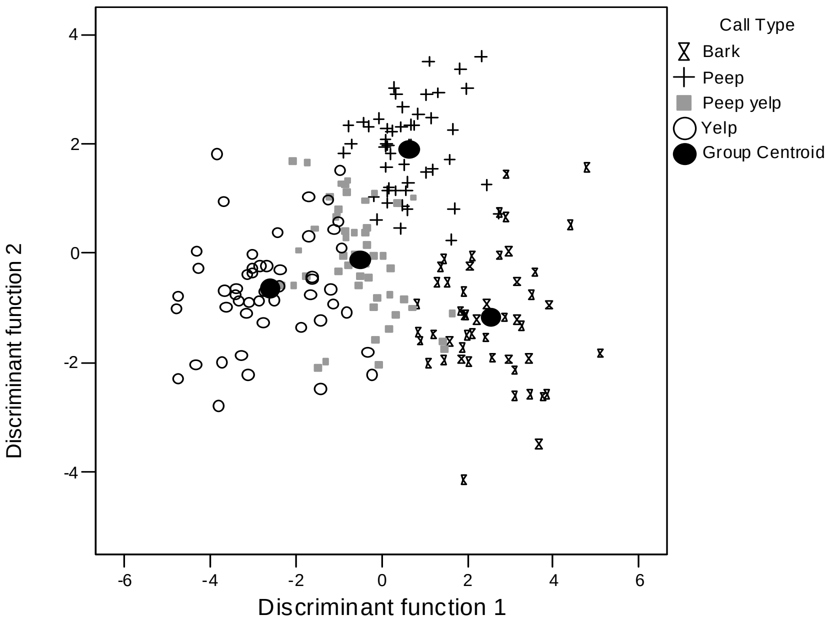


Figure 4.4. Distribution of discriminant scores along the two canonical discriminant functions established to discriminate different bonobo food-associated calls (Eigen values for Function 1 = 3.275; Function 2 = 1.351). Black circles represent group centroids. The four graded call types from the original classification overlay the discriminant function scores.

To examine whether each of the uncorrelated acoustic parameters varied statistically between call types, I conducted one-way related-samples analysis of variance tests with call type as the fixed factor and identity as the random factor. I was able to include grunts in the analyses of mean fundamental frequency and call duration. Both mean fundamental frequency and call duration varied statistically among call types (mean F_0: *F* (4, 36) = 329.409, *P* < 0.001; call duration: *F* (4, 36) = 10.300, *P* < 0.001). I also found that the five remaining acoustic parameters varied consistently amongst the four non-grunt call types (*N* harmonics: *F* (3, 27) = 30.071, *P* < 0.001; peak time: *F* (3, 27) = 6.299, *P* = 0.033; transition onset: *F* (3, 27) = 33.080, *P* < 0.001; transition offset: *F* (3, 27) = 10.894, *P* < 0.001). One acoustic parameter, overall transition, failed to reach significance (*F* (3, 27) = 2.908; *P* = 0.053). Post-hoc pairwise comparisons (with the Sidak-correction) revealed that mean fundamental frequency significantly discriminated among all call types except for the two highest pitched call types, the barks and peeps. Barks were significantly longer in duration and had more harmonic bands visible than other call types. Peeps were the shortest call type and showed significantly fewer harmonics than other call types. Barks had a pointed acoustic shape with steep upward (transition onset) and downward (transition offset) strokes in acoustic energy. Their steep upward stroke distinguished them from peeps, peep-yelps and yelps and their downward stroke distinguished them significantly from peeps and yelps. Yelps showed a distinctive overall downward stroke form, which discriminated them significantly from the acoustically flat peeps in both the onset and offset transition, and from the upward curving peep-yelps in the onset transition. Barks also had a significantly later peak time than peeps or yelps. In contrast to the other graded call types, grunts showed a markedly different structure; they had a distinctly noisy structure, were lower pitch, and were mostly unvoiced. Formants were visible but the harmonic bands and the fundamental frequency were not (table 4.3 and fig. 4.5).

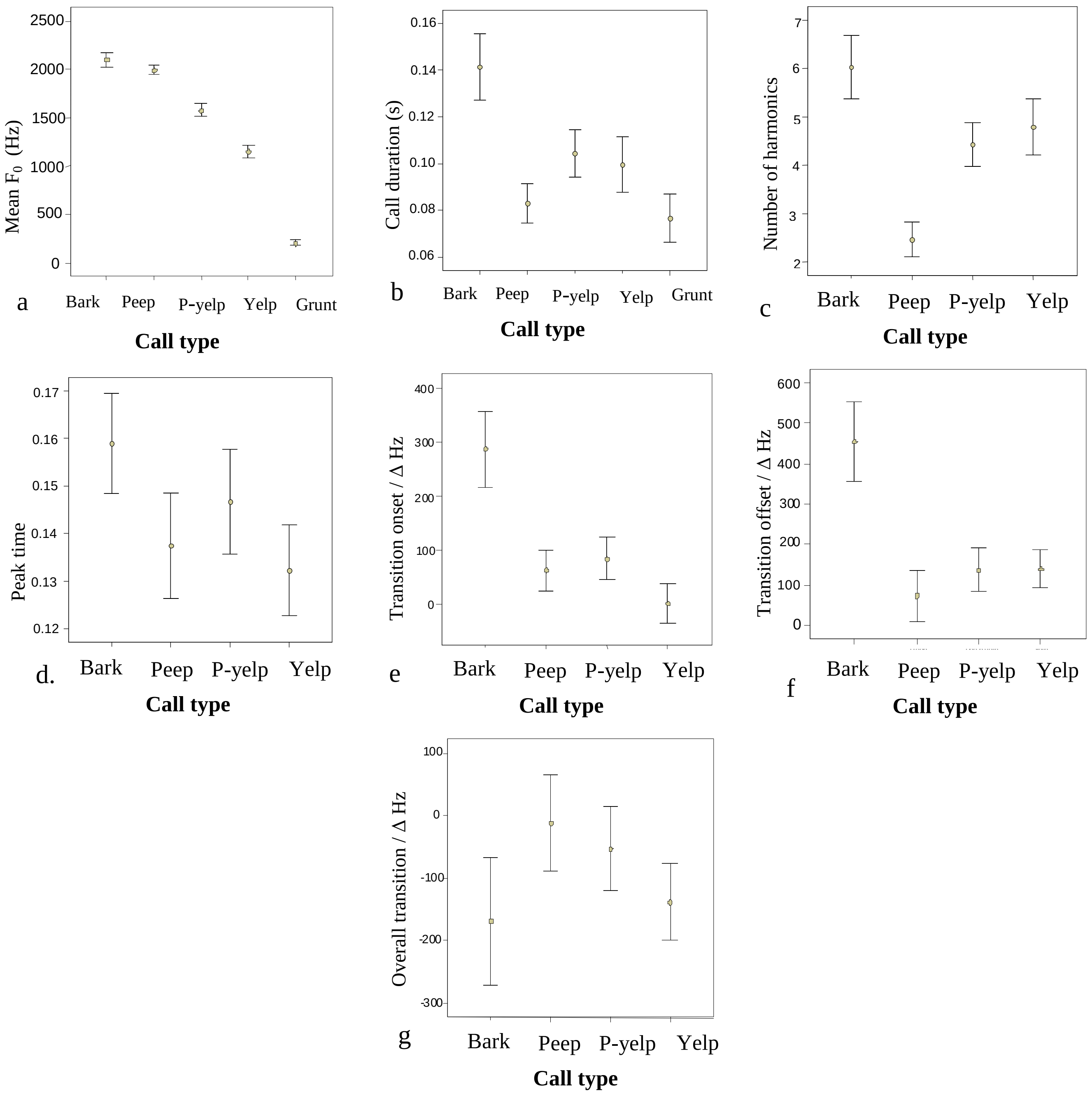


Figure 4.5. Mean values (with error bars) for seven acoustic parameters showing the similarities and differences between the different food-associated call types produced by bonobos at San Diego Zoo and Wild Animal Park: a = fundamental frequency, F_0 (Hz); b = call duration (s); c = number of harmonics; d = peak time; e = transition onset (ΔHz); f = transition offset (ΔHz); g = overall transition (Δ Hz). The last five parameters are missing for grunts because the calculation of the F_0 required to calculate these parameters was not possible (grunts were typically unvoiced and did not possess a distinguishable F_0).

Table 4.2. Results of post-hoc Sidak-corrected comparison tests for differences between sample means of acoustic parameters of five food-associated call types. * *P* <0.05; ** *P* <0.01; *** *P* <0.001

Acoustic parameter	Call type	Bark	Peep	Peep-yelp	Yelp	Grunt
Call duration	Bark		**	*		**
	Peep					
	Peep-yelp					
	Yelp					
	Grunt					
Mean fundamental frequency	Bark			***	***	***
	Peep			***	***	***
	Peep-yelp				***	***
	Yelp					***
	Grunt					
Peak time	Bark		*		**	
	Peep					
	Peep-yelp					
	Yelp					
Number harmonics	Bark		***	**	*	
	Peep			**	**	
	Peep-yelp					
	Yelp					
Transition onset	Bark		***	**	***	
	Peep				*	
	Peep-yelp				*	
	Yelp					
Transition offset	Bark		**		**	
	Peep				**	
	Peep-yelp					
	Yelp					

In addition, I conducted an inter-observer reliability test with two naïve observers to verify whether the original call classification was reliable across human raters. Results indicated that the observers independently attained 97% and 93% agreement with my original classification. Inter-observer reliability scores showed very high levels of agreement (for Observer 1 and 2 respectively: Cohen's $\kappa = 0.96$, $= 0.92$) indicating that human observers could correctly classify calls with a high degree of accuracy.

Structure of call sequences

To describe the different call sequences, I first compared the absolute number of each call type per sequence. Each individual contributed an overall mean per preference class (calculated from the means of three food types, i.e. $N = 9$ for 10 individuals). Results from non-parametric Friedman tests revealed that the absolute frequency of all five call types varied significantly among preference classes (barks: $\chi^2 = 15.077$, $P <$

0.001; peeps: $\chi^2 = 16.632$, $P < 0.001$; peep-yelps: $\chi^2 = 8.6$, $P = 0.012$; yelps: $\chi^2 = 15.436$, $P < 0.001$; grunts: $\chi^2 = 7.913$, $P = 0.017$; for all df = 2). Using a Sidak corrected alpha level of 0.0169, post-hoc Wilcoxon signed-ranks tests revealed that significantly more barks and peeps occurred in sequences associated with high than low preference foods (barks: $Z = -2.521$, $N = 10$, $P = 0.008$; peeps: $Z = -2.803$, $N = 10$, $P = 0.002$) or medium preference foods (barks: $Z = -2.521$: $N = 10$, $P = 0.008$; peeps: $Z = -2.803$: $N = 10$, $P = 0.002$). Significantly more peep-yelps occurred in sequences associated with medium than low preference foods ($Z = -2.803$, $N = 10$, $P = 0.002$) and significantly more yelps occurred in sequences associated with low and medium compared to high preference foods (both: $Z = -2.805$, $N = 10$, $P = 0.002$). Finally, I found trends of increased grunt production in sequences associated with low and medium compared to high preference foods (high to low: $Z = -2.201$, $N = 10$; $P = 0.031$; high to medium: $Z = -2.023$, $N = 10$; $P = 0.063$). Results are shown in fig. 4.6.

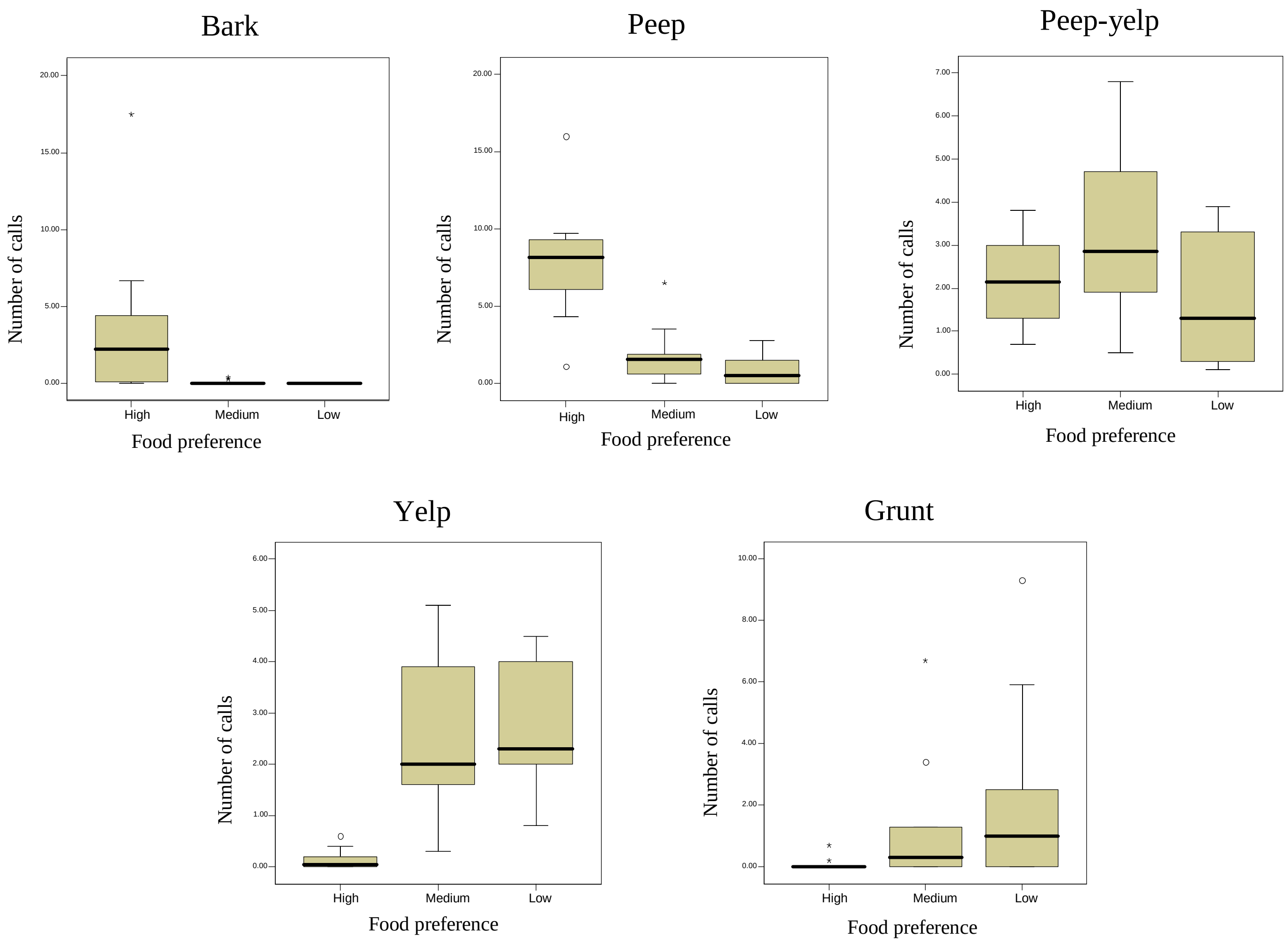


Figure 4.6. Box plots showing the number of times each of the five call types was produced within bonobo food-associated call sequences. Thick black lines represent

medians; box edges represent the upper and lower quartiles; whiskers represent the adjacent values, which are the most extreme values lying within hinges and the normal distribution of the sample. Outliers are marked with circles and extreme cases with asterisks.

To gain more information about the overall composition of the call sequences, I conducted Friedman's test to examine the relative contributions of different call types within the call sequences. When looking at the relative contributions of different call types, I found that the proportion of barks (χ^2 =15.44, df = 2, $P < 0.001$), peeps (χ^2 = 17.90, df = 2, $P < 0.001$), and yelps (χ^2 = 14.00, df = 2, $P < 0.001$) varied significantly amongst preference classes. Proportions of grunts also tended to be associated with preference classes (χ^2 = 5.48, df = 2, $P = 0.061$), but no significant differences were found for peep-yelps. Using a Sidak corrected alpha level of 0.0169, post-hoc Wilcoxon signed-ranks tests analysis revealed significantly higher proportions of both peeps and barks associated with high rather than low preference foods (peeps: $Z = -2.805$, $N = 10$, $P = 0.002$; barks: $Z = -2.521$, $N = 10$, $P = 0.008$) or medium preference foods (peeps: $Z = -2.803$, $N = 10$, $P = 0.002$; barks; $Z = -2.521$, $N = 10$, $P = 0.008$). Significantly higher proportions of yelps occurred in sequences associated with medium than high preference foods ($Z = -2.808$, $N = 10$, $P = 0.002$) and low compared to high preference foods ($Z = -2.66$, $N = 10$, $P = 0.004$). Finally, there was a trend of higher proportions of grunts occurring in sequences associated with low and medium compared to high preference foods ($Z = -2.666$, $N = 10$, $P = 0.046$; $Z = -2.808$; $N = 10$, $P = 0.043$, respectively). Figure 4.7. summarises the results.

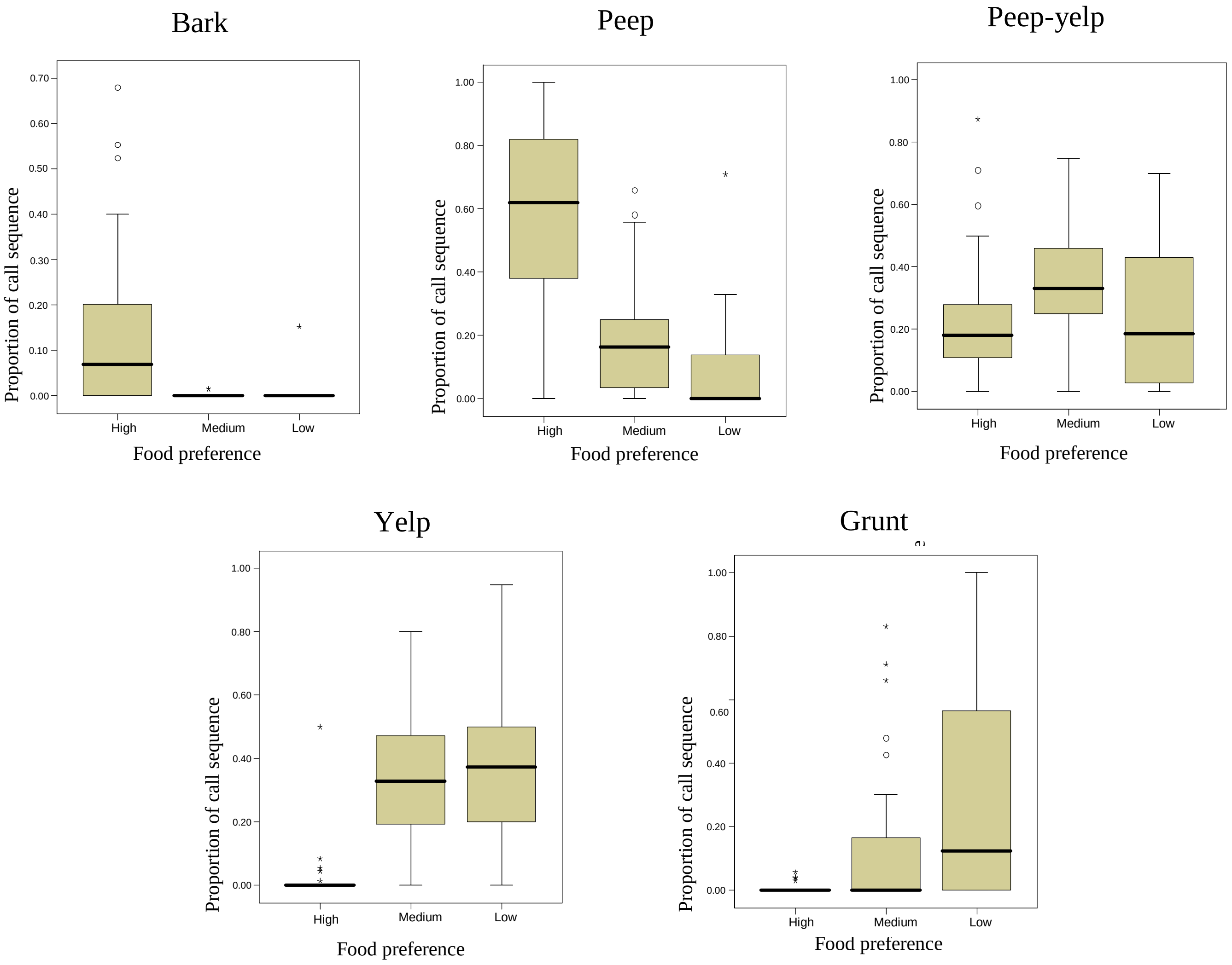


Figure 4.7. Box plots showing the relative proportions of the five call types present in bonobo food-associated calling sequences. Graphical features as described in fig.4.6.

Whilst I found no significant effect of food preference class on inter-call interval (*F* 92, 60) = 3.024, *P* = .073), there was a significant effect of call rate (Friedman's test: χ^2 = 7.2, df = 2; *P* = 0.03). Post-hoc analyses, using Wilcoxon signed ranks tests (Sidak correction) revealed a trend for more calls to be produced in association with high than medium or low preference foods (high vs. medium: *Z* = -2.293, *N* = 10, *P* = 0.02; high vs. low*: Z* = -2.090, *N* = 10, *P* = 0.037), but there was no difference in number of calls produced in association with foods of medium preference compared to low preference.

Discussion

This study demonstrated that captive bonobos at two locations produced five acoustically distinct call types when interacting with food: barks, peeps, peep-yelps, yelps and grunts. Although analyses revealed statistical relationships between call types and levels of perceived food quality, there was considerable overlap in the production of different call types across different food preference classes, indicating that the link between call type and food quality is only probabilistic in bonobos. One consequence is that different food-associated calls may not themselves allow listeners to make strong predictions about the type of food encountered by the caller. However, rather than producing calls singly, bonobos regularly combined different call types together into longer, heterogeneous sequences. Analysis revealed that the production and distribution of different call types within a sequence was not random, but related statistically to the preference score of the food. Barks were produced almost exclusively in association with highly preferred foods, and peeps were given in significantly greater proportions to high compared to medium or low-preference food. Peep-yelps, the intermediary call type, were produced indiscriminately of food preference, although they generally occurred most in sequences for medium to low preference. Significantly higher proportions of yelps were produced in calling sequences associated with medium and low preference foods compared to high preference foods. Whilst the trend was similar for grunts and yelps, these effects were not significant. Furthermore, although statistical discrimination between medium and low preference foods was not possible, I observed trends of increased production of yelps and grunts with decreasing food preference. The general lack of strong distinctions between medium and low preference foods may be due to an insensitivity of the acoustic parameters chosen, or due to the fact that bonobos genuinely only make strong vocal distinctions between high and non-high preference foods.

The five food-associated calls produced by the bonobos in San Diego lay on a graded pitch continuum, with barks at the high end, followed by peeps, peep-yelps, yelps and finally grunts. The grunts I observed were the least common but most acoustically distinct call type, with their more noisy acoustic structure and lack of energy in the fundamental frequency band and harmonics. Barks were longest in duration, characterised by a distinctive pointed shape and numerous visible harmonic bands.

Whilst peeps were also high pitched, they were temporally shorter than barks, with only few harmonic bands and had a flat frequency contour. However, whilst tempting to use the term ‘simplified structure’ here, the low number of visible harmonic bands actually suggests some complex filtering mechanism in the vocal tract may be occurring (e.g. Stevens & Weismer, 2001). Although yelps and peep-yelps were acoustically similar, peeps were noticeably shorter in duration while yelps possessed a marked downward stroke frequency contour, in contrast to the arched contour of the lower-pitched peep-yelps.

Analysis of the inter-call interval indicated that food preference did not affect the speed by which calls were produced per se. However, sequences produced in response to high preference foods contained significantly more calls, suggesting that, although rate does not increase, calls were produced in longer sequences. In a study on rhesus macaques, call rates were explained as an effect of differences in the callers’ hunger levels (Hauser and Marler, 1993a). However, hunger levels were unlikely to play a role in this study as the bonobos were fed the same quantity of food at the same time of day when recordings of the calls were collected.

Food-associated calls in chimpanzees and bonobos

A principal motivation of this study was to compare food-associated calls produced by bonobos with those of their closest relatives, the chimpanzees. Chimpanzees produce one main type of call in response to food, the highly graded ‘rough grunt’ (e.g. Goodall, 1986), which possesses an acoustic structure that relates to perceived food quality (Slocombe & Zuberbühler, 2006). In the current study, I found that bonobos also produced grunts that were acoustically similar to those produced by chimpanzees. However, in contrast to chimpanzees, bonobo grunts were the most infrequent of food-associated calls uttered and were mainly associated with lower preference foods. Furthermore, in contrast to chimpanzees, bonobos appear to communicate information about perceived food quality by producing a range of call types, which are combined together in probabilistic ways within call sequences.

The evolution of this species difference is somewhat difficult to understand and we currently lack empirical data relating to the divergence of the vocal system of the two

Pan species. Some of the acoustic variability between the two species may be accounted for by anatomical and social factors. For example, bonobos are smaller in size than chimpanzees and display a number of neotenous characteristics in their cranio-facial morphology (Cramer, 1977) and regions surrounding the basicranium (Laitman & Heimbuch, 1984). Consequently, bonobos most likely possess smaller vocal tracts than chimpanzees, which may account for the raised pitch of their food-associated calls. However, this feature does not readily explain why bonobos produce a suite of other food-associated vocalisations in addition to the more chimpanzee-like grunt. In terms of social factors, Mitani and Gros-Louis (1995) suggested that the greater degree of group dispersion in chimpanzees compared to bonobos (Nishida & Hiraiwa-Hasegawa, 1987) may favour the production of lower-frequency vocalisations that attenuate less and are transmitted more efficiently than high-frequency vocalisations (Wiley & Richards, 1978). Whilst more research into such questions is needed, results from this study suggest that chimpanzee and bonobo vocal behaviour in the food context has diverged relatively rapidly.

In some ways, the vocal behaviour observed in bonobos in this study shows similarities with patterns previously described in rhesus macaques (Hauser & Marler, 1993a). Rhesus macaques also produce five call types in response to foods, some of which are associated with highly preferred or rare foods (warble, harmonic arches and chirps). Coos and grunts are produced in both food and non-food contexts, and only grunts differ between these contexts. In this study, I found that the production of peep-yelps occurred indiscriminately across preference classes, similar to the rhesus monkeys' coo calls. Peep-yelps were also produced in a range of other non-food contexts, and thus more systematic work examining acoustic morphology is required before making more precise comparisons.

The function and meaning of bonobo food-associated calls

These results suggest that bonobos are able to communicate meaningfully about an important type of external event, the discovery of food. The mechanisms underlying call production, for example, whether the result of a deliberate attempt to inform others or a mere reflection of changes in arousal, largely remain obscure. The signal characteristics of the different food-associated calls are in line with arousal-based explanations of call production (Marler, 1977; Marler et al., 1992; Rendall et al., 2009). For example, the two highest pitched call types, barks and peeps, are reliably given during contact with highly preferred foods, a context which likely provokes a high degree of arousal in the signaller. In chimpanzees, rough grunts given to highly preferred food items were also shown to possess acoustic features, such as higher peak frequencies and first formant frequencies, which would suggest a greater degree of 'arousal' within the signaller (Owren et al., 2010; Slocombe & Zuberbühler, 2006). In this way, it is likely that, to some extent, both bonobo and chimpanzee food-associated vocalisations may provide listeners with a means of assessing the caller's emotional response to the value of the food patch. Nevertheless, results from a host of studies indicate that calls with 'arousing' features, such as may be the case for food discovery, may still provide information to receivers (Seyfarth et al., 2010). Thus, rather than only relying on motivational explanations, which depend upon the elusive concept of 'arousal', that is difficult to quantify and measure experimentally, it appears more useful to adopt the information-based approach, which provides a frame-work in which the informational content of animal signals can be studied scientifically .

Another important observation is that some of the calls described, particularly the peeps and peep-yelps, appear to also be produced in non-food contexts, such as during mother-infant interactions, grooming, alarm, travel and also after agonistic encounters (Bermejo & Omedes, 1999; de Waal, 1988). De Waal (1988) suggested that bonobos frequently respond to and 'comment' on new and interesting objects using peep –like vocalisations. Of course, it is always possible that there is subtle but consistent context-specific acoustic variation within the call types, a topic for future research. Alternatively, it is possible that bonobos use these calls in a range of contexts, suggesting that their communicative significance is broader than referring a listener's attention to the fact that food has been discovered. Bonobos are known to forage more closely together in stable mixed parties than do chimpanzees (e.g. Furuichi, 2009; White & Wrangham, 1988) and it has been suggested that food-associated vocalisations may be used to maintain communication between foraging party members who may lack visual contact (Bermejo & Omedes, 1999).

The function of food-associated calls presents somewhat of an evolutionary conundrum. From the signaller's perspective, such behaviour is costly if it leads to loss of food to competitors (Elgar, 1986b). However, callers could minimise these costs if they took into account, for example, food patch size, divisibility, or composition of the nearby audience (Hauser et al., 1993a, b; Hauser & Wrangham, 1987; Zuberbühler, 2008).

Despite the costs of attracting foraging competitors, there appear to be numerous social benefits to producing these calls. In red-bellied tamarins, it has been suggested that food calls are not solely a function of arousal in the presence of highly desirable food patches, but serve to attract allies, even at the cost of increasing feeding competition (Caine et al., 1995). In chimpanzees, wild males were found to call more in the presence of close allies and also recommenced calling upon their arrival (Slocombe et al., 2010b). This result suggests that chimpanzee food-associated calls may be part of a flexible social strategy to strengthen ally relationships, something particularly important for the male chimpanzee social structure. In a previous study on bonobo food-call production, males who called often attracted females who subsequently mated with them, and it was suggested that by calling, bonobos may also receive benefits from producing food calls by attracting mates as well as potential allies (van Krunkelsven et al., 1996). Further work investigating the influence of social and ecological variables, as well as the influence of audience, is required to explore the adaptive significance of food-associated calls in bonobos.

Whilst there are clearly many avenues still open to explore, this study has made progress by showing that bonobos alter the production of different types of vocal signals as a function of perceived quality of food. Furthermore, although the referential specificity of some of the individual call types appears to be relatively low, the fact that the probabilistic arrangement of the different call types into sequences varies reliably between food preference classes suggests that receivers may be able to make inferences about the nature of an ongoing feeding event by paying attention to the structure of the sequence. In the next chapter (chapter five), I describe a playback experiment which was conducted in order to investigate whether the sequence patterns described here convey meaning to receivers and influence their foraging decisions. If food-associated call sequences do provide information to receivers about the food being eaten, it should be expected that receivers will modify their foraging behaviour based on what they had heard and navigate more effectively to the food associated with the call.

Chapter five: Bonobos extract meaning from food-associated call sequences

Summary

Studies on language-trained bonobos have revealed their remarkable abilities in representational and communication tasks. In contrast, corresponding research into the natural communication of bonobos has largely been neglected. I addressed this issue by conducting the first playback study on bonobo vocal behaviour. In the study outlined in the previous chapter, I demonstrated that bonobos produce five acoustically distinct call types when finding food, which they regularly mix together into longer call sequences. Call types were shown to be relatively poor indicators of perceived food quality, while context-specificity was shown to be greater at the call sequence level. Here, I investigated whether receivers extract meaning about the quality of food encountered by the caller by integrating information across call sequences. I first trained four captive individuals to find two types of foods, kiwi (preferred) and apples (less preferred) at two different locations. I then conducted naturalistic playback experiments, during which I broadcasted sequences of four calls, originally produced by a familiar individual responding to either kiwis or apples. All sequences contained the same number of calls but varied in the composition of call types. Following playbacks, subjects devoted significantly more search effort to the field indicated by the call sequence. The results indicate that bonobos are able to extract meaning about quality of the food encountered by the caller by integrating information from across call sequences.

Results from this study have been submitted for publication as:

Clay, Z., & Zuberbühler, K. Bonobos extract meaning from call sequences. *Submitted*.

Introduction

A growing body of research has demonstrated that the vocalisations of non-human primates can convey a considerably rich amount of information that is meaningful to receivers (e.g. Seyfarth et al., 2010). For instance, field experiments have shown that various species produce acoustically distinct alarm calls, which can inform listeners about specific types of dangers (e.g. Fichtel & Kappeler, 2002; Kirchhof & Hammerschmidt, 2006; Seyfarth et al., 1980; Zuberbühler et al., 1999). In some monkey species, there is evidence that signallers combine strings of acoustically variable calls in ways that alters the signal's meaning (e.g. Arnold & Zuberbühler, 2006b, 2008; Ouattara et al., 2009a, b). For example, male Campbell's monkeys (*Cercopithecus campbelli*) produce acoustically distinct alarm call types in response to eagles and leopards (Zuberbühler, 2001). During less dangerous situations, these monkeys also add a pair of 'boom' calls before the other alarm calls. In a playback experiment, it was shown that Diana monkeys (*C. Diana*), a sympatric species that form mixed-species associations with Campbell's monkeys, cease to respond when a 'boom-boom' series is added (Zuberbühler, 2002). These results indicate that Diana monkeys understand semantic changes brought about by a combinatory rule in the alarm calling system of Campbell's monkeys *(*Zuberbühler, 2002). Subsequent work has also revealed that male Campbell's monkeys produce an array of six different types of loud calls in a range of contexts, which they combine into numerous context-specific sequences. Furthermore, callers have been shown to follow a number of combinatorial principles, such as non-random transition properties of call types (Ouattara et al., 2009a).

Food discovery represents another event type during which some primates produce context-specific vocalisations. Food-associated calls can provide listeners with a useful means to access foraging patches more effectively, while callers appear to gain mainly social benefits (e.g. Caine et al., 1995; Slocombe et al., 2010b). The production of food-associated calls is not restricted to primates but is found in other mammals and birds (e.g. *Gallus gallus*, Evans & Evans, 1999). At the simplest level, food-associated calls are a basic physiological response indicating that the caller has found something desirable, as demonstrated by receivers approaching these calls more rapidly than other calls (Di Bitetti, 2003; Gros-Louis, 2004a) or by triggering foraging behaviour (Evans & Evans, 1999; Kitzmann & Caine, 2009). In some species, food-associated calls appear to provide more detailed information about the food item itself, such as its quality, quantity or divisibility, which can be conveyed by changes in call rates (Boinski & Campbell, 1996; Elowson et al., 1991; Gros-Louis, 2004a; Roush & Snowdon, 2000), or acoustic structure (Benz, 1993; Benz et al., 1992; Hauser et al., 1993a).

Among the great apes, chimpanzees (*Pan troglodytes*) are known to produce specific food-associated calls, known as 'rough grunts' (Goodall, 1963, 1965, 1986). The morphology of rough grunts has been shown to co-vary with the caller's food preference (Slocombe & Zuberbühler, 2006). A naturalistic playback experiment demonstrated that acoustic variation in rough grunts influenced the foraging decisions of a receiver, suggesting that the acoustic structure of this graded signal conveyed meaningful information (Slocombe & Zuberbühler, 2005b).

What exactly governs receiver responses is a matter of ongoing debate. For instance, it is not clear whether receivers respond directly to the calls' physical features or their referential nature, that is to say, the causal relation between calls and contexts (Rendall et al., 2009; Seyfarth & Cheney, 2003a, b). Similarly, signalling is often said to be non-cooperative, with signallers merely producing 'natural' information in response to biologically relevant events, while any representational content is largely generated by the receivers (Stegmann, 2009). These problems are unresolved because the psychological states experienced by primates during call production and perception are rarely investigated.

Results from my observational study, described in chapter four, demonstrated that, like chimpanzees, bonobos vocalize upon encountering food, but that there are important differences between the two *Pan* species. Whilst both chimpanzees and bonobos produce grunts, bonobos give four other acoustically distinguishable tonal calls (barks, peeps, peep-yelps, and yelps) when finding food. Although there were some statistical relationships between call types and perceived food quality, different call types were shown to be produced to a range of different food types. Whilst context specificity at the individual call level therefore appears to be low in bonobos, my results indicated that the composition of longer call sequences, where different call types were combined, relates reliably to food quality.

Although the hypothesis of meaningful call combinations has already been put forward for bonobos, it has never been tested formally (Bermejo & Omedes, 1999; de Waal, 1988). I addressed this in the current study, conducting the first playback experiment on bonobos. Based upon my findings in chapter four, I examined whether listeners were able to extract meaningful information relating to food quality by attending to the composition of these heterogeneous call sequences. To do this, I played back different types of food-associated call sequences to receivers and analysed their subsequent foraging responses.

Methods

Study site and subjects

I conducted this study at Twycross Zoo, UK, over four months, between April and July 2009. During this time, the group was permanently divided into two subgroups of N = 5 individuals (subgroup A) and N = 6 individuals (subgroup B). The subgroups shared the same outdoor enclosure but were temporally separated. Subgroup A had access to the outdoor enclosure in the mornings and subgroup B had access in the afternoons. Full details of the subjects and study site are provided in chapter three.

Design

The basic design was to simulate a member of subgroup A finding food shortly before the midday switchover, in order to investigate whether this influenced the subsequent foraging behaviour of subgroup B members.

The study consisted of four main stages: (1) conducting food preference tests, (2) recording of food-associated calling sequences, (3) establishing two feeding areas, and (4) conducting playback experiments.

1. Food preference tests

I conducted food preference tests for all individuals in both subgroups in order to identify two foods, from eight familiar foods, that were unanimously classed as high and low preference (eight foods = kiwi, banana, apple, orange, carrot, celery, tomato, swede). Full details of the procedure are provided in chapter three. Selecting foods that were unanimously perceived as high and low quality in both groups was necessary in order to ensure that the calls used as stimuli from the 'call producers' in subgroup A corresponded with preferred and less preferred foods of the 'receivers' in subgroup B. It was also necessary to identify two foods that regularly elicited food-associated calls, something that was more challenging for the lesser preferred foods. All vegetables (celery, carrot, tomato, swede) consistently ranked low but, as they only rarely elicited vocalizations, I excluded them from further analyses. Results from the food preference tests indicated that all individuals ranked kiwi as a highly preferred food, followed by banana. Apples consistently ranked as a medium-to-low preference food by all individuals whilst still regularly eliciting vocalisations (see appendix II). I thus selected kiwi and apple as the experimental foods.

2. Recording calls

From April to May 2009, I recorded food-associated call sequences given by all individuals feeding in the outdoor enclosure. This fulfilled two goals. First, recording vocalisations enabled me to build up a sound library of call sequences given to kiwi and apples by individuals of subgroup A that could be used for the subsequent playback experiments. Second, it was necessary to compare the vocal behaviour of the bonobos at Twycross with my previous study of the bonobos at San Diego (chapter four) in order to verify that both groups shared the same vocal behaviour, enabling the hypothesis of meaningful call combinations to be tested. Further information on the protocol for recording vocalisations is provided in chapter three.

3. Foraging training

Starting on the 20th April, I established two outdoor foraging patches for the afternoon subgroup (subgroup B). Each day, before their midday release, a caretaker entered the enclosure and hid finely cut pieces ($1cm^2$ triangular pieces, total 300g) of either apple or kiwi in the grass in one of two $30m^2$ fields, so that they were not visible from a distance. The two fields were on slopes, equidistant to the door (21m); the distance between them was 8m. Both areas were equal in dimensions (length top = 6.5m; width = 4.0m; length bottom = 8.5m), starting with a flat descent and finishing at the concrete border of the enclosure wall (see fig. 5.1). I classified the outer border as the place where the adjoining corner of the other slope edge met the area slope, and the inner edge as the rocky border of an artificial pond located between them.

Daily provisioning of either kiwi or apple pieces was done in a random order so that individuals could not predict which patch was baited and thus had to inspect both areas. Only one food type was provided during a given trial and no other food or enrichment was given. The keeper always visited both areas, even if no food was placed, to prevent individuals from learning noises associated with scattering food. There were 16 training days for each food type, and 10 control days during which the keeper entered the enclosure, but no food was provided.

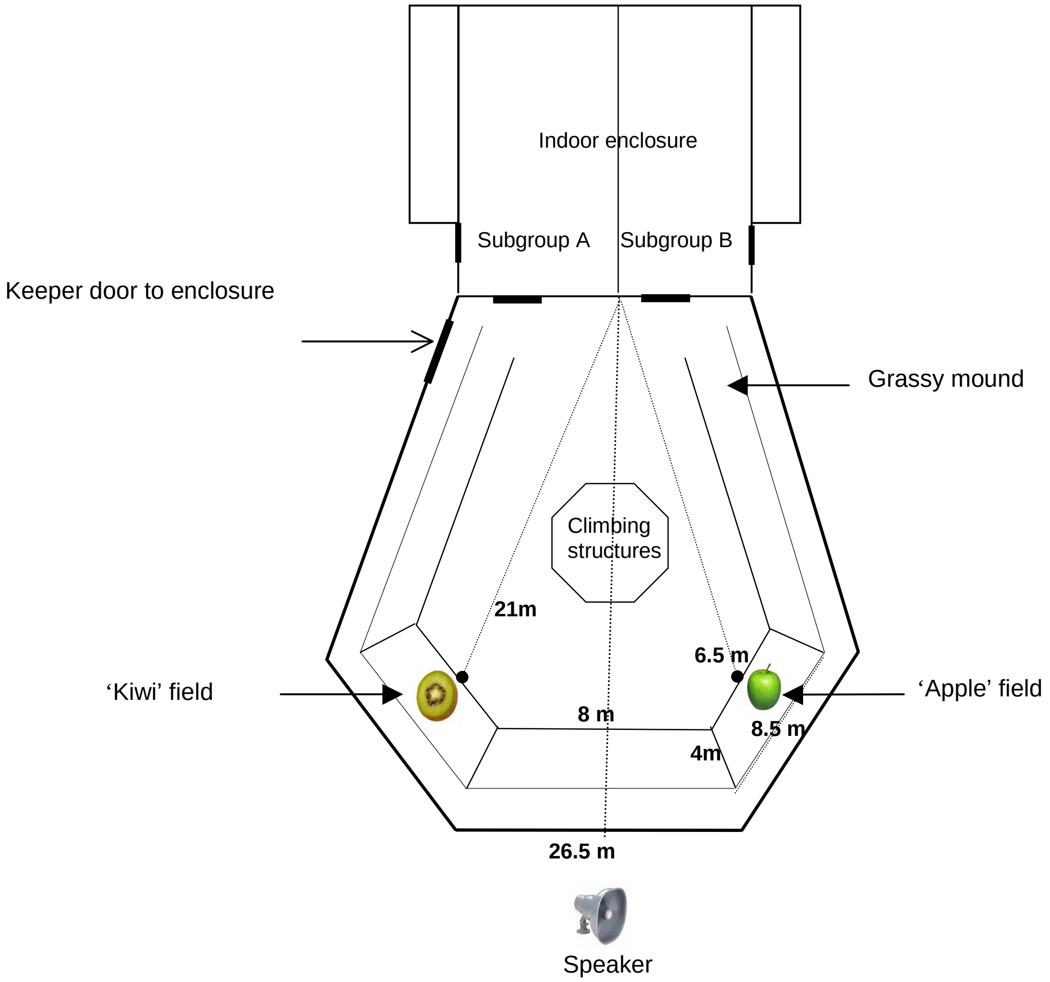


Figure 5.1. Schematic layout of the bonobo facility at Twycross Zoo, including location of playback equipment and artificial food sites.

