INTRA-SEXUAL COMPETITION AND VOCAL COUNTER-STRATEGIES IN WILD FEMALE CHIMPANZEES (PAN TROGLODYTES SCHWEINFURTHII)

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Intra-sexual competition and vocal counter-strategies in wild female chimpanzees (Pan troglodytes schweinfurthii)

Simon W. Townsend

Dissertation submitted to the University of St Andrews
for the degree of Doctor of Philosophy

August 2008

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Abstract

A growing body of behavioural data is beginning to show that, like their male counterparts, female chimpanzees can be competitive and aggressive, particularly when resources come under pressure. These observations are especially surprising because, for a long time, females were simply considered passive pawns of male social manoeuvrings. While we are beginning to understand the complexities surrounding female chimpanzee group living, exactly how females manage these social pressures is unclear. In this thesis I address this by focusing on female competition in wild chimpanzees and the importance of vocal counter-strategies.

I examined two commonly produced female vocalisations: copulation calls and victim screams from chimpanzees (Pan troglodytes schweinfurthii) in the Budongo Forest, Uganda. My results regarding the production and acoustic structure of copulation calls suggests that these vocalisations play a crucial role in the lives of female chimpanzees, dissipating the risks associated with female competition.

During aggression, chimpanzee females commonly produce victim screams and these calls have been shown to vary systematically with the severity of aggression experienced. A playback experiment showed that victim screams are meaningful to females and that listeners do not just respond to the acoustically most salient signals in their environment. Females may use this information to keep track of out-of-sight agonistic interactions and make appropriate social decisions regarding whether to avoid an ensuing attack.

Taken together, I propose that vocalisations may represent important behavioural counter-strategies, enabling females to navigate successfully through their socially intricate world.

Chapter One: General Introduction

Summary

In this first chapter I review what we know about, and address the gaps in our understanding of, female competition in primates. I argue that female competition plays a significant, potentially dangerous role in the day-to-day lives of female chimpanzees and begin to assess how vocalisations may help females manage this little studied social pressure. I focus particularly on copulation calls and scream vocalisations from both the production and comprehension perspective. Finally, I conclude by hypothesising that females may use vocalisations in strategic ways to operate successfully through their socially intricate environment.

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Introduction

The myth of the passive female has plagued primate behaviour studies for decades. In comparison to their male counterparts, females were generally considered peaceful, less gregarious, and solely preoccupied with raising their offspring. The notion that females compete with one another was consistently ignored.

The bias towards studying male competition was bolstered by the assumption that all female primates are uniformly successful at reproduction, because “all females breed” (Wrangham, 1997). In contrast, males can always increase their reproductive success through extra matings (Trivers, 1972; Kahlenberg, 2006). However, cracks in this assumption began to appear with the observations that certain female monkey species show highly variable levels of breeding success, correlating with the individuals life-long rank in the female hierarchy. In essence, higher-ranking females do better (Hrdy and Williams, 1983). Since this discovery, female-female competition in non-human primates has become a major research area, with particular focus on the ways in which females compete and the outcome of such competition.

In this thesis, I look at female-female competition in a community of wild chimpanzees (<u>Pan troglodytes scweinfurthii</u>). Our understanding of the extent to which chimpanzees compete in the wild, the resources they compete over, and the importance of competition in the daily lives of female chimpanzees is still in its infancy in comparison to other primate species. I intend to address this issue, primarily from a vocal perspective.

Studying the vocal systems of non-human primates can give us vital insights into the intricacies of their social lives, allowing us to understand the importance of social processes that would otherwise be impossible to identify (Cheney and Seyfarth, 2007). Combining these two areas of study may elucidate what kinds of pressures female chimpanzees are exposed to, and what strategies they may employ to alleviate such pressures.

Background

Origins of female competition and its effects on female social relationships

The relationship between ecology and social organisation in non-human primates has been studied for over thirty years. These socio-ecological models predominantly focused on the effects of group size on food acquisition and the role of diet on home-range size, group size and population density (Clutton Brock and Harvey, 1977; Koenig, 2002). However, emerging work on female-bonded primates shifted the focus to female-female social relationships (Wrangham, 1979; 1980) and understanding the evolutionary processes driving taxonomic variation in these relationships.

The most popular theoretical model for explaining the evolution of female social relationships and the network of behavioural interactions primarily invokes ecological factors (Wrangham, 1980; Sterck et al., 1997). This socio-ecological framework infers that the pressures associated with predation risk necessitate gregariousness in diurnal non-human primates, which ultimately results in intra- and potentially inter-group competition for resources among females. The majority of the non-human primate literature to date has focused on competition for food, as this is often more easily quantifiable (Wrangham, 1987). Nevertheless, it is highly likely that females may compete for other resources, such as good quality nesting sites and potentially male mating partners.

Scramble or contest?

Competition will not generally occur if resources are so abundant that population growth is not limited (Sterck, 1997). However, as soon as access to resources begins to limit female reproductive output, competition is expected. The nature and severity of these competitive social relationships depends on the overall abundance and distribution of resources within a habitat (Van Schaik and Van Noordwijk, 1988; Janson and Van Schaik, 1988; Isbell et al., 1991).

Scramble competition predominates when limiting resources are either of a low value, highly dispersed or in very large patches relative to the size of the group. In these instances, individuals lose access to resources as other conspecifics have already found and used them. Contest competition on the other hand occurs when resources are monopolisable and, due to competitive superiority, certain individuals can systematically exclude others from the limiting resource, obtaining more of the resource themselves and thereby increasing their fitness levels (Wrangham, 1980).

When scramble competition is the default competitive mode, no overt agonistic interactions over access to resources are expected: all individuals within the group obtain roughly equal shares. In contrast, contest competition does involve an agonistic component and the strength of this competition is thought to explain variation in female social relationships. For example, the potential for aggressive exclusion of resources is likely to select for well-defined female dominance relationships, often with stable linear hierarchies (Van Schaik, 1989; Sterck et al., 1997; Koenig, 2002; Kahlenberg et al., in press a). These relationships can be maintained by long-term alliances between related females (Chapais, 1992) and also mutualistic coalitions with non-relatives. This need for strong female alliances is thought to be one reason why many female primates remain in their natal community groups whilst males transfer (Sterck et al., 1997).

Empirical evidence for female contest competition now exists for numerous primate species: dominants consistently outperform subordinates when resources become scarce (Gouzoules et al., 1982; Harcourt, 1987; Bercovitch and Strum, 1993; Ellis, 1995; Altmann and Alberts, 2003; Creel 2005). This competitive regime is associated with female-aggression and philopatry, and is maintained by alliances among female kin (Emery Thompson et al., 2007).

Despite this growing evidence for female competition, there have been a few female primate holdouts, most notably the chimpanzee (Wrangham, 1997). Despite amassing almost 180 years of research on chimpanzee behaviour and ecology from 7 different field sites (Cote d'Ivoire: Tai; Guinea: Bossou; Tanzania: Mahale, Gombe; Uganda: Budongo, Kanyawara, Ngogo: Muller and Mitani, 2005), our knowledge of the nature of competition between females is limited. Henceforth, I will therefore focus on female competition in chimpanzees, beginning with a brief overview of the study species and its general socio-ecology.

Chimpanzee social structure and ecology

Chimpanzees form large, fluid social groups called “communities”. These can range in size from 20 to 160 individuals (Sugiyama and Koman, 1979b) and are distributed across Africa's equatorial rainforests and woodlands. Within these communities, chimpanzees associate on a fission-fusion basis (Nishida, 1968; Kummer, 1971; Goodall, 1986) where larger groups split into smaller “parties” which can vary in composition and size (Reynolds, 2005).

In contrast to most cercopithecine monkey species, male chimpanzees are philopatric, residing in their natal communities throughout their lives. Females are the dispersing sex, immigrating into new communities when sexually mature (Goodall, 1986; Nishida and Hiraiwa-Hasegawa, 1987; Boesch and Boesch Achermann, 2000; Reynolds, 2005). Females range within unevenly dispersed individual core areas (Wrangham and Smuts, 1980; Williams et al., 2004; Emery Thompson et al., 2007; Kahlenberg et al., in press a). Non-oestrus females spend the majority of their time either in same-sex “mothering” parties (Reynolds, 2005) or alone with their dependent offspring (Goodall, 1986), although the degree of female gregariousness does differ between populations (Wrangham et al., 1992; Boesch, 1996; Doran, 1997; Pepper et al., 1999; Wrangham, 2000; Emery Thompson and Wrangham, in press; Kahlenberg, 2006)

Male chimpanzees are considered more gregarious than females. There is a clear, linear dominance hierarchy among the males of any one community, and because of the potential reproductive and feeding benefits associated with high rank, males spend considerable time maintaining or striving for higher rank. This can be done through grooming, dominance displays, agonistic interactions and alliance formations (Goodall, 1986). Males are territorial, meaning they patrol a large home range incorporating the smaller core areas of multiple females (Chapman and Wrangham, 1993). Inter-community encounters between males may occur during patrols, and are often highly aggressive or even lethal (Goodall, 1986;Wilson et al., 2001; Wilson and Wrangham, 2003).

Chimpanzees are primarily frugivorous (Wrangham et al., 1998; Newton-Fisher, 1999a; Bates, 2005), but they are known to also consume young leaves and terrestrial herb vegetation (Boesch and Boesch Achermann, 2000). Their diet may be sporadically supplemented with meat obtained from hunting, although the frequency at which hunting occurs differs substantially between communities (Guinea Bossou: 5 hunts in 8 years (Sugiyama and Koman, 1987), Tai chimpanzees: 267 hunts in 11 years (Boesch and Boesch Achermann, 2000). Chimpanzees are known to use tools to obtain various nutritious food types such as nuts (Sugiyama and Koman, 1979a; Boesch and Boesch, 1984; Hannah and McGrew, 1987), honey (Nishida and Hiraiwa, 1982) and insects (Goodall, 1964; Nishida, 1973; McGrew, 1974). As with hunting behaviour, the occurrence and frequency of such tool use behaviour varies across chimpanzee study sites and these observations have lead to tool use practices being described as cultural traits (Whiten et al., 1999; Whiten et al., 2001).

Female-female competition in wild chimpanzees

The subject of competition in female chimpanzees is not well understood. Females appear to show high variation in fitness, but this occurs seemingly in the absence of female-female aggression, philopatry or alliances. Several studies on Gombe chimpanzees show that dominant females reproduced more quickly, had higher infant survival and more rapidly maturing daughters than subordinates (Pusey et al., 1997). Furthermore, high-ranking females have been shown to spend less time foraging and have narrower, higher-quality diets in comparison to low-ranked females (Greengrass, 2005; Murray et al., 2006; Kahlenberg et al., in press a). These fitness advantages for high-ranking females suggest female-female competition for resources has a significant contest component in chimpanzees (Kahlenberg et al., in press b). The social relationships between female chimpanzees, however, do not match those predicted by socio-ecological models. Firstly, whilst some females are known to dominate others (Goodall, 1986; Nishida, 1989; Wrangham et al., 1992; Fawcett, 2000; Wittig and Boesch, 2003) dominance interactions are generally rare. In fact, one study on the Kanyawara community of chimpanzees in Uganda recorded no aggressive interactions between females and only a small number of pant grunts in over 680 hours of observations (Muller, 2002). Similarly, in over 22 years of data collected by the Gombe study, some female dyads were not seen to have a single dominance interaction (Pusey et al., 1997; Emery Thompson et al., 2007). Secondly, due to the social organisation of chimpanzee communities, whereby males remain in their natal communities and females transfer at adolescence, adult females are not surrounded by kin (Goodall, 1986) and do not generally form alliances in their new communities (Emery Thompson et al., 2007). It is these observations of the lack of female sociality that have caused some to question the relevance and importance of female competition and dominance for chimpanzees (de Waal, 1982; Baker and Smuts, 1994; Sterck et al., 1997).

Recent observations of female competition

Recent work from a number of chimpanzee communities across Africa suggest it is erroneous to dismiss female competition, instead implying that it is an important component of chimpanzee social lives.

Females residing in the Kanyawara chimpanzee community in Uganda show similar variation in fitness and rank as identified at Gombe (Pusey et al., 1997) and this has been linked to differential use of the community home range. Females were found to form distinct "core areas", with certain core areas having greater access to preferred fruit trees than others (Emery Thompson et al., 2007). Females occupying the richer core areas subsequently demonstrated heightened ovarian hormone levels and hence improved reproductive success, as indexed by inter-birth intervals and infant survivorship. Kahlenberg et al., (in press a) further addressed this relationship, focusing on how females manage to occupy preferred areas. Their results suggest that Kanyawara females do indeed compete directly over long-term access to resources, which are, in this case, specifically core areas containing a higher density of preferred foods (Kahlenberg et al., in press a). Whilst such competition had been previously hypothesised (Pusey et al., 1997), this was the first systematic evidence for direct intra-group female competition in chimpanzees.

This contest competition for resources in Kanyawara occurred under specific socio-ecological conditions. Competition was particularly intense in the months following the immigration of new females into the community. During these times, and most obviously when multiple immigrants were present, rates of aggression between females were almost four times higher than in the absence of such immigration. Whilst this increase in aggression was primarily due to high-ranking residents directing aggression towards immigrants, there were also simultaneous increases in aggression between longer-term residents, often of equal severity. Kahlenberg et al., (in press a) hypothesise that these socio-ecological conditions intensify competition as it essentially presents a challenge to the resource access of resident females occupying the attractive core areas within these regions. At Gombe, increases in female density have also been shown to negatively correlate with reproductive success (Williams et al., 2004). Therefore, by aggressively preventing new females from accessing resources that may overlap with their own, or from putting heightened pressure on pre-existing limited resource supplies, resident females could gain significant fitness advantages (Kahlenberg et al., in press a).

Resources in competition?

So far, the majority of research addressing female competition within primate species and other animal taxa focuses on resources considered to be related directly to the female's or its offspring's own survival. That is, only resources such as food patches, nest sites and safety from predators (Palmobit et al., 2001). The importance of female-female competition for males remains "a vast area of ignorance" (Berglund et al., 1993) and exactly how the competitive interactions between females affects access to this resource remains unknown (Breiehaen and Slagsvold, 1988).

Females are expected to compete for mating access when either the sex ratio is heavily skewed, such that there are more females for each breeding male (Vincent et al., 1992), or if males vary in quality and their ability to provide a limiting resource.

Recent research in species across the animal kingdom has shown that in low-male, multi-female promiscuous mating systems, the resources males can offer, such as their sperm for example, can become a limiting resource. For example, dominant rams (Ovis aries) have been shown to have reduced paternity success due to multiple matings with different females (Preston et al., 2001). Such promiscuous mating is thought to reduce sperm quality and quantity, which subsequently leads to diminished likelihood of fertilisation. Similar sperm limitation has also been suggested in other animal species (e.g. nematodes, (C. elegans), [Van Voorhies, 1992]; moths, (Lepidoptera Pyralidae), [Gage and Cook, 1994]), and non-human primates are no exception. For example, in gelada baboons (Theropithecus gelada) forming one-male breeding units, Dunbar and Sharman (1983) reported an inverse correlation between birth rates and the number of breeding females per male, whilst in captive hamadryas baboons (Papio Hamadryas), also forming one-male breeding units, the number of females in oestrus at any one time negatively correlates with the probability of conception (Zinner et al., 1994). Among chimpanzees, sperm depletion resulting in female-female competition for mating partners is theoretically possible (Matsumoto-Oda et al., 2007). Firstly, males copulate on average four times a day (Short, 1981) and physiological testing in captive chimpanzees has shown that sperm quantity systematically decreases following consecutive copulations (Marson et al., 1989). Secondly, the fact that females immigrate means that during periods of high-immigration (Kahlenberg et al., in press b) the sex-ratio is female-skewed, such that in some cases there can be as many as three adult females for one adult male (see chapter three).

Given that females can cycle simultaneously (Goodall, 1986; Stumpf and Boesch, 2005; Deschner et al., 2003, 2004) access to male partners may therefore be restricted at times.

These socio-physiological factors suggest that sperm in chimpanzee mating systems can become limited. Therefore, as in other animal species, female chimpanzees may compete over this resource, potentially aggressively (Berglund et al., 1993; Rosvall, 2008). Exactly what form the aggression can take is probably dependent on the strength of the competition occurring, though strategies may involve intense physical harassment (Wasser and Barash, 1983) or preventing access to mates (Frame et al., 1979; Rood, 1980; Berglund et al., 1993; Rosvall, 2008).

Females may also compete aggressively not only over male sperm, but also over the males themselves and the potential "help" they can offer. In chacma baboons (Papio ursinus) for example, females have been seen to compete directly for access to particular male "friends" (Palombit et al., 1997, 2001; Palombit 2000). Competition for males differs both proximately and functionally from competition among cycling females for access to sperm. In the former case, females are contending for social bonds with males that may potentially result in some form of post-natal service for the female involved (Palombit et al., 2001). In chimpanzees, due to the "role-reversed" sex ratio, males themselves may be an important resource that can be competed over, in addition to their sperm, but in what context could males provide a post-natal service or support?

Competition for male support

Intra-individual variation in lifetime reproductive success can be explained primarily by offspring mortality (Clutton-Brock et al., 1988) and therefore a male's ability to offer offspring protection is likely to be a very attractive trait for females (Palombit et al., 2001). In birds, males can enhance offspring survivorship by provisioning food or incubating eggs over gestation (Clutton-Brock, 1991); however in mammals alternative forms of post-natal investment predominate (Palombit et al., 2001). Specifically, males may be capable of providing support against infanticide.

Infanticide appears to be a sexually selected strategy that accelerates the return to fertility in lactating females (Struhsaker and Leland, 1985; Pusey and Packer, 1994). This mostly male act (Tuomi et al., 1997) benefits the perpetrator as he increases the chance to sire his own offspring and hence improves his reproductive success. Infanticide is a pervasive feature of most primate societies, including chimpanzees (Hausfater and Hrdy, 1984; Goodall, 1986, see chapter three). Therefore, protection against infanticide may be one attractive service provided by community males.

Chimpanzee males may also be valuable to females for the support they offer during more general agonistic interactions. High-ranking males provide a vital peacekeeping service during intra-community male-female interactions (Goodall, 1986; Boesch and Boesch Achermann, 2000), and, as recent research shows, during female-female aggression (Pusey et al., in press; Kahlenberg et al., in press b). Male chimpanzees therefore provide at least two important forms of post-natal service: protection against infanticide and day-to-day protection against male and female aggression. Given the potential fitness benefits, it is plausible that female chimpanzees compete with one another for access to protector males.

Counter-strategies against female competition

It is now clear that female competition, and the potential aggression that can accompany it, is a considerable risk to female chimpanzees. It is therefore highly likely that selection would favour the evolution of counter-strategies available to less competitively able females, such as low-ranking or immigrant individuals (Pusey et al., in press; Kahlenberg et al., in press b). Research from different mammal species indicates that behavioural counter-strategies are often employed to avoid conflict associated with group living. For example, some female primates are known to mate promiscuously with multiple males in order to confuse paternity (Hrdy, 1979; Van Schaik et al., 2004) and lions (Panthera leo) and hyenas (Crocuta crocuta) (Packer et al., 2001; East et al., 1989) have been shown to avoid the core of the group around parturition – both behavioural counter-strategies against infanticide. However, exactly how female chimpanzees manage the risks associated with intra-sexual competition has, until recently, remained unclear. Kahlenberg et al., (in press a,b) addressed this question specifically by analysing almost 11 years of long-term data from the Kanyawara chimpanzee community. Their analyses have shown that in the face of heightened female aggression, immigrants associate more with adult males and sometimes with other immigrant females. These systematic results mirror more anecdotal findings at other research sites that indicate females seek out the protection of males. Observations at Gombe (Pusey, 1980) and Mahale (Nishida, 1989) both suggest that nulliparous females spend more time with males in comparison to other age-sex classes. From this, Kahlenberg et al., (in press b) suggest that one possible counter-strategy to dissipate the aggression that parallels female competition is to take advantage of male protective services.

The role of vocalisations

Chimpanzees can manage the pressures of female competition using behavioural counter-strategies and vocalisations are likely to play a key role in this. Vocalisations are possibly the most pervasive aspect of chimpanzee life, being produced in almost every social context (Marler and Tenaza, 1977; Goodall, 1986). Furthermore, the dense nature of the forest habitat and the fission fusion nature of the chimpanzee social system mean that vocalisations are probably the most important communicative tool for chimpanzees. Despite their importance and ubiquity, we still know very little regarding the functions vocalisations play in the daily lives of chimpanzees (Slocombe, 2005). This is particularly surprising given the vital insights vocalisations have given us into the social intricacies of other primate species (Cheney and Seyfarth, 1990; 2007; Gouzoules et al., 1986). For example, in baboons, vocalisations represent important social tools, inciting aggression, mediating reconciliation (Wittig et al., 2007), challenging dominance status (Kitchen et al., 2003) and stimulating travel (Rendall et al., 2000). Vocalisations have even been highlighted with facilitating the evolution of complex sociality. Dunbar (1993; 2003) argues that grooming in primates is essential to maintain social bonds and group cohesion. Due to time constraints some social relationships could not be continually serviced through grooming, and consequently could break down. Vocalisations however would allow contact with other group members in the absence of mechanical interaction, and thus maintain social bonds. Complex vocal systems, therefore, may have evolved as a cheap form of “social grooming”, preventing larger social groups from breaking down. McComb and Semple (2005) have provided further evidence for this hypothesis. Their phylogenetic meta-analyses of primate vocal repertoires and grooming time (their measure of sociality) show a clear correlation between vocal and social complexity. Whilst they point out the direction of causality cannot be inferred from correlation analyses, their results are consistent with the hypothesis that the vocal communication system and social complexity are intimately related.

Vocalisations also represent an important medium from which to assess the underlying cognitive sophistication of animals. When animals vocalise, these calls can be used as objective data concerning their "thoughts" and motivations (Griffin, 1991). Hence, focusing on vocalisations could open a previously closed window into the mind of the competitive female chimpanzee.

In this thesis I aim to address these issues in chimpanzees and make progress towards filling the gaps in our knowledge. Specifically, I will ask the questions: how extreme is female-female competition and how do females use vocalisations to manage the risks and pressures associated with such competition? This research will give us a better idea regarding the complexities of female social life and the potential strategies they employ to navigate successfully through their complex social worlds.

The chimpanzee vocal system

Animal vocal systems can vary on a continuum from discretely organised to highly graded, in terms of their acoustic structure. Rhesus macaques were one of the first primate species shown to utilise a graded system with grading between and variation within call types (Rowell and Hinde, 1962). Since then, numerous other primates, including chimpanzees, have been shown to possess a graded vocal repertoire (Red Colobus monkeys, Procolobus badius (Marler, 1970); Baboons, Papio cynocephalus ursinus, (Fischer et al., 2001); Chimpanzees Pan troglodytes schweinfurthii, (Marler, 1976; Marler and Tenaza, 1977). Graded vocal systems differ from discrete systems primarily in the amount of information they can potentially encode. According to Marler (1976), if there is a highly ordered relationship between signal grading and context of production, graded systems can potentially transmit vast quantities of information and hence the scope for vocal complexity is much greater. However, the extremely graded nature of the chimpanzee vocal system has made it very difficult to conduct systematic investigations and to construct a clear vocal repertoire.

The repertoire

Reynolds (1965) identified roughly 12 different call types, a number which was then doubled by Goodall (1968) who isolated 24 specific call variants. These estimations were primarily based on how the call sounded and the context in which it was produced, but lacked a quantitative basis. More objective call categorisation employs mathematical representations of acoustic distinctiveness, which is subsequently put in relation with the context of production (Slocombe, 2005). Marler and Tenaza (1977) undertook this rather significant challenge, identifying over a dozen different call variants – a finding which has recently been confirmed by Slocombe (2005), suggesting this final estimation is robust (see table 1.1 for list of call types)

Table 1.1: The 14 different chimpanzee call variants and their contexts of production (adapted from Marler and Tenaza, 1977 and Slocombe, 2005).

Call type	Context
Pant hoot	Travel, feeding, resting
Pant grunt	Greeting
Laughter	Play
Squeak	Copulation
Scream (incl. SOS screams)	Aggression
Whimper	Conflict/begging
Barks	Social excitement/aggression
Waa bark	Danger
Cough	Stop undesirable behaviour
Rough grunt	Food
Pant	Greeting
Grunt	Resting
Wraa	Not clear
Huu	Unusual events

Female vocalisations

Female chimpanzees, on the whole, are less gregarious than adult males. As previously described, in many populations females spend the majority of their time in small, same-sex parties or alone, only accompanied by their dependent offspring. Due to their less social nature, female chimpanzees do not vocalise at rates comparable to males (Goodall, 1986; Slocombe, unpublished data) and as a consequence, there is a restriction over which call types could be investigated in this thesis. Therefore, I primarily focus on the more common vocalisations produced during evolutionary important events: the female-specific and reproductively important copulation call, and the socially valuable victim scream produced during aggression. As the thesis progresses it will become apparent what role each of these two vocalisations has in helping females manage social pressures.

Female copulation calls

Across the animal kingdom, mating events are accompanied by vocal signals. These so called “copulation calls” have intrigued generations of evolutionary biologists, with much debate surrounding the proximate and ultimate functions of this conspicuous behaviour. Copulation calls are defined as acoustically distinct vocalisations produced prior to, during or just after copulations (Semple, 1998b). Because of their ubiquitous occurrence and often complex acoustic structure, much research has focused on these vocalisations in the primate taxa (Hauser, 1996). Explanations for their pervasiveness range from calls just being incidental by-products of the copulatory act, to calls synchronising orgasms between the mating partners (Hamilton and Arrowood, 1978; see table 1.2). In fact, to date 13 different functional hypotheses have been put forward (see Pradhan et al., 2006 for more details), all of which share a common theme: copulation calls are sexually selected traits that benefit the calling female's reproductive success.

Despite the wide range of explanations, some traditional hypotheses still seem preferred over others. One of the most commonly invoked explanations suggests that these acoustic traits function to alert males to the receptive condition of the female, subsequently inciting competition amongst the males (Hauser, 1990; O'Connell and Cowlishaw; 1994; Henzi, 1996; Semple, 2001; Semple et al., 2002). Competition can occur directly between males, such that the female ends up with the most dominant mating partner, or at a smaller though no less important scale, between sperm. Ultimately the female benefits by getting the best sperm from the best male.

Table 1.2: The functional hypotheses so far presented to explain the adaptive function of primate copulation calls (adapted from Pradhan et al., 2006).

Hypothesis	**Function**	**Reference**
1	Orgasm-like reaction and non-adaptive byproduct of the copulation	Hamilton and Arrowood, 1978
2	Non-adaptive maintained by phylogenetic inertia	Henzi, 1996
3	Self stimulate ovulation	Cheng, 1992
4	Synchronize orgasm	Hamilton and Arrowood, 1978
5	Strengthen the pair bond	Hamilton and Arrowood, 1978
6	Advertise fertility	Aich, 1990
7	Advertise sexual motivation	Gouzoules et al., 1998
8	Promote breeding synchrony between females	Viljoen, 1977
9	Incite male-male competition	Cox and Le Boeuf, 1977; Hauser, 1990
10	Incite sperm competition	O'Connell and Cowlishaw, 1994
11	Incite paternity confusion and protection from infanticide	O'Connell and Cowlishaw, 1994
12	Announce paternity certainty to promote paternal investment	Henzi, 1996
13	Promote mate guarding by preferred mating partners	Maestripieri and Roney, 2005

The majority of the 13 hypotheses put forward to explain the adaptive significance of primate copulation calls, however, have originated from research on monkey species. Only one study to date has assessed these ubiquitous vocalisations in any ape species (Hauser, 1990). This is surprising given the crucial role that apes can play in understanding the adaptive significance and evolution of human behaviour, from a phylogenetic perspective (Tomasello, in press). The results of Hauser's (1990) brief study on chimpanzee copulation calls are inconclusive. From a total of 64 copulations observed over one month, Hauser found females called more with "established" adult males than "young adult" males. Furthermore, females were more likely to receive aggression following vocal copulations with young adult males than established adult males, although this relationship was not significant. Hauser loosely argues that, at some level, female copulation calls may operate to incite competition amongst males, just as they are thought to in other primate species.