During the training phase, I filmed the individuals' foraging behaviour and kept a daily record of each individual's food encounters. To document the amount of learning experience for each individual, I counted the number of events in which an individual had either (a) direct experience with eating or making physical contact with either food, or (b) indirect experience, in which the individual saw another individual feeding without feeding themselves (table 5.1). The individuals appeared to quickly learn the two locations (after two days, the individuals started to run directly to search the locations upon release), and quickly formed a clear preference for the kiwi field. Generally, feeding on both fields was peaceful. Four of the six members of the afternoon subgroup (GM, LU, CK, KH) completed the training, gaining direct experiences in at least two thirds of all training days (table 5.1).

The other two individuals (JS, DT) failed to participate, either due to social exclusion or lack of motivation. JS was bullied by the females in the group to the extent that he rarely entered the outdoor enclosure with the rest of the group. If JS did ever enter, he only did so after significant delay, at which point all the food had already been eaten. DT showed very poor food motivation and lack of interest in approaching the food locations or foraging. Occasionally, she would approach the food locations but after the rest of the group had foraged, and therefore received very little direct experience with the feeding locations.

Table 5.1. Direct and indirect experiences by subgroup B individuals during foraging training phase.

	Individual							
Experience at food site	GM		CK		KH		LU	
	Kiwi	Apple	Kiwi	Apple	Kiwi	Apple	Kiwi	Apple
Direct	9	9	9	9	13	14	14	14
Indirect	2	3	1	1	1	0	1	0
Total	11	12	10	10	14	14	15	14

4a. Creating playback stimuli

Using the library of calls collected from the ‘call producer’ subgroup (A), I created stimuli for the subsequent playback experiments. Each stimulus consisted of a four second series of four equally-spaced calls. I did not use grunts in this study due to their very low occurrence and soft amplitude compared to the other calls. Thus, the playback stimuli were composed of mixtures of up to four different call types: barks, peeps, peep-yelps and yelps (see fig. 5.2).

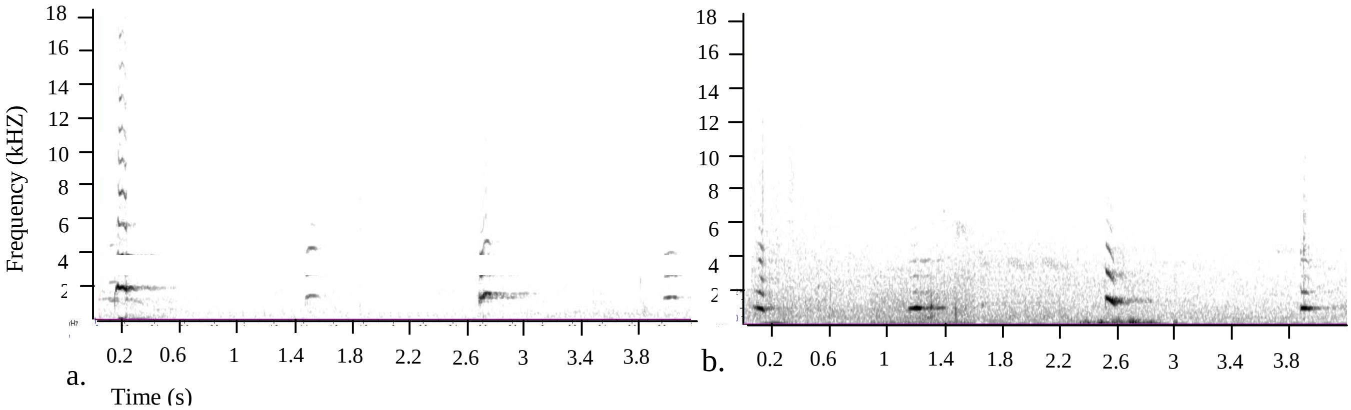


Figure 5.2. Spectrographic illustrations of two playback stimuli. (a) a high value sequence originally given to kiwi (bark/peep/bark/peep) and (b) a low value sequence, originally given to apple (yelp/ peep-yelp/yelp/ peep-yelp).

In order to ensure that the playback stimuli reflected the natural calling behaviour of the bonobos at Twycross, I compiled the playback stimuli so that they reflected the natural range of sequences produced when encountering high and lower value foods (table 5.2). In order to do this, I examined the natural distribution of call types in sequences by the Twycross individuals, by taking a random selection of four call sequences for *N* = 6 individuals (three from each subgroup: subgroup A = KK, KT, BK; subgroup B = KH, DT, CK) given to high and low preference foods. Based on my prior experience with classifying calls, I classified the call types for the first four elements in the sequences. Calls were classified by visually inspecting the spectrograms, verified by a harmonic cursor (on-screen pointer device for indicating spectral frequency), and listening to the calls. Inspection of these sequences indicated that natural call sequences to kiwi contained more peeps and barks but sometimes also peep-yelps and yelps, while sequences to apples contained higher proportions of yelps and peep-yelps, though peeps and barks could also be present (see table 5.2).

When selecting sequences for playback stimuli, I biased the choices towards recordings of the highest quality and ensured that the stimuli covered the natural range of call sequences produced in response to kiwi and apples (table 5.2). For the stimuli, I used a balanced contribution of sequences produced by three individuals (KK, KT, BK) from separate feeding events. I was unable to include calls produced by the other two individuals (MR, BY) due to their low calling rates. Where necessary, I used Adobe Audition to edit unequal inter-call intervals in order to rule out call rate effects.

Table 5.2. Relative frequency of food-associated call types (proportions of call sequences) within natural call sequences given to high and low-value foods by bonobos at Twycross Zoo and the corresponding playback stimuli.

Call Sequence	Food type	Call type				
		Bark	Peep	Peep-yelp	Yelp	Grunt
Natural	High	0.24	0.52	0.22	0.03	0.00
	Low	0.04	0.28	0.42	0.26	0.02
Playback	High	0.29	0.50	0.18	0.04	0.00
	Low	0.05	0.13	0.40	0.43	0.00

If required, undesired ambient sound events were removed (e.g. other animals vocalizing, motor vehicles passing, zoo visitors), provided they did not overlap with the stimulus calls. In some cases, it was necessary to reduce the amplitude of the background noise throughout the entire stimulus using ‘Hann’ band filters. If necessary, the stimulus amplitude was adjusted so that all calls fell within the same amplitude range of 75-80 db. In all cases, amplitude and background noise were only modified if there was no distortion to the overall call sequence, so that the sequence continued to sound natural. For some sequences, I also conducted a number of transplantations, in which individual calls given to apples were replaced with the same call types given to kiwi and vice versa. In doing so, the types of calls or the sequence order was not changed (e.g. a peep from a call sequence to kiwi was replaced by a peep from a call sequence to apple). The purpose was to ensure that the sequence composition, not the acoustic properties of individual calls, was indicative of the food encountered by a caller. If two recordings from the same individual were comparable in terms of levels of background noise, I modified the sequence composition by transplanting a call produced in one series with a call of the same type from another series, using Adobe Audition.

4b. Conducting playback experiments

Finally, I conducted playback experiments in which call sequences of members of the morning subgroup were played to individuals in the afternoon subgroup. Individuals could be exposed to one of three possible conditions: kiwi, apple or control trials. During control trials, all features of the procedure remained the same except that no stimulus was played.

For broadcasting the stimuli, I used a Nagra DSM speaker/amplifier attached to an Apple Ipod shuffle, 2Gb. The speaker was positioned equidistant from the two fields on a large secure tripod, 1.85m off the ground, so that sounds could be broadcast without interference from the 1.8 m glass wall encircling the enclosure (fig. 5.3). The distance between the speaker and the door entrance was 28m. Although facing the door, the speaker was not visible from the door, due to the presence of climbing structures on the mound.

In order to allow the bonobos to habituate to the presence of the playback equipment, I began by setting up the playback equipment daily for 10 days before commencing the experiment. The bonobos quickly habituated to the presence of the speaker, and came to ignore it after several days.

In each trial, the amplitude of the playback stimuli was adjusted so that they sounded natural to experienced observers (myself and two keepers). Within this natural range, the stimulus sequence was arbitrarily reset within a 3db range to control for possible amplitude effects. Prior to the experiment, I conducted sound checks with the assistance of a keeper to ensure that the stimuli played outside were audible through the metal door to the individuals indoors (fig 5.1).

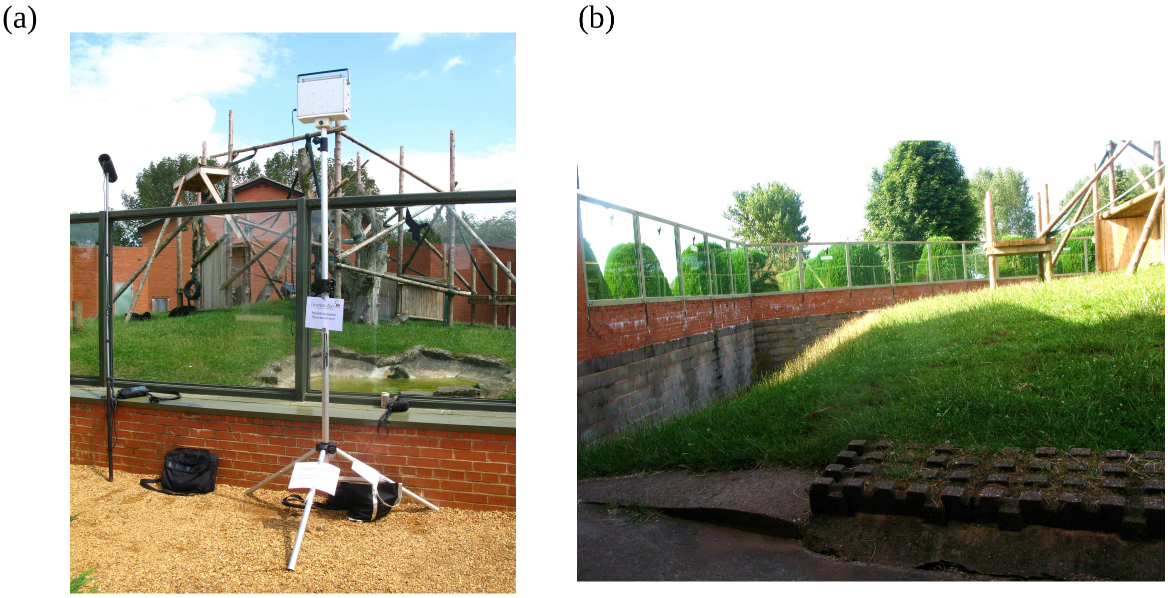


Figure 5.3. Photographs depicting (a) the playback speaker positioned during the experimental phase, (b) the view of the sloped outdoor enclosure from the bonobo exit door (photographs by Z. Clay).

The experimental routine was as follows. Around midday, subgroup A (morning subgroup) was brought inside, as normal, and given a seed feed indoors. Live radio broadcasting was played via an inside keeper door to prevent subjects from subgroup A from hearing the stimuli (i.e. their own calls) in the subsequent experiment. This was effective as no vocal responses were elicited from any individual during playback trials (except for one apple trial, which was excluded from analysis). Meanwhile, individuals from subgroup B (afternoon subgroup) were waiting to be released through their own door. Before their release, three key manipulations were carried out. First, a keeper entered the outdoor enclosure from a side door to mimic placing food (none was provisioned). Individuals were familiar with this routine from the previous foraging training. They could not see the event, but could hear the associated sounds. After the keeper’s return, subjects heard the opening sounds of the door, which connected subgroup A to the outdoor enclosure (to suggest a re-entry of subgroup A), although, in reality, no subject was released.

A trial was conducted only if, (a) no vocalizations had been produced by the morning subgroup for at least one minute, (b) individuals of subgroup B were waiting close (< 1-2m) to the door and were not distracted by social activities (play, agonistic, sex) for at least one minute; (c) there was no rain or excessive wind outdoors. Communication between a keeper, who stayed indoors with the bonobos, and the experimenter, who stayed outdoors, was maintained with two-way radios. If these conditions were not met, the trial was either delayed or abandoned. If conditions were met, I broadcasted a 4s playback of a series of four equally spaced calls extracted from a natural call sequence to either apple or kiwi (to simulate a subgroup A member finding apple or kiwi), played from their outdoor enclosure. One minute after playback (a sufficient time period for the subgroup A to 'return' indoors), subgroup B was released and their foraging behaviour was monitored for up to 10 minutes using a camcorder with additional verbal comments. I simultaneously recorded all vocal responses and provided a commentary using professional sound recording equipment as previously described.

To rule out visually-based foraging, no food was ever provided on either field during experimental and control trials. To reduce the possibility of extinction, I interspersed a number of refresher days between trials, i.e. between 1-4 days during which I provided either kiwi or apple pieces on the corresponding fields, provided in a random order (N = 28 total).

Due to the potential stress provoked, zoo regulations prohibited separation of group members. This meant that all individuals remained in their subgroups throughout the study, and so subjects were released simultaneously into the outdoor enclosure. Therefore, the behavioural responses were collected while individuals interacted as a group.

Analyses

I extracted systematic data on three dependent variables across the different conditions: (a) field first visited (kiwi vs. apple); (b) time spent actively foraging in each field (time trespassing, sitting, resting, or sleeping were subtracted); (c) total number of visits per field (N times entering and exiting the field areas interrupted by at least one bout of foraging). Because data from individuals were inter-dependent (I was unable to separate individuals), my principal analyses were conducted at the group level, using the median scores for individuals combined per trial. The nature of the data distribution meant that only non-parametric statistics were employed.

Whilst measuring the central tendency of the group across trials reduces the problems of data interdependency and type-two clustering errors (Galbraith et al., 2010), the cost is a substantial reduction in statistical power. Furthermore, rather than using the foraging behaviours of receivers as the unit of analysis (upon which my hypothesis is based), the unit of analysis becomes the trials in which the responses of a group of receivers were measured. Given these statistical constraints, I conducted a second, more powerful analysis, using Generalized Linear Models. The Generalized Linear Model is an extension of General Linear Model, in which there is a flexible generalization of ordinary least squares regression. This procedure relaxes the assumptions of normal distribution and the identity link (Nelder & Wedderburn, 1972) and allows nonlinear relations between dependent and independent variables, both of which can have categorical or continuous data distributions (McCullagh & Nelder, 1989). Interdependency prevented me from entering all individuals into one model, thus I conducted Generalized Linear Models (Poisson distribution, log link function) to analyze each individual's performance separately. This second analysis supplemented my group-level analyses, providing a compromise to conduct more powerful statistical analyses of all the data from all four individuals.

To ensure that my behavioural coding was reliable, two naive observers were asked to blind-code a randomly chosen trial for each of the three different conditions. Instructions were provided explaining the criteria used to code the three dependent variables and the coders extracted these measures from the videos. These measures were then compared to the original measures, using a Cronbach's alpha test of inter-observer reliability. Scores of 0.86 (Observer 1) and 0.97 (Observer 2) across trials were obtained, indicating high levels of observer agreement.

Results

A total of 28 trials were conducted; three were discarded due to poor weather (preventing the bonobos from being released), one due to unexpected vocalizations (see before), and one due to an unexpected communication problem between keeper and experimenter. The remaining 23 trials consisted of *N* = 10 apple playback trials, *N* = 7 kiwi playback trials and *N* = 6 control trials, which were completed by four individuals (GM, CK, KH, LU). The remaining two individuals (DT, JS) were excluded from analyses. As previously described, JS did not complete the training phase and due to his social exclusion, he did not enter the outdoor enclosure to participate in the study. DT showed no evidence of having learned the food locations during the training phase. As expected, DT also showed little interest during the playback phase and only completed 5 of 23 trials, which was not enough for statistical analyses.

Foraging behaviour

Following release, there was a strong baseline preference for the highly preferred 'kiwi' field. In the control condition, individuals were more likely to visit the kiwi field first and more often, as well as devoting more foraging effort to it compared to the apple field (fig. 5.4). Despite this baseline bias, comparisons of the median N trials with first arrivals to the Kiwi versus Apple field (per condition, per individual) revealed that playbacks of food-associated calls had a significant effect on the individuals' first choice of fields ($\chi^2 = 16.347$, df =2, $P < .001$; Pearson chi-square, two-tailed, fig. 5.4a). Hearing a call sequence originally given to kiwi resulted in an increase in first entries to the kiwi field compared to control or apple call sequences (median N trials with first arrival to kiwi site per condition, per individual: control = 3.0 (50% of trials); kiwi playback = 6.0 (86%); apple playback = 5.0 (50%), all one-way χ^2 tests: $P > .05$). As described previously, the unit of analysis was the median value for the group response owing to fact that the group foraged together, with level of dependency equal across trials.

After hearing apple call sequences, there was a significant increase in the number of first visits to the apple field, compared to control or kiwi trials (median N trials with first entries to apple site per individual: control trials and kiwi trials = 0.0, apple trials = 4.0 (40%); both control and kiwi vs. apple: $\chi^2 = 13.235$, df =1, $P < .001$, with Sidak corrected alpha = 0.0169). Hearing food-associated call sequences, in other words, influenced the bonobos' foraging decisions against their pre-existing food preference biases.

Next, I determined whether hearing playbacks influenced the number of visits the group made to the two fields (fig. 5.4). Again, I found a significant effect of playback condition on the median number of visits made by the group to both the kiwi field (χ^2 = 6.486, df =2, *P* = .034; two-tailed exact Kruskal-Wallis test) and the apple field (χ^2 = 10.532, df =2, *P* = .002; two-tailed exact Kruskal-Wallis test). Post-hoc, pair-wise comparisons using a Sidak correction (corrected alpha = 0.0169) revealed that individuals visited the 'kiwi' field more often after hearing kiwi call sequences compared to control trials ($\text{median}_{\text{control}}$ = 0.5; $\text{median}_{\text{kiwi}}$ = 1.0; $\text{median}_{\text{apple}}$ =1.0; *N* visits to kiwi field, kiwi playback vs. control: Mann-Whitney U = 4.5, *P* = .015). Conversely, I found that individuals visited the apple field more often after hearing playback of 'apple' call sequences compared to the control condition ($\text{median}_{\text{control}}$ = 0.0; $\text{median}_{\text{kiwi}}$ = 0.5; $\text{median}_{\text{apple}}$ =1.0; *N* visits to apple field, 'apple' playback vs control: U = 3, *P* = .002).

Finally, hearing playbacks of food-associated call sequences had a significant effect on the foraging time devoted by the group at both the kiwi site (χ^2 = 6.902, df =2, *P* = .026; two-tailed exact Kruskal-Wallis test) and the apple site (χ^2= 10.876, df =2, *P* = .002; two-tailed exact Kruskal-Wallis test; fig. 5.4c). Pair-wise comparisons (Sidak corrected alpha = 0.0169) revealed that individuals spent more time at the kiwi location after hearing 'kiwi' call sequences compared to control condition ($\text{median}_{\text{control}}$ = 2.25s; $\text{median}_{\text{kiwi}}$ = 16.50s; $\text{median}_{\text{apple}}$ = 5.75s; kiwi site: kiwi playback vs. control: Mann-Whitney U = 5, *P* = .022,) or hearing 'apple' call sequences (kiwi playback vs. apple playback: U = 15.5, *P* = .058). Likewise, individuals spent more time in the apple field after hearing playbacks of apple call sequences compared to control trials ($\text{median}_{\text{control}}$ = 0.0s; $\text{median}_{\text{apple}}$ = 9.5s; $\text{median}_{\text{kiwi}}$ = 1.5; apple field: apple playback vs. control: Mann-Whitney U = 6, *P* = .015). Although there was a trend for spending more time foraging for apple after hearing apple playbacks compared to kiwi playbacks, the result did not reach significance (apple vs. kiwi playbacks: U = 20, *P* > .05).

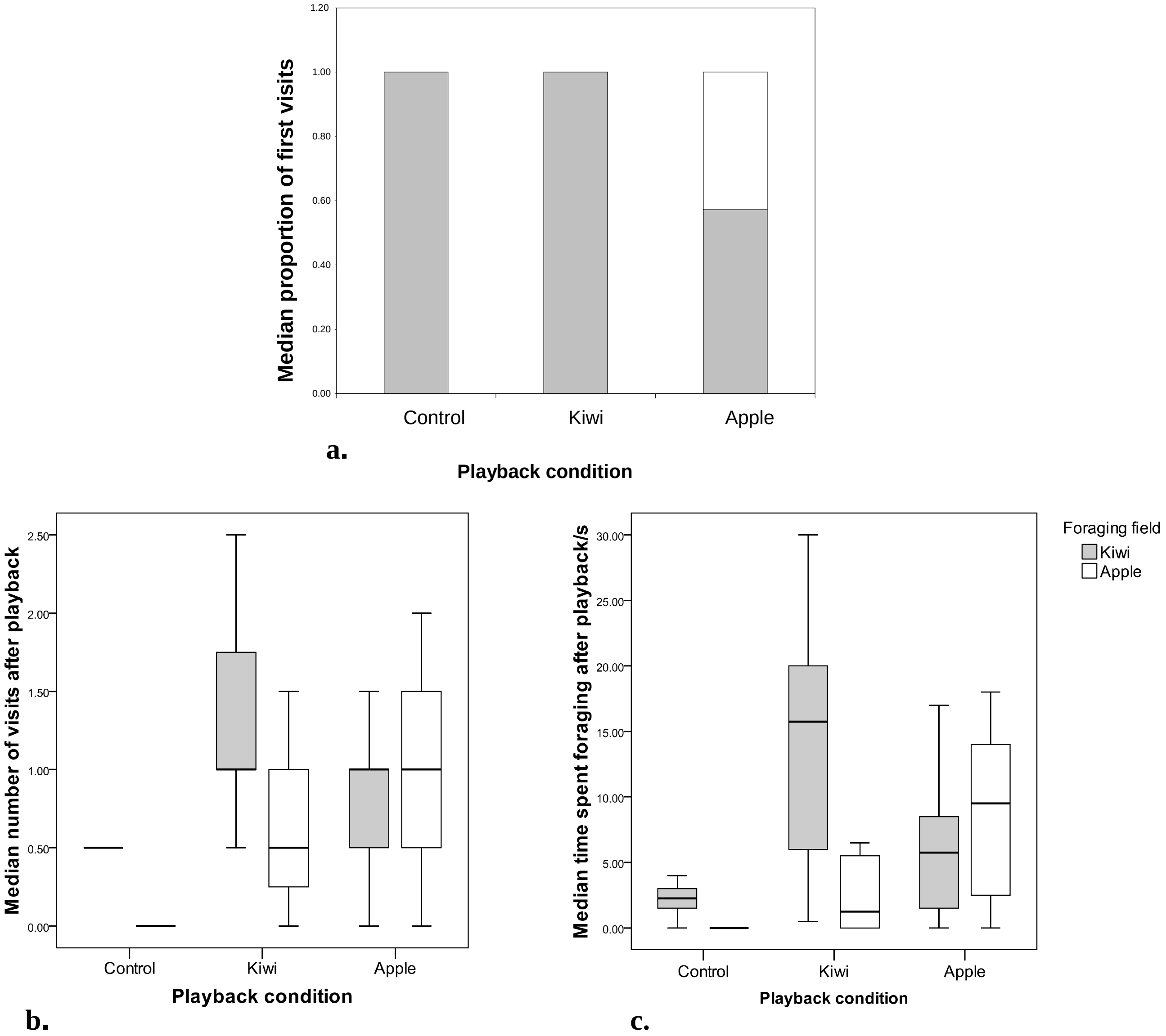


Figure 5.4. Box plots indicating foraging responses (*N* = 4 bonobos) following playbacks of call sequences given to high value (kiwi) or low value (apple) foods. (a) Site of first entry expressed as a median proportion of the individual's median choices per condition; (b) median number of visits per trial; (c) median time spent foraging following playback (s). Boxplots indicate medians (thick black lines), inter-quartile ranges (box edges), and highest and lowest values (whiskers), excluding outliers.

In the above analyses, I reported behaviour at the group level in order to avoid problems with data interdependency and type-two clustering errors (Galbraith et al., 2010), albeit at the cost of a substantial reduction in statistical power. In a second set of analyses, using Generalised Linear Models (Poisson-log, two-tailed), I found that, for each of the four individuals, there was a significant effect of playback type and the number of visits to the two fields (table 5.3, appendix III). Pair-wise comparisons revealed that individuals visited the ‘kiwi’ field more often after hearing kiwi call sequences compared to the control trials, in one case significantly so (CK: *P* = .019; LU: *P* = 0.13; KH: *P* = .084). All individuals visited the apple field significantly more often after hearing apple call sequences compared to the control condition (GM: *P* < .001; CK: *P* = .008; LU: *P* = .016; KH: *P* = .001).

Tables 5.3. Mean number of visits (and SDs) by each individual to the two fields after hearing food-associated call playbacks.

Individual	Kiwi field			Apple field			
	Control	Kiwi PB	Apple PB	Control	Kiwi PB	Apple PB	Likelihood-ratio χ^2
GM	1.00 (0.00)	1.57 (0.20)	1.20 (0.20)	0.00 (0.00)	0.71 (0.18)	1.70 (0.40)	18.471, df = 5, *P = .002*
CK	0.33 (0.21)	1.57 (0.30)	0.90 (0.18)	0.00 (0.00)	0.43 (0.20)	0.70 (0.21)	16.801, df =5, *P* = .005
LU	0.50 (0.22)	1.43 (0.43)	0.70 (0.26)	0.33 (0.21)	0.86 (0.26)	1.40 (0.40)	8.800, df = 5, *P* = .117
KH	0.33 (0.21)	1.14 (0.34)	0.60 (0.16)	0.00 (0.00)	0.57 (0.43)	1.10 (0.23)	13.701, df =5, *P* =.018

(PB = Playback)

Finally, hearing playbacks of food-associated call sequences had a significant effect on the foraging time devoted by each of the four individuals in the two fields (two-tailed Generalised Linear Models, Poisson-log; table 5.4, appendix III). Pair-wise comparisons revealed that individuals spent more time at the kiwi location after hearing kiwi call sequences than apple call sequences (all individuals: *P* < .001) or compared to control trials (GM, KH: *P* < .001; CK, LU: *P* < .005). Likewise, individuals spent more time in the apple field after hearing playbacks of apple call sequences, compared to kiwi call sequences (all individuals: *P* < .001) or compared to control trials (all individuals: *P* < .001).

Table 5.4. Mean time spent (s) (and SDs) by each individual at the two fields after hearing food- associated call playbacks.

Individual	Kiwi field			Apple field			
	Control	Kiwi PB	Apple PB	Control	Kiwi PB	Apple PB	Likelihood-ratio χ^2
GM	6.33 (1.33)	32.86 (15.00)	15.60 (3.75)	2.17 (2.17)	8.28 (2.91)	24.90 (7.25)	328.523, df =5, *P* <.001
CK	0.67 (0.49)	17.57 (5.76)	6.2 (2.56)	0.00 (0.00)	1.86 (0.99)	8.80 (3.27)	259.036, df = 5, *P* < 001
LU	4.00 (1.91)	25.00 9.15	5.3 (1.97)	1.33 (0.99)	5.57 (2.03)	17.20 (5.85)	295.858, df = 5, *P* <.001
KH	1.33 (0.84)	23.57 (11.73)	4.3 (1.71)	0.00 (0.00)	6.86 (5.15)	7.20 (1.66)	305.699, df =5, *P* <.001

(PB = Playback)

Foraging errors and integration

A key indicator of representationally-based signal processing is that subjects sometimes make mistakes, particularly with signals that are ambiguous or only weakly correlated with specific external events (Stegmann, 2009). In my sample, some call sequences were better indicators of high and low food quality than others in terms of their call composition. Thus, if subjects made mistakes, the prediction was that they should be more likely to happen in response to the more ambiguous sequences (e.g. visiting the apple field after hearing a kiwi sequence). To address this, I assigned a cumulative value to each sequence, which was based on its call composition. Each call within the sequence contributed with a value that reflected its association strength with high preference food (tables 5.2, 5.5). I assigned this using ordinal scores, where the calls were ordered according to their associated strength with high preference foods (barks = 4, peeps = 3, peep-yelps = 2, yelps =1). In addition, I calculated cardinal scores, which were based on the frequency of occurrence within natural call sequences to highly preferred foods. This approach resulted in the following values: barks = 6.00, peeps = 1.86, peep-yelps = 0.52, yelps = 0.12 (see fig. 5.5, tables 5.2, 5.5).

Table 5.5. Composition of different call stimuli and resulting behavioural responses in receivers. Receiver foraging effort represents mean time spent foraging at per individual. Cells marked in bold represent ‘response errors’ where individuals exerted more foraging effort in the incongruent field. CVO: Cumulative value (ordinal); CVC: Cumulative value (cardinal); Kiwi bias: Relative bias towards the kiwi field.

Signaller behaviour				Receiver foraging effort (s)		
Food	Sequence	CVO	CVC	Kiwi field	Apple field	Kiwi bias
Kiwi	B B P B	15	19.86	21.0	2.5	9.4
Kiwi	B B P B	15	19.86	6.5	2.5	3.6
Kiwi	B B P PY	13	14.38	28.3	5.0	6.7
Apple	**PY B B PY**	**12**	**13.05**	**20.0**	**12.0**	**2.7**
Kiwi	P P PY P	11	6.10	79.0	18.8	5.2
Kiwi	PY P P P	11	6.10	20.8	1.8	12.6
Kiwi	P PY PY P	10	4.76	1.3	2.5	1.5
Kiwi	P P PY Y	9	4.35	16.5	6.5	3.5
Apple	**PY P PY PY**	**9**	**3.43**	**14.8**	**3.3**	**5.5**
Apple	Y PY PY P	8	3.02	0.0	15.8	1.0
Apple	**Y PY P Y**	**7**	**2.61**	**9.3**	**2.0**	**5.7**
Apple	PY PY Y PY	7	1.69	5.8	20.8	1.3
Apple	Y P Y Y	6	2.20	6.5	14.3	1.5
Apple	Y Y Y P	6	2.20	3.8	40.8	1.1
Apple	PY PY Y Y	6	1.28	9.5	9.0	2.1
Apple	PY Y PY Y	6	1.28	6.5	17.3	1.4
Apple	PY Y Y Y	5	0.87	2.5	10.3	1.2

There was a significant positive correlation between subjects’ foraging effort in the kiwi field and the overall cumulative food value, as assessed by the composition of the sequence (time spent: cardinal scale, Spearman’s rho: $N = 17$ $r_s = 0.585$, $P = .014$, fig. 5.5; ordinal scale: $N = 17$, $r_s = 0.575$, $P = .016$). Inspection at the level of individual trials indicated an almost perfect separation of sequences given to apples and kiwis by the cumulative sequence value generated by the constituent calls. One exception was a call sequence given to apples (PY-B-B-PY), which interestingly also triggered almost twice as much searching in the (wrong) kiwi compared to the apple field. Also interesting were two responses to kiwi sequences, which only triggered weak searching in the kiwi field. However, in both cases, search effort in the apple field was also unusually low, suggesting that subjects were generally unmotivated to forage (table 5.5). In sum, the foraging effort was a strong reflection of the cumulative ‘good food’ score conveyed by the entire sequence.

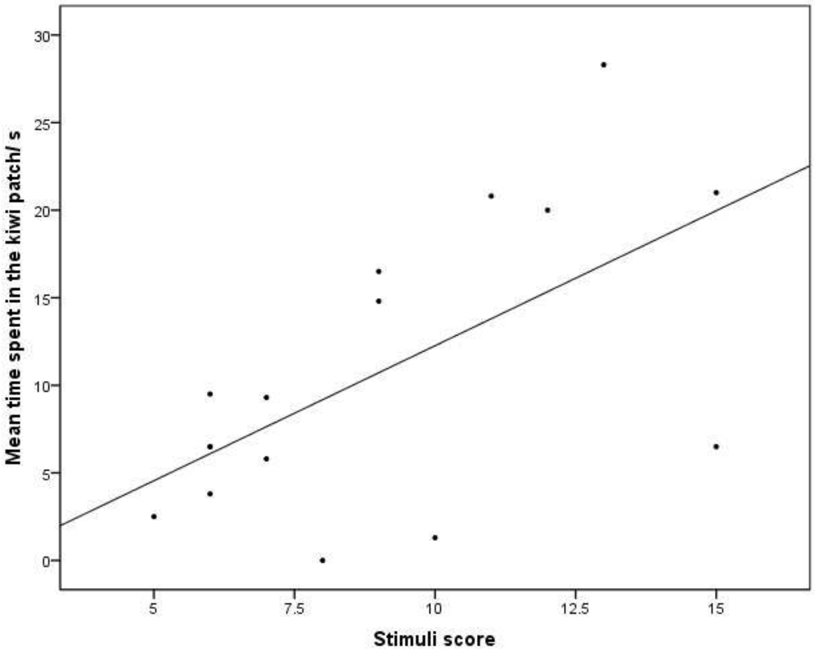


Figure 5.5. Scatter plot showing the relationship between receiver foraging effort and the cumulative value of the stimuli sequence.

Discussion

Language-trained bonobos have long been known for their remarkable representational and communication skills (Savage-Rumbaugh et al., 1986, 1990; Savage-Rumbaugh & Lewin, 1994), but the natural communication system of bonobos has received little attention. This study, focusing on the vocal behaviour of bonobos in the feeding context, provides progress to this end, and shows that bonobos can increase their foraging success by attending to each other’s call sequences. This study followed on from my previous study (chapter four), which demonstrated that bonobo food-associated calls varied reliably with food quality. My key finding here was that call receivers were able to direct their foraging effort to specific locations, according to the call sequence presented to them. Whilst there was an unsurprising baseline preference to the high-preference food site, playbacks of high-preference food call sequences resulted in an even greater amount of foraging effort at this site, indicating that the calls were meaningful to the receivers. Furthermore, although lack of interest at the low-preference food site was to be expected (as was observed in baseline trials), there was a striking increase in search effort at the low-preference food site (apple), which only occurred after hearing sequences associated with low-preference food. These results suggest that individuals incorporated information extracted from the food-associated call sequences to optimise their foraging strategy, in some cases, even against pre-existing foraging biases.

My results also indicate that, although phylogenetically closely related, bonobos and chimpanzees communicate about food in considerably different ways. In contrast to chimpanzees, who produce one acoustically graded call type that co-varies with food quality (Slocombe & Zuberbühler, 2006), bonobos regularly mix several different call types together into heterogeneous vocal strings. Rather than at the level of individual calls, information about food patch quality appears to be related to the probabilistic composition of heterogeneous call sequences. Patterns of receiver behaviour indicate that, rather than attending to individual call types, receivers took into account the relative proportions of different calls within a sequence and extracted meaning by integrating information from across the call units.

In addition, the generation of more foraging errors in structurally ambiguous call sequences (which were less strongly indicative of high or low preference foods) also supports the hypothesis that semantic information extracted from the stimuli sequences influenced the foraging decisions of the receivers. This is consistent with the argument that, in contrast to ‘natural information’, which does not allow for errors, the generation of misrepresentations and errors is a defining feature of what is considered as ‘semantic information’ in animal signals (Stegmann, 2009).

Despite a growing body of evidence indicating that numerous monkey species produce sequences of acoustically variable calls composed in context-specific ways, evidence for meaningful signal combinations in apes has so far been poor (although see Clarke et al., 2006). A recent study of gorilla gestural sequences failed to find any evidence of syntactic organisation or corresponding semantic content (Genty & Byrne, 2010). Results from the current study provide the first empirical evidence that call combinations play a semantic role in bonobo communication in the foraging context. However, it is important to note that I did not find any evidence for syntactic rules nor that the sequencing structure was itself semantically relevant. Thus, although call combinations may represent a means of communicating information in bonobos, the manner in which bonobos use call combinations strikingly contrasts with the way linguistic units are structured hierarchically as sequences in human language. Results from this study therefore highlight some important differences in the linguistic notion of syntax and the manner in which non-human primates, such as bonobos, combine calls together (Szamado et al., 2009).

One of the key questions in the animal communication literature concerns whether signals given in response to external events, such as in this study, should be conceptualised as ‘referential’ or rather a mere readout of a caller’s motivational state (Owren et al., 2010; Rendall et al., 2009; Seyfarth & Cheney, 2003b). Great apes, especially chimpanzees and bonobos, are often described as exceedingly ‘emotional’, suggesting that arousal-based explanations may be more in line with the nature of the phenomenon described here (e.g. Rendall et al., 2009). Furthermore, the vocalisations most closely related with high-preference foods (i.e. barks and peeps) are those which also possess the acoustic properties thought to induce arousal-based responses in listeners (Rendall et al., 2009; Owren et al., 2010). Results here indicated that sequences containing a greater amount of calls with presumably high emotional valence lead receivers to search at the high-value food site. Under arousal-based explanations, receivers may have therefore taken the probabilistic composition of call sequence as an indicator of the receiver’s emotional response to the food. A further study, comparing receiver responses to identical call sequences, taken from high-arousal and low-arousal contexts, could provide further information to address this question.

Although the arousal state of the signaller is likely to play an integral role in call production in contexts such as food discovery (Owren et al., 2010; Rendall et al., 2009; Seyfarth & Cheney, 2003b), gaining meaningful measurements of internal state have proved very challenging and, as so, it has often proved more empirically fruitful to focus on the relation between receiver response and external variables that can be manipulated and measured experimentally (Zuberbühler, 2003; Seyfarth et al., 2010). Furthermore, even calls with high motivational content are still able to inform receivers about the external world. This has been demonstrated by a number of studies showing that, regardless of the caller's motivational state during call production, calls can provide listeners with representational information about external objects and events (Manser et al, 2001; Manser et al., 2002; Seyfarth & Cheney, 2003a; Seyfarth et al., 2010). For example, recent work on the alarm call responses of meerkats (*Suricata suricata*) has demonstrated that both emotional and referential information are coded into the same signal and develop on different ontogenetic time scales (Hollen & Manser, 2007). In future work, meaningful progress will be made by focusing more specifically on the motivational experience of the caller and how this influences signal production.

One important, but unanswered question, concerns the ultimate function of food-associated call production in bonobos. In white-faced capuchins (*Cebus capucinus*), food-associated calls are thought to function to announce food ownership and a willingness to defend, thereby resulting in reducing foraging competition from others (Gros-Louis, 2004b). In red-bellied tamarins (*Saguinus labiatus)* and chimpanzees, food-associated calls may provide social benefits by attracting allies, even at the cost of increasing feeding competition (Caine et al., 1995; Slocombe et al., 2010b). It has also been suggested that bonobos may receive social and reproductive benefits from producing food-associated calls (van Krunkelsven et al., 1996). Further work investigating the interplay and influence of social and ecological variables on the production of bonobo food-associated calls is required to explore the adaptive significance of these calls in this species.

Chapter six: Copulation calls in female bonobos

Summary

During mating events, females of many primate species produce distinct vocalisations known as ‘copulation calls’. In the current study, I investigated copulation calling in bonobos, a species in which females produce these vocalisations during sexual interactions with both male and female partners. I examined the acoustic structure of copulation calls as well as patterns in call production to explore how these signals are used by individuals. Acoustic analyses revealed that, although there was striking variation at the level of the individual caller, copulation calls produced with male and female partners shared the same acoustic morphology and could not be statistically discriminated. Nevertheless, there were subtle differences in call delivery, which discriminated both partner sex and the dominance rank of male, but not female, partners. Effects of partner sex and partner rank were much stronger at the level of call usage. Females were significantly more likely to call with male than female partners and, regardless of partner sex, were significantly more likely to call with high-ranked partners compared to low-ranked partners. Acoustic analyses revealed no relationship between acoustic structure and the size of a female’s sexual swelling. However, female call rates increased with male partners as their sexual swelling sizes increased, while the opposite was found when their partner was female. Overall, my results paint a complex picture of copulation calls in bonobos and suggest that these calls have become partly divorced from their original function in reproduction to take on a greater social significance.

Results from this chapter have been submitted for publication as:

Clay, Z., Pika, S., Gruber, T., & Zuberbühler, K. Female bonobos use copulation calls as social signals. *Biology Letters, In press.*

Clay, Z., & Zuberbühler, K. Informational content of copulation calls in bonobos. *Submitted.*

Introduction

Numerous mammals and birds produce loud and acoustically distinct vocalisations during mating events, generally referred to as ‘copulation calls’ (e.g. Maestripieri & Roney, 2005). Copulation calls are a particularly widespread vocal behaviour amongst female primates, especially in Old World species in which the females are promiscuous, live in multi-male and multi-female groups, and advertise receptivity with pronounced sexual swellings (Dixson, 1998). A broad array of hypotheses has been put forward to explain the prevalence and conspicuous nature of copulation calls (Pradhan et al., 2006), although it is more likely that copulation calls have multiple beneficial effects (e.g. Nikitopoulos et al., 2004). Essentially, all hypotheses converge on the uniting theme that copulation calls are sexually-selected signals that promote the caller’s reproductive success (e.g. Maestripieri & Roney, 2005). Primarily, this is thought to be achieved by advertising female receptivity to potential mates (Aich et al., 1990; Gust et al., 1990; Hauser, 1990; O’Connell & Cowlishaw, 1996; Semple, 1998, 2001), which promotes mate choice benefits by inciting male-male competition, either directly (Cox & Le Bouef, 1977), or indirectly, via sperm competition (Henzi, 1996; O’Connell & Cowlishaw, 1994).