Yet, male-male competition is only one aspect of a large spectrum of social processes that take place in the reproductive context. As previously outlined, female-female competitive interactions over resources (including food and males) and the aggression that accompanies it are now known to be a pervasive and threatening feature of non-human primates, including chimpanzees (Koenig, 2002; Kahlenberg, 2006). Female chimpanzees therefore play a more influential role in the lives of other females than was formerly assumed (Pusey et al., 1997; in press; Kahlenberg et al., in press a). As competition can be detrimental to females, and copulation calls may play some role in maximising an individual female's fitness, it is entirely plausible that female competition may have had an additional impact on the evolution of this reproductively important vocal behaviour.

To address this question, one avenue involves focusing purely on the contexts of copulation call production, as is normally done in studies of this type. However, it would also be valuable to elucidate what additional information is encoded within these calls.

Information content

Research on numerous animal taxa has shown vocalisations can provide listeners with a variety of information sets. For instance, calls can allude to the identity and size of the caller, their maturity, sexual state and condition (Clutton-Brock and Albon, 1979; Reby et al., 2005). Calls can also transmit information regarding the effective state of the caller (Morton, 1977) and their subsequent behaviour (Smith, 1977). For primate copulation calls the following studies have been conducted:

In yellow baboons (Papio cynocephalus ursinus) copulation calls have been shown to vary systematically with the rank of the male mating partner and her identity (Semple, 2001; Semple et al., 2002). Semple et al., (2002) also found that calls varied with the female's proximity to ovulation, e.g. how fertile she was. However, this finding was inferred solely from the size of the sexual swelling (Semple et al., 2002). It has now been shown that the temporal relation between swelling size and proximity to ovulation (when the female is fertile) is not an accurate indicator of reproductive state in primates, (Deschner et al., 2003) and hence this result should be viewed cautiously.

More recently, barbary macaque copulation calls have been shown to acoustically vary primarily with occurrence of ejaculation (Pfefferle et al., 2008a). In this detailed analysis of calling behaviour, Pfefferle et al., (2008a) controlled for numerous confounding variables such as male rank and proximity to ovulation. This time ovulation was systematically elucidated from fecal and urinary hormone analyses (Deschner et al., 2003; 2004; Heistermann et al., 2007), but was found to have no explanatory effect. Subsequent playbacks of these acoustically distinct ejaculatory and non-ejaculatory calls to male subjects suggest that the information content of these calls is indeed salient to listening males, potentially allowing them to make behavioural decisions about when to next copulate (Pfefferle et al., 2008b; see also Semple and McComb, 2000).

No study so far has addressed the acoustic structure of any chimpanzee, or indeed ape, mating vocalisations, despite advances in our understanding of the potential informational content of other call types. For example, chimpanzee pant hoots have been suggested to convey information regarding the behavioural state of the caller (e.g. travelling or feeding) and information about the environment (e.g. presence of a large food source) (Uhlenbroek, 1996). A similar study on these long distance vocalisations performed by Notman and Rendall (2005) gave identical results, although they chose to interpret their findings differently. They dismissed the potential for information transfer and alternatively focussed on the physical mechanisms driving the acoustic variation in the calls. They proposed that the height above the ground and energetic output of the caller might better explain the acoustic differences observed in this call type. Chimpanzee barks might also convey discrete information sets to listening individuals. Crockford and Boesch (2003) examined the circumstances of bark production in adult males of the Tai forest, Ivory Coast, and found clear acoustic subtypes were produced in response to snakes, and while hunting. From this, Crockford and Boesch suggest barks may be capable of informing listeners about external events such as a potential danger, or the occurrence of a hunt. Most recently, Slocombe and Zuberbuhler (2005a; 2005b; 2006) have focused on the food grunts and screams of chimpanzees. With regards to food-associated calls, their work has shown that the acoustic structure of food grunts varies systematically with the quality of food eaten (Slocombe and Zuberbuhler, 2005b; 2006). These acoustic differences were also shown to be meaningful to receivers at some level, suggesting chimpanzees could extract information regarding food type encountered (Slocombe and Zuberbuhler, 2005b). A comparative wild study on scream vocalisations indicated that the role an individual plays in fights and the severity of aggression experienced by the victim might also be encoded within screams (Slocombe and Zuberbuhler, 2005a; 2007). I focus in detail on these particular studies later.

By supplementing the contexts of call production with what information copulation calls may also encode, we are likely to gain a better understanding regarding the function, or role, of these vocalisations in the lives of female chimpanzees (Semple et al., 2002).

Victim screams

Agonistic interactions are a natural outcome of social living and primates can produce acoustically distinctive vocal signals during these events. In dense natural habitats where visual contextual information is limited, such agonistic vocal signals may confer an adaptive function, conveying information regarding the nature of the interaction in progression to potential listeners. Exactly what information is conveyed by these calls has been an area of particular interest in monkey species and more recently in chimpanzees.

Rhesus macaques (Macaca mulatta) have been shown to produce acoustically distinct scream variants as a function of aggression severity and the relatedness and relative rank of the opponent (Gouzoules et al., 1984). Playback experiments of infant screams to mothers further indicated that these screams were indeed meaningful to recipients (as measured by looking duration) and that information regarding the ongoing agonistic interaction could be extracted from the acoustic structure of screams (Gouzoules et al., 1984).

Recent research has shown that chimpanzee screams produced during agonistic interactions also have the potential to convey social information. Male and female chimpanzees produce acoustically distinct screams as a function of the social “role” they play in a fight, specifically whether they are the victim or the aggressor (Slocombe and Zuberbuhler, 2005a). Aggressors seldom vocalise during agonistic interactions in comparison to victims, but when they did, the screams they produced were acoustically very different to victim screams. From this, Slocombe and Zuberbuhler (2005a) postulate that the structural differences make these screams potential candidates for functionally referential signals – signals that refer to objects or events in the external environment (Macedonia and Evans, 1993; Cheney and Seyfarth, 1990). However, before this conclusion can be confirmed, experimental studies are required to systematically show these calls are meaningful to chimpanzees at some level.

Victim screams have also been shown to exhibit considerable variation in their fine acoustic structure. More detailed analyses elucidated that, similarly to rhesus macaques, chimpanzee victim screams varied systematically with the aggression experienced (Slocombe and Zuberbuhler, 2007). Screams produced during severe aggression (beatings, stampings) were higher in frequency, produced more often, and were longer in length than those elicited during mild aggression (chases or bluff displays). Chimpanzee victim screams therefore also have the potential to signal to listening individuals how severe the ongoing aggression is.

In chimpanzees, aggression has traditionally been looked at from the male perspective, primarily due to its more frequent occurrence and sometimes-lethal nature (Goodall, 1986; Wilson and Wrangham, 2003; Fawcett and Muhamuza, 2000; Wilson et al., 2001). Nonetheless, female chimpanzees are equally capable of extreme, intra-sexual aggression, albeit less commonly, with recent reports of coalition formations amongst females (Newton-Fisher, 2005; Kahlenberg et al., in press b) and attempted female-led infanticides (Pusey et al., 1997; in press, see chapter three for more details). Such aggression, it seems, is most apparent when resources become scarce.

It is clear from these recent advances in understanding, that being able to extract information regarding the severity of aggression occurring in the nearby vicinity would confer selective advantages for females. Most importantly, such comprehension would allow females to keep track of potentially lethal intra-sexual agonistic interactions, and the likelihood of the aggression escalating or snowballing towards them. Secondly, attending to female aggression severity also allows females to make informed decisions as to whether to intervene on behalf of their offspring- a behaviour observed often late into the offspring's life (Goodall, 1986; Boesch and Boesch Achermann, 2000; Reynolds, 2005). This would be particularly important in communities where the female offspring of high-ranking females remain resident in their natal community for life (Pusey et al., 1997; Fawcett 2000). Understanding the nature of aggression may therefore play a significant role in the day-to-day lives of female chimpanzees, helping them dissipate the risks associated with female-competition and navigate successfully through a socially challenging world.

Whilst there are clear advantages for processing the information in victim screams, it is as yet unclear whether these screams are meaningful to female listeners. In order to systematically test this, a playback experiment must be employed.

Playback experiments can be designed to reproduce naturally occurring events or to present subjects with a stimulus they normally would be unlikely to encounter (Cheney and Seyfarth, 1990). These experiments represent a powerful technique for investigating the meaning and function of animal vocalisations. Over the last 30 years, playback experiments have made vital contributions to understanding the communicative and cognitive skills of many bird and mammal species (Macedonia and Evans, 1993).

Despite the success of playback experiments in furthering our understanding of animal vocalisations, only a handful of studies have employed playback experiments with any ape species. In fact, only the vocal system of chimpanzees has been experimentally probed in this respect. Firstly, Wilson et al. (2001) and Herbinger (2004) used the long-distance pant-hoot vocalisations of chimpanzees to investigate intercommunity conflict in East and West African chimpanzees. Secondly, and possibly more pertinently, Slocombe and Zuberbuhler (2005b) used playbacks to address chimpanzee call comprehension, demonstrating that food-grunts have the potential to function as referential signals, conveying information regarding food quality. This experiment was conducted in a captive setting where experimental manipulations are often more manageable (Hare et al., 2000). Possibly due to the inherent difficulties associated with conducting playbacks in the wild (Cheney and Seyfarth, 1990, reviewed in chapter six), no experiment has so far addressed ape call comprehension in a naturalistic setting.

Outlook

By combining observational, experimental and acoustic research techniques, I hope to better understand the complexities of the social world in which female chimpanzees live, and how females use vocalisations to successfully manage these demands. In chapter three I will assess how relevant-a-pressure female-female competition is, in the lives of Budongo chimpanzees. In chapter four I will focus on the contexts in which female chimpanzees use copulation calls, whether traditional hypotheses, such as inciting male-male competition, are sufficient to explain call production and function and whether copulation calls are additionally affected by the social pressures accompanying female competition. In chapter five I will build on the findings of chapter four, but rather than purely focusing on the factors that influence call production, I will also take into account what additional information these calls can encode in their fine acoustic structure. Together, chapters four and five will reveal the evolutionary pressures under which chimpanzee copulation calls have evolved and, crucially, what strategic role these vocalisations might play in the day-to-day lives of female chimpanzees. In chapter six I will move away from copulation calls and focus on female understanding of victim screams. By designing and employing a customised playback paradigm I will experimentally test whether female chimpanzees can comprehend the severity of aggression from victim screams and will consider ultimately, what this tells us about the importance of understanding scream vocalisations for female chimpanzees. I hope such research will make vital steps towards overcoming the long-held myth of the passive female chimpanzee.

Chapter two: General methods

This chapter will provide a description of the chimpanzee community studied, the research site in Uganda and a very brief introduction to the more different data collection protocols used in this study. Because certain procedures are specific to each research topic, these are reviewed more extensively with each chapter.

Study Site

Data were collected over a 14-month study period between January 2006-November 2007 on a habituated research group of chimpanzees in the Sonso region (Reynolds, 1992) of the Budongo Forest Reserve, Uganda. The Budongo Forest lies between $31^{o}8$ and $31^{o}42$ East and $1^{o}35$ and $1^{o}55$ North, in the Masindi District of Uganda (figure 2.1 and 2.2). The forest covers an area $428km^2$ and is classified as moist, semi-deciduous tropical forest (Eggeling, 1947). Due to a history of logging, the forest comprises a combination of four forest types: mixed forest, colonizing forest, swamp forest and ironwood forest (Plumptre, 1997). The study site is located at an altitude of 1,100 metres and has a mean annual rainfall of about 1,600 mm (Reynolds, 2005). A short dry season between December and February intersperses two rainy seasons, March-May and July-November (Reynolds, 2005). Monthly maximum and minimum temperatures vary between $32^{o}C$ and $19^{o}C$ (Reynolds, 2005).

Figure 2.1: Map of Uganda with the location of Budongo Forest reserve indicated (courtesy of Slocombe, 2005).

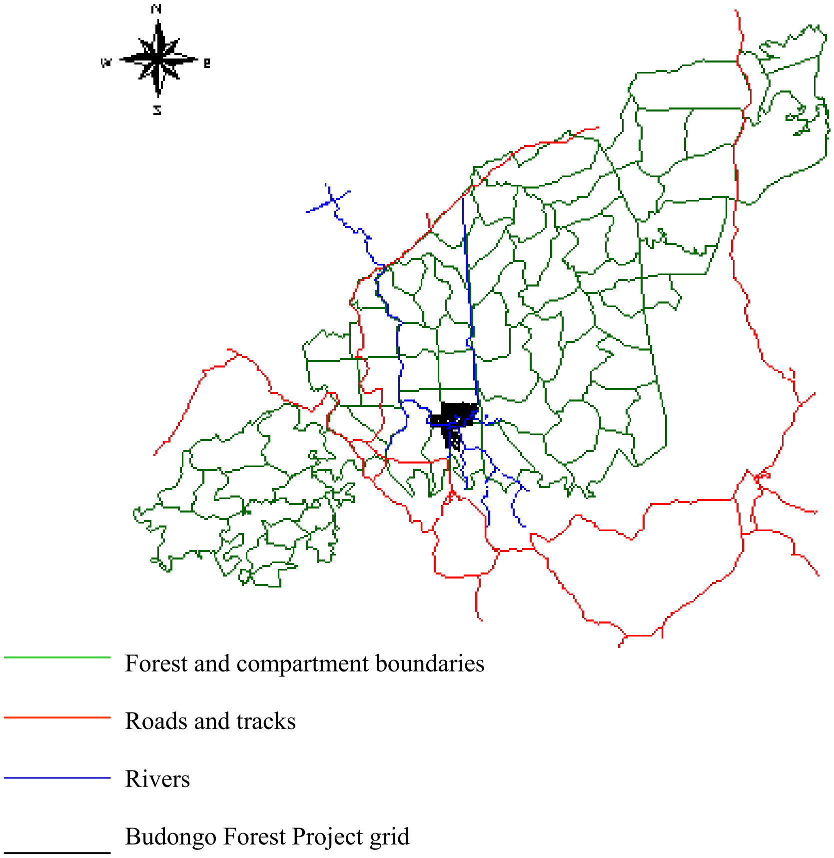

Figure 2.2: Map of the Budongo forest showing the forest edge, compartments, rivers, roads and finally the grid system, centred at the core of the Sonso community's home range (courtesy of www.budongo.org).

Study community

The chimpanzees in the Budongo Forest belong to the subspecies of eastern, or long-haired, chimpanzees (<u>Pan troglodytes schweinfurthii</u>). Similar chimpanzees are found in the Kanyawara and Ngogo communities in Kibale National Park, Uganda and in the Gombe and Mahale National Parks, Tanazania. Whilst there exist almost 650 chimpanzees in the entire Budongo Forest (Reynolds, 2005), only one community, the Sonso community, is sufficiently habituated for human following and research. The Sonso community of chimpanzees are named after the river running through their home range and have been continuously monitored by researchers and field assistants since 1991. A systematic habituation program began at this time, under the supervision of Vernon Reynolds, and provisioning has never been used.

At the time of study (2006-2007) the community consisted of 78 individuals including 8 adult males and ~ 25 adult females (see table 2.1 and 2.2). All individuals are named and given a two-letter code derived from letters of their name. During this period, adult males were the most habituated, permitting researchers to follow them, even when travelling alone. All but a few peripheral adult females were confident when in mixed parties, but the majority remained difficult to follow when travelling just with offspring or in small, same-sex parties.

Table 2.1: The adult and sub-adult males of the Sonso community present during the 14 month study period. Names in bold served as playback subjects.

Adult males	**~Age**	**Known offspring**	**Details**	**Sub-adult males**	**~Age**	**Details**
Nick (NK)	26		Alpha	Kato (KT)	15	
Duane (DN	42	RS,KE,SH,JT,KM	Died March 2008	Kwezi (KZ)	12	
Zefa (ZF)	25			Hawa (HW)	13	
Bwoba (BB)	21			Zalu (ZL)	13	Orphaned August 2007
Maani (MA)	50	KR		Fred (FD)	14	
Musa (MS)	17			Mark (MR)	11	
Bob (BO)	18		Disappeared August 2007	Pascal (PS)	10	
Gashom (GS)	21		Disappeared April 2008	Simon (SM)	15	

Table 2.2: The adult females, their dependent offspring and adolescent females of the Sonso community during the study period. Females in bold served as playback subjects (see chapter six). Asterisks denotes females that served as subjects in the copulation calling study (see chapters four and five).

Adult Female	Age	Offspring	Details	Adolescent female	Age
Biterice (BC)	32	BG		Anna (AN)	15
Banura (BN)	40	BT	Missing July 2007	Rachel (RE)	11
Flora (FL)	29	FA			
		FK			
Gladys (GL)	32	GN			
Harriet (HT)	30	HL			
		HY			
Juliet (JL)*	18				
Janie (JN)	24	JT			
		JS			
Kalema (KL)	29	BH			
		KM			
		KC			
Kewaya (KY)*	24	KA			
		KX			
Kigere (KG)	32	KE			
		KI			
Kutu (KU)*	29	KN			
		KS			
Kwera (KW)	27	KR			
		KB			
Lolla (LL)*	20				
Melissa (ML)	25	MN			
Mukwano (MK)*	28				
Nambi (NB)*	46	NR	Alpha female		
		NT			
Ruhara (RH)	40	RM			
		RS			
Sabrina (SB)	27	SL			
		SN			
		ST			
Sarine (SE)	37	SK			
Wilma (WL)*	27				
Zana (ZN)	27	ZD	Died Aug 2007		
Zimba (ZM)	40	ZG			
		ZK			

The home range habitually used by the community has been estimated as between 6.78 and 14.51km^2 (Newton-Fisher 2002b, 2003 see figure 2.3) and is surrounded by three communities of unknown size and composition. Inter-community relations are in-frequent and there has been no recording of inter-group killings (Reynolds 2005).

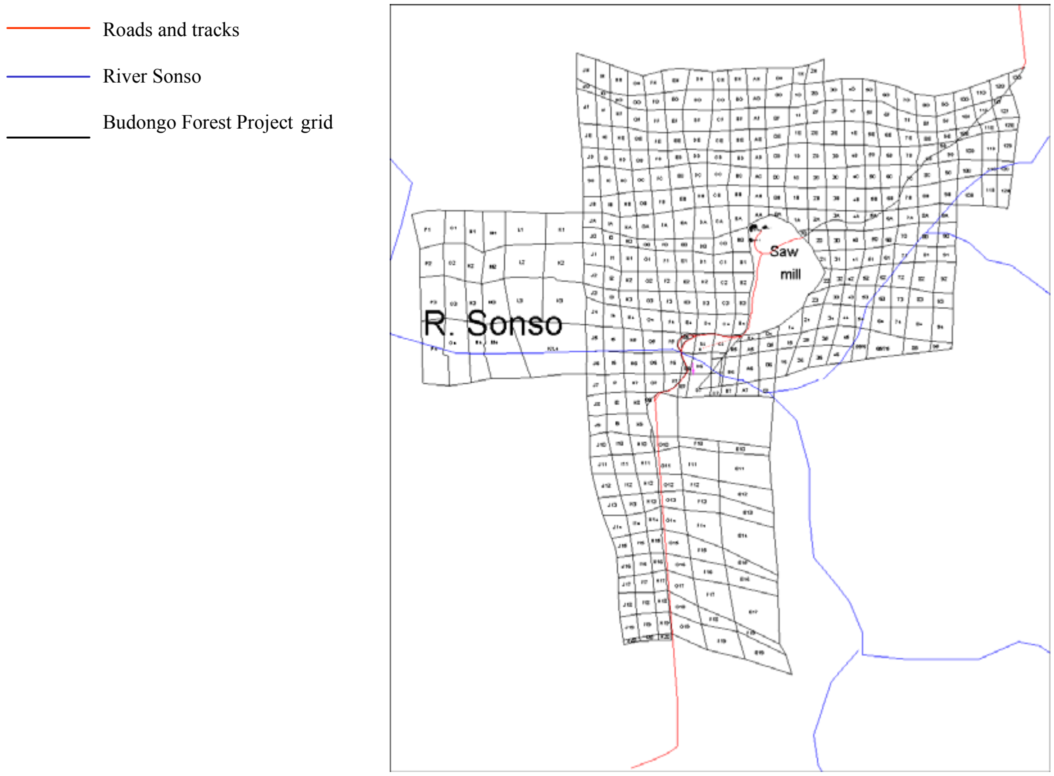

Figure 2.3: Map of the grid system used to navigate the Sonso community home range. Each block covers an area of roughly 100m^2 and is allocated a letter and a number to aide navigation through the forest. The main road indicated is called the "Royal Mile" and provides access to the study site (courtesy of www.budongo.org).

Data collection

Over the 14-month period I collected data on 260 days, constituting approximately 2000 observation hours in the forest. Chimpanzees would be located in the forest though de-nesting previously nested chimpanzee groups or by listening for and following vocal cues.

Sampling methods

When conducting playback experiments and recording the behaviour of oestrus females, both focal and ad libitum animal sampling methods were employed. Focal sampling has been defined as when “attention is directed to one target individual at a time” (Altmann, 1974). This is a particularly useful methodology as it allows all instances of specified behaviours exhibited by that one individual to be recorded. In theory the identity and the duration of focal periods should be specified prior to commencement, though in reality, due to the ranging patterns of wild chimpanzees, this is often not possible. For playbacks, focal samples would last whole days (7am-4pm) and focal individuals were chosen based on a number of factors, particularly when he or she had received their last experimental trial (see chapter six). If multiple focals were present, then one was chosen at random following the protocol outlined in Newton-Fisher (1997). For copulation calling studies, longer whole day samples (6am-7pm) were taken over a period of 14 consecutive days. This was primarily because I had to remain with the female for the duration of her receptive period (see chapter four for more details) and in order to do this, the focal had to be nested and de-nested. This observational technique involves staying with the female until she constructs and rests in a nest. The location is documented and then the same site is returned to early the next morning (approx 6am) before the focal leaves the nest.

Behavioural and acoustic data on copulation calling was supplemented with ad-libitum data. This was only taken if the individual copulating could be clearly seen and did not interfere with focal data sampling. In addition ad-libitum data on chimpanzee pant-grunts were collected. Pant-grunts are submissive vocalisations given by subordinates to dominants and are generally regarded as good indicators of dominance status (Goodall 1986). Frequency, grunter ID and receiver ID would be noted and later entered into a pant-grunt matrix. This allowed systematic dominance relationships to be elucidated (see chapters four and five).

Equipment

To collect acoustic recordings of copulation calls and playback stimuli I used a SENNHEISER ME66 directional microphone and MARANTZ PMD660 solid-state recorder. Recordings were directly transferred as WAV files to a Toshiba Celeron, or Fujitsu Siemens Amilo laptop computer. File editing and quantitative call analyses were conducted with PRAAT software version 4.3.37, including scripts written by M. Owren.

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Playbacks were conducted using a NAGRA DSM speaker/amplifier. Calls to be broadcast were stored and played in uncompressed WAV format on an Ipod Nano. Playbacks and infanticides were filmed using hand held video cameras (Panasonic NV-GS 250 and Canon MVX330i).

For more details on specific methodologies see chapter methods sections.

Chapter Three: Lethal female competition in wild chimpanzees

Summary

Wild chimpanzees exhibit substantial gender differences in behaviour. Adult males typically dominate the females and compete amongst each other for access to resources. As a consequence males can display extremely violent behaviour towards neighbours, other primates, and occasionally community members. In contrast, females are regarded as the more peaceful sex, who lead relatively secluded uncompetitive lives, predominately occupied with raising offspring. I report here recent observations of lethal aggression in the form of infanticide perpetrated by resident females of the Sonso community, Budongo Forest, Uganda. One observed and two inferred cases demonstrate that gender differences in aggressive propensities in our closest living relatives may be much less pronounced than originally thought. Recent research from wild chimpanzee communities suggests that such female aggressive behaviours may be a product of competition for resources. With these observations I directly test this hypothesis in addition to examining a number of other socio-ecological factors that bring out the hidden demonic nature of chimpanzee females.

The results from this chapter have been published in the following paper:

Townsend, S.W., Slocombe, K.E., Emery-Thompson, M. & Zuberbühler, K. (2007). Female-led infanticide in wild chimpanzees. Current Biology 17 (10): 355-356

Introduction

Infanticidal behaviour has been observed in a number of mammalian species and is mostly a male affair (Tuomi et al., 1997). Most functional explanations resort to sexual selection theory, suggesting that males obtain a direct reproductive benefit by shortening the victim female's time to oestrus resumption, thereby increasing the chance to sire his own offspring (Struhsaker and Leland, 1985; Pusey and Packer, 1994). Classic examples for this sort of behaviour come from langurs (Hrdy, 1977) and chacma baboons (Palombit et al., 1997), primates in which males migrate and typically obtain high rank in the new group after arrival.

In chimpanzees, infanticidal behaviour is far less uniform and it has been reported from both males and females (Hiraiwa-Hasegawa & Hasegawa, 1994). In East African chimpanzees, 24 cases of infanticide have been documented, occurring at each of the five long-term study sites (Budongo: Suzuki, 1971; Bakuneeta et al., 1993; Newton-Fisher, 1999b; Gombe: Bygott, 1972; Goodall, 1977, 1986; Mahale: Nishida et al., 1979; Kawanaka, 1981; Norikoshi, 1982; Nishida and Kawanaka, 1985; Takahata, 1985; Hamai et al., 1992; Kanyawara: Clark-Arcadi and Wrangham, 1999; Ngogo: Watts et al., 2002). In 14 cases, observation conditions were sufficient to identify the individuals involved, demonstrating that males acted as aggressors in the majority of cases (N=11). Females were involved only four times, in one case jointly with a male.

What, if any, are the selective advantages for males and females of this extreme form of aggression? For males, competing with conspecifics to maximise mating success is likely to be the most powerful force driving this behaviour. For example, it has been suggested that male infanticide in chimpanzees may be a counter-strategy to female promiscuous mating by coercing resident females into restrictive mating, a way to eliminate potential future competitors, in addition to increasing future mating chances (Hamai et al., 1992; Nishida and Kawanaka, 1985; Takahata, 1985; Clark-Arcadi and Wrangham, 1999). Although these are plausible ideas, the empirical evidence is generally weak. In some occasions, infanticidal males have been identified as the father of the victim (Nishida and Kawanaka, 1985; Takahata, 1985; Clark-Arcadi and Wrangham, 1999) and male infants are not preferentially targeted by infanticidal males (Wilson and Wrangham, 2003). Finally, aggressors have not always had increased mating access to the mothers of the victims (Goodall, 1986). There are also insufficient data that clearly demonstrate that inter-birth intervals are shortened following infanticide, though this is likely to be the case (Clark-Arcadi and Wrangham, 1999; Boesch and Boesch-Achermann, 2000). For females, explanations for this behaviour are even more difficult to formulate because their participation is so rare. Three of the four reported cases of female-involvement come from a mother and daughter dyad, Passion and Pom at Gombe (Goodall, 1986). In all three instances the females ate the offspring and therefore nutrition has been mentioned as a crucial factor, either directly via meat consumption or indirectly via access to high-quality core areas, which ultimately provide them with reproductive advantages (Williams, 1999; Emery Thompson et al., in review). However, given their rarity and the relatedness of the dyad, these infanticides have also been highlighted as potentially just pathological behaviours (Goodall, 1986).