Copulation calls may also represent a sexual counter-strategy against threats from infanticide (Pradhan et al., 2006). Risk of infanticide is a significant problem for many female animals (Muller et al., 2007; Sterck & Korstjens, 2000; van Schaik, 2000) and appears to be an especially powerful selective force in primates (e.g. Thomas langurs, *Presbytis thomasi*, Sterck et al., 2005; chacma baboons, *Papio ursinus*, O’Connell & Cowlishaw, 1994; chimpanzees, *Pan troglodytes,* Townsend et al., 2008). Copulation calls may reduce infanticide risk, either by promoting mate guarding and support from the consort male, or by spreading the likelihood of paternity amongst several males, who might otherwise experience infanticidal motivations (O’Connell & Cowlishaw, 1994). In chimpanzees, females are vulnerable to infanticide by both males (e.g. Goodall, 1986; Muller et al., 2007) and other females (Pusey et al., 2008; Townsend et al., 2007). In a recent study of chimpanzee copulation calls, females called most with high-ranked males, regardless of their fertile state, possibly as a means to confuse paternity and enlist their future support against reproductive competitors (Townsend et al., 2008). At the same time, calling was shown to be inhibited in the presence of high-ranked females, who are also the most likely perpetrators of female-led infanticide (e.g. Pusey et al., 2008), suggesting that the calls may be part of a behavioural strategy used to maximise reproductive success whilst minimising social competition.

One way of exploring the adaptive significance and communicative potential of copulation calls is to examine the relationship between context and acoustic structure. In yellow baboons (*Papio cynocephalus*), the acoustic structure of female copulation calls has been shown to code a range of information, including caller identity, the rank of the mating partner and the size of the sexual swelling (Semple, 2001; Semple et al., 2002). In chimpanzees, the acoustic structure of copulation calls is also a reliable indicator of female identity and to some extent, partner rank (Townsend et al., 2008). In Barbary macaques (*Macaca sylvanus*), copulation calls co-vary acoustically with the occurrence of ejaculation (Pfefferle et al., 2008a), something which was shown to be meaningful to listeners (Pfefferle et al., 2008b). Providing information about identity, receptivity and ejaculatory mating may enable a female to influence the behavioural decisions made by potential mates and promote sperm competition in her favour (Pfefferle et al., 2008b; Semple & McComb, 2000).

Bonobo females also produce copulation calls during mating events (Kano, 1992; Thompson-Handler et al., 1984). This follows the predictions by Dixson (1998), because bonobos live in multi-male and multi-female groups, with the presence of promiscuous females that exhibit pronounced sexual swellings (Furuichi, 1989; Furuichi et al.,1998; Kano 1992). Although empirical data are lacking, bonobos represent an intriguing species to study copulation calls as it is likely that their distinct social behaviour and enhanced levels of socio-sexuality may have influenced the evolution of this vocal behaviour. For example, bonobo females are highly gregarious and form strong affiliations and bonds with one another (e.g. Furuichi, 1989, 2009; Hohmann et al., 1999; Kano, 1992), despite the fact that females are the emigrating sex and so are only distantly related to other group members (e.g. Gerloff et al., 1999; Hohmann et al., 1999). By developing enduring intra-sexual affiliations and coalitions, bonobo females are able to dominate adult males, defend resources and avoid infanticide (e.g. Parish, 1994; White & Wood, 2007; Wrangham, 1993).

One mechanism thought to facilitate affiliations between unrelated females is the performance of homosexual interactions, known as ‘genital contacts’ (Hohmann & Fruth, 2000; Kuroda, 1980). During genital contacts, females embrace each other ventro-ventrally, whilst swinging their hips laterally and keeping their vulvae in contact. Observations in both the wild and captivity have suggested that female genital contact behaviour acts like a ‘social grease’, which enables distantly related individuals to affiliate and coexist peacefully (e.g. Fruth & Hohmann, 2006). For example, genital contacts appear to reduce social tension, as well as providing a means for females to assess each other’s social status and to reconcile conflict (de Waal, 1987; Fruth & Hohmann, 2006; Hohmann & Fruth, 2000; Paoli et al., 2006b; Thompson-Handler et al., 1984). Genital contacts appear to have a particular social relevance for newly immigrating females when trying to integrate and develop affiliations with other unrelated group members (Gerloff et al., 1999; Idani, 1991). During female genital contacts, female bonobos sometimes produce distinct vocalisations, which are thought to acoustically resemble the copulation calls they produce with males (Hohmann & Fruth, 2000; Kano, 1992; Thompson-Handler et al., 1984). The apparent production of copulation calls during homosexual genital contacts is not well explained by current hypotheses of primate copulation calls, which all focus only on their reproductive significance (e.g. Pradhan et al., 2006).

In the current study, I explored how female bonobos use copulation calls during sexual interactions with males and other females. I approached this question in two ways. First, I conducted acoustic analyses comparing copulation calls produced during interactions with male and female partners to investigate what kind of information was conveyed by these signals. I explored whether homo- and heterosexual copulation calls could be statistically discriminated. I also focused on several variables that have been investigated previously, namely caller identity, swelling status and partner rank, thus enabling some comparisons with studies of other primate species, whose copulation calls are assumed to be reproductive in function (e.g. yellow baboons, Semple et al., 2002; chimpanzees, Townsend et al., 2008). In the second part of my analysis, I focused on similar variables to investigate the behavioural patterns in copulation calls.

Methods

Study site and subjects

I conducted my research at Lola Ya Bonobo Sanctuary, Kinshasa (DR Congo) between September and November 2008 and between August and November 2009. I conducted observations on three social groups. In 2008, I observed individuals in enclosure 1, henceforth 'group 1a' (*N* = 9 females, *N* = 9 males), and in 2009, I collected data on two separate groups housed in the two different enclosures; henceforth known as 'group 1b' (*N* = 7 females, *N* = 9 males) and 'group 2' (*N* = 5 females, *N* = 11 males). Full details about the study site, subjects and period of data collection are provided in chapter three. To maximise the sample size available for analysis, I pooled the data set from across the three groups. The majority of dyads in the second year had not encountered each other before and therefore represented independent data points. However, I combined data for any dyads that met again in the second year (*N* = 9 female-female dyads , *N* = 19 male-female dyads).

Observational data collection

I collected observational data on females (*N* = 14) engaging in sexual interactions with both male and female partners. Data collection involved all-occurrence and all-day focal sampling (Altmann, 1974), balanced across individuals (approx. 50 hours per individual). I collected data 6-7 days per week, typically starting at around 7.30-8am and continuing throughout the day, until 4-5pm. Across the entire study period, I collected approximately 1,093 hours of data. Observations were made when the bonobos were in the visible, non-forested areas of the enclosure along the enclosure perimeter, approximately 15% of the total area. Although this was a relatively small area, the bonobos spent the majority of their time there (50-60% of daytime activity; Z.Clay, unpublished data), mainly because food was provisioned there. During hot or rainy periods, the bonobos typically withdrew into the forest, out of sight. During this time, I abandoned data collection, but resumed it when individuals returned to visible observation areas.

Recording sexual interactions

Sexual interactions with males were defined as copulations, which involved both visible intromission and pelvic thrusts, and could take place either in the ventro-ventral position or the dorso-ventral position. Sexual interactions between females were defined as genital contacts, which involved a ventro-ventral embrace, with lateral hip swinging and physical contact of genital swellings (Hohmann & Fruth, 2000; Kuroda, 1980). Genital contacts typically took place in the horizontal plane but could also take place vertically (such as hanging from a tree). I excluded cases of both genital stimulation by body parts other than the genitals (e.g. hands or feet) and sexual interactions involving infants as neither of these behaviours reliably elicited copulation calls.

Recording copulation calls

Using the protocol described in chapter three, I recorded vocalisations given by females during their sexual interactions with both males and females. Bonobo copulation calls typically consist of a single or succession of high-frequency screams that usually begin during the copulation (Hohmann & Fruth, 2000; Kano, 1992; Thompson-Handler et al., 1984; see fig 6.1). To control for context and the possibility of vocalisations being elicited by alternative stimuli, I only considered calls that occurred during the sexual interaction itself. I recorded calls from all females (N = 14) across the entire period of data collection (table 6.1) because bonobo females are sexually active right across their fertile cycles, as well as during non-cycling periods such as pregnancy and lactation (Heistermann et al., 1996; Paoli et al., 2006).

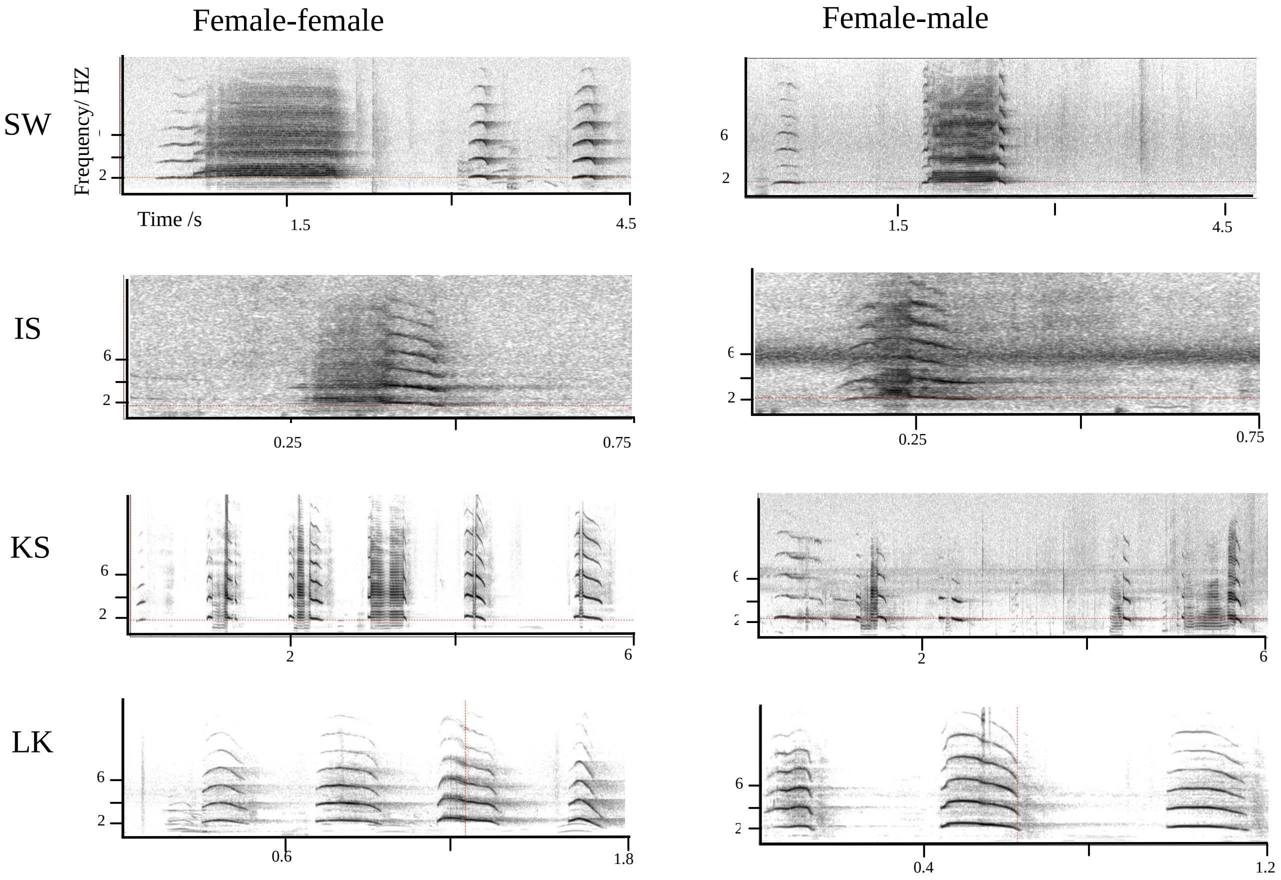


Figure 6.1.Time-frequency spectrograms illustrating copulation calls produced by four female bonobos (SW, IS, KS, LK) during their sexual interactions with female and male partners.

Reproductive states

In order to investigate whether the physical variable of sexual swelling size influenced call production, I collected daily records of female sexual swelling sizes using Furuichi’s (1987) 4-point scale based on degree of wrinkling. Additionally, I kept daily records of the reproductive states of the females, as confirmed by veterinary assessment, to assess whether this influenced copulation calling (table 6.1).

Table 6.1. Reproductive status of females included in this study (with age in years). Definitions: Pregnant = Preg (confirmed by tests or birth); Lactating = Lac; Cycling = Cyc; Parous (already borne viable offspring) = Par; Non-cycling (no evidence of sexual swelling cycle) = non-cyc; Primiparous (first pregnancy) = Pri; Nulliparous (not yet preg / borne viable offspring) = Null. $^{+1}$ = with dependent infant.

Female	Reproductive status	Age (years)
Group 1a		
MM	Preg, par	26
OP^{+1}	Lac, par	13
SW^{+1}	Preg, par	12
BD^{+1}	Lac	11
KL^{+1}	Lac	11
SL	Preg, pri	11
IS	Cyc, null	11
NO	Cyc, null	10
LK	Cyc, null	8
Group 1b		
MY^{+1}	Preg, par	16
OP^{+1}	Non-cyc, par	14
BD^{+1}	Lac	12
KS	Cyc, par	11
SL^{+1}	Lac, par	12
NO	Preg, pri	11
LI	Cyc, null	8
Group 2		
TL^{+1}	Cyc, par	24
SW^{+1}	Preg, par	14
KL^{+1}	Lac	12
IS	Cyc, null	12
MU	Null	6

Dominance

I investigated whether social dominance influenced copulation call production and the acoustic structure of the calls. To do this, I created dominance hierarchies and dominance classes based upon the outcome of agonistic interactions between individuals (e.g. Stevens et al., 2005a, 2007). I used ‘fleeing from aggression’ as a behavioural marker of dominance, following previous studies indicating this to be a suitable dominance measure in bonobos (e.g. Vervaecke et al. 2000a; Stevens et al., 2007). I used the Matman analysis program (Noldus version 1.1) to explore dominance relations and test for the linearity of dominance hierarchies. Extensive details about my procedure and results are provided in chapter three and appendix I.

Part one: Acoustic analyses

For my acoustic analyses, I took a balanced and random sample of copulation calls produced by seven females (SW, BD, KS, SL, NO, LI, LK) during their sexual interactions with males and females. I was unable to include the other females (N = 7) owing to inadequate contributions to the data set. Except for one female, who only contributed N = 7 male-female copulation calls (LI), I analysed N = 8 calling episodes (henceforth copulation calls) for each of the seven females during their interactions with both male and female partners.

Bonobo copulation calls constitute a single call or a sequence of several call units within a longer calling utterance (Kano, 1992; Thompson-Handler et al., 1984; see fig 6.1). Hence, the term ‘copulation call’ in subsequent analyses refers to the overall ‘call episode’, which is composed of one or more ‘call units’. I carried out quantitative analyses of the acoustic structure of each of the call episodes and call units within the copulation call using PRAAT 4.3.17 (www.Praat.org). Following visual inspection of call structure and properties, I used the following analysis settings: pitch: range 1500-4500Hz, optimised for voice analysis; spectrogram: analysis window length 0.025 s, dynamic range 70dB, spectrogram view range: 0–20kHz (to determine the number of harmonics). I performed pitch analysis using a script written by M. Owren (personal communication) and verified the generated values using a harmonic cursor.

For each copulation call, I measured 22 acoustic variables overall (spectral and temporal, see fig.6.2). At the level of calling episode, I measured: (1) episode duration (s): length of total episode from the start of the first call to the end of the last call; (2) number of calls; (3) call rate: number of calls per s; (4) percentage of calls that showed noisy or non-linear properties (see fig 6.2B); (5) mean inter-call interval (s): time between subsequent calls, taken from point of call offset of first call to onset of next call. For individual calls, I measured 18 acoustic parameters, taking spectral measurements from the fundamental frequency (F_0). This analysis included two temporal parameters: (6) call duration (s) and (7) peak time: location in the temporal domain where maximum acoustic energy occurs, expressed as a proportion of the call duration. I analysed 15 spectral parameters: (8) number of harmonics: number of harmonic bands visible in the spectrogram lying above the fundamental frequency; (9) mean fundamental frequency (Hz): average F_0 across the entire call; (10) minimum fundamental frequency (Hz): minimum frequency of F_0 across entire call; (11) maximum fundamental frequency (Hz): maximum frequency of F_0 across entire call; (12) mean amplitude (dB): the mean acoustic energy of the call unit; (13) peak position : temporal position of the max F_0 divided by the call duration; (14) percent of call that was voiced; (15) jitter: measure of the pitch stability or short-term perturbation in the F_0 (perceived as voice roughness); (16) shimmer: measure of sound pressure level perturbation caused by vibratory variations from one vocal fold cycle to the next (perceived as voice hoarseness); (17) peak frequency at call onset (Hz): frequency of maximum energy, as indicated using a spectral slice (fig. 6.2C); (18) peak frequency at call middle; (19) peak frequency at call offset (Hz); (20) transition onset (ΔHz): frequency of maximum energy at call onset minus frequency of maximum energy at call middle; (21) transition offset (ΔHz): frequency of maximum energy at call middle minus frequency of maximum energy at call offset; (22) overall transition (ΔHz); frequency of maximum energy at call end minus frequency of maximum energy at call beginning. Figure 6.2 (overleaf) illustrates the various acoustic parameters.

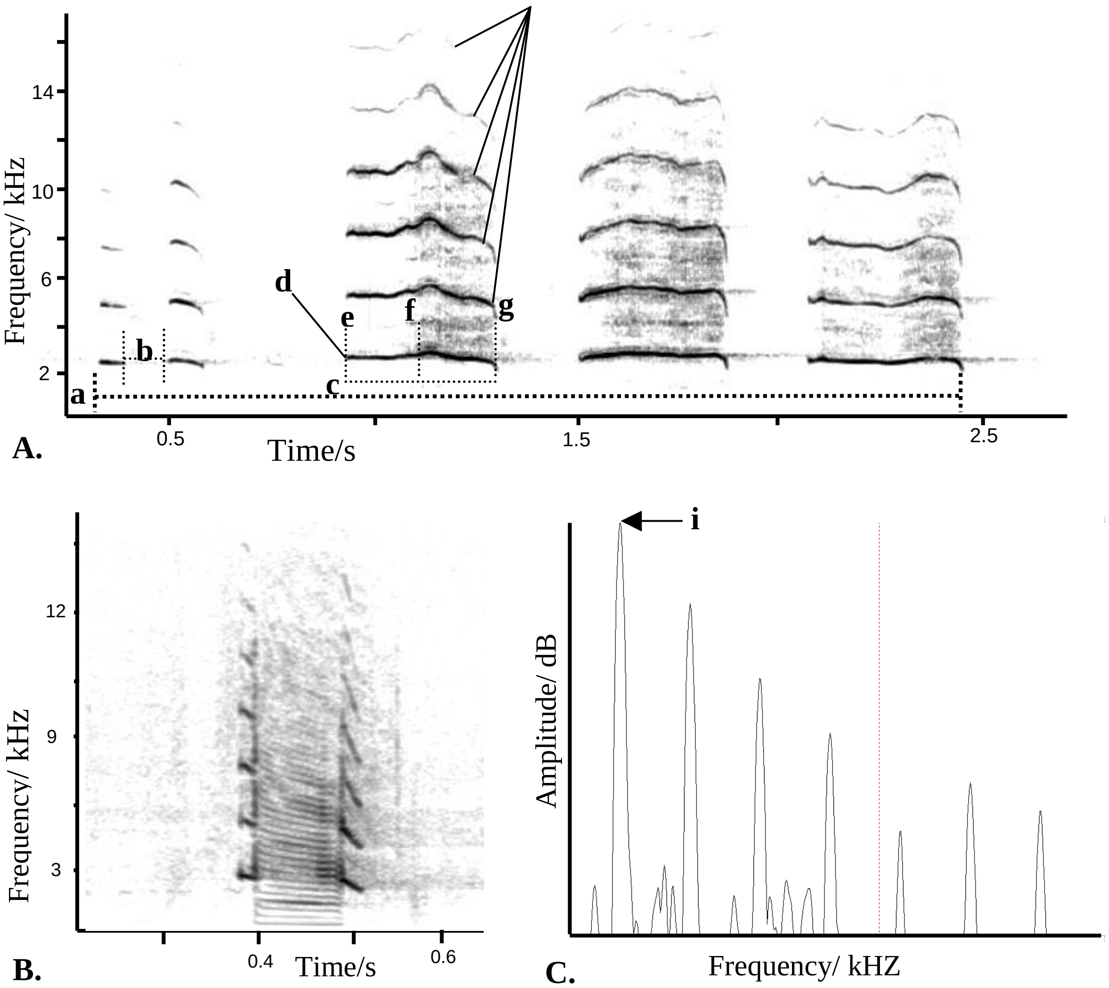


Figure 6.2.(A). Example of a time-frequency spectrogram of a female bonobo copulation call illustrating how some of the acoustic parameters were measured. Copulation call duration = duration of (a) (from start of first call unit to end of final call unit). Inter-call interval = duration of (b) between each call unit. Call unit duration = c (g – e). Fundamental frequency (F_0) upon which all spectral variables were measured, Hz = d. Transition onset (ΔHz) = Frequency of maximum energy at call onset (e) minus at call middle (f).Transition offset (ΔHz) = frequency of maximum energy at call middle (f) at call end (g). Overall transition (ΔHz) = frequency of maximum energy at call end (g) minus at call beginning (e). Number of harmonics = h (e.g. *N* = 5). **(B).** Time-frequency spectrogram of a copulation call unit illustrating non-linear properties. (**C**). Example of spectral slice of a copulation call showing how peak frequency was calculated. Peak frequency (Hz) = (i)

Analysing acoustic differences

My main aims were to investigate the extent to which copulation calls contained information about the type of sexual interaction (female-female genital contact or female-male copulation) and the identities of the individuals involved (caller and partner). In order to account for analysing multiple calls within a given call event, and thus to avoid pseudo-replication, I calculated mean scores per copulation call episode. These were based upon acoustic analyses of each of the individual calls. Before continuing, I first screened the data for outliers by producing standardised Z scores. I rejected any calls with a Z score greater than 3.29 in one or more parameters (Tabachnick & Fidell, 2001). Next, I regressed all parameters to check for multi-co-linearity and singularity, removing any parameters with a variance inflation factor greater than 10.

Female identity

I used the Discriminant Function Analysis (DFA) procedure to test whether the acoustic variables, when combined into one model, could generate discriminant functions that could correctly classify caller identity (N = 7 females). Following the screening procedure, I was able to enter 17 of the original 22 acoustic variables (parameters excluded: maximum $F_{0;}$ transition offset; peak frequency of call onset; peak frequency of call offset) into the DFA for N = 111 calls, with eight calls per female per context (except for one female, LI, who only contributed seven male-female calls). I conducted two separate DFAs to investigate the degree to which caller identity was encoded in copulation calls produced in homo- versus heterosexual interactions (N = 56 female-female interactions, N = 55 female-male interactions). For both analyses, I used the leave-one-out classification procedure in order to cross-validate the discriminant functions that were generated. In this procedure, each call is classified by the functions derived from all calls other than that one.

Sexual interaction type

Next, I investigated whether copulation calls produced during sexual interactions with males could be discriminated from those produced with female partners. For this, I used the DFA procedure, taking interaction type (male-female/female-female) as my test factor (N = 111 calls). Since the data were two-factorial (individual identity; interaction type) and comprised of eight calls per combination of the two factors, Mundry and Sommer (2007) argue that a conventional DFA does not allow for a valid estimation of the overall significance of discriminability. Thus, in order to estimate the significance of the number of correctly classified calls (cross-validated), whilst controlling for female identity, I conducted a permutated DFA (pDFA) with female identity entered as a control factor.

To investigate the finer acoustic structure, I conducted one-way analysis of variance tests (ANOVAs) on each of the non-correlated acoustic parameters to investigate whether different features of the call's acoustic structure varied statistically with the type of sexual interaction. In these analyses, interaction type was entered as a fixed factor and female identity as the random factor. Including female identity as a random factor addressed the problem of pseudo-replication, by controlling for multiple contributions from the same individuals.

Swelling size

I also investigated whether the acoustic structure of copulation calls varied statistically with the size of a female's sexual swelling (an approximate indicator of fertility; e.g. Dixson, 1983; Nunn, 1999). The aim was to conduct a within-subjects analysis comparing a female's call production at high and low swelling states. Unfortunately, the majority of calls available for analysis were produced by females during their mid or maximum swelling states, with very few calls produced at low swelling sizes (see behavioural analyses). Although this imbalance prevented me from conducting a powerful analysis, I was able to conduct some analyses on the limited data set available. This constituted a comparison of the copulation calls produced by four cycling females (LI, IS, KS, LK) when their swelling size was low (sizes zero or one) compared to high (sizes two to three). Each female contributed a minimum of one copulation call during high swelling stages (3-8 calls) and low swelling (1-8 calls) size stages during interactions with males and female partners (female-female interactions: N = 36 calls in total: N = 12 low-swelling calls and N = 24 high-swelling calls; male-female interactions: N = 34 calls in total: N = 11 low-swelling calls and N = 23 high-swelling calls). I conducted two separate pDFAs for interactions with male and female partners to test whether the discriminant functions derived from combining the acoustic variables together could discriminate calls produced during low and high swelling states. Although sample sizes were low, the permutated DFA (pDFA) could control for imbalanced data samples, and female identity was controlled for by entering it as a control factor. I also conducted Wilcoxon related-samples tests on the factor of swelling size for each acoustic parameter to investigate whether there were any differences in acoustic structure.

Partner rank

I investigated whether information about the dominance rank of the partner (high or low) varied statistically with the acoustic structure of the copulation calls. For male partners, I conducted analyses on $N = 54$ copulation calls for five females (other females were excluded owing to inadequate samples or because they were in non-cycling states). In this analysis, each female contributed an equal number of calls with high- and low-ranked male partners (IS, KL, SW = 12 calls, LK= 10 calls, KS = 8 calls). I conducted a pDFA on the 17 non-correlated parameters, controlling for female identity. In addition, I conducted finer-scaled analyses using one-way ANOVAs on each acoustic parameter for the factor of male rank, controlling for female identity (entered as a random factor). For female partners, calling was very rare with low-ranked partners and so inadequate sample size prevented me from conducting a pDFA. However, I was able to examine each of the 17 acoustic parameters individually to investigate whether acoustic structure provided cues to female rank. I conducted Wilcoxon related-samples analyses for five females, based on their mean values for each of the acoustic parameters. These values were based on a total of $N = 55$ calls. Each female contributed a minimum of one call for low-ranked female partners (range 1-5) and seven calls for high ranked partners (range 3-7).

Part two: Behavioural analyses

In this analysis, I investigated whether some of the above mentioned variables also influenced behavioural patterns in the performance of sexual interactions and copulation call production. First, I investigated whether the type of sexual interaction (female-female or male-female) and the rank of the partner (high or low) influenced rates of sexual activity and copulation call production (percent of sexual interactions with calls). To do this, I conducted a two-way repeated measures ANOVA for both rate of sexual activity and production of copulation calls, entering two factors: the type of sexual interaction and partner dominance rank. I was able to enter 11 females in this analysis, with the remaining three excluded due to inadequate sample sizes.

In addition, I investigated whether a female's sexual swelling size influenced her sexual activity and call production, controlling for number of observation days per swelling size. I investigated this for both homosexual and heterosexual interactions and included all females exhibiting visible swelling cycle (N = 9 females), excluding females who lacked swelling cycles due to pregnancy or lactation. I conducted two-way repeated measures ANOVAs for rate of sexual activity and copulation call production (percentage of sexual interactions with call) on the factors of swelling size (size zero to three) and sexual interaction type.

General statistical analyses

I conducted all statistical analyses using SPSS version 17.0, except for the permutated Discriminant Function Analyses, which I computed using R (version 2.5.11, R Core Development Team). Unless otherwise mentioned, all tests were two-tailed and significance levels were set at α= 0.05. For small sample sizes, I calculated exact p-values, as recommended by Mundry and Fischer (1998).

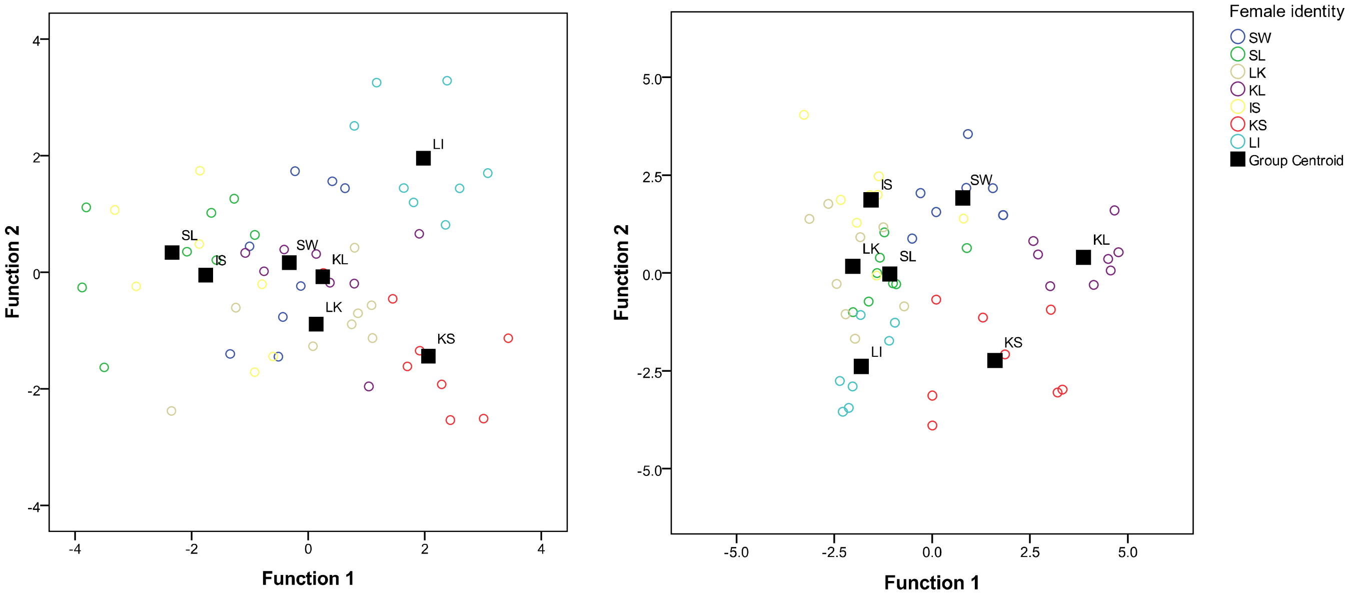
Results

Part one: Acoustic analyses

Female identity

I conducted acoustic analyses on N = 111 copulation call episodes (N = 7 females), where each female contributed a balanced contribution of female-female and male-female copulation calls (N = 8 calls per interaction type, except for one female (LI) who only contributed N = 7 male-female copulation calls). Results from discriminant function analyses (DFAs) indicated that caller identity was reliably conveyed via the acoustic structure of calls produced with both male and female partners, with both models deriving seven significant discriminant functions (male-female interactions:

Wilks lambda: 0.006, χ^2 = 213.224, df = 102, *P* < .001, female-female interactions: Wilks lambda = 0.020, χ^2 = 168.248, df = 102, *P* < .001; see fig.6.3). A cross-validated analysis revealed that copulation calls produced with male and female partners could be significantly discriminated on the basis of caller identity, with cues to identity coded most strongly in copulation calls with male partners compared to with female partners (cross-validated correct classification: male-female = 50.9%: binomial test (0.14) p < .001; female-female = 37.5%: binomial test (0.14) p = .001).



(a) Female-female

(b) Female-male

Figure 6.3 Distribution of the discriminant scores for copulation calls produced by seven female bonobos during (a) female-female genital contacts and (b) female-male copulations. The discriminant scores lie along two discriminant functions established to discriminate female identity in both mating contexts. Group centroids per female are indicated with black squares (two letter code per individual).

Sexual interaction type

Next, I analysed whether copulation calls produced during male-female copulations could be distinguished from those produced during female-female genital contacts. When controlling for female identity, results from a permutated DFA (pDFA), revealed that calls produced during interactions with males could not be reliably discriminated from those produced during interactions with females (cross-validated classification after $N = 1000$ permutations = 7.82, $P > .05$). I also conducted one-way ANOVAs on each acoustic parameter to see if there were any subtler differences at the finer scale (entering interaction type as the test factor and female identity as the control factor). As indicated by the DFAs, I found considerable acoustic overlap for homo- and heterosexual copulation calls, with no statistical differences for the majority of acoustic parameters (15/17 variables, all $P > .05$). However, there were some acoustic differences in call delivery, with significantly longer copulation call episodes (call episode duration: (F (1, 6) = 6.502, $P = .043$) and longer inter-call intervals (F (1, 6) = 4.074, $P = .090$) for heterosexual copulation calls compared to homosexual copulation calls (fig. 6.4.). Overall, these results suggest that although homo- and heterosexual copulation calls share the same acoustic morphology, there are some subtle differences at the level of call delivery.

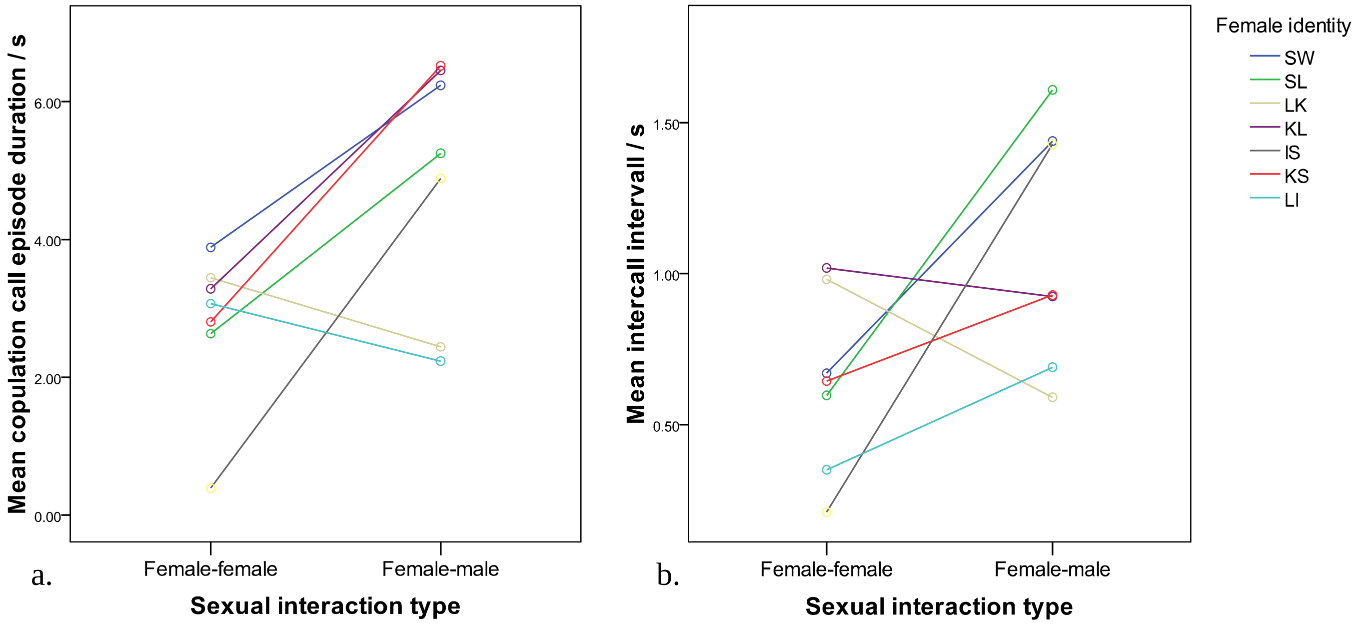


Figure 6.4. Line graphs showing the (a) mean copulation call episode and (b) mean inter-call interval as a function of sexual interaction type for seven female bonobos engaging in sexual interactions with males and females.

<u>Swelling size</u>

Results from pDFA tests on the acoustic structure of calls during homo- and heterosexual interactions revealed that calls produced during low and high swelling phases could not be statistically discriminated from one another (cross-validated classification after *N* = 1000 permutations: female-female = 12.310, *P* > .05; female-male = 15.0, *P* > .05). Further fine scaled comparisons at the level of each acoustic variable included in this analysis again revealed no significant differences (Wilcoxon related-samples tests, all: *P* > .05). Thus, although low sample size prevents strong conclusions, results from this analysis indicate that the acoustic structure of copulation calls does not appear to co-vary with the caller's swelling size.

Partner rank

For male partners, I conducted a pDFA to investigate whether information about the dominance rank of the partner (high or low) co-varied with the acoustic structure of copulation calls. When controlling for female identity, a pDFA failed to classify calls given to high- and low-ranked males with a significant level of accuracy (cross-validated classification after *N* = 1000 permutations = 19.85, *P* > .05). However, results from one-way ANOVA tests revealed several significant differences in how the calls were delivered. During copulations with high-ranked males, copulation call episodes were longer (Sidak corrections for multiple comparisons, F (1, 4) = 36.302, *P* = .001) with faster call rates (F (1, 4) = 17.168, p = .094) and shorter inter-call intervals (F (1, 4) = 4.547, *P* = .095) than calls produced with low-ranking male partners (fig. 6.5). Thus, as with the previous analyses on mating type, although the basic acoustic structure of copulation calls was not shown to differ with partner rank, there appear to be some subtle but striking differences in call delivery.

For female partners, very low call production with low-ranked partners meant there was insufficient data to conduct a pDFA. However, results from Wilcoxon signed-ranks tests (*N* =5 females) revealed no statistical differences for any of the acoustic parameters for the factor of female partner rank (all tests: *P* > .05).

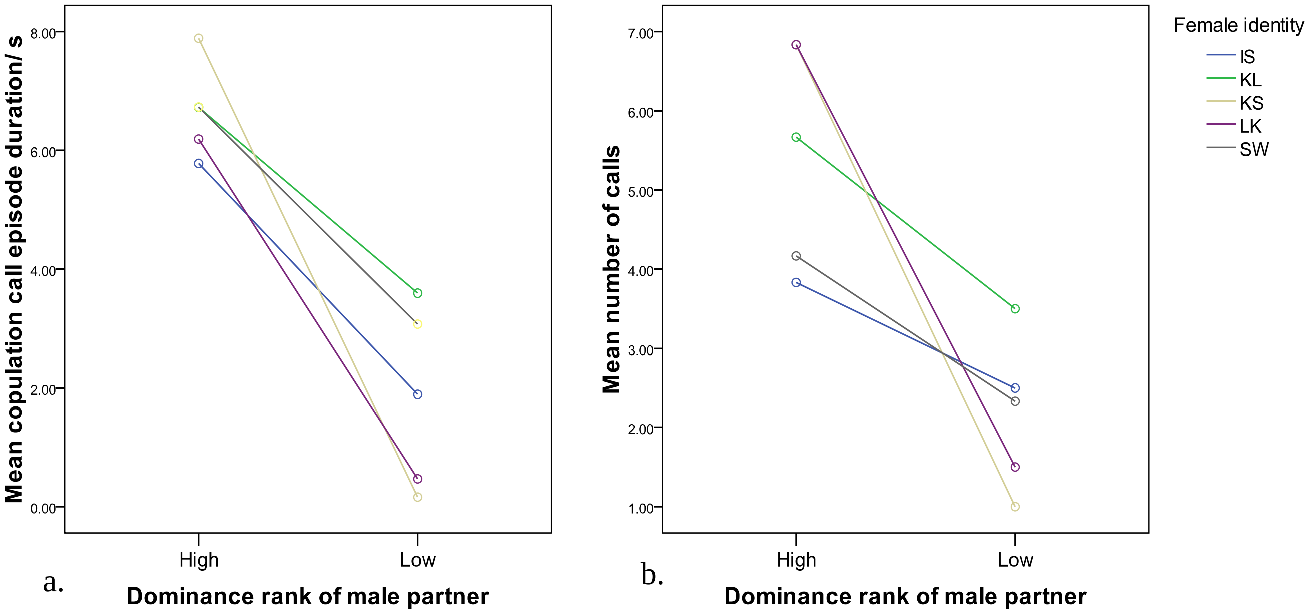


Figure 6.5. Line graphs showing (a) mean copulation call episode and (b) mean number of call units as a function of male partner rank for five female bonobos engaging in sexual interactions with male partners.

Part two: Behavioural analyses

Overall, I observed *N* = 1100 female-male copulations and *N* = 674 female-female genital contacts. However, although the overall number of heterosexual copulations appeared higher than homosexual genital contacts, the difference was not significant (within-subjects t-test: t = 1.378, df =13, *P* > .05).

<u>Sexual interaction type and partner rank</u>

I investigated whether the type of sexual interaction (female-female or male-female) and the dominance rank of the partner (high or low) influenced copulation call production. Results from a two-way repeated measures ANOVA on the factors of interaction type and partner rank (*N* = 11 females, three being excluded due to insufficient data) revealed a main effect of sexual interaction on call production, with females significantly more likely to produce copulation calls during interactions with males than with other females ($X_{\text{call with males}}$ = 32.88 % + 4.28 versus $X_{\text{call with females}}$ = 16.43 % + 2.37: F (1, 10) = 14.621, P = .003). There was a general significant main effect of partner rank, with females more likely to call with high-ranked partners than low-ranked partners, regardless of whether their partner was male or female ($X_{\text{call with high-rank males}}$ = 59.86% + 24.90; and $X_{\text{call with high-rank females}}$ = 28.22% + 16.33; versus $X_{\text{call with low-rank males}}$ = 9.17% + 11.4; and $X_{\text{call with low-rank females}}$ = 2.96% + 4.10: F (1, 10) = 54.734, $P < .001$). Finally, although there was a similar rank effect for calling with both male and female partners, there was a significant interaction between interaction type and partner rank (F (1, 10) = 7.512, P = .021), revealing a steeper decline in call production with low-ranked male partners compared with female partners (fig. 6.6).

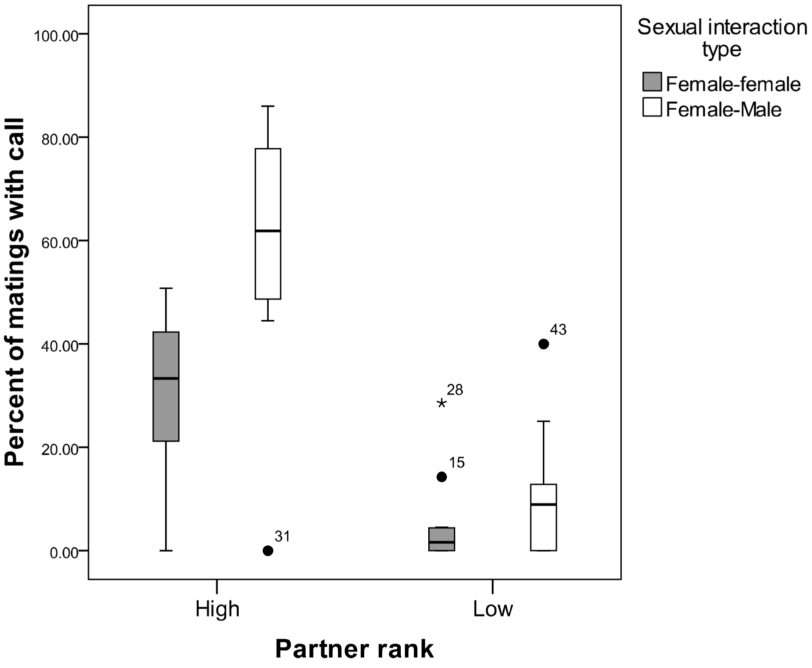


Figure 6.6. Boxplot indicating the percentage of sexual interactions with male and female partners accompanied by copulation calls as a function of partner rank. Thick black lines represent medians, box edges represent inter-quartiles, whiskers represent highest and lowest values within the normal distribution, circles represent outliers and asterisks indicate extreme cases.

Swelling size

Controlling for number of observation days per swelling size, results from a two-way repeated measures ANOVA on the factors swelling size (size zero to three) and sexual interaction type (female-female or male-female) revealed that swelling size had a significant effect on rates of sexual activity (F (3, 24) = 21.362, *P* < .001), with females engaging in more sexual interactions as their swelling sizes increased (pair-wise comparisons of swelling sizes with Bonferroni corrections: zero vs one: *P* = .075; zero vs. two: *P* = .005; zero vs. three: *P* = .002; one vs three: *P* = .013; one vs. two and two vs. three = *P* > .05). There was no significant effect of sexual interaction type on rates of sexual activity (F (1, 8) = 1.170, *P* > .05), but a trend showing that sexual interactions with females increased more steeply during maximum tumescence than compared to the increase of sexual interactions with males (fig 6.7).

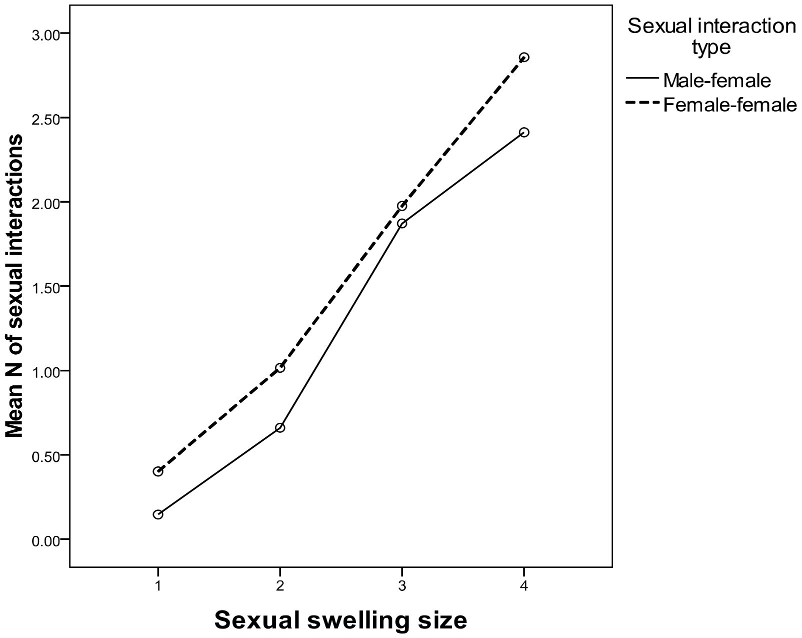


Figure 6.7. Line-graphs showing the effect of a female's sexual swelling size on rates of sexual interactions with males or other females.

Finally, I examined whether changes in sexual swelling size influenced copulation call behaviour. Results from a two-way ANOVA with the factors of swelling size (size one to three, with size zero excluded due to insufficient contributions) and sexual interaction type (female-female or male-female) on the proportion of sexual interactions accompanied by calls (*N* = 6 females) revealed that although females were more likely to call with male partners, female swelling size itself did not significantly increase the overall likelihood of call production (F (2, 10) = .345, $P > .05$). However, although the interaction was not statistically significant, call production increased with increasing swelling size for heterosexual copulations and decreased as swelling size increased for homosexual interactions. It is likely that a larger sample size would have brought this effect into significance (fig. 6.8).

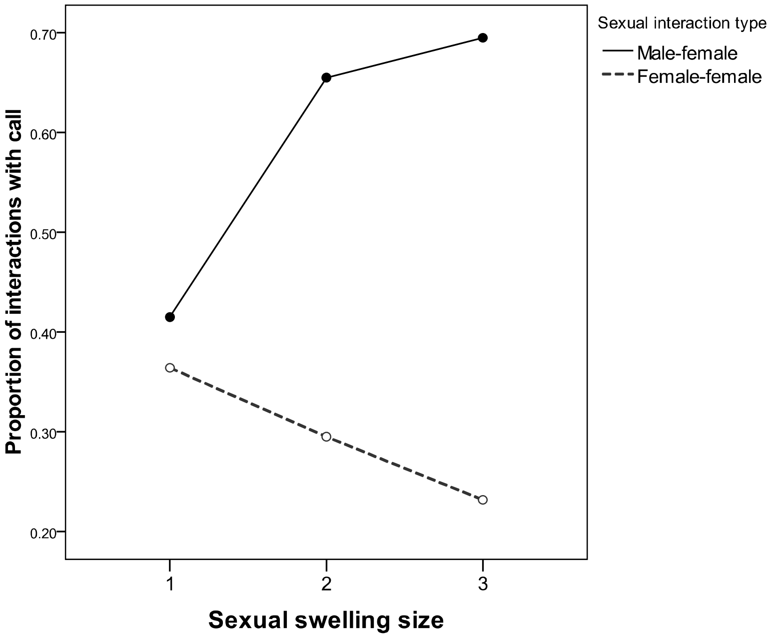


Figure 6.8. Line-graph indicating the proportion of sexual interactions with copulation calls as a function of female swelling size.

Discussion

In this study, I investigated patterns of call production and the acoustic structure of the copulation calls produced by female bonobos during sexual interactions with males and other females. Results highlight the social significance of copulation calls in this species and suggest that, similar to other sexual behaviour, calling has become partly detached from its original reproductive function in bonobos. Acoustic analyses revealed that although copulation calls were individually distinctive, calls produced with male and female partners shared the same acoustic morphology and could not be reliably distinguished from one another. However, there were subtle differences at the level of call delivery that discriminated partner sex as well as the dominance rank of male partners, but not female partners. Effects for partner rank and sex were much stronger in terms of copulation call usage, with females more likely to call with male than female partners, and more likely to call with high-ranked partners, regardless of partner sex. In terms of reproductive state, I found no evidence of any acoustic cues being related to the size of the caller's sexual swelling, an approximate indication of reproductive state (Dixson, 1983; Nunn, 1999). In terms of call usage, sexual swelling size increased sexual activity in general, but corresponding increases in call production only occurred during interactions with males, while they decreased with female partners. In sum, my results suggest that whilst these calls appear to have retained some of their reproductive features, copulation calls are also used within broader social contexts. This pattern deviates from other reports in the literature and therfore represents an intriguing challenge to current theories, which focus only on the reproductive significance of copulation calls (e.g. Maestripieri & Roney, 2005; Pradhan et al., 2006).

Although it is difficult to accurately assess the adaptive significance of bonobo copulation calls and to speculate what their ancestral state may have been, it is likely that these calls evolved as reproductive signals. However, at some point in evolutionary time, these calls appear to have gone through a transition into more general social signals, although still retaining some of their reproductive features. For example, acoustic analyses indicated that although females produced these calls in both contexts, a greater amount of information is coded into the more 'reproductive' (presumably ancestral) form of the call (i.e. there were greater cues to partner rank and caller identity in heterosexual copulation calls than homosexual ones). Furthermore, there was a positive relationship between call production and sexual swelling size in heterosexual interactions but not for homosexual interactions.

In terms of acoustic structure, there could be numerous benefits for a female to signal her identity, in both types of sexual interactions. From a reproductive perspective, alerting males to her location and sexual receptivity could maximize the benefits received from indirect mate choice, either by inciting male-male competition, or by increasing the quality and/or number of partners (O'Connell & Cowlishaw, 1994;

Semple, 1998, 2001, Semple & McComb, 2000). Such a strategy may be especially important for a species, such as the bonobo, in which females regularly overlap in their oestrous cycles and breed non-seasonally (e.g. Altmann et al., 1996). Consistent with this explanation is evidence of individually distinctive copulation calls in numerous other primate species that share similar reproductive ecologies (e.g. female promiscuity, overlapping cycles and non-seasonal breeding). These include chimpanzees, *Pan troglodytes* (Townsend et al. 2008); yellow baboons, *Papio cynocephalus* (Semple, 2001); chacma baboons, *Papio ursinus,* (Hamilton & Arrowood, 1978); sooty mangabeys, *Cercocebus atys*, (Gust et al., 1990); and long-tailed macaques, *Macaca fascicularis* (Deputte & Goustard, 1980).

In chimpanzees, males have been shown to prefer mating with older females (Muller et al., 2006), probably because they require fewer cycles before conception (Deschner & Boesch, 2007). Although data are lacking for bonobos, studies of both wild and captive populations have highlighted significant levels of intra-sexual competition that occur between females, particularly in the context of mating (Hohmann & Fruth, 2003a, Surbeck et al., 2010; Verveacke & van Elsacker, 2000). Thus, in a competitive reproductive climate, providing cues to individual identity may represent a useful means to advertise a female's presence and receptivity to potential consort males.

The finding that information about female identity was acoustically conveyed in copulation calls during female-female interactions challenges the notion of females coding identity for purely reproductive reasons. On the one hand, providing cues to identity during female-female genital contacts may represent a functionless by-product of a call that presumably evolved as a reproductive signal. Nevertheless, advertising individual identity in socio-sexual interactions may also provide benefits. If there are no costs to producing copulation calls, a female may attract both potential reproductive and social partners by advertising her sexual receptivity. In chimpanzees, wild females remain relatively isolated from males and only associate significantly with them during their period of oestrous (e.g. Gilby et al., 2009; Wrangham & Smuts, 1980). For such females, copulation calls may represent a kind of social 'golden pass', advertising their presence and sexual receptivity to individuals that they may not commonly associate with. Such a scenario may also be relevant for female bonobos, who emigrate from their natal groups and are typically unrelated to other group members (Gerloff et al., 1999). This may be especially relevant during the period of immigration, when newly arriving females must integrate with unrelated group members of both sexes (Hohmann et al., 1999; Idani, 1991).

Although acoustic analyses indicated that copulation calls produced in homo- and heterosexual interactions share the same acoustic morphology, differences at the level of call delivery (call duration and inter-call interval) suggest that listeners may still be able to derive some cues to the type of sexual interaction taking place. In Barbary macaques, males have been shown to discriminate calls produced in conjunction with ejaculatory versus non-ejaculatory matings (Pfefferle et al., 2008b). The authors concluded that this could promote sperm competition between potential male mates, which may derive reproductive benefits for the female caller. Sperm competition is likely to play a role in the evolution of copulation calls in bonobos, a highly promiscuous species, and therfore this question certainly requires further investigation. Ultimately, playback experiments are required to determine whether other bonobos can distinguish copulation calls produced during homo- versus heterosexual interactions.

The rank effect observed for call production and, to a lesser extent, for acoustic structure, replicates patterns described in a number of other primates. For example, cues to partner rank have been demonstrated in the calls of yellow baboons and chimpanzees (Semple et al., 2002; Townsend, 2009), as well as other species, showing that females call more with high-ranked compared to low-ranked partners (e.g. Arlet et al., 2007; Nikitopoulos et al., 2004; Oda & Masataka, 1992; Semple et al., 2002; Zhao, 1993). Previously, rank effects were explained as reproductive strategies, such as to promote mate guarding in the consort male (e.g. Pradhan et al., 2006). However, the fact that I found comparable effects in call production during homosexual interactions is incompatible with purely reproductive explanations. In this manner, results from my study highlight the social aspect of copulation calling in bonobos, something that has not received much attention in other studies.

The social use of a reproductive signal is, however, consistent with a broader trend seen in this primate, that is, the transition of sexual behaviour from having a pure reproductive to a more social function (e.g. de Waal 1987, 1995; Hohmann & Fruth, 2000; Kuroda, 1980; Paoli et al. 2006b). In bonobos, sex also serves as a social tool, for example by facilitating the formation of female aggregations and intra-sexual bonds, allowing females to co-exist peacefully, which enables them to form coalitions and exert social power (e.g. Fruth & Hohmann, 2006; Furuichi, 1989; Kano, 1992). In this way, copulation calls may help females to advertise their sexual interactions, especially with high-ranked partners, a behaviour that may be part of a broader strategy to form associations with socially important group members. The social role of copulation calls during genital contacts will be explored in more detail in chapter seven.

In bonobos, the hypothesis that copulation calls are part of a strategy to reduce infanticide risk from males does not appear to apply, as bonobos have never been observed committing infanticide (see Hohmann & Fruth, 2003a). Of course, it is plausible that the absence of evidence for infanticide merely reflects the comparatively small amount of observation hours of wild bonobos (Stanford, 1998). However, behavioural and hormonal studies in the wild and captivity indicate that male bonobos are considerably less aggressive than their chimpanzee counterparts (e.g. Sannen et al., 2003; Vervaecke et al., 2000a), with most of their inter-sexual aggression attempts quickly countered by female defense and/or female coalitionary attacks against them (e.g. Hohmann & Fruth, 2003a). Among females however, significant levels of intra-sexual aggression, particularly in the context of mating, suggest that other females may represent reproductive competitors. For example, there have been numerous cases of females mishandling, abducting and aggressing other females' infants in both the wild and captivity (Hohmann & Fruth, 2003a; Vervaecke & van Elsacker, 2000; Vervaecke et al., 2003; Z. Clay, personal observations). In this way, copulation calls may represent one potential mechanism to cement the support of high-ranked allies against the threats of female-female competition.

In terms of proximate explanations, the findings of differences in call production in relation to partner rank and partner sex may be attributable to more physical mechanisms, such as stimulation and arousal (see Semple et al., 2002). For example, a female's ano-genital region may be more stimulated during the penile intromission and thrusting of heterosexual copulations than during homosexual genital rubbing. This also may be the case for mating with large-bodied, high-ranked males compared to low-ranked males. However, if the level of stimulation influences calling, and the stimulation resulting from copulations with males is assumed to be greater than the external rubbing of genitalia, greater differences in call morphology should have been expected, which is not what was found. These mixed effects suggest that although physical factors may proximately account for some of the structure of copulation calls, there may be other, psychological mechanisms underlying the production of these calls in bonobos.

In sum, my results paint a complex picture of copulation calls in bonobos and suggest that a rich amount of information about the nature of their socio-sexual interactions is conveyed by these calls. Whilst results show that these calls have not entirely lost their reproductive functions, they also highlight the social manner in which copulation calls are used by bonobos, something that has not been thoroughly addressed in the current literature. Previous studies in both the wild and captivity have highlighted the role socio-sexual interactions play in bonobo social life (e.g. de Waal, 1987; Hohmann & Fruth, 2000; Paoli et al., 2006b) and copulation calls may represent an additional avenue for females to advertise their presence and socio-sexual activity within the group. The transition of copulation calls from a reproductive into a social behaviour in bonobos highlights the role that social life can play in shaping communication systems in animals.

Chapter seven: Female bonobos use copulation calls as social signals

Summary

Bonobo females form close affiliations with unrelated females, which enables them to form coalitions to dominate males. In addition to more common social behaviours, such as grooming, the performance of genital contacts appears to be another mechanism that facilitates their social affiliations. During genital contacts, females sometimes produce ‘copulation calls’, which share the same acoustic structure as those given whilst mating with males (chapter six). Here, I focused on female genital contacts and investigated the social rules underlying copulation calls. I found that low-ranked females frequently engaged in sexual interactions with both low- and high-ranked partners, while such interactions between high-ranked females were rare. One interpretation of these results is that genital contacts are a more relevant affiliative mechanism for low-ranked females, whose social position is less stable, compared to high-ranked females. In terms of call production, I found pronounced effects of dominance relations and social intention, with most calls given by low-ranked females when solicited by high-ranked partners. The presence of the alpha female as a bystander also enhanced the likelihood of calling. Two measures relating to physical stimulation, spatial position and genital contact length, had no effect on call production. My results indicate that bonobo females use these calls flexibly by considering their own and their partner’s social positions as well as the composition of the audience. Bonobo copulation calling is an example of an animal vocalisation that has become ritualised away from a purely reproductive function to acquire a broader social significance.

Results from this chapter have been submitted for publication as:

Clay, Z., & Zuberbühler, K. Copulation calls as social cues in bonobos, *Pan paniscus*. *Submitted.*

Introduction

In most old-world primate societies, the prevailing social structure is that of female philopatry, whereby females remain in their natal groups whilst males emigrate (Pusey & Packer, 1987). One apparent consequence of females remaining together within their matrilines is the formation of strong affiliative bonds between females (e.g. Silk et al., 2006; Sterck et al., 1997). Although female migration does occur in a number of primate species (e.g. Moore, 1984; Pusey & Packer, 1986; Sterck & Korstjens, 2000), developing intra-sexual affiliations in the absence of genetic ties is more challenging, leaving relationships between unrelated females typically weak. In addition, female migration is frequently related to despotic systems and risk of infanticide (Sterck et al., 2005; Wrangham, 1980), a consequence being that females tend to remain within small family units and spend less time socialising (e.g. chimpanzees, *Pan troglodytes*, Wrangham & Smuts, 1980).

Bonobos are a species that exhibits female migration, with females typically emigrating as they approach sexual maturity to join new communities (Gerloff et al., 1999; Wrangham & Smuts, 1980). However, despite being unrelated to each other (Gerloff et al., 1999; Hashimoto et al., 1998; Hohmann et al., 1999), female bonobos aggregate and form enduring affiliations with other females (Furuichi, 1989, 2009; Hohmann et al., 1999; Kano, 1992; White & Wood, 2007). The tendency for female bonobos to aggregate in large, mixed groups has aroused considerable interest, particularly as the resulting female coalitions appear to have enabled females to accrue numerous benefits related to resource defence, infanticide avoidance and dominance over males (e.g. Furuichi, 2009; Hohmann & Fruth, 2003a; Parish, 1994, 1996; White & Wood, 2007; Wrangham, 1993).

There appear to be a number of behavioural mechanisms which facilitate the development of affiliations between immigrating females and group members. These include grooming, pronounced levels of adult play, food sharing and to some extent, peering[3] (Palagi & Paoli, 2007; Paoli et al., 2006a; Stevens et al, 2005b; Vervaecke et

---

[3] Peering is a ritualized behaviour in which the actor approaches to stare directly at the receiver’s face from a very close distance, sometime up to several centimetres (Furuichi, 1989; Kano, 1992; Stevens et al., 2005b).

al, 2000a). In addition, the habitual performance of genital contacts is thought to represent another behavioural mechanism that allows females to develop their affiliations and co-exist peacefully (e.g. de Waal, 1987; Kano, 1992; Kuroda, 1980; Thompson-Handler et al., 1984). Although homosexual genital contacts have been observed in all great ape species (*Gorilla gorilla*, Fischer & Nadler, 1978; *Pan troglodytes*, Anestis & Firos, 2004; *Pongo pygmaeus,* van Schaik et al., 2003), female bonobos make particularly strong and habitual use of them, both in the wild and in captivity (de Waal, 1987; Hohmann & Fruth, 2000, Paoli et al., 2006b, Thompson-Handler et al., 1984). Female genital contacts occur during face-to-face embraces when the two females mutually swing their hips laterally, whilst keeping their vulvae in contact (Hohmann & Fruth, 2000; Kuroda, 1980). As described in chapters two and six, genital contacts are thought to have a number of social functions, such as reducing social tension, enhancing social tolerance and food sharing, reconciling conflicts and providing a means for females to assess and express their social relationships (e.g. de Waal, 1987; Fruth & Hohmann, 2006; Furuichi, 1989; Hohmann & Fruth, 2000; Paoli et al., 2006b; Parish, 1994; White & Wood, 2007). The performance of genital contacts appears to be an important part of the integration strategy of newly immigrating females, with these females frequently engaging in genital contacts with new group members, especially with high-ranking, established females (Idani, 1991).

Whilst genital contact behaviours appear to have considerable social relevance for female bonobos, assessing what psychological processes underlie these behaviours remains challenging. One approach to this problem is to examine the communicative signals produced in association with these social interactions, an approach which has proved fruitful in other studies of animal social cognition (Seyfarth & Cheney, 2003a). As demonstrated in chapter six, female bonobos produce specific vocalisations, known as ‘copulation calls’, during their sexual interactions with females as well as with males (Kano, 1992; Thompson-Handler et al., 1984). In addition to sharing the same acoustic morphology, results indicated considerable overlap in their use with male and female partners, indicating that copulation calls have acquired a greater social dimension in this species.

Following these broader comparative analyses, the aim of the current study was to conduct a more detailed exploration of female genital contact behaviour and the social use of copulation calls in this homosexual context. I explored the influence of several social variables on genital contact performance and call production, including the dyadic dominance relationship of the caller and her partner, the direction of solicitation and the presence of an audience. In addition, I also investigated whether genital contacts and associated call production were influenced by the more physical features of the interaction, such as the spatial position of the partners (top versus bottom) and the genital contact length. In addition to my main data set, which was composed of naturalistic observations, I conducted an additional focused study of genital contact behaviour in a controlled environment where I manipulated dyad and audience composition.

If genital contacts are representative of a migration strategy for females to integrate and affiliate with other group members, I expected low-ranked females (most representative of wild, immigrating females) to be more sexually active than high-ranked females, who are already established in the group. Furthermore, if the vocalisations accompanying genital contacts relate to the expression and acknowledgment of social status, as has been suggested for the genital contact event itself (Hohmann & Fruth, 2000), callers should be expected to be sensitive to rank relations. Specifically, if low-ranked females are more motivated to advertise their sexual interactions using copulation calls, they should be expected to call more compared to high-ranked females. In terms of spatial position, I tested the hypothesis, suggested by Hohmann and Fruth (2000), that high-ranked females are more likely to take the top position during their interactions with low-ranked females as a means to express their social status (Hohmann & Fruth, 2000; although see Paoli et al., 2006b). From a more arousal-based perspective, I examined whether, in terms of genital stimulation, call production is also influenced by spatial position and genital contact length.

Methods

Study site

I conducted this study at Lola ya Bonobo Sanctuary, Kinshasa (DR Congo), between September and November 2008 and between August and November 2009. All details about the study site and dietary information are provided in my general methods chapter (chapter three). The genital contacts interactions upon which these analyses are based represent the same data set previously used in chapter six and have therefore been already described in detail. To summarise, I collected data from sexually mature females or females approaching sexual maturity (*N =14)* from three social groups over two periods. In 2008, I collected data on nine females from a group of 22 individuals housed in enclosure 1 (henceforth 'group 1a'). In 2009, I collected data on seven females from a group of 20 individuals housed in enclosure 1 and collected data on five females from a group of 19 individuals housed in enclosure 2 (henceforth 'group 1b' and 'group 2'). All details of group composition are provided in chapter three. To maximise sample size, I pooled the data set from across the three groups, resulting in *N* = 58 female-female dyads. The majority of dyads in the second year had not encountered each other before so represented independent data points. However, I combined data for any dyads that met each other again in the second year (*N* = 9 dyads), thus reducing the total N of dyads from 67 to 58.

Data collection

As methods for data collection have been presented in chapters three and six, I will only give a brief overview here. All observations (approx. 1,093 hours) were conducted at the largest two enclosures. Data collection involved all-occurence and all-day focal sampling (Altmann, 1974), balanced across individuals (approx. 50 focal hours per individual).

Recording genital contacts and copulation calls

I considered a genital contact between two females to be a ventro-ventral embrace with physical contact of genital swellings and lateral hip swinging (Hohmann & Fruth, 2000; Kuroda, 1980). I excluded cases of genital stimulation by any body part other than the genitals. For each genital contact event, I recorded the following information: partner identities, their spatial positions (top or bottom), call production, associated behaviours; identities of audience members within 15m and the behavioural context. Contexts included feeding, pre and post-feeding (15 minutes before and after feeding), social disturbances (group alarm or tension), food stealing (i.e. a female initiates a genital contact with another, then during or immediately afterwards, takes their target’s food), travel, arrival (i.e. meeting of separated individuals or arrival at new, non-feeding, location), play, agonism, post-agonism (reconciliation) and rest.

Additionally, I recorded the identities of the initiator and the target of the interaction. There was a diverse range of signals that females used to initate a genital contact, ranging from a single gestural behaviour to a more elaborate sequence of a multitude of different behaviours. In order to assign the identity of the initiator, I developed an inititation ethogram, based upon directed gestural behaviours (table 7.1). The initiator identity was only marked if at least one of these behaviours was observed and done in a way directed specifically at the taget individual.

Table 7.1. Ethogram describing the initiation behaviours which resulted in a genital contact interaction between the initiating female and her target female.

Initiation behaviour directed at target	Description/details
Exaggerated forward roll	Lying/sliding onto stomach in front of target, then rolling 180° onto back. Normally accompanied by leg/arm waving
Squat leg presentation with/without thrust	Standing in front of target with squatted legs whilst thrusting hips. May involve thrusting legs by using arms to hold body. Can be without thrust
Back slide	Sliding onto back in front of target. Can be accompanied by any combination of the following: legs straight up, legs shaking, arms up and open, arms shaking
Bipedal stance with open arms	Arms may be straight or waving. Bipedal stance can be whilst standing or walking to target with open arms, with or without contact. May lead into walking or leading the target to a location using bipedal dorsal embrace.
Bipedal dorsal embrace	Approach and embrace of target, may involve squat thrust
Dorso-ventral presentation	Presenting swelling dorso-ventrally. May involve looking/head-turn to target. May involve crouching
Contact on target	Tapping, poking, stroking of target with leg/foot/ hand/arm
Directed shake	Directed shake of the leg/foot/arm/hand towards the target
Extend	Leg/foot/arm/hand extend toward target, without contact

Dominance

I investigated the influence of the social dominance of caller and her partner on call production. Investigating the dyadic dominance relationship required accurate assessment of individual cardinal ranks. In order to calculate dominance ranks, I created dominance hierarchies for the three social groups, based upon the outcome of agonistic interactions between females (e.g. Stevens et al., 2007). I used the Matman analysis programme (Noldus, version 1.1) to examine dominance relationships and the linearity of hierarchies. Following this, I then calculated cardinal rank scores for individual females based upon normalised David's Scores, corrected for chance. All details of these analyses have been previously presented in chapter three, with results shown in appendix I.

Statistical analyses

Parametric analyses were conducted wherever possible, but non-parametric statistics were used where necessary. Non-parametric statistics were required for much of the data owing to low sample sizes and unbalanced individual contributions. For proportions data where the resulting value was equal to 0 or 1, I re-scaled the values using the following substitutions: where $x = 1$, the value was replaced with $x = 1 - (1/4N)$; where $x = 0$, the value was replaced with $x = 1/4N$). Following this, I then applied the arcsine transformation uniformly across the data set. These steps improved the homogeneity of variance distribution, rendering the data suitable for parametric analyses. All tests were two-tailed and unless otherwise mentioned, significance levels were set at $\alpha = 0.05$. For small sample sizes, I used exact tests (Mundry & Fischer, 1998). All statistical analyses were conducted using SPSS v. 17.0.

Part one: Patterns of genital contact performance

I first examined the behavioural patterns in genital contact performance. In addition to examining rates of performance and context of usage, I explored the effects of three main factors: the social rank; spatial position (top vs. bottom position); and the direction of initiation (which individuals initiates/is target).

To explore social rank, I used a goodness of fit test to compare rates of genital contacts against the expected frequencies for three dyad types: two low-ranked females; two high-ranked females; and a high- with a low-ranked female (henceforth referred to as 'asymmetric dyads'). Expected frequencies were calculated using expected proportions for each dyad class, based on the total number of dyads possible for each dyad type (two low-ranked females: $N = 17$ dyads; two high-ranked females: $N = 9$ dyads; asymmetric dyads: $N = 32$ dyads).

In terms of spatial position, I examined whether high-ranked females were more likely to take the 'top' position than low-rank females (following Hohmann & Fruth, 2000).

In addition, to investigate whether there were rank asymmetries in the direction of initiation, I compared the rates of initiation by high and low-ranked females during their interactions with one another (asymmetric dyads). To examine whether the initiation effect occurred more generally than just in dyads with large rank differences, I used the cardinal rank scores (David's Scores) to compare frequencies of initiations for the higher and lower ranked females within dyads composed of females from the same absolute rank class (i.e. the higher and lower-ranked of two females who both belonged to the low-ranked or high-ranked class). Non-parametric statistics were employed to investigate these broader behavioural patterns.

Part two: Patterns of calling behaviour

Social dominance

To investigate whether partner rank influenced call production, I conducted a repeated-measures analysis of variance test (ANOVA) comparing the proportion of genital contacts with calls for interactions with high- versus low-ranked partners. Owing to insufficient sample size for high-ranked females, I was unable to include caller rank as a factor in this analysis (there were only N = 20 interactions involving three high-high dyads, with two of the six high-ranked individuals never engaging in genital contacts with other high-ranked females). Thus, in order to investigate the effect of caller rank on call production, I conducted a Spearman's correlation to compare each female's cardinal rank score in her respective group (normalised David's Scores, corrected for chance) against the proportion of genital contacts in which she called. Because David's Scores are an absolute value for a given time period, I only entered data for each female once (to avoid pseudo-replication) with her accompanying David's Score (taken from her first data entry year, N = 14 females). Supplementary analyses of rank scores for both years for all females are indicated in appendix V.

Spatial position

To investigate whether spatial position influenced call production, I analysed the proportion of genital contacts accompanied by calling when the female took the top versus the bottom position (Wilcoxon signed-ranks test). I excluded any ambiguous cases where the females were in a more equal or upright position.

Initiation

To investigate whether the direction of initiation influenced call production (which female initiated the interaction), I conducted a two-way ANOVA on the factors of direction of initiation (initiate vs. target) and partner rank (high vs. low) on the proportion of genital contacts accompanied by calls. I assigned initiator identity using the behavioural ethogram described previously.

Audience effects

I also examined whether the presence of bystanders influenced call production. In order to control for the effects of dyadic dominance rank, I analysed interactions between low- and high-ranked females, which also represented the dyad type in which calling was most likely. Taking the perspective of the low-ranked caller, I randomly selected a balanced number of genital contacts for six low-ranked females (N = 20 for five females: LK, LI, IS, NO, KL, and N =18 for one female, KS), i.e. N = 118 events in total. The two other low-ranked females (MU and SL) were excluded from analysis owing to inadequate sample sizes. I compared the audience composition for silent and vocal genital contacts using the following variables: size of group present; number of females present; number of males present. I also investigated the influence of the social position of the audience. For this, I analysed the proportion of genital contacts accompanied by calls in which the following audience members were present compared to absent: dominant females (one or more high-ranked females present, excluding alpha-female); subordinate females (one or more low-ranked female/s present but high-ranked females and alpha female absent); the alpha female; and the alpha male. In order to assess the value of the alpha female as a bystander, it was necessary to exclude all interactions which involved the alpha female.

In addition to these separate analyses, I examined which audience variable most strongly predicted call production if all variables were combined in one model. To do this, I conducted the Generalized Linear Model analysis (binomial-logit) on the dependent variable of calling (call versus no call) with the above-mentioned predictor variables. I was able to enter data for all low-ranked females (*N* = 8) in this analysis and accounted for female identity by entering it as a covariate in the model. In order to analyse the effect of alpha female presence, I excluded all cases in which the alpha female was involved, which resulted in *N* = 206 interactions available for analysis.

Part three: Experimental study with controlled group composition

In order to further investigate the variables described in the main analysis, I conducted an additional, focused study of female genital contact performance and accompanying vocal behaviour in a controlled environment, where dyad and audience composition were controlled. To investigate the hypothesis that copulation calls during genital contacts are a female-directed behaviour used to express social status, I recorded genital contacts and associated calls for female dyads in the presence of female-only audiences.

I conducted this study inside the dormitory facility connected to Enclosure 1 over a 30-day period. The dormitory facility for Enclosure 1 was a 15m^2 room, divided into 9 sub-rooms. Rooms were separated by metal bar partitions, but everything was visible/audible to the other individuals (see fig. 7.1). There were wire tunnels connecting adjacent rooms as well as three tunnels to exit the dormitory from different places.

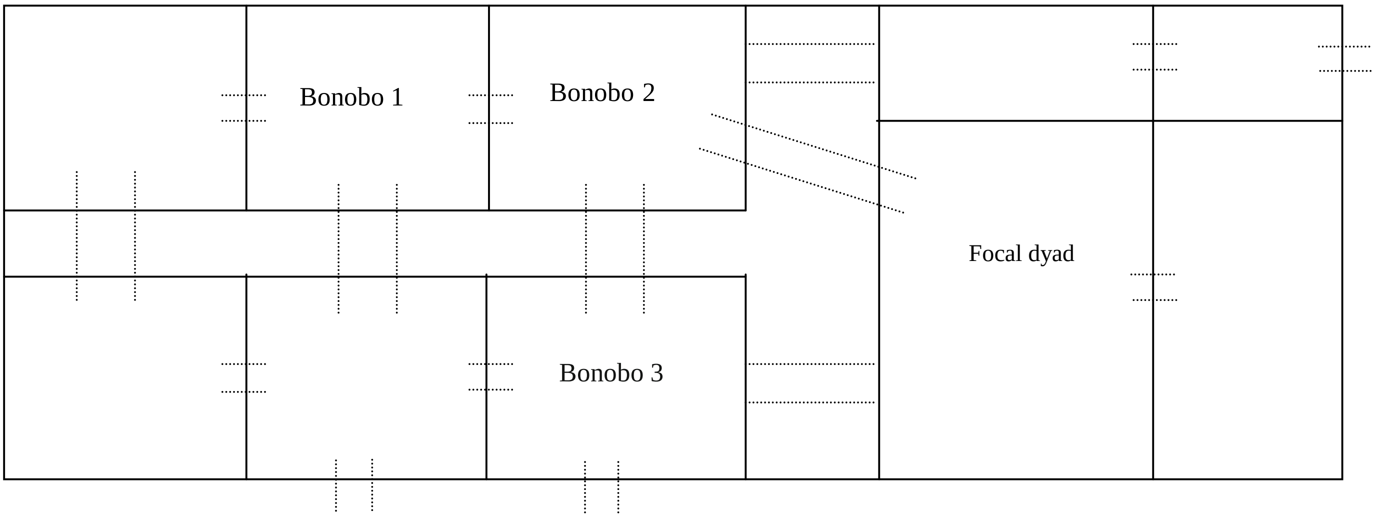


Figure 7.1. Layout of indoor dormitory for the focal study of genital contacts with controlled audience composition. Dotted lines represent passing tunnels.

In each trial, I recorded the genital contact behaviors and copulation calls that occurred between a focal dyad. Every female in group 1b was involved, as both an audience member and as part of the focal dyad (*N* = 7 females: three high-ranked: OP, BD, MY; and four low-ranked: KS, NO, SL, LI). Five females were present within the dormitory facility in each trial: three females as audience members, each housed in separate rooms, and two females as the focal dyad, housed in one room. Although separated, all females were visible to one another as only wire bars divided the caged rooms. In order to encourage sexual interactions, I began a trial by letting two females join one another in one room. Mothers (*N* = 4 females) were accompanied by their dependent offspring. Upon meeting, the two females would typically approach one another and commence genital contact behaviours, without any other intervention. However, if necessary, I waited several minutes until it was clear that no contact was being made and then provided banana slices in order to encourage behavioural interactions between the females. In all trials, I recorded the interactions using a camcorder and made verbal commentaries. I also made audio recordings using sound equipment as previously described. During a trial, the female dyad frequently performed a whole sequence of sexual interactions over several minutes. In order to control for context across trials, I only counted copulation call behaviour during the first genital contact interaction. Sex with offspring occasionally occurred, but was excluded from analysis. After completing a trial, either as a part of a focal dyad or as a bystander, a female was allowed to exit the dormitory and join the outdoor enclosure. Participation was voluntary and subjects could refuse to participate at any time, at which point they could exit the building. No female was ever forced to move rooms against their will or remain somewhere where they seemed uncomfortable. However, in general, the females appeared to enjoy participating in this study. Transferring between rooms was a normal part of their daily routine and individuals were cooperative in moving rooms.

In total, I conducted 90 trials balanced across all seven females in group 1b, with every possible dyad meeting at least once (19/21 dyads met at least twice) on separate days (mean: 4 trials per dyad). As with my main data set, I analysed genital contact performance and call production as a function of dyad composition (social rank), spatial position, direction of initiation and audience composition. For trials in which a genital contact interaction occurred, I analysed the factor of audience at three levels: (1) only low-ranked females present (i.e. visible); (2) one or more high-ranked females present without the alpha female; (3) alpha female present. Due to the low-sample sizes, I conducted non-parametric statistics throughout

Genital contact length

In order to further address the effect of physical stimulation on call production, I examined whether the length of the genital contact influenced call production. Using the close-range video-footage in this indoor study (in slow-frame settings on VLC media player), I compared the length of genital contacts (s) for interactions in which the focal female produced a copulation call or remained silent. Due to a rank bias in caller identity (all callers in this study were low-ranking), I was only able to examine data from low-ranked females. This resulted in a balanced sample of $N = 6$ call and $N = 6$ no-call events for 3 females (KS, LI, NO), with a given genital contact event entered only once (the other low-ranked female, SL, was excluded owing to inadequate sample size). Due to the low number of subjects available, I conducted separate Wilcoxon signed-ranks tests (exact, two-tailed) for each individual to compare genital contact length for vocal versus silent genital contacts.

Results

Rates of genital contacts

Overall, I observed $N = 674$ genital contacts between females; with every female ($N = 14$) engaging in at least one sexual interaction with two or more partners. Of the 674 genital contacts observed, 67% occurred within the feeding context, followed by 11% in the pre-feed period and 7% during rest phases. Genital contacts also occurred during socio-sexual play (5%), arrival (4%), non-agonistic social disturbances (2%) as well as a range of other contexts (all < 2% or lower) such as during agonism, post-agonism (reconciliation), food stealing, post-feeding and travel (see appendix IV).

Controlled for group size and observation time, the highest rates of genital contacts occurred in group 2, followed by group 1a and 1b (*N* genital contacts per female per hour: group 2 = 0.12; group 1a = 0.09; group 1b = 0.06). Heightened performance of genital contacts has been shown to be associated with periods of social instability and tension (de Waal, 1987; Hohmann & Fruth, 2000), something which may account for the raised levels of sexual activity in group 2 compared to the other groups. Group 2 experienced the greatest amounts of disturbances to its social structure compared to the other groups. For instance, there were 19 changes to the composition of group 2 (10 losses and 9 gains) one month before data collection commenced (owing to the departure of eight bonobos into a wild release programme and the subsequent reshuffling of remaining individuals). During the study period, group 1b was comparatively less affected, undergoing only eight changes (2 losses and 6 gains). In addition, social tension may have also been enhanced in group 2 owing to a particularly strong male presence (11 males compared to 5 females), as well as the presence of three dominant males that frequently provoked social instability and tension (KZ, MK, FZ). Likewise, the presence of a dominant and aggressive male (TT) in group 1a frequently resulted in social disturbances and tension. In contrast, lower levels of social tension in group 1b may also have been attributable to a higher proportion of more established females in the group and the absence of aggressive males (owing to the death of TT, the more placid beta male, MN, assumed the top male position).

Part One: Patterns of genital contact performance

Social rank:

The majority of genital contacts occurred between two low-ranked females (58%, *N* = 390) followed by asymmetric dyads (39%, *N* = 264). Interactions between two high-ranked females were rare, occurring just 20 times (3%). When taking into account the total number of dyads possible for each dyad type (two low-ranked females: *N* = 17 dyads; two high-ranked females: *N* = 9 dyads; asymmetric dyads: *N* = 32 dyads), genital contacts between two low-ranked females occurred more often than expected by chance, and interactions for asymmetric dyads and dyads with two high-ranked females occurred less frequently than expected by chance (goodness of fit test: G_2 = 283.464, df = 2 , $P < .001$; fig. 7.2).