More recent observations of intense aggression amongst high-ranking Gombe females, including apparent attempts at infanticide, led to the hypothesis that increased competition for resources can lead to violent behaviour amongst females (Pusey et al., 1997). Here, in collaboration with Melissa Emery Thompson and Katie Slocombe, I describe three new cases of female-led infanticide in wild chimpanzees. These results provide a direct test of Pusey et al.,'s hypothesis and ultimately suggest that females may have similar propensities for extreme physical violence as previously described for male chimpanzees.

Methods

Observations were made as part of the ongoing behavioural research with the free-ranging Sonso community in Budongo Forest, Uganda. Long-term data are collected on an interval basis, whilst important events, such as infanticidal attacks, are recorded on an ad libitum basis. The cases described here occurred between March 2004 and July 2006. In two of them, it was possible to film parts of the events using hand-held video camcorders (2004: Sony CCD-TR728E; 2006: Canon MVX330i).

Results

(1) Resident females attack an immigrant mother and kill her infant son (see also Reynolds 2005, p. 152)

On 12th March 2004 at 13:50, Katie Slocombe and a field assistant, Raymond Ogen (KS and RO), were with a party of four adult females (KU, ML, WL, alpha female NB with adolescent son MS), all in a Cynometra alexandrii tree. Three minutes later, continuous screams could be heard from a second party to the South. All individuals descended rapidly from the tree and rushed towards the source. After seven minutes of continuous screaming, KS and RO located the party, consisting of a group of adult females (ZM, BN, MK, KL), and their juveniles, now joined by the first party of females (NB, KU, ML, WL). They also saw an adult male (ZF) displaying in a tree. The females then moved into a vine tangle and, when followed, blood was seen on the ground. The adult female ZM was first seen carrying a dead male infant, approximately 1 week old. She was charged by NB, and lost possession of the carcass to her. NB's adolescent daughter (NR) then took the carcass and initiated a play fight with an adolescent male (KT), each trying to drag and pull it off each other. NB then regained possession and sat with the carcass. When KT approached she threatened him, and the adolescent male ran screaming to the presumed mother of the infant, the adult female (FL), who was lying in thick undergrowth with a fresh bleeding gash 2-3 inches long on her left upper arm. FL was a recent immigrant who came into the Sonso community about 10 months earlier with two older male offspring (approximately 4 and 9 years of age). She is missing her right hand, making defence of an infant difficult.

NB retained possession of the carcass for just under an hour, grooming it and keeping the flies away from it. She allowed KU, MK, and WL to inspect it but threatened FL and KZ when they tried to approach it. The adult males ZF and MA were resting within 10m of NB and the carcass and never showed any interest in the carcass and never approached. No attempt was made by any of the females to eat the infant. At 14.42 NB moved off without the carcass, allowing us to inspect it. The body was intact, with puncture wounds to the head.

Although we cannot completely rule out that the infant belonged to an unknown stranger female who disappeared during the incident, we consider it highly likely that FL was the infant’s mother who sustained her wounds whilst unsuccessfully trying to defend her infant son. Although it was too late to witness the actual killing, we strongly suspect that the five adult females ZM, KL, ZN, BN, MK initiated it. NB, ML, WL and KU fought over the body and may have been involved in delivering the fatal bite to the head. The only adult male present during the whole event was ZF. MA arrived after. Following male-led infanticides, the perpetrators paid great attention to the dead infant, vying for access to the body (Newton-Fisher 1999b). In this instance, neither male showed any interest in the dead infant and despite resting in the very close vicinity, they did not approach. From these observations, we were confident that the males had not played any part in the lethal attack.

(2) Resident females attack a stranger female and kill her infant daughter

On 3rd February 2006, at approximately 13.00 hours, we (myself, Katie Slocombe and field assistant Monday Gideon) were with the adult male ZF who was feeding in a Cynometra alexandrii tree. When hearing screams about 30m away, ZF descended and moved directly towards a party of screaming individuals. Approximately 3 minutes later, ZF moved away from the screaming party, pilo-erect, travelling towards another nearby feeding party. Then, the young adult male BB approached the now westward moving screaming party, again pilo-erect. Due to poor visibility, direct observations were not possible until 13.05, when we saw contact aggression between various screaming females. Within the group of fighting females, we observed a stranger female with an approximately one-week old female infant. The mother had a wounded and bleeding ano-genital region that was not swollen. The adult male (NK) displayed close to the females and the young adult male BB, pilo-erect, produced SOS screams (Goodall, 1986) about 5m from the females. At 13.09 the stranger female managed to escape and ran approximately 25m away, chased by six resident adult females (NB, RH, KW, KU, WL and ZM). All but WL had infants under three years clinging ventrally. The females soon caught the stranger, pounded her back, thumping and stamping her, whilst the stranger female was lying on the ground shielding her infant from the ensuing attack.

During this attack, the adult males BB, NK and ZF were following the females, displaying, buttress drumming and screaming continuously. One male charged right through the females, hitting at least one of the females, who crouched on the ground screaming for several seconds, however the females quickly regrouped to continue the attack. At 13.14 an old adult male

(MA) appeared and tried to disrupt the assault on the stranger by repeatedly forcing the females apart.

At 13.16, the females successfully removed the infant from the mother and the resident alpha female (NB) ran along the ground carrying it. The mother was no longer seen after this point. The females continued to scream and compete for possession of the infant. The adult male MA was no longer visible, but the adult males NK, ZF and BB continued to display. At 13.18 ZM, with her male infant ZK, now riding dorsally, carried the limp infant by the pelvic girdle. ZM sat on a log, lifted the infant up, and delivered a single bite spanning the head and neck, probably killing it. The adult male BB immediately charged at her and hit her in the face with considerable force. ZM was knocked backwards and hit the infant hard against the log as she recovered her balance. She immediately chased BB, giving aggressor screams. The adult male MA then chased ZM away with the dead infant, whilst ZF continued to display close by. For the rest of the day, we were unable to follow the females as they moved through impenetrable forest, but could hear them calling from a fruiting Ficus mucuso tree at 17.30. Two days later, after considerable movement throughout their home range, the chimpanzees returned to this same tree again and at 10.00 we discovered the body of the killed infant in the adjacent tree, 20m off the ground in a fork. Although in a state of partial decomposition and with significant injuries to the lateral side of the head and neck, the cadaver remained intact with no signs of attempted consumption.

(3) Resident females kill an infant

On 2nd July 2006, at approximately 09.00, two of our field assistants heard loud screams from the centre of the Sonso home range. They rushed towards the screaming party and found fresh drops of blood and part of an infant's hand along the trail. They also saw a low ranking resident female (MK), known to be near her pregnancy term, screaming loudly. Further down the trail, towards the sounds of the screaming, retreating chimpanzees, a portion of maxilla with two unerupted incisors was found. The rest of the infant's body was never seen or recovered. We suspect MK may be the victim's mother, as she was seen later in the same day with signs of recent parturition (sagging, gaping sexual skin, less pronounced belly). MK is a low ranking female, with no close relationships with other females and no offspring, who is believed to move between Sonso and neighbouring communities. We have strong reasons to believe that this, like the previous incidents, was perpetrated by Sonso females. Since the event occurred in the centre of the community's home range and close to the research camp, it is very unlikely that males from the unhabituated neighbouring community were responsible for this case of infanticide or that an individual carried the infant from the periphery. In addition, Melissa Emery Thompson and field assistants could confirm that during the event, all adult males of the community were approximately 800m away, as part of a large feeding party, suggesting that the infant was killed by resident females. The high ranking females NB, KU, KL, KW, RH, and ZM, who were involved in the previous killings, were absent from this large feeding party. Their whereabouts during the killing are unknown, meaning they may have been involved.

(4) Timescale of infanticides

Figure 3.1 shows the timescale of the reported female-led infanticides in the last decade. The sex ratio of the community is also plotted over the same time scale, using long term community composition data. The occurrence of infanticides coincides with local peaks in the community sex ratio.

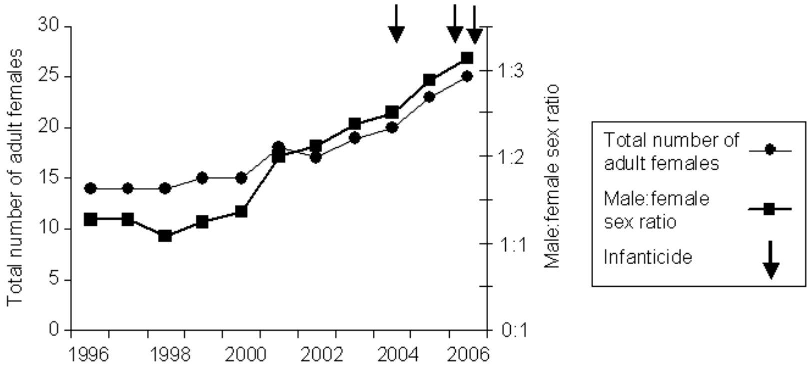

Figure 3.1. Relationship between the adult female and male sex ratio and the occurrence of female led infanticide in the Sonso community of wild chimpanzees, over the last decade. Arrows denote the occurrence of a female-led infanticide.

Discussion

I have provided observational evidence for coalitionary lethal aggression in female chimpanzees. The three instances of infanticide described here were observed, or strongly inferred, to be led by the resident females of the community and in at least two cases the same high-ranking females were responsible whilst the victims' mothers were either a stranger or a recently immigrated female. In all cases, the adult males were not involved in the killing. Instead in two cases they displayed in the vicinity or they even intervened and attacked the females to impede the infanticide, fulfilling a possible peace-keeping role.

In all three cases, the remains of the attacked infants showed significant bites to the head, almost certainly the fatal wound in the first two cases. Thus, I conclude that these were purposeful, not accidental, killings. It is also notable that, together, we encountered three such events in only 28 months. Since July 2006, one further "attempted" infanticide has also been observed. In February 2008, high-ranking resident females (NB, ML, RH) were seen to attack and attempt to remove the ~1week old infant of an immigrant female, in the SE periphery of the Sonso home range (Monday Gideon, Pers.comm). However, whilst this is relevant, it is not included with the three previous cases as the survival of the offspring is unknown.

What was the impetus behind these infant killings and attempted killings, why did the same high-ranking females participate, and why did some of the males directly or indirectly attempt to disrupt the killing? I can think of several explanations, some of which can be ruled out by our observations:

<u>Nutritional gain</u>:

In contrast to the other instances of female-led infanticide, such as the well-known Gombe cases (Goodall 1986), our females made no attempt to consume the infants after killing them, ruling out the idea of short-term nutritional gain as an explanation for this behaviour.

<u>Inter-community aggression</u>:

The females' behaviour could be hypothesized as an extension of inter-community aggression, a well-known feature of chimpanzee behaviour (Clark-Arcadi and Wrangham, 1999). However, the most recent victim was a low ranking resident of Sonso and in the observed cases, our females were clearly fixated on removing the infant from the mother in order to kill it, whilst injury to the mother seemed incidental. Moreover, aggression to the mother terminated as soon as the infant was taken, ruling out intercommunity aggression as a feasible explanation.

Intra-group female competition:

Increased competition is a more likely explanation for these attacks. In the last few years, the Sonso community has had an unusually high influx of female immigrants who have brought one or more dependent offspring with them. An estimated 5-10 parous females immigrated between 2001-03, and this number increased even further from 2004-2006, with a total of 13 stranger females having now taken up residence (Emery Thompson et al., 2006). The recent influx has dramatically increased the community size in a short period of time, suggesting that a critical threshold may have been surpassed. Males are not normally hostile to these immigrants, presumably because they increase their mating success. Contrary to traditional views of male chimpanzee behaviour, however, they have not shown any serious aggression towards the offspring of these females, including males as old as 10. It is also relevant that the community is probably unable to expand its current home range to access additional resources because the number of adult males has simultaneously gone down.

In what ways could heightened female density provide a competitive challenge for resident females? Access to food and sexual partners are promising candidates, but it is difficult to assess the relative importance of each. Concerning food, several studies have found that the home range of the Sonso community has a particularly rich and stable food supply with relatively little seasonal variation (Newton-Fisher, 2003; Bates, 2005), perhaps making this community particularly attractive for immigrants. However, the home range of this community is relatively small (Newton-Fisher, 2003), so competition for access to high-quality core feeding areas may still be considerable. Second, like other communities the Sonso chimpanzees have a female-skewed sex ratio, but this has now increased from approximately 1:1 in 1996 to almost 1:3 in 2006 (figure 3.1), heightening the chance that several females will be in oestrus at a given time, possibly compromising resident females in their ability to mate with preferred males (Goodall, 1986). Recent research has indicated that in promiscuous mating systems, when the sex-ratio is skewed, males and their sperm can become a limiting resource (Brauch et al., 2007; Wedell et al., 2002; Pfefferle et al., 2008a). This, compounded by the fact that the three observed infanticides occurred when the adult female:male sex ratios were highest suggests that competition for male chimpanzees could be a real challenge for females in this community. It is also relevant that most females that participated in these killings were relatively old and high-ranking individuals (Newton-Fisher, 2005). These females are generally more competitively able than lower-ranking females (Pusey et al., 1997, in press) and should thus be most interested in maintaining their access to such resources. The observations presented here suggest escalated aggression may be one such strategy.

Male peacekeepers

The behaviour of the adult males during these infanticidal attacks is also of interest (see Wrangham & Peterson, 1996). We never observed any participation of the adult males in these infanticides. In contrast, adult males actively attempted to disrupt, not advance, the progression of the infanticide. Captive male orangutans (Zuker, 1987) and gorillas (Hoff, 1985) have been observed to intervene during female-female aggressive interactions, however such mediation behaviour has not yet been documented in wild chimpanzees. It is possible that this was a direct result of males recognising the stranger female as a previous or potential mating partner. Indeed, the adult male MA, who showed the strongest motivation to stop the March 2006 infanticide, was not sighted with the rest of the community during the stranger female's time of conception (July-August 2005), suggesting that he may have copulated with her during that time. The two peace-keeping males, MA and BB, were joined by higher-ranking males, NK and ZF, but these males only displayed in the vicinity of the event without directly intervening. It is therefore possible that these males have never had contact with the stranger female. Thus, these males would enjoy no immediate fitness benefits from intervention although there are numerous other explanations for why they remained neutral during the conflict.