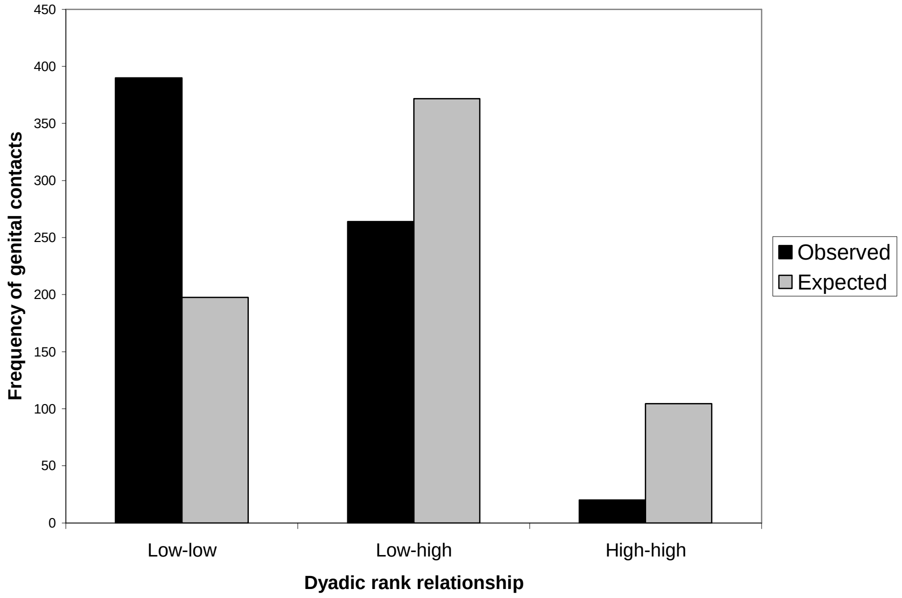


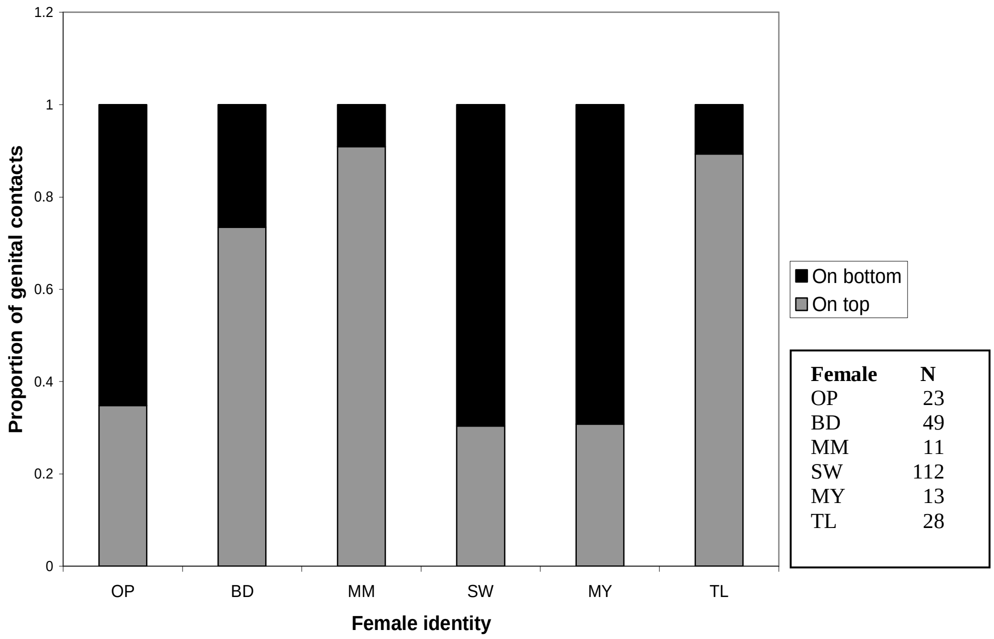
Figure 7.2. Frequency of genital contacts between: (1) two low-ranked females; (2) asymmetric dyads of a low- with a high-ranked female; (3) two-high ranked females.

Spatial position:

There was no significant difference between the spatial position (top or bottom) taken by low-ranked females ($N = 8$) compared to high-ranked females ($N = 6$) (Mann-Whitney U = 14, $P > .05$, table 7.2). In an analysis of the spatial position of high-ranked females ($N = 6$) within asymmetric dyads, there was significant variation in their individual preferences for spatial position, with no overall trend for them to take the top position ($\chi^2 = 56.022$, df = 5, $P < .001$, fig 7.3)

Table 7.2. Proportion of genital contacts in which the individual took the top position

Rank	Female	Proportion
Low	LK	0.66
	IS	0.69
	KS	0.12
	LI	0.92
	SL	0.15
	KL	0.25
	MU	0.00
	NO	0.66
High	OP	0.33
	BD	0.73
	SW	0.26
	TL	0.93
	MM	0.91
	MY	0.36



Female	N
OP	23
BD	49
MM	11
SW	112
MY	13
TL	28

Figure 7.3. Proportion of genital contacts when the high-ranked female took the top position during interactions with low-ranked females. Sample sizes are indicated in the text box (range: 3-5 partners per female)

Initiation

Of the 390 genital contacts that occurred between asymmetric dyads (high-with low), high-ranked females were significantly more likely to initiate to the low-ranked females than vice-versa ($X_{\text{high-rank female initiate}}$ + SD = 6.5 + 2.86 vs. $X_{\text{low-rank female initiates}}$ + SD = 1.75 + 2.86; Wilcoxon signed-ranks test, exact-two-tailed: Z = -3.006, N = 32, P = .002). However, there were no statistical differences in the direction of initiation for dyads composed of either two low-ranked females or two high-ranked females (two low-ranked females: $X_{\text{higher-rank female initiate}}$ + SD = 9.29 + 8.93 vs. $X_{\text{lower-rank female initiates}}$ + SD = 13.65 + 14.64; Wilcoxon signed-ranks test, exact-two-tailed: Z = -.911, N = 17, $P > .05$; two high-ranked females $X_{\text{higher-rank female initiate}}$ + SD = 1.44 + 3.97 vs. $X_{\text{lower-rank female initiates}}$ + SD = 0.78 + 1.71; Wilcoxon signed-ranks, exact-two-tailed: Z = -.535, N = 9, $P > .05$).

Part two: Patterns of calling behaviour

Of the $N = 674$ genital contacts recorded, $N = 124$ were accompanied by a copulation call (group 1a: 12.7%, $N = 424$; group 1b: 17.9%, $N = 151$; group 2: 43.4%, $N = 99$). As with genital contact performance, rates of calling were highest in group 2, followed by group 1a and 1b (N genital contacts with calls per female per hour: group 2 = 0.05; groups 1a and 1b = 0.01).

Social dominance

I investigated whether the dominance rank of the partner influenced call production. A repeated measures ANOVA revealed that females were significantly more likely to call with high-ranked partners compared to low-ranked partners (mean proportion of genital contacts with calls: $X_{\text{high-rank female}}$ + SD = 0. 38 + 0.18 vs. $X_{\text{low-rank female}}$ 0.04 + 0.06: $F(1, 11) = 31.897$, $P < .001$).

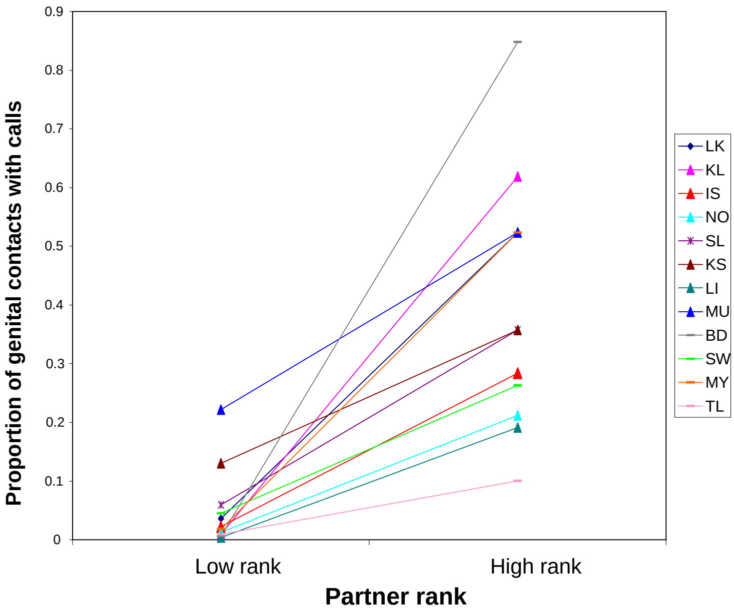


Figure 7.4. Line graph showing the influence of partner rank on copulation call production during female genital contacts. High-ranked females (BD, SW, MY, TL) are indicated with flatter graph symbols. Low-ranked females (all others) are indicated with triangular symbols.

In terms of caller rank, there was a significant negative correlation between female rank and call production (Spearmans rho r_s = - 0.662, *N* = 14, *P* = .010) indicating that females with lower rank scores were more likely to call than higher ranked females (fig 7.5, appendix V).

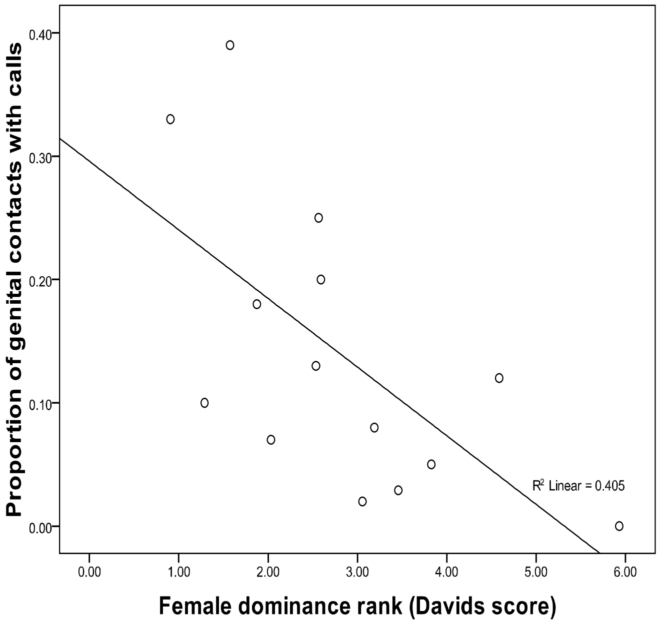


Figure 7.5. Scatter-plot showing the relationship between a female's dominance rank and copulation call production during female genital contacts.

Spatial position

I found no significant relationship between call production and spatial position within the dyad (*N* of calls in top position: *X* +SD = 5.25 + 4.43 vs. bottom position: *X* + SD = 4.41 + 4.94: Wilcoxon signed-ranks test: Z = -0.591, df = 12, *P* > .05).

Initiation

Results from a two-way analysis of variance revealed that the direction of initiation (initiate vs. target) as well as partner rank (high vs. low) had a significant effect on a female's likelihood to call (proportion of genital contacts with calls) (Initiation: F (1, 8) = 6.064, *P* = .039; Partner rank: F (1, 8) = 27.293, *P* = .001). Although the interaction between partner rank and initiation just failed to reach significance (F (1, 8) = 4.619, *P* = .064), results indicated that the effect of initiation was strongest for high-ranked partners, with females calling more when they were targeted by a high-ranked female compared to when they initiated the interaction (fig 7.5).

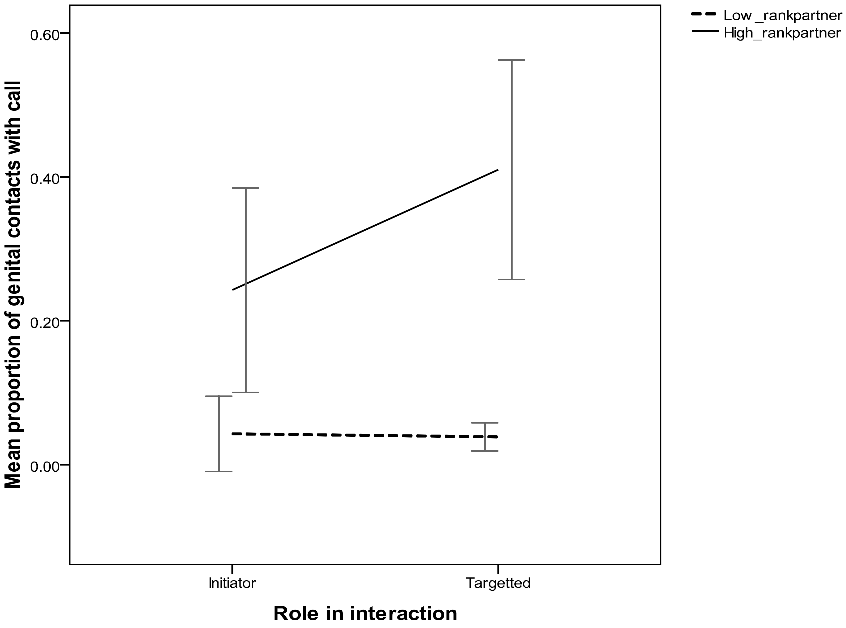


Figure 7.6. Line-graph (with standard error bars) showing the effect of initiation on call production during female genital contacts (*N* = 9 females).with high-ranked and low-ranked partners

Audience effects

I investigated whether the presence of bystanders influenced call production. Group size had no significant effect on call production (paired t-test: t = 2.050, df= 5, *P* > .05), in terms of both number of females or males (paired t-tests: for *N* females, t = 0.819, df = 5, *P* > .05; for *N* males, t = 2.341, df = 5, *P* > .05). However, there was a strong effect of alpha female presence, with females significantly more likely to call when the alpha female was present rather than absent (paired t-test on proportion of events with calls when the alpha female was present vs. absent: t = 4.931, df = 5, *P* = .005). However, the effect appeared to be restricted to alpha female presence alone, as neither the presence of other dominant females nor the presence of subordinate females had a significant effect on call production (paired t-tests: dominant female presence, t = -0.46, df = 5, *P* > .05; subordinate female presence, t= 2.140, df = 5. *P* > .05). The presence of the alpha male also had no significant effect on call production (paired t-test, t = 0.617, df = 5, *P* > .05, table 7.4).

Table 7.4. Influence of audience on calling during female genital contacts (GCs). The top half indicates mean number of bystanders (+ SDs) for vocal vs. silent GCs (N = 6 females). The bottom half indicates proportion of GCs with calls in which the given audience member was present vs. absent. Asterisk indicates significant effect.

Audience variable	Vocal GCs	Silent GCs
Group size	8.51 (2.23)	6.52 (0.59)
N females	2.95 (1.01)	2.60 (0.55)
N males	5.55 (1.43)	3.91 (0.55)
	Proportion GCs with calls when present	Proportion GCs with calls when absent
*Alpha female	0.54 (0.14)	0.22 (0.08)
Alpha male	0.34 (0.26)	0.27 (0.16)
Dominant females	0.35 (0.19)	0.36 (0.33)
Subordinate females	0.35 (0.18)	0.20 (0.19)

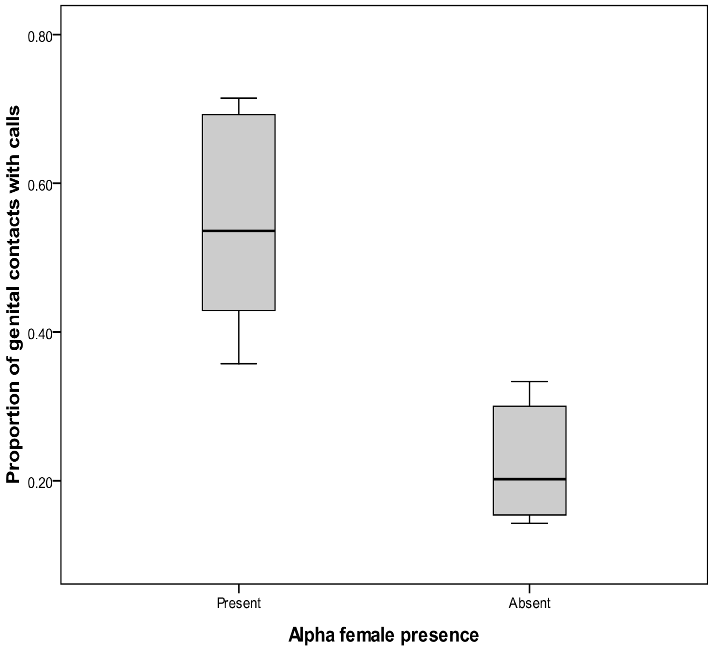


Figure 7.7. Boxplot indicating the proportion of genital contacts accompanied by copulation calls (*N* = 6 females) in which the alpha female was present in the audience versus absent.

Results from a Generalized Linear Model (binomial-logit) with calling (call versus no call) as the binomial dependent variable revealed that alpha female presence was the only audience-related variable that contributed significantly to the model (alpha female presence: Wald χ^2 = 4.579, df = 1, P = .032). Although the effect of female identity was also just significant (Wald χ^2 = 4.161, df = 1, P = .041), all audience-related variables, except for alpha female presence, were non-significant (all: $P > .05$).

Part three: Experimental study with controlled group composition

I conducted 90 trials in which a pair of females had the chance to interact in the presence of different audiences. Every female met every other female at least twice and interactions between females of the same or different rank class were approximately balanced according to the number of dyads possible (43 trials for 12 low-high rank dyads, 37 trials for six low-low dyads, 10 trials for three high-high dyads). Overall, patterns in these experimentally induced genital contacts mirrored the natural behaviours observed outdoors, although effects were enhanced. Rates of genital contacts were very high (64.4% of trials, 58/90) and in 16 of all possible 21 dyads, genital contacts occurred in at least one trial. Patterns in genital contact performance differed according to dyad composition (Fishers exact test on rates of genital contact performance for dyads of two low-ranked females vs. two high-ranked females vs. asymmetric dyads: *P* = .001, two-tailed). Upon meeting one another, genital contact performance for dyads composed of two low-ranked females or asymmetric dyads was significantly higher than expected by chance (67% of trials between two-low ranked females, binomial test: (0.5) p = .047; 74% of trials for asymmetric dyads: binomial test (0.5), *P* = .002). In contrast, sexual activity between two high-ranked females was very rare, occurring in just 10% of trials, a number significantly lower than expected by chance (binomial test (0.5), *P* = 0.021).

Of the 58 trials with sex, 29 (50.0%) were accompanied by copulation calls. In *N* = 26 of these, only one individual produced a call and in *N* = 3 both females called simultaneously. To reduce ambiguity, I excluded cases of co-calling and thus based my analyses on a total of *N* = 55 trials, of which 26 trials were accompanied by calling (52.7%). Again, there were strong rank effects for both caller and partner. Call production was solely restricted to the four low-ranking females and in 20 of the 26 cases with calling, callers interacted with high-ranked partners (call production with high- vs. low-ranked partners: $\chi^2 = 6.48$, df = 1, *P* = .014).

In terms of other factors, spatial position had no influence on call production (*N* instances when caller on top vs. bottom: $\chi^2 = 1.46$, df = 2, *P* > .05), but there was a significant effect of initiation (call when initiate versus when being targeted: $\chi^2 = 3.85$, df = 1, *P* = .050). For analyses of audience effects, small sample sizes meant that data from all interactions were entered together (*N* = 55 genital contact events). Although there was no effect concerning the presence of subordinate females ($\chi^2 = 0.53$, df =1, *P* > .05) nor the presence of dominant females ($\chi^2 = 0.01$, df = 1, *P* > .05), females were significantly more likely to call when the alpha female was present in the audience ($\chi^2 = 5.106$, df = 1, *P*= .024, with the *N* = 20 interactions involving alpha female excluded from analysis).

Genital contact length

I also analysed whether the length of the genital contact event itself influenced call production. I compared the length of genital contact interactions for *N* = 6 silent and vocal interactions for $N = 3$ females (LI, KS, NO; total $N = 36$ interactions). Results indicated no relationship between genital contact length and call production (Wilcoxon signed-ranks tests: all $P > .05$).

Table 7.5. Mean length of silent vs. vocal genital contacts (GCs), with standard deviations in parentheses.

Female	Vocal GC length (s)	Silent GC length (s)
KS	12.3 (4.03)	13.0 (2.52)
NO	11.5 (5.54)	13.8 (3.54)
LI	11.17 (4.57)	16.3 (5.88)

Discussion

Results from this study highlight the social relevance of genital contacts and associated call production for female bonobos. Low-ranked females were the most motivated to engage in genital contacts, both with other low-ranked females and high-ranked partners. In contrast, genital contacts between high-ranked females were very rare. These results suggest that genital contacts may be a more important affiliative mechanism for low-ranking females, whose social position is less stable, compared to high-ranked females, who already have more established positions with each other and within the group. These rank effects were also mirrored in call production. During genital contacts, copulation call production was biased towards low-ranked females and was related to a number of variables, such as social dominance, direction of initiation and audience composition. Overall, my results suggest that females possess considerable social awareness of their own, as well as their partner's social position during genital contacts, which is consequently expressed in their accompanying vocal signals. Whilst primate copulation calls are traditionally assumed to be tightly linked to reproductive contexts (Maestripieri & Roney, 2005; Pradhan et al., 2006), results from this study highlight the social use of copulation calls in this species.

Although the majority of copulation calls were produced by low-ranked females during their interactions with high-ranked partners, the same low-ranked females rarely called with low-ranked partners. This pattern indicated that, rather than only their own rank, females were sensitive to the dyadic dominance relationship of the interaction they were engaging in. In terms of initiation behaviours, low-ranked females were sensitive to the direction of initiation, calling more when invited to engage in a genital contact by their high-ranked partner rather than the other way around. Beyond the dyad composition itself, there were also female-driven audience effects, with the presence of the alpha female in the audience enhancing call production. Although arousal is likely to play a role in this vocal behaviour, I actually found no significant effects for two measures of physical stimulation (spatial position and genital contact length), indicating that arousal alone does explain call production.

Results from the additional experimental study, where the social variables of audience and dyad composition were controlled, reliably replicated these effects. In this study, I found enhanced levels of genital contact performance and call production in a context where males were absent. Genital contacts were, again, extremely rare between high-ranked females and all copulation calls were produced by low-ranked females. Alpha female presence also enhanced call production. These results complemented the main results, indicating that copulation calls during genital contacts may be a female-driven affair that does not require male presence.

As discussed in chapter six, the production of copulation calls in social contexts is not well explained by current theories of primate copulation calls, and is inconsistent with previous conclusions that focus only on their reproductive significance (Pradhan et al., 2006). For instance, the effect of female partner rank mirrors what has previously been observed in chimpanzees (Townsend et al., 2008), as well as in a number of other primates (see Maestripieri & Roney, 2005; Pradhan et al., 2006). Previously, authors have concluded that females call more with high-ranked partners as a means to potentially reduce threats of infanticide (e.g. Pradhan et al., 2006) or to encourage sperm competition between high-ranked males, that typically travel together (e.g. Townsend et al., 2008). The comparable rank effect is more difficult to explain in this purely social setting. On the one hand, copulation calls during homosexual interactions may have retained the same features as for heterosexual copulations, maintained through phylogenetic inertia. However, it is also possible that these calls are used to advertise associations with socially important, high-ranking group members.

Whilst my results indicate that physical stimulation did not drive call production, I do not of course discount the effect that the caller’s arousal state may have on this calling behaviour (e.g. Rendall et al., 2009). As with previous studies, I found that genital contacts occurred frequently during food discovery (e.g. Hohmann & Fruth, 2000; Kano, 1992; Paoli et al., 2006b; Parish, 1994), and thus it is likely that associated arousal influences vocal behaviour. Furthermore, socially driven arousal effects may also influence call production. Such an approach could proximately explain the effects of both dyadic dominance rank and alpha female presence. For example, low-ranked females may perceive close contacts with high-ranked females as somehow more ‘dangerous’ or ‘risky’, and the consequential increase in arousal levels (‘fear’ or ‘excitement’) is reflected in an increase in call production. Such an interpretation would be compatible with the hypothesis put forward by Wrangham (1993), who suggested that genital contacts represent a means of testing the willingness of another individual to interact fairly, by exposing a vulnerable part of their body. Furthermore, although quite rare, female-directed aggression at other females and their offspring does sometimes occur and when it does, is typically directed down the hierarchy (Paoli & Palagi, 2008; Vervaecke et al., 2003).

Although it is difficult to ascribe a functional explanation without further empirical testing, my results do point to a number of possibilities. From a social perspective, rank-related asymmetries in call production mirror patterns in genital contact performance itself (Hohmann & Fruth, 2000) and suggest that homosexual copulation calls may provide an additional means for females to express the social dynamics of their relationships. Ultimately, playback experiments are required to assess whether these calls are meaningful to receivers.

In particular, these calls appear to be especially relevant for low-ranked females and may provide a means to express and acknowledge their social position, as well as potentially advertising their association with high-ranked females. Greater call production by low-ranked females is consistent with the suggestion that newly immigrating females use homosexual interactions to facilitate their integration and affiliation with unknown and unrelated females in their new groups (Furuichi, 1989; Idani, 1991). In wild populations, young immigrant females invest highly in developing a strong bond with older and more dominant females and frequently engage in genital contacts with them (Idani, 1991). Although the females in the current study coexisted together in artificially formed groups, the females that called most were those that were most representative of the immigrating females described in wild studies. Currently, data on wild bonobo copulation calls is lacking and requires investigation. Conducting further work on rank related asymmetries between established and immigrating females would shed important light on the question of how homosexual copulation calls may be used within the framework of female social assessment and integration.

From another perspective, my results also suggest that copulation calls during genital contacts may signal the acknowledgement of social status by female bonobos. Unlike chimpanzees, bonobos appear to lack a formal vocal signal of submission (Furuichi & Ihobe, 1994). In chimpanzees, individuals use the ‘pant grunt’ vocalisation as a formal vocal signal of greeting and sub-ordinance (e.g. Bygott, 1979). There is some evidence that chimpanzees take the potential effects on their audience into account, although this was only shown in male-female interactions (Laporte & Zuberbühler, 2010). Although not used as habitually and ritualistically as the chimpanzee pant grunt, similar patterns of rank-related asymmetries indicate that calls during female genital contacts may enable low-ranked females to express their perceived social position in relation to that of their female partner. In bonobo society, a female’s social status in the group crucially depends on developing and maintaining alliances with other group members, especially other females (e.g. Kano, 1992; Parish, 1994). Gaining affiliation and proximity with high-ranked females can be especially beneficial in terms of enhanced status, access to food and agonistic support (Fruth & Hohmann, 2006).

Another effect I observed in this study was the sensitivity of callers to the presence of the alpha female. The alpha female occupies an important position in bonobo society (e.g. Furuichi, 1989) and these results highlight the awareness other females apparently have of the significance of her position. In this manner, one more adaptive interpretation is that being solicited by a high-ranking partner for sex is judged as a social success, and something that females wish to acknowledge publicly to socially relevant others. Females who have been chosen by a higher-ranking partner may become more attractive to others, which would explain why females are particularly keen to call when the alpha female is present. The prediction here is that females who have been sexually successful (and have advertised this to others) will be more highly preferred partners in future interactions compared to sexually successful individuals who have not advertised their success vocally. In the wild, it would be interesting to monitor the development of affiliative relations between females in relation to copulation calling, particularly from new immigrants.

In sum, the way in which bonobo copulation calls have become partly detached from their reproductive function to be used additionally, as social signals, both complements and develops existing theories that focus solely on the reproductive significance of primate copulation calls by highlighting their social relevance. More generally, the social use of a reproductive signal represents an intriguing deviation from the typically tight relationship that exists between animal vocal signals and evolutionarily important biological functions (e.g. alarm calls, Zuberbühler, 2003). Although more work is required, results from the current study indicate that female bonobos possess considerable levels of awareness about their social worlds, which is expressed via their vocal signals. In this way, this study further emphasises the central role of vocal communication in the study of social cognition (Seyfarth & Cheney, 2003a).

Chapter eight: General discussion

Summary

In this chapter, I discuss and reflect upon my empirical findings described in previous chapters in order to address the original research questions and to examine the contributions that my work has made to the study of bonobo vocal communication. In particular, I discuss the question of whether bonobos can produce vocalisations and vocal sequences that convey information to receivers. I also discuss some of the social roles and functions of vocalisations in bonobos, using insights from the studies of copulation calls. More generally, I reflect on the broader implications of my work, especially in relevance to the evolution of primate vocal communication. Finally, I consider the limitations of my work, how these could be addressed, and what future studies could be conducted in order to advance our understanding of vocal communication in this species.

Objectives

Compared to a relatively rich understanding of the communication and cognition of one of our closest living relatives, the chimpanzees (e.g. Lonsdorf et al., 2010), current understanding of our other close relative, the bonobo is strikingly limited in this area. Current estimations have indicated that at least 20 times more research has been conducted on chimpanzees compared to bonobos (Hare, 2009). Part of the reason for this disparity no doubt stems from the wide dispersal of chimpanzees across Africa, enabling more opportunities for studies to be conducted. In contrast, bonobos live in a more limited and remote ranging area, which lies within the DR Congo, a country that has been riddled with war and instability. In captivity, bonobos are also much scarcer, with the number of captive bonobos representing the equivalent of just 11% of the number of captive chimpanzees (International Species Information System, 2010; www.isis.org). In terms of what is known about bonobos, the most significant progress has been made in understanding their socio-ecology and social behaviour (Furuichi & Thompson, 2008), whereas research into their natural communication, particularly in the vocal domain, has received little attention. The relative absence of research on their vocalisations formed the key motivation for this thesis. Using the premise that vocalisations provide a window into underlying cognition, I focused on two of the most important biological problems faced by all animals: food discovery and sex. I used these areas in order to examine whether bonobos are able to communicate meaningful information about their worlds, both in terms of their interactions with external objects, as well as with social others.

Food-associated calls

Previous research on food-associated calls in bird and mammal species has indicated that these vocalisations represent promising signals to study vocal complexity and vocal function in non-human animals. In a number of species, food-associated calls have been shown to convey an array of information concerning the presence of food, as well as its quantity, divisibility and quality (e.g. Benz et al., 1992; Caine et al., 1995; Di Bitetti, 2003; Gros-Louis, 2004a; Roush & Snowdon, 2000). In chimpanzees, the acoustic structure of food-associated calls has been shown to relate statistically to food quality (Slocombe & Zuberbühler, 2006) in a way that is meaningful to listeners (Slocombe & Zuberbühler, 2005b).

In the first two empirical chapters (chapters four and five), I studied food-associated vocalisations in order to examine whether bonobos, like chimpanzees, produce vocalisations that relate reliably to external events and, if so, what information these vocalisations convey to receivers. In chapter four, I studied food-associated calls from the perspective of the signaller, and in chapter five, from the perspective of the receiver. In terms of signal production, my results suggest that, although bonobos and chimpanzees are very closely related (diverging 0.9 million years ago: Won & Hey, 2005), there appears to have been considerable divergence in how the two *Pan* species vocalise about food. Unlike chimpanzees, who produce one main food-associated call, the 'rough grunt' (Goodall, 1986), bonobos were shown to produce a range of distinct vocalisations in response to foods of different qualities. Using acoustic analysis techniques, I statistically discriminated five distinct call types (barks, peeps, peep-yelps, yelps and grunts). Results indicated that individuals frequently combine these calls together into longer, mixed sequences. Whilst there were statistical relationships between call types and food quality, context-specificity was shown to be greater at the level of call sequences, with the probabilistic composition of food-associated call sequences relating reliably to food quality. In addition to highlighting some important differences between bonobos and chimpanzees, this study also indicated that bonobo food-associated call sequences may be able to provide information relating to the quality of the food encountered by the signaller.

In chapter five, I described a playback study, which was conducted in order to investigate the receivers' responses to food-associated call sequences. Following on from chapter four, the main aim was to test the hypothesis that bonobo food-associated call sequences convey meaningful information about food quality to receivers. After training four subjects to learn the locations of a high and a low quality food, I conducted playback experiments, where subjects heard a familiar individual producing food-associated calls in response to one of these foods in their outdoor enclosure. The stimuli were composed of heterogeneous call sequences, so that the receivers had to attend to the whole sequence in order to extract information about the food eliciting the calls. Upon release, individuals were more likely to visit and exert more foraging effort at the site associated with the call sequence heard, indicating that bonobos are able to extract information about food quality by integrating across call sequences. These results highlight the meaningful role that call combinations appear to play in bonobo communication, something that has been suggested previously (Bermejo & Omedes, 1999; de Waal, 1988), but has never before been formally demonstrated.

Overall, these studies on food-associated calls represent a relevant contribution to the study of vocal communication in bonobos, providing detailed and systematic work on their natural vocal behaviour, which goes beyond the scope of what has been conducted so far. Moreover, the experimental study presented in chapter five represents the first playback experiment ever conducted with bonobos. The encouraging results from this study highlight the potential for using the playback paradigm in future studies of bonobos.

Copulation calls

In the second section of my research (chapters six and seven), I examined how females use vocalisations during their sexual interactions. Females of many primate species produce distinct vocalisations, known as ‘copulation calls’, during mating events with males (Pradhan et al., 2006). However, in addition to producing copulation calls with male partners, female bonobos also produce them during their sexual interactions with other females. Previous studies have considered copulation calls as sexually-selected signals, which promote the caller’s reproductive success (Pradhan et al., 2006). Whilst there is evidence supporting this general hypothesis for a number of species (e.g. yellow baboons, *Papio cynocephalus,* Semple, 1998, 2001; Barbary macaques, *Macaca sylvanus,* Pfefferle et al., 2008a; chimpanzees, *Pan troglodytes,* Hauser, 1990), the fact that bonobos also produce these calls with female partners, where there is no reproductive advantage, is not well accounted for by current ideas. My research aimed to examine the usage of copulation calls in female bonobos, focusing on both homosexual and heterosexual encounters. Although retaining some of their reproductive features, my results highlight the apparently social significance of these calls in bonobos. The social use of a reproductive signal is not well explained by current theories, and thus provides a new perspective for future debates regarding the evolutionary significance of primate copulation calls.

In terms of acoustic structure, females were shown to produce individually distinctive copulation calls, but produced acoustically similar copulation calls with both male and female partners. Furthermore, although females were shown to call more with males, there was an overriding effect of partner rank, showing that females called more with high-ranked partners, irrespective of partner sex. Acoustic and behavioural analyses indicated that, although swelling size did not relate statistically to call structure, call production varied as a function of swelling size, depending on the sex of the partner. At the level of call delivery, I found differences in relation to partner sex and rank, suggesting that sequence structure may be able to convey some information about the sex of the mating partner. Overall, whilst copulation calls still appear to convey information that is relevant in a reproductive context, these calls appear to have adopted a more social role in bonobos.

In the following chapter (chapter seven), I further explored the social usage of copulation calls, examining how these calls are used during homosexual genital contacts between females. The main part of this study involved naturalistic observations, although I supplemented this with a more focused study of call production, when the composition of the dyad and the audience were controlled. Beyond partner rank, results highlighted the relevance of the dyadic dominance rank relationship itself, with the majority of calls being produced by low-ranked females during their interactions with high-ranked partners. I also found that calling females were sensitive to both the direction of solicitation of the interaction as well as the presence of the alpha female in the audience. However, neither the spatial position nor the genital contact length were shown to influence call production, suggesting that arousal-based explanations do not solely account for this vocal behaviour. Beyond physical stimulation alone, results indicated that calling was mediated by an underlying social awareness, both in terms of the caller’s own social position and that of their partner, as well as the presence of specific group members. The social manner in which copulation calls were shown to be used by females highlights the impact that social life has had on the evolution of vocal communication in this species.

Insights into bonobo vocal communication

Broader studies concerning the bonobo vocal repertoire have been conducted both in captivity (de Waal, 1988) and in the wild (Bermejo & Omedes, 1999), although both studies were only descriptive and lacked empirical data or spectrographic analyses. Nevertheless, these studies have made some important contributions to the field of bonobo vocal communication and provided the foundations for my own studies. During feeding, as well as in other contexts, Bermejo and Omedes (1999) showed that bonobos regularly combine vocalisations together in a range of different contexts. The authors identified 19 different vocal sequences, although unfortunately, they never addressed the relevance of these call sequences empirically. Likewise, de Waal (1988) commented on the notable range of different vocalisations produced by bonobos, especially during feeding, and suggested that these rapid vocal commentaries may be meaningful to others. Following these suggestions, my work has provided further empirical support of the notion for meaningful call combinations in bonobos.

In a study of wild bonobos in Lomako, DR Congo, Hohmann and Fruth (1994) showed that, during long-distance vocal communication, individuals were sensitive to the vocalisations of conspecifics. In their study, individuals were found to respond to the vocalisations of distant conspecifics in more than 50% of occurrences, suggesting that these vocalisations may have conveyed some information to them. In addition, the study indicated that individuals used their vocalisations with some flexibility, synchronising their own hoot vocalisations with those they heard. Although long-distance communication was not studied in this thesis, my results have empirically demonstrated that in another context, that of food discovery, bonobo vocalisations are meaningful to receivers. Furthermore, in my analyses of copulation calls, I found that patterns in acoustic structure and call production co-varied statistically with a number of variables, particularly social ones. Thus, although playback experiments on copulation calls are required, it is likely that this acoustic information is also meaningful to receivers.

Vocalisations as a window into cognition

One of the underlying themes threading through this thesis is the notion that the vocalisations of non-human animals provide a window into their cognition (Seyfarth & Cheney, 1990, 2003a). Following the assumption that cognition and communication are tightly linked, researchers have made considerable progress in examining the cognitive abilities of animals, especially those of non-human primates.

Studies of the vocalisations of monkey and ape species have demonstrated sophisticated levels of underlying cognition (e.g. Seyfarth & Cheney, 2003a, 2008). For example, long-term behavioural research on wild baboons (*Papio hamadryas ursinus*) has revealed that these primates possess considerable social knowledge, which impacts on their vocal communication (Seyfarth & Cheney, 2008). Using playback experiments, baboons have been shown to recognise each other’s' dominance ranks (Cheney et al., 1995a), distinguish kin relationships (Cheney & Seyfarth, 1999) as well as recognise how these kin relationships impact on their social interactions (Cheney et al., 1995a; Wittig et al., 2007). For instance, after a fight, dominant baboons often approach subordinates and emit a specific type of soft grunt (Cheney et al., 1995b). Playback experiments have demonstrated that after hearing these grunts, subordinates are more likely to approach the dominant and regain proximity, indicating that these grunts function for reconciliation (Cheney & Seyfarth, 1997). Furthermore, grunts of close relatives of the aggressor appear to promote reconciliation between the original aggressor and the victim. In a playback experiment, victims who heard the reconciliatory grunts of their aggressor's close relative looked longer at the speaker compared to the control and were less likely to behave submissively to either the aggressor or their grunting relative in the hour after aggression (Wittig et al., 2007). These results indicated that baboons are able to recognise kin-based relationships in other group members and may use vocalisations of one kin member as a proxy for another. Subsequent playback experiments using threat-grunts and screams have also shown that baboons can discriminate within-family conflicts from between-family conflicts, demonstrating that their knowledge of kin and rank-based relationships extends to an understanding of the hierarchical organisation of their social groups (Bergman et al., 2003).

So far, the communication-cognition approach has been largely neglected in studies of bonobos. Results from the investigations of bonobo vocal communication described in this thesis provide progress to this end, revealing that bonobos are able to both use and understand vocalisations in complex ways. Furthermore, the way the bonobos use vocalisations reveals a considerable underlying awareness of their social worlds.

Results from my studies of food-associated calls indicate considerable acoustic variation, both at the level of the call units and at the level of call sequences. Furthermore, whilst finding statistical relationships between call type and food quality, it is likely that, in such a graded vocal system as that of bonobos, there may also be more subtle variation within the signals themselves. In a number of primate species, acoustic analyses have revealed a number of acoustic variants in what have appeared to be unitary call types (e.g. Gouzoules et al., 1984; Owren et al., 1997; Seyfarth & Cheney, 1984; Snowdon & Pola, 1978). In subsequent playback experiments, these call variants have been shown to be meaningful to listeners (e.g. Fischer, 1998; Fischer et al., 2001; Gouzoules et al., 1984). For example, vervet monkeys (*Cercopithecus aethiops*) have been shown to produce and understand four subtly different grunt variants in response to four different social situations (Cheney & Seyfarth, 1982; Seyfarth & Cheney, 1984). These include responding to a dominant versus a subordinate, as well as responding to an animal moving into an open area or in response to another group. Although further acoustic analyses and playback experiments are needed, it is likely that bonobos are also able to produce and comprehend subtle differences in acoustically similar call variants.

Whether or not bonobos only perceive vocalisations based on their acoustic properties, or rather on their semantic features, is open to further investigation. Nevertheless, results from my playback study indicated that, despite considerable variation in call units and sequence structure, receivers reacted to the playback stimuli as if they had conveyed meaningful information about two discrete categories (high or low quality food). In this manner, these results are consistent with the hypothesis that listeners can acquire information from vocalisations and form mental representations about the eliciting stimuli, which they can incorporate into their behavioural responses (e.g. Seyfarth & Cheney, 2003a). The notion that receivers judge signals with different acoustic properties to be semantically similar has also been demonstrated in a number of primates, in a range of contexts (see Cheney & Seyfarth, 1988; Fischer, 1998; Hauser, 1998; Rendall et al., 1996). Diana monkeys (*Cercopithecus diana*) normally respond to the growls of leopards by producing a leopard alarm call. However, if they first hear a monkey's alarm call in response to leopard and then hear the leopard growl from the same place, they do not respond to this predator. In contrast, if they first hear a monkey's alarm call in response to an eagle, and then hear the leopard growl, they respond strongly to the leopard (Zuberbühler et al., 1999). Thus, despite clear acoustic differences between leopard growls and alarm calls in response to leopards, receivers treat them as semantically similar.

Whilst the Diana monkey alarm calls system is composed of discrete vocal units (Zuberbühler et al., 1997), results from my study suggest that bonobos may be able to derive categorical information from within a graded vocal system. How bonobos perceive vocalisations still remains to be explicitly addressed and, thus far, the assumption of semantic categorisation can only be inferred from the behavioural responses of listeners. Although further studies are required to assess how bonobos perceive their vocalisations, research on rhesus macaques (*Macaca mulatta*), another primate with a graded vocal system, has demonstrated that individuals categorise calls based on their meaning, rather than their acoustic structure alone (Hauser, 1998).