To summarise, past copulatory experience appears to be the best explanation for the unusual peace-keeping behaviour in some males. Concerning the females' behaviour, the emerging picture is that the Sonso females respond with extreme physical violence to increased intra-group female-female competition caused by high rates of immigration. For female chimpanzees such competition may therefore represent a significant threat associated with social living. These observations provide further evidence that chimpanzee females are able to form alliances with non-kin (Emery Thompson & Wrangham, in press; Newton-Fisher, 2005), in this instance to attack other females and their infants. Coalitionary and severe female aggression may not be as rare as previously thought, in fact, recent observations of very similar behaviours have now been documented from other study sites (Gombe: Pusey et al., in press; Mitumba: Pusey et al., in press; Kanyawara: Kahlenberg et al., in press a,b; Tai: Boesch et al., 2008). In the case of Budongo however, this aggression, which is probably part of the wider female behavioural repertoire, was facilitated by an extremely skewed sex-ratio and high density. This may have led to increased food and reproductive competition between females.

Chapter Four: Female chimpanzees use copulation calls flexibly to prevent social competition

Summary

The adaptive function of copulation calls in female primates has been debated for years. One influential idea is that copulation calls are a sexually selected trait, which enables females to advertise their receptive state to males. Male-male competition ensues and females benefit by getting better mating partners and higher quality offspring. However, whilst these adaptive explanations address a number of important theoretical points their focus is on how the female's calls affect the nearby male mating partners. The fact that the female is usually part of a complicated social network, consisting of relatives, offspring and social competitors, is not normally considered. Female primates are now known to play crucial roles in the social fabric of the group, and it is therefore somewhat surprising that this has never been properly considered as a selection factor in this reproductively important vocalisation. In this study, I analysed the copulation calling behaviour of wild female chimpanzees at Budongo Forest, Uganda, but found no support for the male-male competition hypothesis. Hormone analysis further showed that the calling behaviour of copulating females was unrelated to their fertile period and likelihood of conception. Instead, females called significantly more whilst with high-ranking males, but suppressed their calls if high-ranking females were nearby. Copulation calling may therefore be one potential strategy employed by female chimpanzees to advertise receptivity to high-ranked males, confuse paternity and secure future support from these socially important individuals. In chapter three I have shown that competition between females can be dangerously high in wild chimpanzees, and my results here indicate that females use their copulation calls strategically to minimise the risks associated with such competition.

The results from this chapter have been published in the following paper:

Townsend S.W., Deschner T., Zuberbuhler K. (2008). Female chimpanzees use copulation calls flexibly to prevent social competition. PLoS ONE 3(6): e2431

Introduction

In various animal species copulations are accompanied by a distinct vocal behaviour, the copulation call (e.g. African elephants (Loxodonta africana) [Poole et al., 1988]; lions (Panthera leo) [Schaller, 1972]; elephant seals (Mirounga angustirostris) [Cox and Le Boeuf, 1977]; and humans (Homo sapiens) [Hamilton and Arrowood, 1978]. Due to their prevalence, considerable debate has surrounded the adaptive significance of these conspicuous acoustic signals. In primates, copulation calls are loud, acoustically distinctive vocalisations emitted prior to, during or just after copulation. Calls can be produced by both males and females participating in the copulation, however in Old World monkeys and apes, it is more commonly females that vocalise (Hauser, 1996; Semple, 2001; Pradhan et al., 2006). Interestingly, not all copulations are accompanied by calling behaviour, suggesting that females have some control over call production.

A number of different hypotheses have been put forward to explain the adaptive significance of copulation calls (Pradhan et al., 2006), although it is unlikely that any one hypothesis in isolation is sufficient to explain call evolution. Indeed, copulation calls may operate at more than one level with multiple functions (Semple, 1998b). The most common hypothesis invoked to account for the evolution of such calls is that they are sexually selected traits to alert males, other than the mating partner, to the receptive condition of the female caller (Cox and Le Boeuf, 1977; Hauser, 1990; 1996; O'Connell and Cowlishaw, 1994; Oda and Masataka, 1995; Semple, 1998b; 2001) with the result of inciting competition amongst them. The "incitation of male-male competition" hypothesis (Cox and Le Boeuf, 1977) can operate at two distinct levels, which are not mutually exclusive (Semple et al., 2002). Firstly, calls may operate to stimulate overt competitive interactions between males so that, indirectly, the female ends up with the most dominant partner (Henzi, 1996). Copulations accompanied by a call are then predicted to primarily occur with low-ranking, less desirable males and increase subsequent levels of male aggression. Aggressive interactions can also occur during or after copulation to prevent insemination or future matings (Hauser, 1990). Secondly, copulation calls may lead to multiple mating partners, and this could generate additional benefits for the female due to sperm competition (O'Connell and Cowlishaw, 1994). Under this scenario, males do not attempt to prevent insemination per se, but they will be particularly motivated to mate with the female shortly after a successful mating by another male. If female calling behaviour has been shaped by sperm competition, females should call to advertise ejaculation (O'Connell and Cowlishaw, 1994) and such calling should lead to a decrease in the time period between successive matings (Semple, 1998b).

Polyandrous mating, and sperm competition that follows from it, increases paternity confusion for individual males, and it has been argued that this lowers the risk of male infanticide (O'Connell and Cowlishaw, 1994). In contrast to the male-male competition hypothesis, however, the paternity confusion hypothesis makes no predictions about females trying to increase the quality of partners or sperm. Instead, females are primarily interested in receiving copulations from as many socially important partners as possible, safeguarding them from their infanticidal tendencies and gaining their future support. In many primate species females are notoriously vulnerable to infanticide (Van Schaik, 2000; Muller et al., 2007), suggesting that there are strong selective pressures acting on females to evolve behavioural or sexual counter-strategies to protect their infants: copulation calls may well be one such counter-strategy.

Although the theoretical reasoning behind the incitement of male-male competition and the paternity-confusion hypotheses is sound, the desired empirical support is weak, especially for chimpanzees. Most empirical work so far has been done with different monkey species, which are typically matrilineally bonded (Hauser, 1993; 2007; O'Connell and Cowlishaw, 1994; Henzi, 1996; Semple, 1998b; Nikitopoulos et al., 2004), in contrast to male-bonded chimpanzees. A second relevant point is that if copulation calls function to increase a female's reproductive success, or confuse paternity amongst multiple males, then it is reasonable to predict that callers should take into account (a) at which stage in their cycle they are; and (b) whether the desired mating partners are present in the audience. A number of studies have investigated the influence of the female reproductive stage on vocal production. For example female-alpine accentors, Prunella collaris, sing only during their fertile time-period (Langmore et al., 1996) and the stereotyped 50kHz vocalisations produced by female brown rats are only given during pro-oestrus (Matochik et al., 1992). In primates, it has also been suggested that copulation calls change based on female sexual status (O'Connell and Cowlishaw, 1994; Semple et al., 2002), but hormonal data are not usually available to determine the precise time of ovulation.

Very little is known about the degree to which female primates adjust calling behaviour in relation to the composition of the audience. A growing body of evidence suggests that female-female competition, and the aggression that accompanies it, is far more pervasive in chimpanzee societies than previously thought (See chapter three, Kahlenberg et al., in press a; b; Pusey et al., 1997; in press). Females are likely to compete with each other over access to resources and in mating systems where promiscuity is high, males and their sperm may be one such limiting resource (Pfefferle et al., 2008a). Female competition may therefore represent a significant social pressure in the lives of wild female chimpanzees. For lower ranking, less competitively able females, it may thus not be beneficial to advertise successful matings with copulation calls if other females are nearby, especially if this increases the likelihood of aggression. Our pilot observations revealed that females often remained silent during copulations, although the reasons for this behaviour remained largely unknown (Hauser, 1990). Based on these considerations, I hypothesised that females adjusted their copulation calls, to maximise paternity confusion by soliciting copulations from nearby males on the one hand, and to minimise the effects of social competition caused by other females on the other hand. To address these points, I conducted a study on the copulation calling behaviour of wild female chimpanzees from the Sonso community of the Budongo Forest, Uganda.

Materials and Methods

Study site and animals

I studied the sexual behaviour of a number of individuals belonging to the Sonso community of the Budongo Forest, Uganda (Reynolds 2005), during two field seasons (January 2006-April 2006 and October 2006-March 2007). As mentioned in chapter two, at the time of this study, the group comprised 78 individuals including 8 adult males and 25 adult females. Of the 25 adult females, data were collected from 7 adult females. Three additional females also had sexual swelling and copulated during the study but were excluded from analyses due to low copulation frequency (<15 copulations).

Copulation calls, behaviour and determination of female swelling size

Around the time of ovulation, female chimpanzees exhibit sexual swellings. The average duration of the maximum swelling period is about ten days (Tutin, 1979; Hasegawa and Hiraiwa-Hasegawa, 1983; Deschner et al., 2003) and females` sexual activity is usually confined to this period (Goodall, 1986). Female chimpanzees mate promiscuously with multiple males (Tutin, 1979; Goodall, 1986), but they do not produce copulation calls every time (Hauser, 1990). Copulation calls consist of a rhythmic succession of high-frequency squeaks or screams and typically begin during the copulation, after mounting and intromission (figure 4.1). Copulation calls can be reliably identified by human observers and are audible in forest habitats up to about 50m.

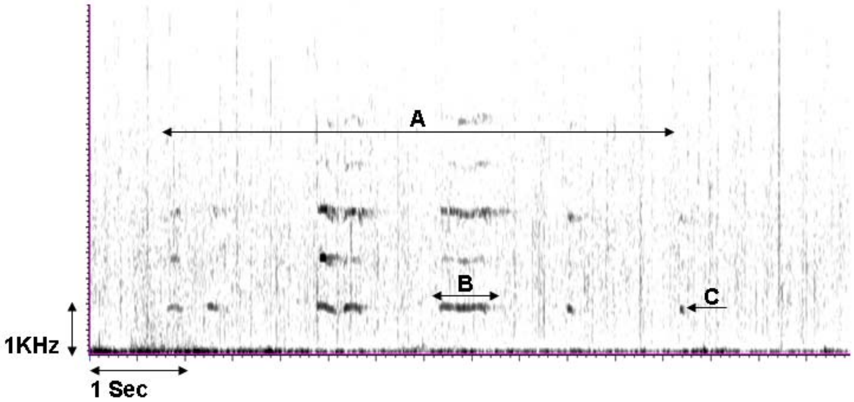

Figure 4.1: Time-frequency spectrogram of a female copulation call from Budongo Forest during maximum tumescence. Filter bandwidth: 159Hz, Frequency resolution: 86.1Hz. Depicted is (A) a complete copulation calling bout of approximately 6.5s and (B) a single copulation call of approximately 0.6s by the female JL. (C) The lowest visible band is the fundamental frequency from which acoustic measurements were taken with three visible harmonic bands. Copulation calls have a frequency range of 700-1000Hz.

Copulations from cycling adult females were collected using all day focal follows on each day of the female's maximum tumescence phase. Given that only one female could be followed for this duration, yet more than one female could cycle at any one time, ad-libitum observations of copulations were also taken. Only copulations occurring during the maximum tumescence phase were considered. Maximum tumescence was determined following Furuichi's (1987) method, which uses degree of wrinkling of the sexual swelling (on a 4 point scale at Budongo) as the main parameter, rather than labial occlusion (Dahl, 1999). Sexual skin swelling characteristics were recorded every morning through visual inspection of the perineal area. Inter-observer agreement between myself and field assistant Monday Gideon (MG) was a pre-requisite for final assessment of female swelling size. In addition to swelling size, I noted the following variables: identity of mating partners, presence/absence of copulation call, temporal occurrence of call in relation to copulation, aggressive behaviours following a copulation, duration to next copulation and composition of the audience during copulation. Only calls that occurred during the copulation were considered to control for the vocalisation being elicited by an alternative stimulus other than the copulation.

Urine sample collection, hormone analysis, and assessment of the fertile period

To determine approximate timing of ovulation and its potential effects on calling behaviour, I collected regular urine samples during the period of maximum tumescence, with sampling gaps of no greater than two days. Samples were collected directly after an individual had been observed urinating by aspiration of the urine from plastic sheets or vegetation using disposable plastic pipettes. They were stored in 2-ml polypropylene Cryotubes in liquid nitrogen until shipment on dry ice to the laboratory. Although I did familiarise myself with the laboratory procedure, unfortunately there was not enough time to conduct assays alone. Therefore, samples were analysed by Tobias Deschner and colleagues (MPI-EVAN), for immunoreactive pregnanediol glucuronide (PdG), using enzyme immunoassay procedures (Heistermann, 1996). The sensitivity of the assay at 90% binding was 12.5 pg. Serial dilutions of urine samples of the follicular and luteal phase gave displacement curves parallel to those obtained with the appropriate standard. Intra- and inter-assay coefficients of variation, calculated from replicate determinations of quality controls were, 7.94 and 6.52% (high) and 13.31 and 11.26% (low), respectively. To compensate for variations in the volume and concentration of urine samples, all hormone levels were divided by the urinary creatinine concentration as described in Bahr et al., (2000). Based on the defined postovulatory rise in PdG levels, the day of ovulation was presumed as the day preceding the day of PdG increase (Deschner et al., 2003; 2004), figure 4.2). Based on human data regarding the survival time of ovum and sperm, the fertile period (POP) was defined as the day of ovulation plus the three preceding days (Deschner et al., 2003), with the post-ovulation period being the period of maximum tumescence following POP.

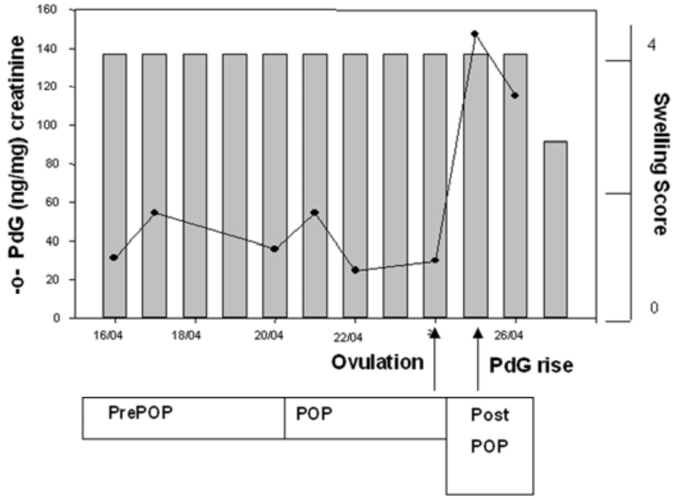

Figure 4.2: Profiles of urinary pregnandiol in ng/mg creatinine and perineal swelling for the adult female WL during April 2007. POP: periovulatory or fertile period, defined as the day of ovulation plus the three preceding days; PrePOP: period of maximum tumescence prior to POP PostPOP: period of maximum tumescence following POP.

Behavioural observations

Male-male aggression

I scored all instances of aggression during copulations, and during the subsequent 10-minute time-window, provided I could identify a target of aggression. Aggressive events could range from ‘mild’, such as arm raises or displays, to ‘severe’, such as chases or stamping and beatings (Slocombe and Zuberbuhler, 2007).

Sperm competition

In wild chimpanzees, it is difficult to determine reliably whether or not ejaculation has occurred (O'Hara and Lee, 2006). Sperm competition has alternatively been assessed indirectly, by measuring the time interval between successive copulation events (Semple, 1998b). The prediction is that sperm competition increases as the time interval decreases.

Male rank

Male rank is known to affect the production of copulation calls in many primate species (Pradhan et al., 2006). In chimpanzees, dominance rank is usually assessed by using the occurrence and direction of pant-grunt vocalisations. The direction of these vocalisations is regarded as a good indicator of relative social status (Bygott, 1979; De Waal, 1982; Newton-Fisher, 1997; Boesch and Boesch-Achermann, 2000). Because of the instability of the male hierarchy at the time of study, it made little sense to attempt to construct a linear dominance hierarchy. Instead I determined the status to each male by calculating the proportion of other males in the community from whom he received pant grunt vocalisations, allowing us to assign each individual with a 'dominance value' (DV=arcsine of the square root of the proportion; Beilharz and Mylrea, 1963). Eight of the community adult males received pant-grunts from other males. There were two clusters of individuals (see table 4.1) with similar DV scores; 5 high-ranking males (NK, DN, ZF, BB, MA) and 3 low ranking males (GS, MS, BO). Juvenile and sub-adult males were not observed to receive any pant-grunts.

Table 4.1: Adult males, dominance value scores and rank groups for the adult males of the Sonso community over the study duration.

Male	DV Score	Rank group
NK	0.5	**High**
DN	0.48	**High**
ZF	0.48	**High**
BB	0.45	**High**
MA	0.38	**High**
MS	0.2	**Low**
BO	0.14	**Low**
GS	0.14	**Low**

Audience effects

Previous work has shown that wild chimpanzees can adjust call production depending on who is likely to listen to their calls (Slocombe and Zuberbuhler, 2007). They usually travel in small family groups, consisting of a mother and her dependent offspring, or in mixed-sex parties of different sizes, usually around 10 individuals. Party composition is relatively fluid, with individuals joining or leaving regularly, and group members are often not in direct visual contact. To determine whether the audience had an impact on copulation calling I noted party composition at 15-minute intervals when following a female. A party was defined as any individual within a 50m radius (Reynolds, 2005) of the focal female. Every time a copulation event occurred, my field assistant and I conducted an additional and more detailed search of the area to account for individuals that might have joined or left the party since the previous scan. This was particularly important for copulations that occurred in trees, where the female has a better observational vantage point than observers on the ground.

Female rank

Female rank was determined in a previous study of female-male aggression (Newton-Fisher, 2006, see table 4.2). Rank relations between female chimpanzees are more stable than between males (Wittig and Boesch, 2003), and there was no evidence of any significant changes since that study.

Statistical analyses

Whenever possible I conducted parametric analyses. If the data failed to meet conditions for parametric analyses, before and after transformation, I used non-parametric statistics. Because the calling behaviour data were scored as a binary response (ie “yes” or “no”) and I was interested in the independent and potentially interactive effect of the different explanatory variables, I also employed a binary logistic regression. Logistic regression makes no assumption about the distribution of the independent variables, that is, whether they are normally distributed, linearly related or of equal variance within each group. The following variables were incorporated into the model: female ID, female audience composition, male rank and male audience number (Wilson et al., 2001). All tests were two-tailed and significance levels were set at $\alpha= 0.05$. For small sample sizes, I calculated exact p-values, as recommended by Mundry and Fischer (1998). All described statistical analyses were done using SPSS v. 15.0 and R version 2.5.1 (R Core Development Team, 2007).

Results

Mating behaviour of female chimpanzees

All seven monitored females gave copulation calls during mating, but only in a minority of cases: The females copulated a total of 287 times and produced copulation calls during only 104 (36%) of copulations (table 4.2). The females were more likely to produce copulation calls when they mated with high-ranking adult males than low-ranking males (Wilcoxon exact test $N_{\text{females}} = 7$, $Z = -2.37$, $p=0.016$, figure 4.3), with all seven females showing the same pattern (Cronbach’s alpha test for reliability = 0.791, figure 4.4). There was no difference in calling behaviour when females copulated with low-ranked adult males and even lower-ranking subadult males (Wilcoxon exact test $N_{\text{females}} = 7$, $Z = -0.405$, $p=0.813$).

Table 4.2: Rank and copulation calling behaviour of seven adult females of the Sonso community, Budongo Forest, Uganda (adapted from Newton-Fisher, 2005).

Female	**Female rank**	**Total number of copulations**	**% copulations accompanied by a call**
LL	Low	66	53
WL	Low	68	34
NB	Alpha	50	38
MK	Low	37	35
KU	Low	18	11
KY	High	29	24
JL	Mid	19	26
Total		287	36

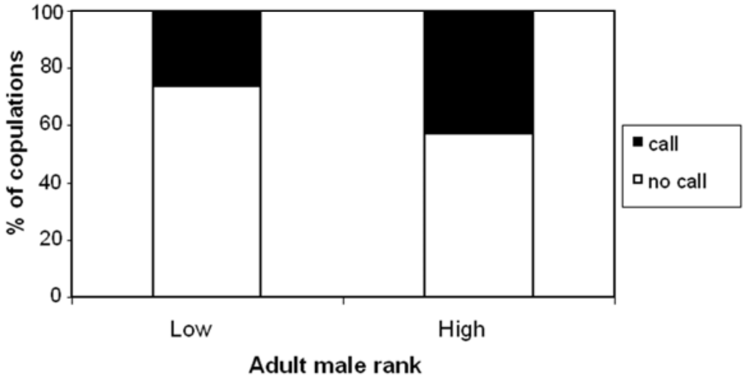

Figure 4.3: Copulation calls and the effect of male rank. Bar graphs showing the percentage of copulations accompanied by calls given by seven females when copulating with high (N=5) and low (N=3) ranking males.

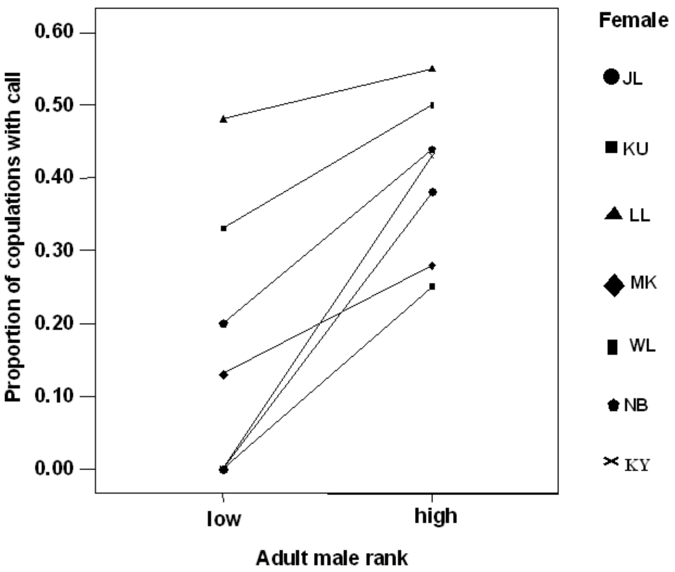

Figure 4.4: Individual variation in copulation calling behaviour. Line graphs showing the proportion of copulations accompanied by a call when copulating with high (N=5) and low (N=3) ranking males for each of the seven females.

35 (12%) observed copulations elicited aggression by a third party individual, either leading to interruption of the copulation or to targeted aggression to one of the mating partners within 10 min. There was no difference in the occurrence of aggression after silent or vocal matings (controlled for copulation number: N_{silent}=26, N_{vocal}=9, binomial test (0.63), p=0.2, two-tailed). Out of the nine instances of aggression following a vocalisation, four were caused by high-ranking females, three by high-ranking males, and two by low ranking males. These four cases of female-caused aggression were particularly severe and always directed at a low-ranking female. If the same four low-ranking females copulated, but remained silent, then the high-ranking females never responded with aggression. In no case were they likely to see the copulation event (Fishers exact test, two-tailed, N_{silent} = 4, N_{vocal} =4, p=0.02).

Finally, I found no relation between the time interval between successive copulations with different males and the likelihood of a female producing copulation calls (Wilcoxon exact test; Z=-0.314, N_{silent}=6, N_{vocal}=6, p=0.844).

Hormonal analyses

In collaboration with Tobias Deschner, we were able to analyse the hormonal profiles of six complete oestrus cycles (LL: N=1; WL: N=3, NB: N=2), which allowed us to determine the exact time of ovulation. Females called prior to the fertile peri-ovulatory period (Pre-POP), during the fertile peri-ovulatory period (POP) and after ovulation (Post-POP). Because one female (WL) did not exhibit a Post-POP period and another (NB) did not exhibit a Pre-POP period, only five cycles were included for each analysis. I found no significant difference in the calling rate between Pre-POP and POP periods (Binomial GLMM with female ID as a random factor Z=-0.789, N=121, p=0.430) or between POP and Post-POP (Binomial GLMM with female ID as a random factor, Z=-1.344, N=117, p=0.181).

Audience effects

To test for audience effects, I randomly selected for each of the seven females an equal number of copulations (N=18), which were subjected to analyses, i.e. N=126 total. Adult male audience size had no effect on call production by the copulating female (Mean $males_{silent}$ = 3.6, Mean $males_{vocal}$ = 3.45, Wilcoxon Exact test Z=-1.10, $N_{females}$ =7, p=0.328; figure 4.5), despite the fact that there were consistently more high-ranking males present when a female copulated with a high-ranked male (Paired T test; t=-4.916, $N_{females}$ = 7, p <0.001). In contrast, the number of adult females in the party had a significant effect on call production (Mean $females_{silent}$ = 3.41, Mean $females_{vocal}$ = 2.3, Mann Whitney U test: U= 536, N_{silent} = 62, N_{vocal} = 28. $N_{females}$= 5, p=0.04, figure 4.5); females called less the more adult females were in the party. Sample sizes were too small for two females (NB, KY), who were excluded from this analysis. Both were high-ranking females and there were indications that they behaved differently in the presence of other females, compared to the other five lower-ranking females. The observed audience effect was mainly driven by the social position of listening females. Females called significantly less if they were surrounded by a female audience that contained individuals of equal or higher rank than themselves (Mean $\text{females}_{\text{silent}}$ = 3.38, Mean $\text{females}_{\text{vocal}}$ = 2.01, Mann Whitney U test: U= 516, $N_{\text{silent}} = 62$, $N_{\text{vocal}} = 28$, $N_{\text{females}} = 5$, p=0.025).

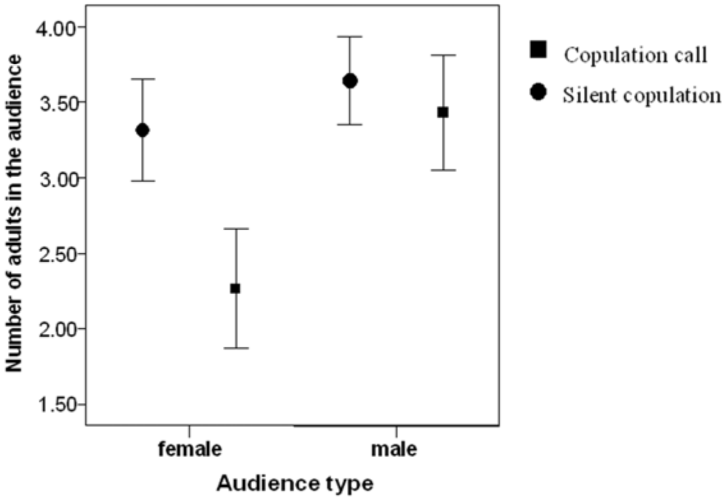

Figure 4.5: Mean number of individuals in the audience in the presence/absence of a copulation call. Female audience ($N_{\text{females}} = 5$, $N_{\text{copulations}}=90$): the number of adult females present. Male audience ($N_{\text{females}}=7$, $N_{\text{copulations}}=126$): the number of adult males present. Error bars represent Mean +-1 SE.

I was particularly interested in how female audience composition affected calling behaviour. To identify the independent and potentially interactive influence of the determining variables I conducted a binary logistic regression. Of the variables tested male rank, female audience composition and male rank*female audience composition explained a significant proportion of the overall variance (binary logistic regression with female ID as a random factor χ^2 = 8.595, N=90, Nagelkerke r^2 =0.421, male rank p= 0.004, female audience composition p=0.029, male rank*female audience composition p=0.043). The model explained variation in female calling behaviour with 82% accuracy, a rate significantly higher then that when running the model with no explanatory variables (Binomial (0.7), p= 0.024, two-tailed). The significant interaction effect suggested that the females' response to female audience composition also depended on the rank of the male mating partner. Whilst there was a trend to call less when more high-ranking females were in the audience for both rank groups, this was most apparent when females copulated with high-ranked males (figure 4.6).