Studies with language-trained bonobos

Despite relatively few prior studies of the natural communication of bonobos, there has been considerable attention devoted to how bonobos deal with spoken human language and artificial language systems (Savage-Rumbaugh & Lewin, 1994). Studies of language-trained bonobos have highlighted their abilities in this communicative domain, revealing sophisticated underlying cognition. Kanzi, the most famous of these language-trained bonobos, is able to use a lexigram based upon hundreds of artificial symbols, indicating his ability in mastering arbitrary signal-referent relationships (Savage-Rumbaugh et al., 1986; Savage-Rumbaugh & Lewin, 1994). Kanzi also exhibits striking competence comprehending human language and it has also been suggested that he can participate meaningfully in discourse interactions with humans (Benson et al., 2002a; Taglialatela et al., 2003) as well as process human symbolic lexico-grammar (Benson et al., 2002b). In the realm of vocal communication, two studies have suggested that Kanzi is able to modify species-typical vocalisations in context-specific ways (Taglialatela et al., 2003) and that he can produce vocalisations unheard in non-language trained subjects (Hopkins & Savage-Rumbaugh, 1991). The authors concluded that due to his extensive training with human language, Kanzi has acquired greater vocal flexibility and is capable of vocal learning. However, results from my studies, as well as those done previously, highlight the considerable range of individual variation present in bonobo vocalisations, as well as the array of subtly different vocalisations within their vocal repertoire (Bermejo & Omedes, 1999; de Waal, 1988). In this way, these previous studies (Hopkins & Savage-Rumbaugh, 1991; Taglialatela et al., 2003) may have been rather tapping into the individually distinctive vocalisations that Kanzi produces, which may still fall within the range of species-typical vocalisations. Whether or not Kanzi's vocalisations fall within the natural range of bonobo call types still has to be investigated. Thus far, failing to address these issues prevents any conclusions that Kanzi's vocalisations were novel and learned.

Whilst Kanzi's abilities in the domain of vocal production may have been over-estimated, it is still possible that his intensive language training and human-enculturated upbringing has resulted in some changes in his vocal repertoire. Data from other non-human primate species have indicated that learning may play some role in shaping vocal production and that individuals can learn to produce certain calls in specific contexts (Crockford et al., 2004; Fischer et al., 1998; Marshall et al., 1999; Mitani et al., 1992; Seyfarth & Cheney, 1986). For example, Wich and colleagues showed that a captive orangutan was capable of copying a human whistle upon command, something which it appeared to have acquired spontaneously, without training (Wich et al., 2008).

Nevertheless, although such results from other primate species indicate some degree of scope for vocal learning, the manner in which Kanzi appears to understand and use communicative signals still appears much more limited than patterns observed in language-learning children. In particular, Kanzi has required years of intense linguistic training in order to acquire his communicative skills with human and artificial languages. In contrast, human children are able to develop language with even the minimum of input and may even create it from scratch (e.g. Senghas et al., 2004). Furthermore, although many of the studies focus on Kanzi's communicative abilities in 'commenting' on aspects of his world, Greenfield and Savage-Rumbaugh (1991) revealed that his communicative 'comments' actually account for just 4% of his communications. Thus, in contrast to human language learners, who use their language to communicate a multitude of information and intentions to others, the majority of Kanzi's communications are imperative, meaning he wants something done, rather than wanting to communicate per se (Goldin-Meadow, 1996).

Bonobo vocalisations as a social tool?

Results from my studies of copulation calls suggest that bonobos possess considerable knowledge of their social relationships. Evidence of audience effects also indicates that females may be sensitive to the social composition of their audience, particularly concerning the presence of the alpha female. Audience effects also suggest that bonobos may have some degree of control over call production and also an awareness of the impact their signal has upon listeners. Although more data are certainly required, results from my studies of copulation calls highlight the possibility that females can use these calls strategically, as a means to advertise their affiliations and proximity to high-ranked partners.

Previously, partner rank effects in copulation calls have been explained as reproductive strategies, such as for promoting mate guarding by the consort male (e.g. Semple, 1998, 2001). However, evidence of strong rank effects with female partners in my research suggests that a more social, rather than reproductive explanation may be appropriate for this effect. One interpretation is that gaining alliance and affiliation with high-ranked group members represents an important strategy in many social animals, and therefore, it may be advantageous to female bonobos to announce this using copulation calls. Furthermore, evidence of audience effects in this context suggests that females may be especially motivated to advertise their activities when the most relevant female group member, the alpha female, is present.

Advertising socio-sexual encounters with high-ranked group members, regardless of their sex, may be advantageous in terms of advertising an affiliative interaction with a potential ally. Female bonobos are known to form strong affiliations with other females (Kuroda, 1980; Parish, 1996), although they also form them with males (Furuichi, 1989, 1997; Hohmann et al., 1999; Hohmann & Fruth, 2003a). Both intra-sexual and inter-sexual alliances are thought to contribute to the raised status of females in bonobo groups (e.g. Vervaecke et al., 2000b). Inter-sexual bonds are especially strong between mothers and sons, although they also extend beyond this kin relationship (Furuichi, 1989). In an analysis of the social and genetic associations in a community of wild bonobos, Hohmann and colleagues found that, in addition to associations among females, inter-sexual associations were also strong and actually more stable over time (Hohmann et al., 1999). For males, bonding with females may increase their reproductive success and rank acquisition (e.g. Furuichi, 1989; Surbeck et al., 2010). For females, inter-sexual bonds may derive benefits related to reduced food competition and gaining alliance-based support. Inter-sexual alliances are common when a female attacks another resident male (Hohmann & Fruth, 2003a; Vervaecke & van Elsacker, 2000) although they may also be formed in defence against male intruders (Hohmann et al., 1999). In this way, developing enduring bonds with males, as well as other females, may serve to protect females against infanticide, a common pattern found in other primates (Wrangham, 1979, 1986; van Schaik, 2000; van Schaik & Kappeler, 1997). Although infanticide has not been directly observed in bonobos, female harassment of other females and their offspring has been observed in both the wild and in captivity (Hohmann & Fruth, 2003a; Vervaecke & van Elsacker, 2000; Vervaecke et al., 2003).

Hypotheses pertaining to strategic call production are of interest, as they suggest that females may have some control over call production and use their vocal signals to manoeuvre their social landscapes. The notion that primates use their social expertise in strategic ways has been developed in the theory of ‘Machiavellian intelligence’ (Byrne & Whiten, 1988). The Machiavellian intelligence hypothesis proposes that primate intelligence is primarily an adaptation to deal with the complexities of primate social life. Although numerous studies have indicated other primates are able to employ social and communicative behaviours strategically (see Byrne & Whiten, 1988, 1990; Hauser, 1997; Whiten & Byrne, 1988), more data are certainly required in order to convincingly demonstrate strategic call use in bonobos.

Wider contributions

In addition to addressing the contributions that these studies have made to our understanding of bonobo communication and cognition, it is also important to reflect upon what contributions my work has made to primatology and comparative psychology more generally. In particular, how do my results complement and contrast with previous theories, and what new light do they shed on vocal communication in non-human primates?

Referential communication

My studies of food-associated calls have revealed that bonobos can both produce and comprehend vocalisations that convey information about an event in their external world. The possibility of semantic vocal communication in animals has generated a considerable research interest and has also stimulated a lively debate (e.g. Rendall et al., 2009; Scarantino, 2010; Seyfarth et al., 2010). The centre of controversy rests upon the notion of functionally referential signals and their relevance to theories of the evolution of language. Functionally referential calls are defined as those possessing a specific acoustic structure, which are selectively produced in a specific context and elicit specific responses in listeners (Evans, 1997; Macedonia & Evans, 1993). As discussed in chapter one, referential calls have been demonstrated in a number of different animal taxa, in a range of different contexts (reviewed in Zuberbühler, 2003), including food discovery (e.g. Di Bitetti, 2003; Evans & Evans, 1999; Kitzmann & Caine, 2009; Slocombe & Zuberbühler, 2006). Although functionally referential calls are qualitatively different from language (i.e. words) in the sense that animal signallers appear to lack the same flexibility and communicative intention (Seyfarth & Cheney, 2003a), they nevertheless function to provide relevant information about objects or events in the external world (Marler et al., 1992). The ability to communicate information about external stimuli is thought to mark a key milestone in the evolution of semantic communication and represents an important precursor to language (Zuberbühler, 2005). From a cognitive perspective, functionally referential communication also suggests that some aspects of animal communication may be conceptually-driven (e.g. Cheney & Seyfarth, 1990; Zuberbühler et al., 1999).

Although my results suggest that bonobos can combine calls together in meaningful, context-specific ways, their food-associated calling system does not meet the strict criteria required to be classed as functionally referential (Macedonia & Evans, 1993). For instance, call types were not restricted to one food type, but were rather produced in response to a range of different food types. Furthermore, a whole range of different structured sequences of different lengths could be potentially produced in response to the same food type suggesting that the relation between stimulus and signal is only probabilistic in bonobos. Although more empirical work is required, my recent pilot observations have also indicated that some of these vocalisations (such as peeps), may also be produced in non-food contexts (Z. Clay, personal observations), something also suggested by Bermejo and Omedes (1999).

The finding that bonobo food-associated calls do not fulfil the original requirements for functional reference (Macedonia & Evans, 1993) adds to a growing body of evidence that is challenging the strict notion of production specificity, indicating that the original definition may be too narrow to encompass the apparently broader use of animal signals which convey information. In particular, whilst some studies conclude that alarm calls to different predator types (i.e. aerial or terrestrial) are highly specific (Macedonia, 1990; Seyfarth et al., 1980; Zuberbühler 2000, 2001), evidence from other species has shown that calls types produced to specific predator types may also be given in a range of other circumstances. This includes responding to various different disturbances, such as falling trees and non-predatory animals (Arnold & Zuberbühler, 2006a; Wheeler, 2010), but also in response to social disturbances, such as agonistic encounters with other conspecific groups (Digweed et al, 2005; Fichtel & Kappeler, 2002; Fichtel & van Schaik, 2006), as well as in eliciting hunting (Crockford & Boesch, 2003) and during habitual dawn choruses (Marler, 1972). Rather than conveying highly specific information to receivers, these calls may function more to direct the attention of the receiver to a particular stimulus from which they can draw their own inferences (Arnold & Zuberbühler, in prep).

Particularly for calls with low referential specificity, context may also play a more important role in deriving call meaning than has been previously acknowledged (Smith, 1965). In some recent work, playback experiments with putty-nosed monkeys (*Cercopithecus nictitans*) have indicated that individuals extract meaning from conspecific alarm calls by integrating additional contextual information about what was likely to have elicited the call (Arnold & Zuberbühler, in prep). For example, male putty-nosed monkeys produce loud calls, known as 'pyows', which are regularly used in the alarm context in response to terrestrial predators (i.e. leopards), but are also used in response to a range of other disturbances (Arnold & Zuberbühler, 2006a; Arnold et al., in prep). In the absence of contextual information, subjects in a playback experiment spent much longer looking towards the source of the pyows than when contextual cues were present (Arnold et al., in prep). This result indicated that contextual information enables these monkeys to determine whether these calls are functioning as alarm calls or not. Likewise, in my playback experiment, it is likely that the bonobos integrated information from the call sequence with their prior contextual knowledge of the foraging task. For example, individuals may have already been expecting to enter their enclosure in order to find either a high quality or a low quality food in locations known to them. Therefore, by combining their prior expectations about the feeding event with the information extracted from the call, receivers were able to make informed foraging decisions.

Call combinations

One of the main differences between human language and animal communication is said to be the presence of syntax and complex grammatical organisation in human language but an absence of it in animal communication systems (Chomsky, 1981; Pinker, 1994; Hauser et al., 2002). Syntax is a hugely complex system, involving a great number of processes (see Bickerton, 2009 for a review). To briefly summarise, it is said to 'consist of a process of progressively merging words into larger units, upon which are superimposed algorithms that determine the reference of items (in various types of structural configuration) that might otherwise be ambiguous or misleading' (Bickerton, 2009: p11). Although the communication systems of some birds and mammals exhibit higher-order structure, the hierarchical organisation of syntax goes far beyond the capacities shown in non-human animal communication (e.g. Bickerton, 2009; Hilliard & White, 2009).

Whilst complex syntax appears to be absent in non-human communication systems, its precursor, combinatorial signalling, has been shown to play an important role in a number of species. For example, structured songs that combine stereotyped sound elements have been demonstrated in passerine birds as well as in whales and in gibbons (Aitchison, 2000; Catchpole & Slater, 2003; Clarke et al., 2006; Geissmann, 2002; Suzuki et al., 2006). For example, the nightingale (*Luscinia megarhynchos*) is considered one of the most impressive of signallers among the songbirds, possessing up to 200 song types, with each song typically composed of 1000 different elements (Kipper et al., 2004). However, unlike human language, where the number of sentences far exceeds the number of available words, the number of combinatorial signals in nightingale song is still much smaller than the elements that make up the signals.

In some cases, hierarchical organisation has been demonstrated, although in general, animal and bird song structures appear to lack the flexibility of syntactical constructions in language. Furthermore, the relationship between acoustic structure and communicative function in birds and animals continues to remain elusive. For instance, in most cases, signals tend to lose their communicative function if the structure of the sequence is artificially altered (e.g. Vallet et al., 1998; Holland et al., 2000). In this sense, the songs of birds and some other animals may be combinatorial, but unlike human language, they are not semantically compositional, in the sense that the elements that make up their utterance carry specific meaning (Számado et al., 2009).

Call combinations are also a common feature of the vocal communication systems of non-human primates, and in some cases, may even play a semantic role (e.g. Arnold & Zuberbühler, 2006a, b). In Campbell’s monkeys (*Cercopithecus campbelli*), males produce an array of context-specific call combinations, some of which demonstrate syntactic-like properties. For example, Zuberbühler (2001) showed that these monkeys produce acoustically distinct alarm calls to their two principal predators, leopards and eagles. However, for non-imminent dangers (such as a branch fall in the vicinity), the callers add a pair of ‘boom’ calls at the beginning of the sequence. Playback experiments demonstrated that by adding the boom-boom prefix, listeners respond to the call sequence as if its meaning had changed to indicate the presence of only non-imminent danger (Zuberbühler, 2002). Since this discovery, a long-term observational study of Campbell’s monkeys has revealed that males produce up to six different loud call types, which may be combined into highly context-specific call sequences that discriminate between different types of dangers and disturbances. (Ouattara et al., 2009a, b). The authors have also found evidence of some other systematic structuring ‘rules’, including non-random transition properties of call types, adding specific calls to a sequence to transform it to a different one, and recombining two sequences together to form a third.

Despite being our closest living relatives, evidence for call combinations in apes has been quite weak. A notable exception is the complex song structures of gibbon song (*Hylobates* sp). For example, agile gibbons (*Hylobates agilis*) produce individually-distinctive songs that are organised into complex sequences, composed of several phases (Oyakawa et al., 2007). Analyses of white-handed gibbon song (*Hylobates lar*) has indicated context-specificity in acoustic structure of predator-induced versus typical songs (Clarke et al., 2006). In chimpanzees, Crockford and Boesch (2003) analysed context-specific bark variants and demonstrated that context-specificity could be achieved through variation in the acoustic signal as well as by creating context-specific call combinations. In another study, the same authors also highlighted the frequent use of call combinations in chimpanzees in a range of different contexts (Crockford & Boesch, 2005), although context-specificity was not explored in detail.

Results from my studies contribute novel data to the ape literature in this domain, highlighting the role that call combinations play in bonobo vocal communication. My results complement previous work by Crockford and Boesch (2003, 2005), although they go one step further by empirically demonstrating that call combinations can be meaningful to receivers. The probabilistic manner in which bonobos combine calls also shows similarities with the alarm calling system of colobus monkeys (*Colobus polykomos* and *C. guereza*). In the alarm context, Colobus monkeys produce two call types in response to leopards and crowned eagles (Schel et al., 2009). Whilst both call types can be produced in response to both predators, observational and experimental evidence, using playback experiments, has shown that changes in probabilistic call composition convey information to listeners relating to a range of information, such as predator type, response urgency, and the caller's imminent behaviour (Schel et al., 2010).

In sum, patterns of call combinations in the feeding context by bonobos are consistent with evidence from other apes and monkeys indicating that, unlike human syntax, most primate vocal sequences do not follow fully predictable patterns and tend to based more on probabilistic combinations (e.g. Arnold & Zuberbühler, 2006b; Crockford & Boesch, 2003; 2005; Schel et al., 2009). However, although bonobo vocal signalling does not appear to share the properties of human syntax in terms of production, results from my playback study indicate that listeners are nevertheless able to extract differential information by attending to the different combinations of call units. This suggests that, despite differences in the structures underlying call production, some of the cognitive processes required for the comprehension of syntactic structures are also present in the natural communication systems of our close relatives, the bonobos. In this sense, my work reiterates some of the important differences, but also similarities, between human language and animal communication systems (e.g. Owings & Morton, 1997, 1998; Rendall et al., 2009; Számado et al., 2009).

Social influences on the evolution of vocal communication

How vocal systems evolve is an extremely complex problem. It is likely that a multitude of variables influence and shape the evolution of vocal communication, from ecological changes, anatomy, social life, predation, brain size, and so on (Fitch, 2010). One hypothesis is that increases in social complexity consequently lead to the evolution of vocal complexity (Dunbar, 1998). The 'social-complexity hypothesis', as it is known, has had a significant impact on theories of language evolution (e.g. Dunbar, 1998, 2003; Pinker, 2003). Dunbar has argued that human language first evolved as a means to service social relationships, at the point when primate groups became too large for social grooming to effectively serve this function (Dunbar, 2003). In addition to its impact on theories of language evolution, the social-complexity hypothesis may provide a useful framework for explaining more general variation in the vocal systems of animal species.

So far, the majority of evidence supporting the social-complexity hypothesis has been either comparative or correlational (e.g. Blumstein & Armitage, 1997; Maestripieri, 1999; Wilkinson, 2003). McComb and Semple (2005) conducted a phylogenetically-controlled meta-analysis of non-human primates, which indicated that evolutionary increases in vocal repertoire were positively related to increases in social bonding (using group size and time spent grooming as proxies). Whilst such correlational evidence is important, experimental evidence validating the hypothesis has been demonstrated only recently. Freeberg (2006) studied the influence of group size on the complexity of the ‘chick-a-dee’ call in Carolina chickadees (*Poecile carolinensis*). In both un-manipulated field settings and in aviaries (where he manipulated group size), Freeberg found that individuals in larger groups gave calls of greater vocal complexity than those in smaller groups. In support of the social complexity hypothesis (Dunbar, 1998), Freeberg’s results indicated that social complexity can influence communicative complexity in this species.

The social-complexity hypothesis may have relevant implications for the evolution of vocal communication in bonobos. Bonobos use a diverse array of vocal signals and regularly combine them into long and complex vocal sequences, something which may be influenced by patterns in their socio-ecology (e.g. Bermejo & Omedes, 1999). In particular, vocal diversity in bonobos may have been influenced by their complex social systems, pro-social tendencies and cohesive ranging strategies (e.g. Furuichi, 2009). In their phylogenetic comparisons of vocal and social complexity of non-human primate species, McComb and Semple (2005) reported that bonobos exhibited both the largest vocal repertoire and the largest group sizes. Whilst the repertoire size they quote (N = 38), taken from Bermejo and Omedes (1999), appears to have been inflated by the addition of vocal sequences, it nevertheless suggests that the complex social worlds bonobos live in may require complex vocal communication.

Compared to chimpanzees, wild bonobos typically travel in more cohesive groups centred around closely-bonded female aggregations and form more stable foraging parties (Furuichi et al., 1998; Kano, 1992; Nishida & Hiraiwa-Hasegawa, 1987).

Furthermore, during foraging, chimpanzees tend to disperse among several fruiting trees, whereas bonobos tend to maintain closer spatial proximity and forage cohesively (White, 1998). The increased cohesiveness and social tolerance of bonobos, facilitated by other features of their socio-ecology, may have resulted in the evolution of their diverse, close-range vocalisations. In the context of feeding, these vocalisations may enable individuals to maintain contact with each other. Such a hypothesis shows compatibility with results from my studies during the feeding context, which highlighted the diversity of vocalisations produced by individuals. Previous studies have also highlighted the conversational manner in which bonobos vocalise during feeding contexts. De Waal (1988) remarked that bonobos frequently ‘comment’ and respond to food items, as well as other objects or events of interest to them. Furthermore, a study of wild bonobos showed that individuals often forage closely together and appear to use food-associated calls to maintain contact with fellow foragers and to coordinate group movements (Bermejo & Omedes, 1999). For example, when foraging on the ground, bonobos were shown to regularly emit peep-yelps, soft barks, barks, peeps and grunts as well as combining them into a sequence known as a ‘soft mixed series’ (Bermejo & Omedes, 1999). Production of the ‘soft mixed series’ was observed frequently when foragers lost visual contact with other foragers. During group progression, Bermejo and Omedes also found that the bonobos regularly emitted peep-like vocalisations, which appeared to facilitate the maintenance of contact between individuals during their foraging activities. In this sense, whilst food-associated vocalisations may carry information specific to the feeding context, they may also play a relevant social role within this context for facilitating group cohesion. In bonobos, relaxed feeding competition may also reduce the costs of advertising food and potentially favour the evolution of more diverse vocalisations.

Socio-ecological features, such as reduced foraging competition and a more predictable ecological environment (Furuichi, 2009; White, 1998; White & Wrangham, 1988) are also thought to have influenced the evolution of bonobo social cognition and behaviour (Furuichi, 2009). Consistent with the notion of ecological predictability, experiments have shown that bonobos value future food pay-offs less than chimpanzees (Rosati et al., 2007), avoid risky feeding decisions (Heilbronner et al., 2008), are more willing to co-feed with each other (Hare & Kwetuenda, 2010, but see Jaeggi et al., 2010) and are more competent than chimpanzees in performing cooperative tasks (Hare et al., 2007).

Study limitations and further work

Whilst my work provides new and relevant data concerning vocal communication in bonobos, my studies were not without their own limitations. It is important to first identify these weaknesses before future progress can be made.

Studies of food-associated calls

In addition to food quality, it is likely that other factors, which I did not investigate, may also influence food-associated call production in bonobos. In particular, although factors such as food quantity and divisibility remained constant during my studies, time constraints prevented me from examining them empirically. Future work should address whether food-associated calls convey information about other features of the feeding event and which factors are the most powerful in explaining call production.

Beyond features of the food item, my study did not address the impact of social variables on food call production. However, bonobos are a highly social species and there is already some evidence that social factors impact on vocal production in this context (van Krunkelsven et al., 1996). Previous work on a number of species has demonstrated that food-associated call production is influenced by social factors, such as the presence of allies as well as potential feeding competitors (Gros-Louis, 2004b; Hauser & Marler, 1993b; Pollick et al., 2005; Slocombe et al., 2010b). Future work exploring the social variables that influence call production and the broader social function of these calls represents a necessary and important next step.

In particular, studies examining audience effects and the social repercussions of food-associated call production could provide data pertaining to function. To test the influence of audience, playback studies could be used to simulate the presence or arrival of a potential ally or non-ally. In addition, more attention to social factors relating to caller identity may also explain some variation in call acoustic structure and call behaviour. This includes, for example, taking into account the callers' age, their sex and their social status. In white-faced capuchins (*Cebus capucinus*), low-ranking individuals are more likely to call if a higher-ranked individual approaches them and are less likely to receive aggression by them, when compared to individuals who remain silent (Gros-Louis, 2004b). In bonobos, pilot observations that I have conducted do not indicate clear differences between the sexes but do suggest that high-ranked individuals may be more vocal during feeding compared to low-ranked individuals. Although this must be demonstrated empirically, my pilot observations suggest that the social factors underlying call production in bonobos may differ to those observed in capuchins or other primates with differing socio-ecologies. If calling is mediated by rank, and high-ranking individuals call more, it is more likely that calls signal a willingness and ability to defend food resources. Furthermore, by signalling the presence of food, high-ranking individuals may attract potential allies, whilst their high social status protects them from the risk of having their food stolen.

My playback experiment on food-associated calls had a number of methodological limitations which could be addressed in future work. Two significant problems were the small sample size and the inter-dependency of the subjects' responses. Small sample size could be addressed by conducting this study at a larger facility or at more than one facility. However, finding facilities with the conditions suitable for playback experiments is no simple task. In both Europe and the USA, most facilities have thick protective glass surrounding their enclosures, making it difficult to record and play vocalisations. In addition to the large group (*N* =11), the open-air enclosure was one of the main reasons I selected Twycross Zoo. However, I had to deal with the problem of interdependency, in that I was unable to separate individuals under Zoo policy. However, this limitation also functioned to keep the situation as natural and stress-free as possible for the bonobos. Furthermore, food motivation appears to be generally quite low in bonobos (B. Hare, personal communication; Z. Clay, personal observation) and thus it is likely that even if isolation were possible, a subject may not fully participate in a foraging task in the absence of group members.

One alternative to the problem of data inter-dependency would be to only collect data from the first individual, taking them as the focal subject. This strategy has been used in a number of studies, generating some important findings in a range of species (e.g. Harley et al., 2003; Pepperberg, 2002; Savage-Rumbaugh & Lewin, 1994; Weir et al., 2002). In their study of chimpanzee food-associated calls, Slocombe and Zuberbühler (2005b) based their conclusions on the behavioural responses of a single subject. However, even putting aside the statistical flaws of basing conclusions on an *N* of 1, the single-subject approach was not practical for my experiment as I found that it was not always the same individual who arrived first.

Another alternative approach could be to conduct a playback experiment using single subjects, within individual testing rooms. Such an approach may be possible in sanctuaries and captive facilities where individuals are used to being kept alone within test rooms (often their sleeping rooms) and participating in tests. For instance, the subject could be given a food choice task, where they are able to choose from one of two cups, having learned that one contains high-quality food and the other low-quality food. The manipulation would be whether or not they heard an unseen group member (behind an occluder) participating in the same task and responding to finding food in one of the two cups. If food-associated calls provide information about food quality, subjects may be more likely to choose the cup associated with the call. In order for this to be realistic, the subject would have to have experience in conducting the test whilst seeing a group member simultaneously doing the task next door.

Another issue that I was unable to address in my playback experiment was the issue of arousal (Owren et al., 2010; Rendall et al., 2009; Seyfarth & Cheney, 2003b). In particular, it was difficult to ascertain whether the individuals were responding to the emotional rather than the informational content of the calls. Whilst arousal-based explanations cannot be ruled out, it is relevant to acknowledge that even calls of high emotional valence may also still be able to convey referential information (see my discussion of screams in chapter one, pp. 6-7.). One experimental approach to this problem would be to first establish food preferences to two foods and then de-value the high quality food (by providing it repeatedly until the subjects cease to have high emotional reactions to it). Playback experiments could demonstrate whether it was more the emotional or referential content that the receivers were responding to.

Finally, although my study indicated that receivers were able to integrate information from across sequences, time constraints prevented me from investigating their reactions to each of the individual call types. It is possible that some calls, even in the absence of others, are sufficient to convey information relating to the food. In order to further test whether it is the combination of calls together, or the presence of particular calls that conveys information, playback studies could be conducted whereby subjects either heard homogeneous strings or heterogeneous ones.

Studies of copulation calls

One of the key issues that still needs to be addressed in future studies of copulation calls concerns whether female bonobos are using these calls strategically (i.e. calling has advantageous consequences to the caller. Future work could test whether females who produce copulation calls are more successful in forming alliances with other group members, and whether copulation call production predicts who will be supported during agonistic encounters. One hypothesis is that females producing copulation calls are more likely to develop bonds with their sexual partners, remain proximate to them, and gain support from them compared to other females.

My results have highlighted the particular relevance of these calls to subordinate females, whose social positions are less stable. These females are also the most representative of immigrating females in the wild. In the wild, immigrating females are known to be highly sexually active, particularly focusing their sexual interactions on higher-ranked females (Idani, 1991). It would be interesting to study copulation call behaviour in the wild to test whether copulation calls are used strategically by females during the period of immigration and whether calling is related to more successful integration.

Beyond needing to demonstrate strategic call use, there were also a number of other methodological limitations in these studies. As before, results suffered from low sample sizes that often prevented powerful statistical comparisons. This problem was particularly apparent in the indoor study described in chapter seven (this study only involved seven subjects, of which only four subjects vocalised). Unfortunately, this problem is difficult to remedy. Lola Ya Bonobo Sanctuary, where I collected my data for studies of copulation calls, is the largest bonobo facility in the world and thus already represents an optimal location for conducting such a study, which requires a large number of females. The number of bonobos in captivity remains low, indicating that the problem of sample size would be even more problematic. According to the International Species Information System (www.isis.org), there are currently only 175 captive bonobos held worldwide, compared to 1528 chimpanzees (plus 9 bonobo + 11 chimpanzee new-borns). Among the 18 captive facilities worldwide that house bonobos, the average number of females is 5.7. Furthermore, this already low figure does not discriminate adults from infants or juveniles, indicating the number of potential study females to be even lower. In the future work, the best sample sizes are therefore more likely to be from wild studies, which would also additionally bring the crucial ecological validity required for these studies.

From an acoustic perspective, I was unable to address whether copulation calls provide meaningful information to receivers. Playback studies are required in order to investigate what information about the sexual interaction is conveyed to receivers. For example, in my analyses, I found that female copulation calls produced with male and female partners shared the same acoustic morphology but differed in how they were delivered. Playback experiments, using the violation-of-expectancy paradigm (e.g. Hauser & Carey, 1998), could be used in order to determine whether listeners are able to distinguish calling context. This approach could also be used to determine whether calls convey information about caller identity and partner rank.

In studies of vocal communication such as these, it would also be interesting to study the influence of other physiological variables, namely hormones. Faecal and urinary hormonal analyses could be used to accurately determine whether copulation calls provide information about timing of ovulation (e.g. Deschner et al., 2003; 2004; Nikitopoulos et al., 2005; Townsend et al., 2008). In addition to cues to reproductive state, hormonal analyses could be used to investigate whether raised levels of stress or arousal are correlated with call production. Measuring levels of glucocorticoids, a biomarker of stress, could be used to compare call and non-call events (controlling for context). Hormonal analyses could also be used to investigate the hypothesis that socio-sexual interactions enhance social affiliation (e.g. de Waal, 1987; Parish, 1994). This is important, as the social-bonding hypothesis forms the basis of a number of my arguments for the social significance of copulation calls. The hormone oxytocin is released by many socio-sexual stimuli and has been shown to play a role in socially affiliative interactions between conspecifics (e.g. Campbell, 2008; Carter et al., 1998).

If socio-sexual interactions do promote affiliation, a relationship between sexual activity and corresponding changes in oxytocin levels should be expected. Levels of oxytocin could also be examined for call and non-call interactions to see if calling is related to greater social affiliation.

Conclusion

Despite being one of our closest living relatives, research into the natural behaviour of bonobos has been somewhat neglected, especially when compared to the considerable progress that has been made in our understanding of chimpanzees, the sister species of bonobos. In this thesis, I addressed this issue by examining one of the least studied aspects of bonobo behaviour, their vocal communication. Taking the contexts of food discovery and sex, I explored how bonobos use vocalisations to communicate about their physical and social worlds and what their vocal behaviour can reveal about their underlying cognition. My results have revealed that bonobos are able to communicate meaningfully about objects and events in their external world and appear to have a sophisticated awareness of their social relationships, which is consequently expressed in their vocal signals. As well as providing novel data to the field of bonobo vocal communication, my results contribute to a growing body of literature that highlights the important role that vocalisations play as tools for primates to navigate their social landscapes. Systematic research into bonobo vocal communication is still in its infancy, and future work should focus more on the interaction between communication and cognition in this little understood, but fascinating species of great ape.

References

Aich, H., Moos-Heilen, R., & Zimmermann, E. (1990). Vocalizations of adult gelada baboons (*Theropithecus gelada*): Acoustic structure and behavioural context. *Folia Primatologica, 55*, 109-132.

Aitchison, J. (2000). *The seeds of speech: Language origin and evolution*. Cambridge: Cambridge University Press.

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour, 49*, 227-267.

Altmann, J., Alberts, S. C., Haines, S. A., Dubach, J., Muruthi, P., Coote, T., Geffen, E., Cheesman, D. J., Mutata, R. S., Saiyalel, S. N., Wayne, R. K., Lacy, R. C., & Bruford, M. W. (1996). Behavior predicts genetic structure in a wild primate group. *Proceedings of the National Academy of Sciences of the United States of America*, *93*(12), 5797-5801.

André, C., Kamate, C., Mbonzo, P., Morel, D., & Hare, B. (2008). The conservation value of Lola ya Bonobo Sanctuary. In T. Furuichi & J. Thompson (Eds.), *The bonobos: Behaviour, ecology and conservation* (pp. 303-322). New York: Springer.

Anestis, S. F. (2004). Female genito-genital rubbing in a group of captive chimpanzees. *International Journal of Primatology, 25*(2), 477-488.

Arbib, M. A., Liebal, K., & Pika, S. (2008). Primate vocalization, gesture, and the evolution of human language. *Current Anthropology, 49*(6), 1052-1075.

Arlet, M. E., Molleman, F., & Chapman, C. (2007). Indications for female mate choice in grey-cheeked mangabeys, *Lophocebus albigena johnstoni*, in Kibale National Park, Uganda. *Acta Ethologica, 10*(2), 89-95.

Arnold, K., & Zuberbühler, K. (2006a). The alarm-calling system of adult male putty-nosed monkeys, *Cercopithecus nictitans martini*. *Animal Behaviour, 72*(3), 643-653.

Arnold, K. & Zuberbühler, K. (2006b). Semantic combinations in primate calls. *Nature, 441*, 303.

Arnold, K., & Zuberbühler, K. (2008). Meaningful call combinations in a non-human primate. *Current Biology 18*(5), R202-R203.

Arnold, K., & Zuberbühler, K. Inference enables wild monkeys to determine the cause of alarm calls. *In prep.*

Audenaerde, D. F. E. (1984). The Tervuren Museum and the pygmy chimpanzees. In R. L. Susman (Ed.), *The pygmy chimpanzee: Evolutionary biology and behaviour* (pp. 3-11). New York: Plenum Press.

Aujard, F., Heistermann, M., Thierry, B., & Hodges, J. K. (1998). Functional significance of behavioral, morphological, and endocrine correlates across the ovarian cycle in semifree ranging female Tonkean macaques. *American Journal of Primatology, 46*(4), 285-309.

Badrian, A., & Badrian, N. (1984). Social organization of *Pan paniscus* in the Lomako Forest, Zaire. In R. L. Susman (Ed.), *The pygmy chimpanzee: Evolutionary biology and behavior* (pp. 325-346). New York: Plenum Press.

Badrian, N., & Malenky, R. K. (1984). Feeding ecology of *Pan paniscus* in the Lomako forest, Zaire. In R. L. Susman (Ed.), *The pygmy chimpanzee: Evolutionary biology and behaviour* (pp. 275-299). New York: Plenum Press.

Barclay, R. M. R., & Thomas, D.W. (1979). Copulation call of *Myotis lucifugus*: A discrete situation-specific communication signal. *Journal of Mammalogy, 60*(3), 632-634.

Bates, E. (1976). *Language and Context: The acquisition of pragmatics*. New York: Academic Press.

Becquet, C., Patterson, N., Stone, A. C., Przeworski, M., & Reich, D. (2007). Genetic structure of chimpanzee populations. *PLoS Genetics, 3*(4), e66.

Benson, J., Fries, P., Greaves, W., Iwamoto, K., Savage-Rumbaugh, S., & Taglialatela, J. (2002). Confrontation and support in bonobo-human discourse. *Functions of Language, 9*(1), 1-38.

Benson, J., Greaves, W., O’Donnell, M., & Taglialatela, J. (2002). Evidence for symbolic language processing in a bonobo (*Pan paniscus*). *Journal of Consciousness Studies, 9*(12), 33-56.

Benz, J. J. (1993). Food-elicited vocalizations in golden lion tamarins: design features for representational communication. *Animal Behaviour, 45*, 443-455.

Benz, J. J., Leger, D. W., & French, J. A. (1992). Relation between food preference and food-elicited vocalizations in golden lion tamarins (*Leontopithecus rosalia*). *Journal of Comparative. Psychology, 106*, 142-149.

Bergman, T. J., Beehner, J. C., Cheney, D. L., & Seyfarth, R. M. (2003). Hierarchical classification by rank and kinship in baboons. *Science, 302*(5648), 1234-1236.

Bermejo, M., Illera, G., & Pí, J. S. (1995). Animals and mushrooms consumed by bonobos (*Pan paniscus*): New records from Lilungu (Ikela), Zaire. *International Journal of Primatology, 16*(1), 879-898.

Bermejo, M., & Omedes, A. (1999). Preliminary vocal repertoire and vocal communication of wild bonobos (*Pan paniscus*) at Lilungu (Democratic Republic of Congo). *Folia Primatologica, 70*(6), 328-357.

Bickerton, D. (1990). *Language and species*. Chicago: University of Chicago Press

Bickerton, D. (2009). Syntax for non-syntactiticians: A brief primer. In D. Bickerton, & E. Szathmáry (Eds.), *Biological foundations and origin of syntax* (pp. 3-14). Cambridge, MA: The MIT Press.

Blount, B. G. (1990). Issues in bonobo (*Pan paniscus*) sexual behavior. *American Anthropologist, 92*(3), 702-714.

Blumstein, D. T. (1995). Golden-marmot alarm calls: The production of situationally specific vocalizations. *Ethology, 100*(2), 113-125.

Blumstein, D. T., & Armitage, K. B. (1997). Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. *American Naturalist, 150*(2), 179-200.

Boesch, C. (1999). The hunting apes: Meat eating and the origins of human behavior. *Nature, 399*(6737), 653-653.

Boesch, C., Hohmann, G., & Marchandt, L. F. (Eds.). (2002). *Behavioral diversity in chimpanzees and bonobos*. Cambridge: Cambridge University Press.

Boinski, S., & Campbell, A. F. (1996). The huh vocalization of white-faced capuchins: a spacing call disguised as a food call? *Ethology, 102*(6), 826-840.

Boinski, S., & Campbell, A. F. (1995). Use of trill vocalisations to coordinate troop movement among white-faced capuchins – a 2nd field test. *Behaviour, 132*, 875-901.

Brakke, K. E., & Savage-Rumbaugh, E. S. (1995). The development of language skills in bonobos and chimpanzees: Comprehension. *Language and Communication, 15*(2), 121-148.

Brown, C. R., Brown, M. B., & Shaffer, M. L. (1991). Food-sharing signals among socially foraging cliff swallows. *Animal Behaviour, 42*, 551-564.

Bugnyar, T., Kijne, M., & Kotrschal, K. (2001). Food calling in ravens: are yells referential signals? *Animal Behaviour, 61*, 949-958.

Bygott, D. (1979). Agonistic behavior and dominance among wild chimpanzees. In D. Hamburg & E. McCown (Eds.), *The great apes* (pp. 405-427). Menlo Park, California: B. Cummings.

Byrne, R. W., & Whiten, A. (1988). *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans*. Oxford: Oxford University Press.

Byrne, R. W., & Whiten, A. (1990). Tactical deception in primates: The 1990 database. *Primate Report, 27,* 1-101.

Caine, N. G., Addington, R. L., & Windfelder, T. L. (1995). Factors affecting the rates of food calls given by red-bellied tamarins. *Animal Behaviour, 50*, 53-60.

Call, J., & Tomasello, M. (2007). *The gestural communication of apes and monkeys*. New Jersey: Lawrence Erlbaum.

Campbell, A. (2008). Attachment, aggression and affiliation: The role of oxytocin in female social behavior. *Biological Psychology, 77*(1), 1-10.

Capranica, R. R. (1978). Sound communication and auditory physiology in anurans. *Journal of the Acoustical Society of America, 64*, S2-S3.

Carter, S. (1998). Neuroendocrine perspectives on social attachment and love. *Psychoneuroendocrinology, 23*(8), 779-818.

Catchpole, C. K., & Slater, P. J. B. (2003). *Bird song: Biological themes and variations*. Cambridge: Cambridge University Press.

Chalmers, N. (1968). The visual and vocal communication of free-living managabeys in Uganda. *Folia Primatologica, 9*, 258-280.

Chapman, C. A., & Lefebvre, L. (1990). Manipulating foraging group size: Spider monkey food calls at fruiting trees. *Animal Behaviour, 39,* 891-896.

Cheney, D. L., & Seyfarth, R. M. (1982). How vervet monkeys perceive their grunts: Field playback experiments. *Animal Behaviour, 30*(3), 739-751.

Cheney, D. L., & Seyfarth, R. M. (1988). Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Animal Behaviour, 36*(2), 477-486.

Cheney, D. L., & Seyfarth, R. M. (1990). *How monkeys see the world*. Chicago: Chicago University Press.

Cheney, D. L., & Seyfarth, R. M. (1997). Reconciliatory grunts by dominant female baboons influence victims' behaviour. *Animal Behaviour, 54*(2), 409-418.

Cheney, D. L., & Seyfarth, R. M. (1999). Recognition of other individuals' social relationships by female baboons. *Animal Behaviour, 58,* 67-75.

Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995a). The role of grunts in reconciling opponents and facilitating interactions among adult female baboons. *Animal Behaviour, 50*(1), 249-258.

Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995b). The responses of female baboons (*Papio cynocephalus ursinus*) to anomalous social interactions: Evidence for causal reasoning? *Journal of Comparative Psychology, 109*(2), 134-141.

Cheng, M. F. (1992). For whom does the female dove coo: A case for the role of vocal self-stimulation. *Animal Behaviour, 43*(6), 1035-1044.

Chomsky, N. (1981). Knowledge of language: its elements and origins. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 295*(1077), 223-234.

Clarke, E., Reichard, U. H., & Zuberbühler, K. (2006). The syntax and meaning of wild gibbon songs. *PLoS One, 1*(1), e73.

Clutton-Brock, T. H., Albon, S. D., Gibson, R. M., Guinness, F. E.(1979). The logical stag: Adaptive aspects of fighting in red deer. *Animal Behaviour, 27*, 211-225.

Coolidge, H. J. (1933). *Pan paniscus,* pygmy chimpanzee from south of the Congo River. *American Journal of Physical Anthropology, 18*, 254-264.

Corballis, M. C. (2003). *From hand to mouth: The origins of language*. Princeton, NJ: Princeton Univeristy Press.

Cox, C. R., & LeBoeuf, B. J. (1977). Female incitation of male competition: a mechanism in sexual selection. *American Naturalist, 111*, 317-335.

Cramer, D. L. (1977). Craniofacial Morphology of *Pan paniscus. Contributions to Primatology,* 10:1–64.

Crockford, C., & Boesch, C. (2003). Context-specific calls in wild chimpanzees, *Pan troglodytes verus*: Analysis of barks. *Animal Behaviour, 66*, 115-125.

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

Crockford, C., Herbinger, I., Vigilant, L, & Boesch, C. (2004). Wild chimpanzees produce group-specific calls: A case for vocal learning? *Ethology, 110*(3), 221-243.

Dahl, J. F. (1986). Cyclic perineal swelling during the intermenstrual intervals of captive female pygmy chimpanzees (*Pan paniscus*). *Journal of Human Evolution, 15*(5), 369-385.

Dahlin, C. R., Balda, R. P., & Slobodchikoff, C. (2005). Food, audience and sex effects on pinyon jay (*Gymnorhinus cyanocephalus*) communication. *Behavioural Processes, 68*(1), 25-39.

David, H. A. (1987). Ranking from unbalanced paired-comparison data. *Biometrika, 74*(2), 432-436.

Dawkins, R., & Krebs, J. R. (1978). Animal signals: Information or manipulation? In J.R. Krebs & N.B. Davis (Eds.), *Behavioural Ecology: An evolutionary approach* (pp. 282-309). Sunderland, MA: Sinauer.

Delgado, R. A. (2007). Geographic variation in the long calls of male orangutans (*Pongo* spp.). *Ethology*, 113(5), 487-498.

de Vries, H. (1998). Finding a dominance order most consistent with a linear hierarchy: A new procedure and review. *Animal Behaviour, 55*(4), 827-843.

de Vries, H., Stevens, J. M. G., & Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour, 71*(3), 585-592.

de Waal, F. B. M. (1987). Tension regulation and nonreproductive functions of sex in captive bonobos. *National Geographic Research, 3*(3), 318-335.

de Waal, F. B. M. (1988). The communicative repertoire of captive bonobos (*Pan* paniscus) compared to that of chimpanzees. *Behaviour, 106*(3-4), 183-251.

de Waal, F. B. M. (1989). Behavioral contrasts between bonobo and chimpanzee. In P. G. Heltne & L. A. Marquardt (Eds.), *Understanding chimpanzees* (pp. 154-175). Cambridge, MA, and London, UK: Harvard University Press in cooperation with the Chicago Academy of Sciences.

de Waal, F. B. M. (1995). Sex as an alternative to aggression in the bonobo. In P. R. Abramson & S. D. Pinkerton (Eds.), *Sexual nature, sexual culture*. Chicago: University Press of Chicago.

de Waal, F. B. M. (1997). *Bonobo. The forgotten ape*. Berkeley: University of California Press.

Deputte, B. L., & Goustard, M. (1980). Copulatory vocalizations of female macaques (*Macaca fascicularis*): variability factors analysis. *Primates, 21*(1), 83-99.

Deschner, T., & Boesch, C. (2007). Can the patterns of sexual swelling cycles in female Taï chimpanzees be explained by the cost-of-sexual-attraction hypothesis? *International Journal of Primatology, 28*(2), 389-406.

Deschner, T., Heistermann, M., Hodges, K., & Boesch, C. (2003). Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees, *Pan troglodytes verus*. *Animal Behaviour, 66*, 551-560.

Deschner, T., Heistermann, M., Hodges, K., & Boesch, C. (2004). Female sexual swelling size, timing of ovulation, and male behavior in wild West African chimpanzees. *Hormones and Behavior, 46*(2), 204-215.

Di Bitetti, M. S. (2003). Food-associated calls of tufted capuchin monkeys (*Cebus apella nigritus*) are functionally referential signals. *Behaviour, 140*, 565-592.

Di Bitetti, M. S. (2005). Food-associated calls and audience effects in tufted capuchin monkeys, *Cebus apella nigritus*. *Animal Behaviour, 69*, 911-919.

Digweed, S. M., Fedigan, L. M., & Rendall, D. (2005). Variable specificity in the anti-predator vocalizations and behaviour of the white-faced capuchin, *Cebus capucinus*. *Behaviour, 142*, 997-1021.

Dittus, W. P. (1984). Toque macaque food calls: semantic communication concerning food distribution in the environment. *Animal Behaviour, 32*(2), 470-477.

Dixson, A. F. (1998). *Primate sexuality*. Oxford: Oxford University Press.

Dixson, A.F. (1983). Observations on the evolution and behavioral significance of sexual skin in female primates. *Advances in the Study of Behavior*, *13*, 63-106.

Dunbar, R. (1998). Theory of mind and the evolution of language. In J. R. Hurford, M. Studdert-Kennedy, & C. Knight (Eds.), *Approaches to the evolution of language* (pp. 92–110). Cambridge: Cambridge University Press.

Dunbar, R. (2003). The social brain: mind, language, and society in evolutionary perspective. *Annual Review of Anthropology, 32*, 163-181.

Elgar, M. A. (1986a). The establishment of foraging flocks in house sparrows: risk of predation and daily temperature. *Behavioral Ecology and Sociobiology, 19*(6), 433-438.

Elgar, M. A. (1986b). House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. *Animal Behaviour, 34*, 169-174.

Elowson, A. M., Tannenbaum, P. L., & Snowdon, C. T. (1991). Food-associated calls correlate with food preferences in cotton-top tamarins. *Animal Behaviour, 42*(6), 931-937.

Engelhardt, A., Pfeifer, A. B., Heistermann, M., Niemitz, C., van Hooff, J.A.R.A.M., & Hodges, J. K. (2004). Assessment of female reproductive status by male longtailed macaques, *Macaca fascicularis*, under natural conditions. *Animal Behaviour, 67*, 915-924.

Evans, C. S. (1997). Referential signals. In D. H. Owings, M. D. Beecher & N. S. Thompson (Eds.), *Perspectives in ethology* (Vol. 12, pp. 99-143). New York: Plenum Press.

Evans, C. S, & Evans, L. (1999). Chicken food calls are functionally referential. *Animal Behaviour, 58*(2), 307-319.

Evans, C. S, & Evans, L. (2007). Representational signalling in birds. *Biology Letters, 3*(1), 8.

Evans, C. S., Evans, L., & Marler, P. (1994). On the meaning of alarm calls: functional reference in an avian vocal system. *Animal Behaviour, 45*, 23-38.

Evans, C. S., & Marler, P. (1994). Food calling and audience effects in male chickens, *Gallus gallus*: Their relationships to food availability, courtship and social facilitation. *Animal Behaviour, 47*, 1159-1170.

Fichtel, C., & Kappeler, P. M. (2002). Anti-predator behavior of group-living Malagasy primates: Mixed evidence for a referential alarm call system. *Behavioral Ecology and Sociobiology, 51*(3), 262-275.

Fichtel, C., & van Schaik, C. P. (2006). Semantic differences in Sifaka (*Propithecus verreauxi)* alarm calls: A reflection of genetic or cultural variants? *Ethology, 112*, 839-849.

Fischer, J. (1998). Barbary macaques categorize shrill barks into two different call types. *Animal Behaviour, 55*, 799-807.

Fischer, J. (2004). Emergence of individual recognition in young macaques. *Animal Behaviour, 67*, 655-661.

Fischer, J., Hammerschmidt, K., & Todt, D. (1998). Local variation in Barbary macaque shrill barks. *Animal Behaviour, 56*, 623-629.

Fischer, J., Metz, M., Cheney, D. L., & Seyfarth, R. M. (2001). Baboon responses to graded bark variants. *Animal Behaviour, 61*, 925-931.

Fischer, R. B., & Nadler, R. D. (1978). Affiliative, playful, and homosexual interactions of adult female lowland gorillas. *Primates, 19*(4), 657-664.

Fitch, W. T. (2010). *The evolution of language*. Cambridge: Cambridge University Press.

Flower, T. *In press*. Fork-tailed drongos use deceptive mimicked alarm calls to steal food. *Proceedings of the Royal Society B- Biological Sciences*.

Franz, C. (1999). Allogrooming behavior and grooming site preferences in captive bonobos (*Pan paniscus*): Association with female dominance. *International Journal of Primatology, 20*(4), 525-546.

Freeberg, T. M. (2006). Social complexity can drive vocal complexity. *Psychological Science, 17*(7), 557.

Fruth, B., & Hohmann, G. (2002). How bonobos handle hunts and harvests: Why share food? In C. Boesch, G. Hohmann & L. F. Marchandt (Eds.), *Behavioral diversity in chimpanzees and bonobos* (pp. 231-243). Cambridge: Cambridge University Press.

Fruth, B, & Hohmann, G. (2006). Social grease for females? Same-sex genital contacts in wild bonobos. In V. Sommer & P. Vasey (Eds.), *Homosexual behaviour in animals: An evolutionary perspective* (pp. 294-315). Cambridge: Cambridge University Press.

Furuichi, T. (1987). Sexual swelling, receptivity, and grooming of wild pygmy chimpanzee females at Wamba, Zaire. *Primates, 28*(3), 309-318.

Furuichi, T. (1989). Social interactions and the life history of female *Pan paniscus* in Wamba, Zaire. *International Journal of Primatology, 10*(3), 173-197.

Furuichi, T. (1997). Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba. *International Journal of Primatology, 18*(6), 855-875.

Furuichi, T. (2009). Factors underlying party size differences between chimpanzees and bonobos: A review and hypotheses for future study. *Primates, 50*(3), 197-209.

Furuichi, T., & Hashimoto, C. (2002). Why female bonobos have a lower copulation rate during estrus than chimpanzees. In C. Boesch, G. Hohmann & L. F. Marchandt (Eds.), *Behavioral diversity in chimpanzees and bonobos* (pp. 156-167). Cambridge: Cambridge University Press.

Furuichi, T., & Hashimoto, C. (2004). Sex differences in copulaton attempts in wild bonobos at Wamba. *Primates, 45*(1), 59-62.

Furuichi, T., Idani, G., Ihobe, H., Kuroda, S., Kitamura, K., Mori, A., Enomoto, T., Okayasu, N., Hashimoto, C., & Kano, T. (1998). Population dynamics of wild bonobos (*Pan paniscus)* at Wamba. *International Journal of Primatology, 19*(6), 1029-1043.

Furuichi, T., & Ihobe, H. (1994). Variation in male relationships in bonobos and chimpanzees. *Behaviour, 130*, 212-228.

Furuichi, T, & Thompson, J. (Eds.). (2008). *The bonobos: Behavior, ecology, and conservation*. New York: Springer.

Galbraith, S., Daniel, J. A., & Vissel, B. (2010). A study of clustered data and approaches to its analysis. *Journal of Neuroscience, 30* (32), 10601.

Gardner, R. A. & Gardner, B. (1969). Teaching sign language to a chimpanzee. *Science, 165*, 664–672.

Gautier, J. P. (1974). Field and laboratory studies of vocalizations of Talapoin monkeys (*Miopithecus Talapoin*). *Behaviour, 51*(3-4), 209-271.

Gautier, J. P. (1988). Interspecific affinities among guenons as deduced from their vocalizations. In A. Gautier-Hion, F. Bourliere & J.-P. Gautier (Eds.), *A primate radiation: Evolutionary biology of the African guenons* (pp. 194-226). Cambridge: Cambridge Univeristy. Press.

Geissmann, T. (2002). Duet-splitting and the evolution of gibbon songs. *Biological Reviews, 77 (1): 57-76.*

Genty, E., Breuer, T., Hobaiter, C., & Byrne, R. W. (2009). Gestural communication of the gorilla (*Gorilla gorilla*): Repertoire, intentionality and possible origins. *Animal Cognition, 12*(3), 527-546.

Genty, E., & Byrne, R. W. (2010). Why do gorillas make sequences of gestures? *Animal Cognition, 13*(2), 287-301.

Gerloff, U., Hartung, B., Fruth, B., Hohmann, G., & Tautz, D. (1999). Intracommunity relationships, dispersal pattern and paternity success in a wild living community of bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. *Proceedings of the Royal Society of London Series B-Biological Sciences, 266*(1424), 1189-1195.

Gilby, I. C. (2006). Meat sharing among the Gombe chimpanzees: Harassment and reciprocal exchange. *Animal Behaviour, 71*, 953-963.

Gilby, I. C., Machanda, Z. P., & Wrangham, R. (2009). Long-term inter-sexual association patterns among wild chimpanzees. *American Journal of Physical Anthropology, 138*(S48), 180.

Glenn, M. E., Matsuda, R., & Bensen, K.J. (2004). Unique behavior of the Mona monkey (*Cercopithecus mona*): All-male groups and copulation calls. In M. E.

Glenn & M. Cords (Eds.), *The guenons: Diversity and adaptation in African monkeys* (pp. 133-145). New York: Plenum Press.

Goldfoot, D. A., Westerborg-van Loon, H., Groeneveld, W., & Koos Slob, A. (1980). Behavioral and physiological evidence of sexual climax in the female stump-tailed macaque (*Macaca arctoides*). *Science, 208,* 1477-1479.

Goldin-Meadow, S. (1996). Kanzi: The ape at the brink of the human mind. *International Journal of Primatology, 17*(1), 145-148.

Goodall, J. (1965). Chimpanzees of the Gombe stream reserve. In I. DeVore (Ed.), *Primate behavior: Field studies of monkey and apes*. New York: Holt, Rinehart, and Winston.

Goodall, J. (1968). A preliminary report on expressive movements and communication in the Gombe Stream chimpanzees. In P. C. Jay (Ed.), *Primate studies in adaptation and variability*. New York: Holt, Rinehart and Winston.

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

Gouzoules, S., Gouzoules, H., & Marler, P. (1984). Rhesus monkey (*Macaca mulatta*) screams: Representational signalling in the recruitment of agonistic aid. *Animal Behaviour, 32*(1), 182-193.

Gouzoules, H., Gouzoules, S., & Tomaszycki, M. (1998). Agonistic screams and the classification of dominance relationships: Are monkeys fuzzy logicians? *Animal Behaviour, 55*(1), 51-60.

Gouzoules, H., Gust, D. A., Donaghey, B., & St. Andre, E. (1998) Estrus vocalizations in two primate species (*Cercocebus torquatus atys* and *Macaca nemestrina*): Evidence for an effect of intrasexual competition. *Evolution and Communication,* 2, 189–215.

Greenfield, P. M., & Savage-Rumbaugh, E.S. (1991). Imitation, grammatical development and the invention of protogrammar by an ape. In N. Krasnegor, D. Rumbaugh, R. Schiefelbusch, & M. Studdert-Kennedy (Eds.). *Biological and behavioural determinants of language development* (pp. 235-262). Hillsdale, NJ: Erlbaum,

Grice, H. P. (1961). The causal theory of perception. *Proceedings of the Aristotelian Society*, Supplementary Vol. 35.

Grice, H. P. (1969). Utterer's meaning and intention. *The Philosophical Review, 78*(2), 147-177.

Gros-Louis, J. (2004a). Responses of white-faced capuchins (*Cebus capucinus*) to naturalistic and experimentally presented food-associated calls. *Journal of Comparative Psychology, 118*(4), 396-402.

Gros-Louis, J. (2004b). The function of food-associated calls in white-faced capuchin monkeys, *Cebus capucinus,* from the perspective of the signaller. *Animal Behaviour, 67,* 431-440.

Groves, C. P. (2001). *Primate taxonomy*. Washington: Smithsonian Institution Press.

Gruber, T., Clay, Z., & Zuberbühler, K. (2010). A comparison of bonobo and chimpanzee tool use: evidence for a female bias in the Pan lineage. *Animal Behaviour*, 80, 1023-1033.

Gust, D. A., Busse, C. D., & Gordon, T. P. (1990). Reproductive parameters in the sooty mangabey (*Cercocebus-Torquatus Atys*). *American Journal of Primatology*, *22*(4), 241-250.

Gyger, M., & Marler, P. (1988). Food calling in the domestic fowl, *Gallus gallus* : The role of external referents and deception. *Animal Behaviour, 36*(2), 358-365.

Halperin, S. D. (1979). Temporary association patterns in free ranging chimpanzees: An assessment of individual grouping preferences. In D. A. Hamburg & E. McCown (Eds.), *The great apes* (pp. 491-499). Palo Alto, CA: Benjamin Cummings.

Hall, K. R. L., & DeVore, I. (1965). Baboon social behavior. In I. DeVore (Ed.), *Primate behavior*. New York: Holt, Rinehart & Winston.

Hamilton, W. D. (1963). The evolution of altruistic behavior. *American Naturalist., 97,* 354-356.

Hamilton, W. J. III, & Arrowood, P. C. (1978). Copulatory vocalizations of chacma baboons (*Papio ursinus*), gibbons (*Hylobates hoolock*), and humans. *Science, 200,* 1405-1409.

Hammerschmidt, K., & Fischer, J. (1998). The vocal repertoire of Barbary macaques: A quantitative analysis of a graded signal system. *Ethology, 104,* 203-216.

Hanby, J. P. (1977). Social factors affecting primate reproduction. In J. Money & H. Mustaph (Eds.), *Handbook of sexology* (pp. 461-484). Amsterdam: Excerpta Medica.

Harcourt, A. H., Harvey, P. H., Larson, S. G., & Short, R. V. (1981). Testis weight, body weight, and breeding system in primates. *Nature, 293*(5827), 55-57.

Hare, B. (2009). What is the effect of affect on bonobo and chimpanzee problem solving? *Neurobiology of “Umwelt”*, 89-102.

Hare, B., & Kwetuenda, S. (2010). Bonobos voluntarily share their own food with others. *Current Biology, 20*(5), R230-R231.

Hare, B., Melis, A. P., Woods, V., Hastings, S., & Wrangham, R. W. (2007). Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology, 17*(7), 619-623.

Hare, J. F. (1998). Juvenile Richardson's ground squirrels, *Spermophilus richardsonii*, discriminate among individual alarm callers. *Animal Behaviour, 55*, 451-460.

Harley, H. E., Putman, E. A. & Roitblat, H. L. (2003). Bottlenose dolphins perceive object features through echolocation. *Nature, 424*, 667-669.

Hashimoto, C. (1997). Context and development of sexual behaviour of wild bonobos (*Pan paniscus*) at Wamba, Zaire. *International Journal of Primatology, 18*(1), 1-21.

Hashimoto, C., Furuichi, T., & Takenaka, O. (1996). Matrilineal kin relationship and social behavior of wild bonobos (*Pan paniscus*): Sequencing the D-loop region of mitochondrial DNA. *Primates, 37*(3), 305-318.

Hashimoto, C., Tashiro, Y., Kimura, D., Enomoto, T., Ingmanson, E. J., Idani, G., Furuichi, T. (1998). Habitat use and ranging of wild bonobos (*Pan paniscus*) at Wamba. *International Journal of Primatology, 19*(6), 1045-1060.

Hauser, M. D. (1990). Do chimpanzee copulatory calls incite male-male competition? *Animal Behaviour, 39*(3), 596-597.

Hauser, M. D. (1992). Costs of deception - cheaters are punished in Rhesus monkeys (*Macaca mulatta*). *Proceedings of the National Academy of Sciences of the United States of America, 89*(24), 12137-12139.

Hauser, M. D. (1993). Rhesus monkey copulation calls: honest signals for female choice? *Proceedings for the. Royal. Society of London B- Biological Sciences, 254*, 93-96.

Hauser, M. D. (1997). Minding the behaviour of deception. In A. Whiten, & R. W. Byrne (Eds.), *Machivellian intelligence II: Extensions and evaluations* (pp. 112-143). Cambridge: Cambridge University Press.

Hauser, M. D. (1998). Functional referents and acoustic similarity: field playback experiments with rhesus monkeys. *Animal Behaviour, 55*, 1647-1658.

Hauser, M. D., & Carey, S. (1998). Building a cognitive creature from a set of primitives: Evolutionary and developmental insights. In D. Cummins, & C. Allen, *The evolution of mind* (pp. 51-106). Oxford: Oxford University Press.

Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The faculty of language: What is it, who has it, and how did it evolve? *Science, 298*(5598), 1569-1579.

Hauser, M. D., & Marler, P. (1993a). Food-associated calls in rhesus macaques (*Macaca mulatta*): I. Socioecological factors. *Behavioral Ecology, 4*(3), 194-205.

Hauser, M. D., & Marler, P. (1993b). Food-associated calls in rhesus macaques (*Macaca mulatta*): II. Costs and benefits of call production and suppression. *Behavioral Ecology, 4*, 206-212.

Hauser, M. D., & Wrangham, R. W. (1987). Manipulation of food calls in captive chimpanzees: A preliminary report. *Folia Primatologica, 48,* 24-35.

Heilbronner, S. R., Rosati, A. G., Stevens, J. R., Hare, B., & Hauser, M. D. (2008). A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos. *Biology Letters, 4*(3), 246.

Heinrich, B., & Marzluff, J. M. (1991). Do common ravens yell because they want to attract others? *Behavioral Ecology and Sociobiology, 28*(1), 13-21.

Heistermann, M., Brauch, K., Mohle, U., Pfefferle, D., Dittami, J., & Hodges, K. (2008). Female ovarian cycle phase affects the timing of male sexual activity in free-ranging Barbary macaques (*Macaca sylvanus*) of Gibraltar. *American Journal of Primatology, 70*(1), 44-53.

Heistermann, M., Mohle, U., Vervaecke, H., van Elsacker, L., & Hodges, J. K. (1996). Application of urinary and fecal steroid measurements for monitoring ovarian function and pregnancy in the bonobo (*Pan paniscus*) and evaluation of perineal swelling patterns in relation to endocrine events. *Biology of Reproduction, 55*(4), 844-853.

Henzi, S. P. (1996). Copulation calls and paternity in chacma baboons. *Animal Behaviour, 51*, 233-234.

Herrmann, E., Hare, B., Call, J., Tomasello, M., & Emery, N. J. (2010). Differences in the cognitive skills of bonobos and chimpanzees. *PloS One, 5*(8), 563-571.

Hill, W. C. O. (1969). In: G. H. Bourne (Ed.), *The chimpanzee*, Volume 1 (pp. 22–49). Basel, New York: S. Karger.

Hilliard, A. T., & White, S. A. (2009). Possible precursors of syntactic components in other species. In D. Bickerton, & E. Szathmáry (Eds.), *Biological foundations and origin of syntax* (pp. 161-184). Cambridge, MA: The MIT Press.

Hohmann, G. (1989). Vocal communication of wild bonnet macaques (*Macaca radiata*). *Primates, 30*(3), 325-346.

Hohmann, G., & Fruth, B. (1993). Field observations on meat sharing among bonobos (*Pan paniscus*). *Folia Primatologica, 60,* 225-229.

Hohmann, G., & Fruth, B. (1994). Structure and use of distance calls in wild bonobos (*Pan paniscus*). *International Journal of Primatology, 15*(5), 767-782.

Hohmann, G., & Fruth, B. (2000). Use and function of genital contacts among female bonobos. *Animal Behaviour, 60,* 107-120.

Hohmann, G., & Fruth, B. (2003a). Intra- and inter-sexual aggression by bonobos in the context of mating. *Behaviour, 140,* 1389-1413.

Hohmann, G., & Fruth, B. (2003b). Culture in bonobos? Between-species and with-species variation in behavior. *Current Anthropology, 44*(4), 563-571.

Hohmann, G., & Fruth, B. (2008). New records on prey capture and meat eating by bonobos at Lui Kotale, Salonga National Park, Democratic Republic of Congo. *Folia Primatologica, 79*(2), 103-110.

Hohmann, G., Gerloff, U., Tautz, D., & Fruth, B. (1999). Social bonds and genetic ties: Kinship, association and affiliation in a community of bonobos (*Pan paniscus*). *Behaviour, 136,* 1219-1235.

Hohmann, G., & Herzog, M. (1985). Vocal communication in lion-tailed macaques (*Macaca silenus). Folia Primatologica., 45,* 148-178.

Hohmann, G., Mundry, R., & Deschner, T. (2009). The relationship between socio-sexual behavior and salivary cortisol in bonobos: Tests of the tension regulation hypothesis. *American Journal of Primatology, 71*(3), 223-232.

Holland, J., Dabelsteen, T., & Lopez Paris, A. (2000). Coding in the song of the wren: Importance of rhythmicity, syntax and element structure. *Animal Behaviour, 60,* 463-470.

Hollén, L. I, & Manser, M. B. (2007). Motivation before meaning: Motivational information encoded in meerkat alarm calls develops earlier than referential information. *American Naturalist, 169,* 758-767.

Hopkins, W. D, & Savage-Rumbaugh, E. S. (1991). Vocal communication as a function of differential rearing experiences in *Pan paniscus*: A preliminary report. *International Journal of Primatology, 12*(6), 559-583.

Hsu, M. J., Lin, J. F., Chen, L. M., & Agoramoorthy, G. (2000). Copulation calls in male Formosan macaques: Honest signals of male quality? *Folia Primatologica, 73*(4), 220-223.

Idani, G. (1991). Social relationships between immigrant and resident bonobo (*Pan paniscus*) females at Wamba. *Folia Primatologica, 57,* 83-95.

Ihobe, H. (1992). Observations on the meat-eating behavior of wild bonobos (*Pan paniscus*) at Wamba, Republic-of-Zaire. *Primates, 33*(2), 247-250.

Ingmanson, E. J. (1996). Tool-using behavior in wild *Pan paniscus*: Social and ecological considerations. In A. E. Russon & K. A. Bard (Eds.), *Reaching into thought: The minds of the great apes* (pp. 190-210). Cambridge: Cambridge University Press.

Jaeggi, A. V., Stevens, J. M. G., & van Schaik, C. P. (2010). Tolerant food sharing and reciprocity is precluded by despotism among bonobos but not chimpanzees. *American Journal of Physical Anthropology, 143*(1), 41-51.

Judd, T. M., & Sherman, P. W. (1996). Naked mole-rats recruit colony mates to food sources. *Animal Behaviour, 52*(5), 957-969.

Kano, T. (1980). Social behaviour of wild pygmy chimpanzees (*Pan paniscus*) of Wamba: A preliminary report. *Journal of Human Evolution, 9*, 243-260.

Kano, T. (1982). The social group of pygmy chimpanzees (*Pan paniscus*) of Wamba. *Primates, 23*(2), 171-188.

Kano, T. (1989). The sexual behavior of pygmy chimpanzees. In P. G. Heltne & L. A. Marquardt (Eds.), *Understanding chimpanzees* (pp. 176-183). Cambridge, MA, and London, UK: Harvard University Press in cooperation with the Chicago Academy of Sciences.

Kano, T. (1992). *The last ape: Pygmy chimpanzee behavior and ecology*. Stanford: Stanford University Press.

Kano, T., & Mulavwa, M. (1984). Feeding ecology of the pygmy chimpanzees (*Pan paniscus*) of Wamba. In R. L. Susman (Ed.), *The pygmy chimpanzee: Evolutionary biology and behavior* (pp. 233-274). New York: Plenum Press

Kendon, A. (2004). *Gesture: Visible action as utterance*: Cambridge: Cambridge Univeristy Press.

Kipper, A. U., Mundry, R., Hultsch, H. & Todt, D. (2004). Long-term persistence of song performance rules in nightingales (*Luscinia megarhynchos*): A longitudinal field study on repertoire size and composition. *Behavior, 141*, 371- 390.

Kirchhof, J., & Hammerschmidt, K. (2006). Functionally referential alarm calls in tamarins (*Saguinus fuscicollis* and *Saguinus mystax*)–evidence from playback experiments. *Ethology, 112*(4), 346-354.

Kitamura, K. (1983). Pygmy chimpanzee asociation patterns in ranging. *Primates, 24*(1), 1-12.

Kitzmann, C. D., & Caine, N. G. (2009). Marmoset (*Callithrix geoffroyi*) food-associated calls are functionally referential. *Ethology, 115*(5), 439-448.

Kripke, S. (1977). Speaker's reference and semantic reference. *Midwest Studies in Philosophy, 2*(1), 255-276.

Kuroda, S. J. (1980). Social behavior of the pygmy chimpanzees. *Primates*, *21*(2), 181-197.

Kuroda, S. J. (1984). Interaction over food among pygmy chimpanzees. In R. L. Susman (Ed.), *The pygmy chimpanzee: Evolutionary biology and behavior* (pp. 301-324). New York: Plenum Press.

Laitman, J., & Heimbuch, R. (1984). A measure of basicranial flexion in *Pan paniscus*, the pygmy chimpanzee. In R. L. Susman, *The pygmy chimpanzee: Evolutionary biology and behavior* (pp. 49-63). New York: Plenum Press.

Lancaster, J. B. (1975). *Primate behavior and the emergence of human culture*. New York: Holt, Rinehart and Winston.

Langergraber, K., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology, 71*(10), 840-851.

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

Leavens, D. A., Hopkins, W. D., & Thomas, R. K. (2004). Referential communication by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 118*(1), 48-57.

Lehmann, J., & Boesch, C. (2009). Sociality of the dispersing sex: the nature of social bonds in West African female chimpanzees, *Pan troglodytes*. *Animal Behaviour, 77*(2), 377-387.

Lieberman, P. (1968). Primate vocalizations and human linguistic ability. *Journal of the Acoustical Society of America, 44*(6), 1574-1584.

Lieberman, P. (1998). Speech evolution: Let barking dogs sleep. *Behavioral and Brain Sciences, 21*(4), 520.

Lindburg, D. G. (1990). Proceptive calling by female lion-tailed macaques. *Zoo Biology, 9*(6), 437-446.

Liszkowski, U. (2005). Human twelve-month-olds point cooperatively to share interest with and provide information for a communicative partner. *Gesture, 5*(1, 2), 135-154.

Liszkowski, U., Carpenter, M., Striano, T., & Tomasello, M. (2006). Twelve and 18-months-olds point to provide information for others. *Journal of Cognition and Development, 7*(2), 173-187.

Lonsdorf, E. V., Ross, S.R., Matsuzawa, T. (Eds.) (2010). *The mind of the chimpanzee: Ecological and experimental perspectives*. Chicago: University of Chicago Press.

Macedonia, J. M. (1990). What is communicated in the antipredator calls of lemurs: Evidence from playback experiments with ring-tailed and ruffed lemurs. *Ethology, 86*, 177-190.

Macedonia, J. M., & Evans, C. S. (1993). Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology, 93*, 177-197.

Maestripieri, D. (1999). Primate social organization, gestural repertoire size, and communication dynamics. In B. J. King (Ed.), *The origins of language: What nonhuman primates can tell us* (pp. 55-77). Santa Fe: School of American Research Press.

Maestripieri, D., Leoni, M., Raza, S. S., Hirsch, E. J., & Whitham, J. C. (2005). Female copulation calls in guinea baboons: Evidence for postcopulatory female choice? *International Journal of Primatology, 26*(4), 737-758.

Maestripieri, D., & Roney, J. R. (2005). Primate copulation calls and postcopulatory female choice. *Behavioral Ecology, 16*(1), 106.

Mahurin, E. J., & Freeberg, T. M. (2009). Chick-a-dee call variation in Carolina chickadees and recruiting flockmates to food. *Behavioral Ecology, 20*(1), 111-116.

Malenky, R. K., Kuroda, S., Vineberg, E. O., & Wrangham, R. W. (1994). The significance of terrestrial; herbaceous foods for bonobos, chimpanzees, and gorillas. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal & P. G. Heltne (Eds.), *Chimpanzee cultures* (pp. 59-75). Harvard, England: Harvard University Press.

Manser, M. B., Bell, M. B., & Fletcher, L. B. (2001). The information that receivers extract from alarm calls in suricates. *Proceedings of the Royal Society of London Series B-Biological Sciences, 268*(1484), 2485-2491.

Manser, M. B. , Seyfarth, R. M., & Cheney, D. L. (2002). Suricate alarm calls signal predator class and urgency. *Trends in Cognitive Sciences, 6*(2), 55-57.

Manson, J. H., Perry, S., & Parish, A. R. (1997). Nonconceptive sexual behavior in bonobos and capuchins. *International Journal of Primatology, 18*(5), 767-786.

Marler, P. (1961). The logical analysis of animal communication. *Journal of Theoretical Biology,, 1*, 295-317.

Marler, P. (1970). Vocalizations of East African monkeys. I. Red colobus. *Folia primatologica., 13*, 81-91.

Marler, P. (1972). Vocalizations of East African monkeys: II. Black and white colobus. *Behaviour, 42*, 175-197.

Marler, P. (1976). Social organization, communication and graded signals: The chimpanzee and the gorilla. In P. P. Bateson & R. A. Hinde (Eds.), *Growing points in ethology*. Cambridge: Cambridge University Press.

Marler, P. (1977). The evolution of communication. In T. S. Sebeok (Ed.), *How animals communicate* (pp. 45-70). Bloomington & London: Indiana University Press.

Marler, P., Dufty, A., & Pickert, R. (1986). Vocal communication in the domestic chicken: II. Is a sender sensitive to the presence and nature of a receiver? *Animal Behaviour, 34*, 194-198.

Marler, P., Evans, C., & Hauser, M. D. (1992). Animal signals: reference, motivation, or both? In H. Papoucek, U. Jürgens & M. Papoucek (Eds.), *Nonverbal vocal communication: Comparative and developmental approaches* (pp. 66-86). Cambridge: Cambridge University Press.

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

Marshall, A. J., Wrangham, R. W., & Arcadi, A. C. (1999). Does learning affect the structure of vocalisations in chimpanzees? *Animal Behaviour, 58*(4), 825-830.

Marzluff, J. M., & Heinrich, B. (1991). Foraging by common ravens in the presence and absence of territory holders - an experimental-analysis of social foraging. *Animal Behaviour, 42*, 755-770.

McComb, K., & Semple, S. (2005). Coevolution of vocal communication and sociality in primates. *Biology Letters, 1*(4), 381-385.

McCullagh, P., & Nelder, J. A. (1989). *Generalized linear models (Monographs on statistics and applied probability 37*). London: Chapman Hall.

McNeill, D. (1992). *Hand and mind.* Chicago: The University of Chicago Press.

Miles, H. L. (1990). The cognitive foundations for reference in a signing orang-utan. In S. T. Parker, & K. R. Gibson (Eds.), *Language and intelligence in monkeys and apes* (pp. 511-539). Cambridge: Cambridge University Press,

Milton, K. (1985). Mating patterns of woolly spider monkeys, *Brachyteles arachnoides*- Implications for female choice. *Behavioral Ecology and Sociobiology 17*:53–59

Mitani, J. C., & Gros-Louis, J. (1995). Species and sex differences in the screams of chimpanzees and bonobos. *International Journal of Primatology, 16*(3), 393-411.

Mitani, J. C., Hasegawa, T., Gros-Louis, J., Marler, P., & Byrne, R.W. (1992). Dialects in wild chimpanzees? *American Journal of Primatology, 27*(4), 233-243.

Mitani, J. C., Merriwether, A. D., & Zhang, C. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Animal Behaviour, 59*, 885-893.

Montgomerie, R., Thornhill, R. (1989). Fertility advertisement in birds: a means of inciting male–male competition? *Ethology,* 81:209–220.

Moore, J. (1984). Female transfer in primates. *International Journal of Primatology, 5*(6), 537-589.

Moos-Heilen, R., & Sossinka, R. (1990). The influence of oestrus on the vocalizations of female gelada baboons (*Theropithecus gelada*). *Ethology, 84,* 35-46.

Mori, A. (1983). Comparison of the communicative vocalizations and behaviors of group ranging in eastern gorillas, chimpanzees and pygmy chimpanzees. *Primates, 24*(4), 486-500.

Muller, M. N., Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2007). Male coercion and the costs of promiscuous mating for female chimpanzees. *Proceedings of the Royal Society B-Biological Sciences, 274*(1612), 1009.

Muller, M. N., Thompson, M. E., & Wrangham, R. W. (2006). Male chimpanzees prefer mating with old females. *Current Biology, 16*(22), 2234-2238.

Mundry, R. & Fischer, J. (1998). Use of statistical programs for nonparametric tests of small samples often leads to incorrect P values: Examples from animal behaviour. *Animal Behaviour, 56*(1), 256.

Mundry, R., & Sommer, C. (2007). Discriminant function analysis with nonindependent data: consequences and an alternative. *Animal Behaviour, 74*(4), 965-976.

Munn, C. A. (1986). Birds that "cry wolf". *Nature, 319*, 143-145.

Myers-Thompson, J. A. (2002). Bonobos of the Lukuru Wildlife Research Project. In T. Furuichi & J. Thompson (Eds.), *Behavioural diversity in chimpanzees and bonobos (*pp. 61-70). Cambridge: Cambridge University Press.

Nelder, J. A., & Wedderburn, R. W. M. (1972). Generalized linear models. *Journal of the Royal Statistical Society. Series A (General), 135*(3), 370-384.

Newman, J. A., & Caraco, T. (1989). Co-operative and non-co-operative bases of food-calling. *Journal of Theoretical Biology, 141*(2), 197-209.

Nikitopoulos, E., Arnhem, E., van Hooff, J.A. R. A. M., & Sterck, E. H. M. (2004). Influence of female copulation calls on male sexual behavior in captive *Macaca fascicularis. International Journal of Primatology, 25*(3), 659-677.

Nikitopoulos, E., Heistermann, M., de Vries, H., van Hooff, J. A. R. A. M., & Sterck, E. H. M. (2005). A pair choice test to identify female mating pattern relative to ovulation in longtailed macaques, *Macaca fascicularis*. *Animal Behaviour, 70,* 1283-1296.

Nishida, T., & Hiraiwa-Hasegawa, M. (1987). Chimpanzees and bonobos: Cooperative relationships among males. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R.W. Wrangham & T.T. Struhsacker (Eds.), *Primate societies* (pp. 165-177). Chicago: The University of Chicago Press.

Noe, R., de Waal, F. B. M., & van Hooff, J. A. R. A. M. (1980). Types of dominance in a chimpanzee colony. *Folia Primatologica, 34*(1-2), 90 - 110.

Nunn, C. L. (1999). The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Animal Behaviour, 58*(2), 229-246.

O'Connell, S. M., & Cowlishaw, G. (1994). Infanticide avoidance, sperm competition and mate choice: The function of copulation calls in female baboons. *Animal Behaviour, 48*(3), 687-694.

O'Grady, W., Dobrovolsky, M., & Katamba, F. (1997). *Contemporary linguistics: An introduction*. Essex: Addison Wesley Longman Limited/ St. Martin's Press Inc.

Oda, R., & Masataka, N. (1992). Functional significance of female Japanese macaque copulatory calls. *Folia Primatologica, 58*(3), 146-149.

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009a). Campbell's monkeys concatenate vocalizations into context-specific call sequences. *Proceedings of the National Academy of Sciences of the Uinted States of America, 106*(51), 22026.

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009b). Campbell's monkeys use affixation to alter call meaning. *PLoS One, 4*(11).

Owings, D. H. , & Morton, E. S. (1997). The role of information in communication: An assessment/management approach. In H. Donald & M. D. Owings (Eds.), *Perspectives in ethology, Vol. 12: Communication* (Vol. 12, pp. 359-390). New York: Plenum Press.

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

Owren, M. J., & Rendall, D. (2001). Sound on the rebound: Bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary Anthropology., 10,* 58-71.

Owren, M. J., Rendall, D, & Ryan, M. J. (2010). Redefining animal signaling: Influence versus information in communication. *Biology and Philosophy,* 1-26.

Owren, M. J., Seyfarth, R. M., & Cheney, D. L. (1997). The acoustic features of vowel-like grunt calls in chacma baboons (*Papio cyncephalus ursinus*): Implications for production processes and functions. *Journal of the Acoustical Society of America, 101*(5), 2951-2963.

Oyakawa, C., Koda, H., Sugiura, H. (2007). Acoustic features contributing to the individuality of wild agile gibbon (*Hylobates agilis agilis*) songs. *American Journal of Primatology, 69,* 777- 790.

Palagi, E., & Paoli, T. (2007). Play in adult bonobos (*Pan paniscus):* Modality and potential meaning. *American Journal of Physical Anthropology, 134*(2), 219-225.

Palagi, E., Paoli, T., & Borgognini Tarli, S. (2004). Reconciliation and consolation in captive bonobos (*Pan paniscus*). *American Journal of Primatology, 62*(1), 15-30.

Palombit, R. A., Seyfarth, R. M., & Cheney, D. L. (1997). The adaptive value of 'friendships' to female baboons: Experimental and observational evidence. *Animal Behaviour, 54*, 599-614.

Paoli, T., & Palagi, E. (2008). What does agonistic dominance imply in bonobos? In T. Furuichi & J. Thompson (Eds.), *The bonobos: Behaviour, ecology and conservation* (pp. 39-54). New York: Springer.

Paoli, T., Palagi, E., & Tarli, S. M. B. (2006a). Reevaluation of dominance hierarchy in bonobos (*Pan paniscus*). *American Journal of Physical Anthropology, 130*(1), 116-122.

Paoli, T., Palagi, E., Tacconi, G., & Tarli, S. B. (2006b). Perineal swelling, intermenstrual cycle, and female sexual behavior in bonobos (*Pan paniscus*). *American Journal Of Primatology, 68*(4), 333-347.

Parish, A. R. (1994). Sex and food control in the uncommon chimpanzee - How bonobo females overcome a phylogenetic legacy of male-dominance. *Ethology and Sociobiology, 15*(3), 157-179.

Parish, A. R. (1996). Female relationships in bonobos (*Pan paniscus*) - Evidence for bonding, cooperation, and female dominance in a male-philopatric species. *Human Nature - An Interdisciplinary Biosocial Perspective, 7*(1), 61-96.

Patterson, F. (1978). Conversations with a gorilla. *National Geographic, 154*(4), 438-465.

Paul, A. (1989). Determinants of male mating success in a large group of Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. *Primates, 30*(4), 461-476.

Pepperberg, I. M. (2002). *The Alex studies: Cognitive and communicative abilities of grey parrots*. Cambridge, MA: Harvard University Press.

Pereira, M. E., & Macedonia, J. M. (1991). Ringtailed lemur anti-predator calls denote predator class, not response urgency. *Animal Behaviour, 41*, 543-544.

Pfefferle, D., Brauch, K., Heistermann, M., Hodges, J. K., & Fischer, J. (2008a). Female Barbary macaque (*Macaca sylvanus*) copulation calls do not reveal the fertile phase but influence mating outcome. *Proceedings of the Royal Society B- Biological Sciences, 275*(1634), 571-578.

Pfefferle, D., Heistermann, M., Hodges, J. K., & Fischer, J. (2008b). Male Barbary macaques eavesdrop on mating outcome: a playback study. *Animal Behaviour, 75*(6), 1885-1891.

Pika, S., Liebal, K., & Tomasello, M. (2005). Gestural communication in subadult bonobos (*Pan paniscus*): Gestural repertoire and use. *American Journal of Primatology, 65*(1), 39-51.

Pika, S., & Mitani, J. (2006). Referential gestural communication in wild chimpanzees (*Pan troglodytes*). *Current Biology, 16*(6), R191-R192.

Pika, S., & Zuberbühler, K. (2008). Social games between bonobos and humans: Evidence for shared intentionality? *American Journal of Primatology, 70*(3), 207-210.

Pinker, S. (1994). *The language instinct. How the mind creates language*. New York: Morrow.

Pinker, S. (2003). Language as an adaptation to the cognitive niche. *Language Evolution*, 16-37.

Pollick, A.S, de Waal F. B. M. (2007). Ape gestures and language evolution. *Proceedings of the National Academy of Sciences of the United States of America 104*(19), 8184-8189.

Pollick, A. S., Gouzoules, H., & de Waal, F. B. M. (2005). Audience effects on food calls in captive brown capuchin monkeys, *Cebus apella*. *Animal Behaviour, 70*, 1273-1281.

Pollick, A. S., Jeneson, A., & Waal, F. B. M. (2008). Gestures and multimodal signaling in bonobos. In T. Furuichi & J. Thompson (Eds.), *The bonobos: Behaviour, ecology and conservation* (pp. 75-94). New York: Springer.

Poole, J. H., Payne, K., Langbauer, W. R., & Moss, C. J. (1988). The social contexts of some very low-frequency calls of African elephants. *Behavioral Ecology and Sociobiology, 22*(6), 385-392.

Pradhan, G. R., Engelhardt, A., van Schaik, C. P., & Maestripieri, D. (2006). The evolution of female copulation calls in primates: A review and a new model. *Behavioral Ecology and Sociobiology, 59*(3), 333-343.

Pruetz, J. D., & Bertolani, P. (2007). Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Current Biology, 17*(5), 412-417.

Pulliam, H. R., & Caraco, T. (1984). Living in groups: Is there an optimal group size? In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology* (pp. 122-147). Oxford: Blackwell.

Pusey, A. E., Murray, C. M., Wallauer, W., Wilson, M. L., Wroblewski, E., & Goodall, J. (2008). Severe aggression among female chimpanzees at Gombe National Park, Tanzania. *International Journal of Primatology, 29*, 949-973.

Pusey, A. E., & Packer, C. (1986). Dispersal and philopatry. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primate societies* (pp. 250-266). Chicago: University of Chicago Press.

Rendall, D., Rodman, P. S., & Emond, R. E. (1996). Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour, 51*, 1007-1015.

Rendall, D., Owren, M. J., & Ryan, M. J. (2009). What do animal signals mean? *Animal Behaviour, 78*(2), 233-240.

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

Ridley, A. R., & Raihani, N. J. (2007). Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. *Behavioral Ecology, 18*(2), 324-330.

Rosati, A. G., Stevens, J. R., Hare, B., & Hauser, M.D. (2007). The evolutionary origins of human patience: Temporal preferences in chimpanzees, bonobos, and human adults. *Current Biology, 17*(19), 1663-1668.

Roush, R. S., & Snowdon, C. T. (2000). Quality, quantity, distribution and audience effects on food calling in cotton-top tamarins. *Ethology, 106*, 673-690.

Ruxton, G. D. (1995). Foraging on patches: Are groups disadvantaged? *Oikos, 72*(1), 148-150.

Ryan, M. J., Tuttle, M. D., & Rand, A. S. (1982). Bat predation and sexual advertisement in a neotropical anuran. *American Naturalist, 119*(1), 136-139.

Sannen, A., Heistermann, M., van Elsacker, L., Mohle, U., & Eens, M. (2003). Urinary testosterone metabolite levels on bonobos: A comparison with chimpanzees in relation to social system. *Behaviour, 140*, 683-696.

Savage-Rumbaugh, S. (1986). *Ape language from conditioned response to symbol*. New York: Columbia University Press.

Savage-Rumbaugh, S. (1987). A new look at ape language: Comprehension of vocal speech and syntax. Nebraska Symposium on Motivation (1987, Lincoln, Nebraska). *Nebraska Symposium on Motivation, 35*, 201-255.

Savage, S., & Bakeman, R. (1978). Sexual morphology and behavior in *Pan paniscus Proceedings of the Sixth International Congress of Primatology* (pp. 613-616). New York: Academic Press.

Savage-Rumbaugh, S. & Lewin, R. (1994). *Kanzi. The ape at the brink of the human mind*. New York: Wiley.

Savage-Rumbaugh, S., McDonald, K., Sevcik, R. A., Hopkins, W. D., & Rubert, E. (1986). Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*Pan paniscus*). *Journal of Experimental Psychology: General, 115*(3), 211-235.

Savage-Rumbaugh, S., Sevcik, R. A., Brakke, K. E., & Rumbaugh, D. M. (1990). Symbols: Their communicative use, comprehension, and combination by bonobos (Pan paniscus). *Advances in Infancy Research., 6,* 221-278.

Savage-Rumbaugh, S., Wilkerson, B. J., & Bakeman, R. (1977). Spontaneous gestural communication among conspecifics in the pygmy chimpanzee (*Pan paniscus*). *Progress in Ape Research*, 97–116.

Scarantino, A. (2010). Animal communication between information and influence. *Animal Behaviour, 30*, 1e5.

Schaller, G. B. (1972). *The Serengeti lion*. Chicago: University of Chicago Press.

Schel, A. M., Candiotti, A., & Zuberbühler, K. (2010). Predator-deterring alarm call sequences in Guereza colobus monkeys are meaningful to conspecifics. *Animal Behaviour, 80*(5), 799-808.

Schel, A. M., Tranquilli, S., & Zuberbühler, K. (2009). The alarm call system of black-and-white colobus monkeys. *Journal of Comparative Psychology, 123*, 136-150.

Semple, S. (1998). The function of Barbary macaque copulation calls. *Proceedings of the. Royal. Society. London. B- Biological Sciences., 265*(1393), 287-291.

Semple, S. (2001). Individuality and male discrimination of female copulation calls in the yellow baboon. *Animal Behaviour, 61*(5), 1023-1028.

Semple, S., & McComb, K. (2000). Perception of female reproductive stale from vocal cues in a mammal species. *Proceedings of the Royal Society of London Series B-Biological Sciences, 267*(1444), 707-712.

Semple, S., McComb, K., Alberts, S., & Altmann, J. (2002). Information content of female copulation calls in yellow baboons, *American Journal of Primatology, 56*, 43-56).

Senghas, A., Kita, S., & Ozyurek, A. (2004). Children creating core properties of language: Evidence from an emerging sign language in Nicaragua. *Science, 305*(5691), 1779.

Setia, T. M., & van Schaik, C. P. (2007). The response of adult orangutans to flanged male long calls: Inferences about their function. *Folia Primatologica,* 78(4), 215-226.

Sevcik, R. A., & Savage-Rumbaugh, S. (1994). Language comprehension and use by great apes. *Language & Communication, 14*(1), 37-58.

Seyfarth, R. M., & Cheney, D. L. (1984). The acoustic features of vervet monkey grunts. *Journal of the Acoustical Society of America, 75*(5), 1623-1628.

Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal Behaviour, 34*, 1640-1658.

Seyfarth, R. M., & Cheney, D. L. (2003a). Signalers and receivers in animal communication. *Annual Review Of Psychology, 54*(1), 145-173.

Seyfarth, R. M., & Cheney, D. L. (2003b). Meaning and emotion in animal vocalizations. In P. Ekman, J. J. Campos, R. J. Davidson & F. de Waal (Eds.), *Emotions inside out: 130 Years after Darwin's "The expression of the emotions in man and animals"* (Vol. 1000, pp. 32-55). New York: New York Academy of Sciences.

Seyfarth, R. M., & Cheney, D. L. (2008). Primate social knowledge and the origins of language. *Mind & Society*, *7*(1), 129-142.

Seyfarth, R. M., Cheney, D. L., Bergman, T., Fischer, J., Zuberbühler, K., & Hammerschmidt, K. (2010). The central importance of information in studies of animal communication. *Animal Behaviour, 80*(1), 3-8.

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. *Science, 210*(4471), 801.

Shanker, S. T., Savage-Rumbaugh, E. S., & Taylor, T. J. (1999). Kanzi: a new beginning. *Animal Learning and Behavior., 27*(1), 24-25.

Sherman, P. W. (1977). Nepotism and the evolution of alarm calls. *Science, 197,* 1246-1253.

Silk, J. B., Alberts, S. C., & Altmann, J. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology, 61*(2), 197-204.

Sloan, J. L., Wilson, D. R., & Hare, J. F. (2005). Functional morphology of Richardson's ground squirrel, *Spermophilus richardsonii*, alarm calls: The meaning of chirps, whistles and chucks. *Animal Behaviour, 70*, 937-944.

Slocombe, K. E., Kaller, T., Call, J., & Zuberbühler, K. (2010a). Chimpanzees extract social information from agonistic screams. *PLoS One, 5*(7) e11473

Slocombe, K. E., Kaller, T., Turman, L., Townsend, S. W., Papworth, S., & Squibbs, P., & Zuberbühler, K. (2010b). Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. *Behavioral Ecology and Sociobiology*, 64(12), 1959-1966

Slocombe, K. E., Townsend, S. W., & Zuberbühler, K. (2009). Wild chimpanzees (*Pan troglodytes schweinfurthii*) distinguish between different scream types: Evidence from a playback study. *Animal Cognition*, *12*(3), 441-449.

Slocombe, K. E., & Zuberbühler, K. (2005a). Agonistic screams in wild chimpanzees (*Pan troglodytes schweinfurthii)* vary as a function of social role. *Journal of Comparative Psychology, 119*(1), 67-77.

Slocombe, K. E., & Zuberbühler, K. (2005b). Functionally referential communication in a chimpanzee. *Current Biology*, *15*(19), 1779-1784.

Slocombe, K. E., & Zuberbühler, K. (2006). Food-associated calls in chimpanzees: Responses to food types or food preferences? *Animal Behaviour, 72,* 989-999.

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

Smith, J. W. (1965). Message, meaning and context in ethology. *American Naturalist, 99*, 405-409.

Snowdon, C. T., & Pola, Y. V. (1978). Interspecific and intraspecific responses to synthesized marmoset vocalizations. *Animal Behaviour, 26*, 192-206.

Stanford, C. B. (1998). The social behavior of chimpanzees and bonobos - Empirical evidence and shifting assumptions. *Current Anthropology, 39*(4), 399-420.

Stanford, C. B., Wallis, J., Mpongo, E., & Goodall, J. (1994). Hunting decisions in wild chimpanzees. *Behaviour, 131*, 1-18.

Steenbeek, R., Piek, R. C., van Buul, M., & van Hooff, J. A. R. A. M. (1999). Vigilance in wild Thomas's langurs (*Presbytis thomasi*): The importance of infanticide risk. *Behavioral Ecology and Sociobiology, 45*(2), 137-150.

Stegmann, U. E. (2009). A consumer based teleosemantics for animal signals. *Philosophy of Science, 76*, 864-875.

Sterck, E. H. M., & Korstjens, A. H. (2000). Female dispersal and infanticide avoidance in primates. In C. P. van Schaik, & C. H. Janson, *Infanticide by males and its implications* (pp. 293-321). Cambridge: Cambridge University Press.

Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology, 41*(5), 291-309.

Sterck, E. H. M., Willems, E. P., van Hooff, J. A. R. A. M, & Wich, S. A. (2005). Female dispersal, inbreeding avoidance and mate choice in Thomas langurs (*Presbytis thomasi*). *Behaviour, 142*, 845-868.

Stevens, J. M. G., Vervaecke, H., de Vries, H., & van Elsacker, L. (2005a). The influence of the steepness of dominance hierarchies on reciprocity and interchange in captive groups of bonobos (*Pan paniscus*). *Behaviour, 142*(7), 941-960.

Stevens, J. M. G., Vervaecke, H., de Vries, H., & Van Elsacker, L. (2005b). Peering is not a formal indicator of subordination in bonobos (*Pan paniscus*). *American Journal of Primatology, 65*(3), 255-267.

Stevens, J. M. G., Vervaecke, H., de Vries, H., & van Elsacker, L. (2006). Social structures in *Pan paniscus*: Testing the female bonding hypothesis. *Primates, 47*(3), 210-217.

Stevens, J. M. G., Vervaecke, H., de Vries, H., & van Elsacker, L. (2007). Sex differences in the steepness of dominance hierarchies in captive bonobo groups. *International Journal of Primatology, 28*(6), 1417-1430.

Stevens, J. M. G., Vervaecke, H., & Elsacker, L. (2008). The bonobo's adaptive potential: social relations under captive conditions. In T. Furuichi & J. Thompson (Eds.), *The bonobos: Behaviour, ecology and conservation* (pp. 19-38). New York: Springer.

Stevens, K. N., & Weismer, G. (2001). Acoustic phonetics. *Journal of the Acoustical Society of America, 109*, 17.

Stokes, A. W., & Williams, H. W. (1971). Courtship feeding in gallinaceous birds. *The Auk, 88*(3), 543-559.

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

Surbeck, M., Fowler, A., Deimel, C., & Hohmann, G. (2009). Evidence for the consumption of arboreal, diurnal primates by bonobos (*Pan paniscus*). *American Journal of Primatology, 71*(2), 171-174.

Surbeck, M., & Hohmann, G. (2008). Primate hunting by bonobos at Lui Kotale, Salonga National Park. *Current Biology, 18*(19), R906-R907.

Surbeck, M., Mundry, R., & Hohmann, G. (2010). Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus). Proceedings of the Royal Society B-Biological Sciences*.

Suzuki, R., Buck, J. R., & Tyack, P. L. (2006). Information entropy of humpback whale songs. *Journal of the Acoustical Society of America, 119,* 1849.

Számado, S., Hurford, J., Bishop, D. V. M., Deacon, T. W., d'Errico, F., Fischer, J., Okanoya, K., Szathmáry, E., & White, S. A. (2009). What are the possible biological and genetic foundations for syntactic phenomena? In D. Bickerton, & E. Szathmáry (Eds.), *Biological foundations and origin of syntax* (pp. 207-226). Cambridge, MA: The MIT Press.

Tabachnick, B. G., & Fidell, L. S. (2001). *Using multivariate analysis.* California State University Northridge: Harper Collins College Publishers.

Taglialatela, J. P., Savage-Rumbaugh, S., & Baker, L. A. (2003). Vocal production by a language-competent *Pan paniscus*. *International Journal of Primatology, 24*(1), 1-17.

Takahata, Y., Ihobe, H., & Idani, G. (1996). Comparing copulations of chimpanzees and bonobos: Do females exhibit proceptivity or receptivity. In W. C. McGrew, L. F. Marchandt & T. Nishida (Eds.), *Great ape societies* (pp. 146-155). Cambridge: Cambridge University Press.

Templeton, C. N., Greene, E., & Davis, K. (2005). Allometry of alarm calls: Black-capped chickadees encode information about predator size. *Science, 308*(5730), 1934-1937.

Thompson-Handler, N. T., Malenky, R. K., & Badrian, N. (1984). Sexual behavior of *Pan paniscus*. In R. L. Susman (Ed.), *The pygmy chimpanzee: Evolutionary biology and behavior* (pp. 347-368). New York: Plenum Press.

Thompson-Handler, N. T., Malenky, R. K., & Reinartz, G. E. (1995). *Action plan for Pan paniscus. Report on free ranging populations and proposal for their preservation*. Milwaukee: Zoological Society of Milwaukee County.

Todt, D., Hammerschmidt, K., Ansorge, V., & Fischer, J. (1995). *The vocal behavior of Barbary macaques (Macaca sylvanus): Call features and their performance in infants and adults*. New York: Plenum Press.

Tomasello, M. (1999). Having intentions, understanding intentions, and understanding communicative intentions. In P. D. Zelazo, J. W. Astington, & D. R. Olson (Eds.), *Developing theories of intention: Social understanding and self-control* (pp. 63–75). Mahwah, NJ: Lawrence Erlbaum.

Tomasello, M. (2008). *Origins of human communication*: Cambridge, MA: The MIT Press.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences, 28*(5), 675-735.

Tomasello, M., Carpenter, M., & Liszkowski, U. (2007). A new look at infant pointing. *Child Development, 78*(3), 705-722.

Tomasello, M., & Rakoczy, H. (2003). What makes human cognition unique? From individual to shared to collective intentionality. *Mind & Language, 18*(2), 121-147.

Townsend, S.W. (2009). *Intra-sexual competition and vocal counter-strategies in wild female chimpanzees (Pan troglodytes schweinfurthii).* PhD Thesis, University of St Andrews, UK.

Townsend, S. W., Deschner, T., & Zuberbühler, K. (2008). Female chimpanzees use copulation calls flexibly to prevent social competition. *PLoS One, 3*(6), 2431.

Townsend, S. W., Slocombe, K. E., Emery Thompson, M., & Zuberbühler, K. (2007). Female-led infanticide in wild chimpanzees. *Current Biology, 17*(10), 355.

Tuomi, J., Agrell, J., & Mappes, T. (1997). On the evolutionary stability of female infanticide. *Behavioral Ecology and Sociobiology, 40*(4), 227-233.

Vallet, E., Beme, I., & Kreutzer, M. (1998). Two-note syllables in canary songs elicit high levels of sexual display. *Animal Behaviour, 55*(2), 291-297.

van Hooff, J. A. R. A. M. (1973). A structural analysis of the social behaviour of a semi-captive group of chimpanzees. In M. von Cranach & I. Vine (Eds.), *Social communication and movement: Studies of interaction and expression in man and chimpanzee* (pp. 75-162). London & New York: Academic Press.

van Hooff, J. A. R. A. M., & van Schaik, C. P. (1994). Male bonds: Afilliative relationships among nonhuman primate males. *Behaviour, 130, 3*(4), 309-337.

van Hooff, J. A. R. A. M., & Wensing, J.A.B. (1987). Dominance and its behavioral measures in a captive wolf pack. In H. W. Frank (Ed.), *Man and wolf* (pp. 219-252). Dordrecht: Junk Publishers.

van Krunkelsven, E., Dupain, J., van Elsacker, L. , & Verheyen, R. F. (1996). Food calling by captive bonobos (*Pan paniscus). International Journal of Primatology, 17*(2), 207-217.

van Schaik, C. P. (2000). Infanticide by male primates: the sexual selection hypothesis revisited. In C. P. van Schaik & C. H. Janson (Eds.), *Male infanticide and its implications* (pp. 27-60). Cambridge: Cambridge University Press.

van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B. M., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S. & Merrill, M. (2003). Orangutan cultures and the evolution of material culture. *Science, 299,* 102-105.

van Schaik, C. P., & Kappeler, P. M. (1997). Infanticide risk and the evolution of male-female association in primates. *Proceedings of the Royal Society B-Biological Sciences, 264*(1388), 1687.

van Schaik, C. P., van Noordwijk, M., Nunn, C. L . (1999). Sex and social evolution in primates. In: P. C. Lee (Ed.), *Comparative primate socioecology* (pp. 204–240). Cambridge: Cambridge University Press.

Vasey, P. L. (1995). Homosexual behaviour in primates: A review of evidence and theory. *International Journal of Primatology, 16*(2), 173-.

Vervaecke, H., de Vries, H., & van Elsacker, L. (2000a). Dominance and its behavioral measures in a captive group of bonobos (*Pan paniscus*). *International Journal of Primatology, 21*(1), 47-68.

Vervaecke, H., de Vries, H., & van Elsacker, L. (2000b). Function and distribution of coalitions in captive bonobos (*Pan paniscus*). *Primates, 41*(3), 249-265.

Vervaecke, H., Stevens, J., & van Elsacker, L. (2003). Interfering with others: Female-female reproductive competition in *Pan paniscus*. In C. B. Jones (Ed.), *Sexual selection and reproductive competition in primates: New perspectives and directions* (pp. 231-253). New York: Alan R. Liss.

Vervaecke, H., & van Elsacker, L. (2000). Sexual competition in a group of captive bonobo (*Pan paniscus*). *Primates, 41*(1), 109-115.

Viljoen, S. (1977). Factors affecting breeding synchronization in an african bush squirrel (*Paraxerus cepapi cepapi*). *Journal of Reproduction and Fertility, 50*(1), 125-127.

Warkentin, K. J., Keeley, A. T. H., & Hare, J. F. (2001). Repetitive calls of juvenile Richardson's ground squirrels (*Spermophilus richardsonii*) communicate response urgency. *Canadian Journal of Zoology, 79*(4), 569-573.

Watts, D. P. (2002). Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour, 139,* 343-370.

Weir, A., Chappell, J., & Kacelnik, A. (2002). Shaping of hooks in New Caledonian crows. *Science, 297,* 981-983.

Wheeler, B. C. (2009). Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. *Proceedings of the Royal Society B-Biological Sciences, 276*(1669), 3013-3018.

Wheeler, B. C. (2010). Production and perception of situationally variable alarm calls in wild tufted capuchins (*Cebus apella nigritus*). *Behavioral Ecology and Sociobiology, 64*(6), 989-1000.

White, F. J. (1988). Party composition and dynamics in *Pan paniscus*. *International Journal of Primatology, 9*, 179-193.

White, F. J. (1989). Social organization of pygmy chimpanzee. In P. G. Heltne & L. A. Marquardt (Eds.), *Understanding chimpanzees* (pp. 194-207). Cambridge, MA, and London, UK: Harvard University Press in cooperation with the Chicago Academy of Sciences.

White, F. J. (1996). Comparative socio-ecology of *Pan paniscus*. In W.C. McGrew, L.F. Marchandt & T.Nishida (Eds.), *Great ape societies* (pp. 29-41). Cambridge: Cambridge University Press.

White, F. J. (1998). Seasonality and socioecology: The importance of variation in fruit abundance to bonobo sociality. *International Journal of Primatology, 19*(6), 1013-1027.

White, F. J., & Burgman, M. A. (1990). Social-organization of the pygmy chimpanzee (*Pan-Paniscus*): Multivariate-analysis of intracommunity associations. *American Journal of Physical Anthropology, 83*(2), 193-201.

White, F. J., & Lanjouw, A. (1992). Feeding competition in Lomako bonobos: Variation in social cohesion. *Topics in Primatology, 1*, 67-79.

White, F. J., & Wood, K. D. (2007). Female feeding priority in bonobos, *Pan paniscus,* and the question of female dominance. *American Journal of Primatology, 69*(8), 837-850.

White, F. J., & Wrangham, R. W. (1988). Feeding competition and patch cize in the chimpanzee species *Pan-Paniscus* and *Pan-Troglodytes*. *Behaviour, 105*, 148-164.

Whiten, A., & Byrne, R. W. (1988). Tactical deception in primates. *Behavioral and Brain Sciences, 11*(2), 233-273.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C,. E. G., Wrangham, R. W., & Boesch, C. (1999). Cultures in chimpanzees. *Nature, 399*, 682-685.

Wich, S. A., & de Vries, H. (2006). Male monkeys remember which group members have given alarm calls. *Proceedings of the Royal Society B-Biological Sciences, 273*(1587), 735-740.

Wich, S. A., Swartz, K. B., Hardus, M. E., Lameira, A. R., Stromberg, E., & Shumaker, R. W. (2009). A case of spontaneous acquisition of a human sound by an orangutan. *Primates, 50(1),* 56-64.

Wildman, D. E., Uddin, M., Liu, G., Grossman, L. I., & Goodman, M. (2003). Implications of natural selection in shaping 99.4% nonsynonymous DNA identity between humans and chimpanzees: Enlarging genus Homo. *Proceedings of the National Academy of Sciences of the United States of America, 100*(12), 7181.

Wiley, R. H., & Richards, D. G. (1978). Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behavioural. Ecology and. Sociobiology., 3*, 69-94.

Wilkinson, G. S. (2003). Social and vocal complexity in bats. In F. B. M. de Waal, & P. L. Tyack (Eds.), *Animal social complexity: Intelligence, culture, and individualized societies* (pp. 322–341). Cambridge, MA: Harvard University Press.

Wilkinson, G. S., & W. Boughman, J. (1998). Social calls coordinate foraging in greater spear-nosed bats. *Animal Behaviour, 55*(2), 337-350.

Williams, J. M., Pusey, A. E., Carlis, J. V., Farm, B. P., & Goodall, J. (2002). Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. *Animal Behaviour, 63*, 347-360.

Wittig, R. M., Crockford, C., Wikberg, E., Seyfarth, R. M., & Cheney, D. L. (2007). Kin-mediated reconciliation substitutes for direct reconciliation in female baboons. *Proceedings of the Royal Society B-Biological Sciences, 274*(1613), 1109.

Wobber, V., Wrangham, R. W., & Hare, B. (2010). Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees. *Current Biology, 20*(3), 226-230.

Won, Y. J., & Hey, J. (2005). Divergence population genetics of chimpanzees. *Molecular Biology and Evolution, 22*(2), 297-307.

Wrangham, R. W. (1979). Evolution of ape social-systems. *Social Science Information Sur Les Sciences Sociales, 18*(3), 335-368.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour, 75*, 262-299.

Wrangham, R. W. (1985). Chimpanzees. In D. Macdonald (Ed.), *Primates* (pp. 126-131). New York: Torstar Books.

Wrangham, R. W. (1986). Ecology and social relationships in two species of chimpanzees. In D. I. Rubenstein & R. W. Wrangham (Eds.), *Ecological aspects of social evolution: Birds and mammals* (pp. 352-278). Princeton: Princeton University Press.

Wrangham, R. W. (1993). The evolution of sexuality in chimpanzees and bonobos. *Human Nature, 4*(1), 47-79.

Wrangham, R. W. (1999). Evolution of coalitionary killing. *Yearbook of Physical Anthropology* (Vol. 42, pp. 1-30).

Wrangham, R. W. (2002). The cost of sexual attraction: is there a trade-off in female *Pan* between sex appeal and received coercion? In C. Boesch, G. Hohmann, & L. Marchant (Eds.). *Behavioural diversity in chimpanzees and bonobos (*pp. 204–215). Cambridge: Cambridge University Press.

Wrangham, R. W., & Smuts, B. B. (1980). Sex differences in the behavioral ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal for Reproductive Fertility, 28*, 13-31.

Zhao, Q. K. (1993). Sexual behavior of Tibetan macaques at Mt. Emei, China. *Primates, 34*(4), 431-444.

Zuberbühler, K. (2000). Referential labelling in Diana monkeys. *Animal Behaviour, 59*(5), 917-927.

Zuberbühler, K. (2001). Predator-specific alarm calls in Campbell's guenons. *Behavioral Ecology and Sociobiology, 50,* 414-422.

Zuberbühler, K. (2002). A syntactic rule in forest monkey communication. *Animal Behaviour, 63*(2), 293-299.

Zuberbühler, K. (2003). Referential signaling in non-human primates: Cognitive precursors and limitations for the evolution of language. *Advances in the Study of Behavior, 33*, 265-307.

Zuberbühler, K. (2005). The phylogenetic roots of language: Evidence from primate communication and cognition. *Current Directions in Psychological Science, 14*(3), 126-130.

Zuberbühler, K. (2008). Audience effects. *Current Biology, 18*, R189-R190.

Zuberbühler, K. (2009). Survivor signals: The biology and psychology of animal alarm calling. *Advances in the Study of Behavior, Vol 40* (pp. 277-322). San Diego: Elsevier Academic Press Inc.

Zuberbühler, K., Cheney, D. L., & Seyfarth, R. M. (1999b). Conceptual semantics in a nonhuman primate. *Journal of Comparative Psychology, 113*(1), 33-42.

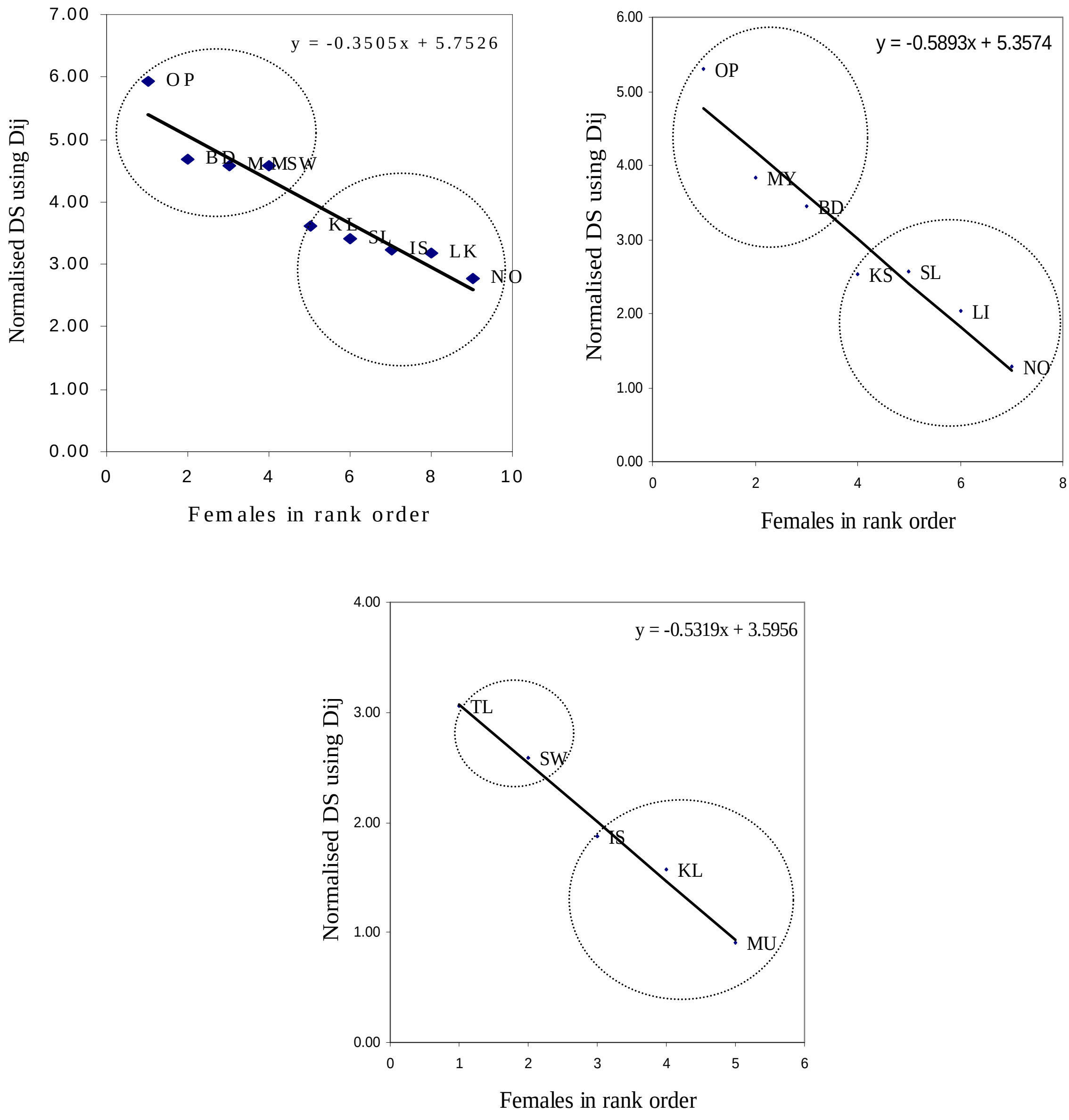
Zuberbühler, K., Jenny, D., & Bshary, R. (1999a). The predator deterrence function of primate alarm calls. *Ethology, 105*(6), 477-490.

Zuberbühler, K., Noe, R., & Seyfarth, R. M. (1997). Diana monkey long-distance calls: Messages for conspecifics and predators. *Animal Behaviour, 53*, 589-604.

Appendices

Appendix I. Results of the analyses of social dominance for the three social groups of bonobos at Lola Ya Bonobo Sanctuary, DR Congo.

For females, my analyses were based upon *N* = 181 cases of one female fleeing from aggression by another (group 1a: *N* = 62; group 1b: *N* = 92; group 2: *N* = 27). Analyses using the Matman matrix analysis programme revealed significantly linear dominance hierarchies in all three groups, headed each by a clear alpha female (appendix I: fig. 1, table 2). Landau's linearity indices h′ (corrected for unknown relationships) were high and significant in all groups, and significantly different from non-linearity where analyses could be conducted (group 1a: h′ = 0.98, $P < .0037$; group 1b: h′ = 0.78, $P < .008$; group 2 consisted of only N=5 females, which violated the analysis requirements, but see appendix fig.1). Based on these linear hierarchies, I then assigned a cardinal rank score to each individual based on normalised David's Scores, corrected for chance. For each group, I divided the hierarchy into two classes, high-ranked and low-ranked females, at the place where there was the clearest divide in dominance scores. This resulted in *N* = 4 high-ranked females and *N* = 5 low-ranked females for group 1a, *N* = 3 high-ranked and *N* = 4 low-ranked females for group 1b; and *N* = 2 high-ranked and *N* = 3 low-ranked females for group 2.



Appendix I: figure 1. Results of simple linear regressions showing the linear dominance hierarchies of females in the three study groups at Lola Ya Bonobo Sanctuary (group 1a: N = 9; group 1b: N = 7, group 2: N = 5), calculated using normalized David's scores based on the dyadic dominance index, corrected for chance. Dashed circles indicate the separation of dominance classes, with individuals in the left hand circle being 'high' rank and individuals in the right-hand circle being 'low' rank.

For males, analyses were based upon a total of *N* = 268 agonistic interactions (group 1a: *N* = 104, groups 1b and 2: both *N* = 82). Analyses revealed significant linearity in only one of the three groups (Landau’s linearity index, corrected for unknown relationships h`: Group 1a = 0.76 (*P* = 0.13); Group 1b = 0.51 (*P* > .05); Group 2 = 0.39, *P* > .05: see appendix I, table 2). The absence of significant linearity amongst males appeared to be mostly due to a high number of unknown relationships, something attributable to the large number of younger, sub-adult males in all groups. In males, whilst I observed reliable numbers of submissive fleeing in response to a cluster of older and more established males, the large group of sub-adult and juvenile males had not begun to engage in proper dominance interactions with one another. Thus, although these males showed clear submissive behaviours towards the small number of more established males, agonistic interactions between them were largely playful, with absence of victim fleeing behaviour. In sum, the dominance hierarchy amongst males could effectively be thought of as a steeply pyramidal at the top, collapsing into a wide base of un-ordered males at the bottom. To account for this, I assigned males to high and low rank classes based on whether they were dominated more than 50% of the males in the group (scored by submissive fleeing). This method amounted to *N* = 4 high-ranked males in group 1a, *N* = 1 high-ranked male in group 1b and *N* = 3 high-ranked males in group 2b. The remaining males were all classed as low-ranking (group 1a: *N* = 5; group 1b: *N* = 8; group 2: *N* = 8). See table 1 below.

Appendix I: table 1. Table of males and their dominance classes (high = H, low = L) for the three social groups at Lola Ya Bonobo Sanctuary, DR Congo.

Group 1		Group 1b		Group 2	
Individual	Rank	Individual	Rank	Individual	Rank
TT	H	MN	H	MK	H
MN	H	KW	L	KZ	H
KW	H	MA	L	FZ	H
BN	H	MD	L	TB	L
MI	L	DL	L	LM	L
MA	L	BO	L	AP	L
KD	L	KG	L	BL	L
KG	L	LZ	L	MB	L
IB	L	VG	L	IB	L
				YL	L
				BY	L

Appendix I: table 2. Results from Matman tests for linearity of dominance hierarchies calculated for the three bonobo groups at Lola Ya Bonobo Sanctuary.

	Females			Males		
	Group 1a (*N* = 9)	Group 1b (*N* = 7)	Group 2 (*N* = 5)	Group 1b (*N* = 9)	Group 1b (*N*=9)	Group 2 (*N* = 11)
Matrix total	62	92	27	104	82	82
h′	0.98	0.78	0.85	0.76	0.51	0.39
p (1-tailed)	0.0037	0.008	0.23	.013	0.14	0.19
DCI	0.97	1	0.93	0.98	0.97	0.97
Total N dyads	21	36	10	36	36	55
% unknown relationships	9.52	33.3	20	22.2	63.89	67.27
% 1-way relationships	85.71	66.67	70	75.0	33.3	30.91
% 2-way relationships	4.76	0	10	2.78	2.78	1.82
% tied relationships	0	0	0	0	0	0

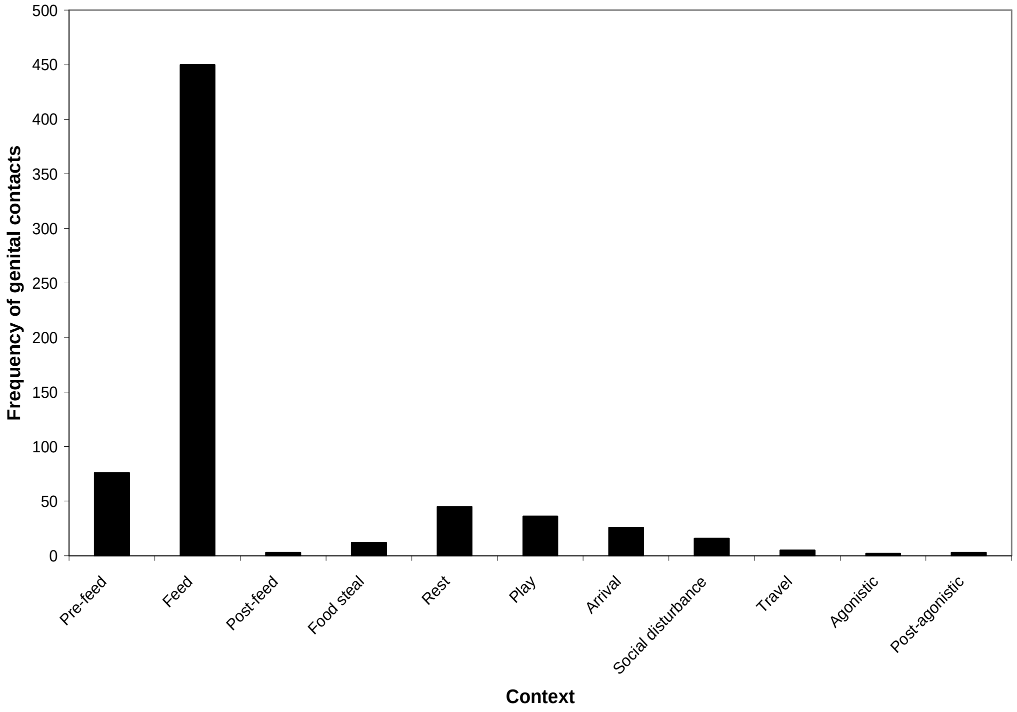
Appendix II. Results of food preference tests conducted at Twycross Zoo, UK. Scores represent the percentage that the given food was chosen other food types

Subgroup A (call producers)										
	KK		KT		MR		BY		BK	
Food	Food rank	Preference score	Food rank	Score	Food rank	Score	Food rank	Score	Food rank	Score
Kiwi	1	65.0	1	67.5	1	67.5	1	70.0	1	70
Banana	1	65.0	2	62.5	2	62.5	2	60.0	2	60
Orange	2	45.0	3	50.0	3	47.5	3	47.5	3	45
Apple	2	45.0	4	40.0	4	42.5	4	42.5	3	45
Subgroup B (call receivers)										
	DT		KH		CK		LU		GM	
Food	Food rank	Preference score	Food rank	Score	Food rank	Score	Food rank	Score	Food rank	Score
Kiwi	1	70.0	1	70.0	1	70.0	1	70.0	1	70
Banana	2	60.0	2	60.0	2	60.0	2	60.0	2	60
Orange	3	50.0	3	47.5	3	47.5	3	50.0	3	47.5
Apple	4	40.0	4	42.5	4	42.5	4	40.0	4	42.5

Appendix III. Results of Generalised Linear Models for the (a) time and (b) number of visits to the apple and kiwi fields for *N* = 4 subjects in the playback experiment, conducted at Twycross Zoo, UK.

a	**Time spent**			
ID	Likelihood ratio χ^2	Wald χ^2: Playback	Wald χ^2: Site	Wald $\chi^{2:}$ Interaction
GM	328.523, df =5, *P* < .001	98.405, df = 2, *P* < .001	29.064, df =1 *P* < .001	114.352, df =1, *P* < .001
CK	259.036, df = 5, *P* < .001	31. 525, df = 2, *P < .001*	31.976, df = 1, *P < .001*	59.946, df = 1, *P < .001*
LU	295.858, df = 5, *P < .001*	53.921, df = 2, *P < .001*	9.088, df = 1, *P* = .003	134.678, df = 1, *P < .001*
KH	305.699, df = 5, *P* < .001	81.021, df = 2, *P* < .001	8.079, df = 1, *P* = .004	47.834, df = 1, *P* < .001
b	**Number of visits**			
GM	18.471, df = 5 *P* = .002	1.319, df = 2 *P* > .05	0.447, df =1 *P* > .05	2.984, df =1 *P* = .084
CK	16.801, df = 5 *P* = .005	2.951, df = 2 *P* > .05	3.545, df =1 *P* = .060	1.619, df = 1 *P* = .203
LU	8.800, df = 5, P > .05	3.779, df =2, P > .05	0.038, df =1 P > .05	3.346, df =1 *P* > .05
KH	13.701, df = 5, *P* =.018	1.446, df = 2 *P* > .-5	0.012, df =1, *P* > .05	2.669, df = 1, *P* > .05

Appendix IV. Frequency of female-female genital contacts in different behavioural contexts (for *N* =14 females, total *N* = 674 genital contacts).



Appendix V. Scatter-plot showing the relationship between a female's dominance rank and copulation call production during female genital contacts. Spearman's correlation: $r_s = -0.670$, $N = 21$, $P = .001$.