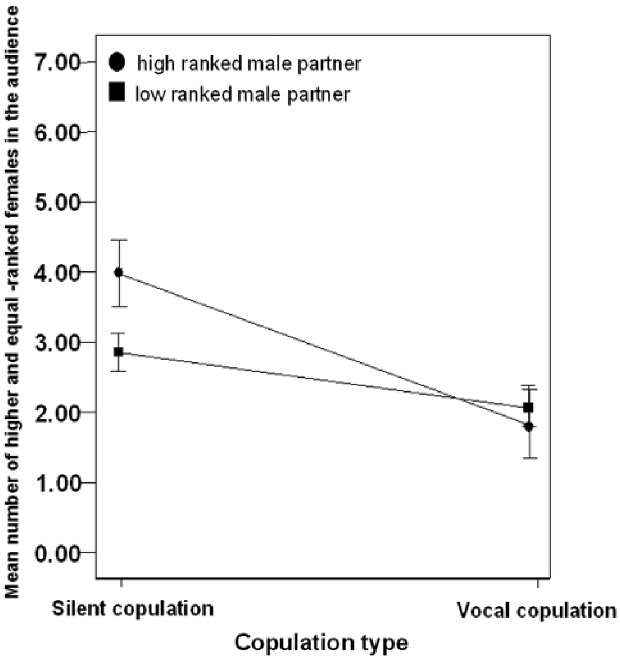

Figure 4.6: Line graphs showing the mean number of high and equal ranked females in the audience when copulating with a) high ranked males and b) low ranked males. Error bars represent Mean +-1SE.

Discussion

Overall, this study lent no support to the ‘male-male competition’ hypothesis of copulation calling (Cox and Le Boeuf, 1977) despite its prominence in the sexual behaviour literature. Specifically, females did not produce calls when mating with low-ranked males in order to instigate disruption by high-ranked individuals (Nikitopoulos et al., 2004; Pradhan et al., 2006). Instead, they called more when mating with higher-ranked males, an effect also reported in other primate species (O’Connell and Cowlishaw, 1994; Oda and Masataka, 1995; Semple et al., 2002; Nikitopoulos et al., 2004). In this sample, copulation calls did not lead to increased levels of aggression towards the mating pair. I also found no evidence that chimpanzee copulation calls operated at the ‘sperm competition’ level (O’Connell and Cowlishaw, 1994). Whilst it was virtually impossible to determine the occurrence of ejaculation, the duration to the next copulation was unrelated to the female’s calling behaviour. Instead, females produced copulation calls preferably when mating with high-ranked adult males, but suppressed calls if high-ranked females were present. Hormonal analysis showed that female calling behaviour was unrelated to their fertile period and likelihood of conception.

If the male-male competition hypothesis does not explain copulation calling behaviour, then why do females call? My results suggest that other social variables are important in driving these vocalisations. Females call significantly more when copulating with high- compared to low-ranked partners, and since other dominant males are usually nearby in these circumstances, calling is one potential strategy allowing a female to signal her receptivity to a large audience of high-ranked males. Although females appear to be motivated to advertise their receptivity, they do not provide any information about the timing of their ovulation, a pattern that also holds for Barbary macaques where precise information on the timing of ovulation is not available in copulation calls (Pfefferle et al., 2008a). By calling in the presence of high-ranking adult males and by concealing ovulation, females may prevent monopolisation by a single male and to increase paternity confusion amongst other males.

Research from long-term field studies increasingly shows that chimpanzee females are exposed to severe social pressure from other group members, especially when resources are limited. In chapter three I have shown that female chimpanzees can suffer substantially from infanticide-related threats. In this context, confusing paternity, particularly amongst socially important males, has a two-fold advantage. Firstly, it reduces the probability that males will attack infants potentially sired by them (O'Connell and Cowlishaw, 1994). Secondly, it is likely to improve a male's general willingness to provide support, including during female-initiated agonistic encounters. Possibly because of their previous mating history, high-ranking males have been observed to intervene during female aggressive events, which in some cases have resulted in female-led infanticidal attacks, at Gombe (Pusey, 1980, Pusey et al., in press), Mahale (Nishida, 1989) and Budongo (see chapter three). My data are consistent with the idea that chimpanzee females use copulation calls as a vocal counter-strategy to minimise these threats.

Chimpanzees produce copulation calls at much lower rate than other primates (Pradhan et al., 2006), suggesting females take other factors into account, apart from trying to increase paternity confusion. My data suggest that lower ranking females refrained from calling when mating with high-ranking males if high-ranking females were nearby, suggesting that they were trying to conceal their sexual activity in these circumstances.

Unlike most other primates, chimpanzee females leave their natal group at adolescence to immigrate into neighbouring communities. Immigration can affect the adult sex ratio of a group (see chapter three), increasing competition for resources between females, such as high-quality foraging areas (Pusey et al., 1997; Kahlenberg et al., in press a), and possibly the amount and quality of available sperm (Nakatsura and Kramer, 1982; Dewsbury, 1982; Van Voorhies, 1992; Gage and Cook, 1994; Preston et al., 2001; Weddell et al., 2002; Marson et al., 1989). As a consequence, more competitively able high-ranking females should have an interest in maximising their own access to such resources and escalated aggression may be one strategy (see chapter three, Pusey et al., 1997; in press; Kahlenberg et al., in press b). One counter-strategy for lower-ranked females is to form short-term associations with the adult males of the community (Kahlenberg, Pers. comm.; in press b) and, as suggested by this study, to modify their copulation calling behaviour (De Waal, 1982) when high-ranking resident females are likely to witness their sexual activities.

To conclude, female copulation calls in primates and other groups of animals have usually been interpreted as male-directed signals, for example to advertise fertility and incite male-male competition, but my findings in wild chimpanzees do not support this view. In this study, chimpanzee females adjusted their calling behaviour in flexible ways, potentially to avoid aggression from other females and possibly to secure future benefits from the socially important males. Data from more females and different study sites will be required to test this hypothesis more thoroughly (see chapter seven). For many years, female chimpanzees have been regarded as the more peaceful sex. However, there is increasing evidence from a number of communities studied in the wild, which indicates that female competition plays an important role in dictating female behaviour and these data provide further support for this view. My results indicate that the social pressures deriving from resource competition have acted as an important selective force, shaping the copulation calling behaviour in wild chimpanzees.

Chapter Five: Copulation calls in female chimpanzees convey social information

Summary

Copulation calls are a relatively common feature of female primate behaviour. As shown in the previous chapter, wild oestrous chimpanzees produce these calls probably to avoid monopolisation by single males and to minimize aggression by other females. In this chapter, I investigated to what further degree such social demands were reflected in the calls' use and acoustic structure. Although females were generally reluctant to produce copulation calls when mating with low-ranking males, they called regularly in trees where furtive mating with these males was not possible. Hormonal analyses showed that the acoustic structure of copulation calls did not covary with the ovulatory status of the calling female, further confirming my previous findings that the calls functioned to confuse paternity. However, the calls' acoustic structure reliably encoded the identity of the calling female and to some extent whether her male partner was of high or low social rank. In sum, chimpanzee females may be providing honest information to other group members about their sexual activity although they appeared to act strategically as to when to provide this information.

The results from this chapter have been submitted for publication:

Townsend, S.W, Deschner, T., & Zuberbuhler, K. (Submitted). Copulation calls in females chimpanzees convey social information.

Introduction

In many primates copulation calls are thought to alert nearby males to the female's receptive state, inciting competition amongst them (O'Connell and Cowlishaw, 1994; Henzi, 1996; Semple, 1998b; Semple et al., 2002). However in the previous chapter I have shown that male-male competition is probably just one of a number of social factors that influence reproduction and its accompanying behaviours. Females called most when with high-ranking males, regardless of their exact fertile phase, possibly to confuse paternity and enlist future support from socially important males against aggressively competitive female chimpanzees. Since high-ranking males have the power to avert infanticidal attacks by other group members (primarily females at Budongo), oestrous females should thus be particularly interested in mating with them, especially if males use their mating history as a measure of paternity certainty (Murray et al., 2007; see chapter three).

Infant chimpanzees are most vulnerable in the first few months after birth, particularly due to infanticide by other group members (Goodall, 1986; Reynolds, 2005). However, chimpanzee offspring depend on their mothers for more than a decade and subsequently both rely on males in a number of contexts, such as encounters with predators (Boesch, 1991b), raids from neighbouring communities (Mitani & Watts, 2005), or during competition over resources (Kahlenberg et al., in press a). Given that male rank relations can change rapidly with young males typically rising through the ranks in a few years, choosing to mate with young low-ranking males may be part of a successful longer-term social strategy for any female, confusing paternity more widely amongst the males (Goodall, 1986; Boesch and Boesch-Achermann, 2000; Reynolds, 2005).

In all chimpanzee communities, oestrous females have been observed to mate with low-ranking males. This female strategy sets up an inevitable conflict of interest between males and oestrus females. As a result, high-ranking males tend to aggressively exclude lower ranking males from mating, usually by harassing the female (Goodall, 1986; Hauser, 1990; Watts, 1998; Boesch and Boesch-Achermann, 2000; Van Schaik et al., 2004; Kahlenberg, 2006; Duffy et al., 2007). Perhaps due to this additional social threat, matings with low-ranking males are ostensibly cryptic and females often refrain from producing copulation calls. At Sonso, females have been seen sneaking away from the main party, in order to copulate silently with a low-ranking male and then return to the rest of the group (Reynolds, 2005), a behaviour also observed at other research sites (Gombe: Goodall 1986; Tai: Boesch and Boesch Achermann, 2000). However, females sometimes call during copulations with low-ranked males, a finding that was hard to explain from the previous study and something that I was particularly interested in investigating.

Copulation calls play an important role in the lives of female chimpanzees helping them to avoid social conflict and secure reproductive success. Given the unusually long chimpanzee inter-birth intervals in comparison to other non-human primates (Tutin, 1979), natural selection is likely to favour mechanisms that enhance any such function. Encoding social information within the acoustic structure of these calls is one potential mechanism.

As described in chapter one, animal vocalisations are capable of encoding varied information sets. Despite this potential, to date, most copulation call studies have focused primarily on the contexts eliciting production with little attempt made to assess what additional information may be encoded within the acoustic structure of these calls. This is a vital piece of the puzzle that needs to be addressed if we are to better understand exactly why female chimpanzees produce copulation calls and, more broadly, how they function in their daily lives.

In this study, I was interested in elucidating what information copulation calls conveyed to the listening audience and how this related to the adaptive function of these vocal signals.
In their natural forest habitat, chimpanzees typically travel in family units or small parties of less than a dozen individuals and individuals rarely have direct visual contact with all other group members. Since females sometimes overlap in their oestrous cycles and because their relationships are individualised (Goodall, 1986; Muller et al., 2006), I expected females to provide acoustic cues that revealed their individual identity, as already described in female baboons (Semple, 2001). In the previous study (see chapter four) it was shown that female chimpanzees tried to maximise paternity confusion amongst males. I thus predicted that natural selection should act against signalling the fertile period as this would lead to monopolisation by the most powerful male and decrease paternity certainty of others (Pradhan and van Schaik, 2008). Hence, in addition to call rates, there should also be no acoustic differences in copulation calls given by a female during her ovulatory phase and after ovulation, when conception is impossible (Pfefferle et al., 2008a). Finally, if high-ranking males aggressively exclude low-ranking males from mating, females should behave strategically when mating with low-ranking males (Pradhan et al., 2006). One possible strategy for females therefore is to remain silent if furtive mating is possible or, if this is not, produce copulation calls but honestly signal the rank of the male with whom they are mating (Semple et al., 2002).

To systematically investigate the potential information content conveyed in these signals and to further understand in what ways female chimpanzees use their copulation calls, I analysed the acoustic structure of wild female chimpanzee copulation calls from the Budongo Forest, Uganda.

Methods

Study site and animals

I studied a number of individuals residing in the Sonso community of the Budongo Forest, Uganda, between Jan -Apr 2006 and Oct 2006-Mar 2007. During this period, I observed 287 copulations to which females produced calls on 104 occasions. Recordings of calls were collected from 6 adult cycling females using all day focal follows throughout the female's maximum tumescence phase. If more than one female was in oestrus, additional ad-libitum copulation call recordings were taken.

Urine sample collection, hormone analysis, and assessment of fertile period

To determine approximate timing of ovulation, I collected regular urine samples during the period of maximum tumescence, with sampling gaps of no greater than two days. Through Enzyme immuno-assaying (EIA) PdG levels in urine, Tobias Deschner and colleagues could reliably identify the day of ovulation and hence the female's fertile period. For more details regarding hormonal analysis see chapter four.

Male rank

As explained in chapter four, I determined the status of each male by calculating the proportion of other males in the community from whom he received pant grunt vocalisations. There were two clusters of individuals with similar dominance value scores (see chapter four); 5 high-ranking males (NK, DN, ZF, BB, MA) and 3 low ranking males (GS, MS, BO). Juvenile and sub-adult males were not observed to receive any pant-grunts.

Acoustic analyses

Using PRAAT software I focused on the following temporal parameters: 1) Call bout length (s): total duration of the copulation calling bout, 2) N call units: number of individually distinct call units within the calling bout and 3) inter-call interval (s): time duration between each successive call unit. The following frequency measurements were taken: (1) Peak fundamental frequency: location in the frequency domain where maximum acoustic energy occurred in the F0 in the call middle (Hz); (2) Peak frequency at call beginning: frequency where maximum acoustic energy occurs at call beginning (Hz); (3) Peak frequency of the call at call middle: frequency where maximum acoustic energy occurs at call middle (Hz); (4) Peak frequency of the call at call end: frequency where maximum acoustic energy occurs at call end (Hz); (5) transition onset: frequency modulation between call beginning and middle (Hz); (6) transition offset: frequency modulation between call middle and call end (Hz); (7) Mean Pitch: average pitch over call unit (Hz) (see figure 5.1 and 5.2). Measurements of the frequencies at which maximum acoustic energy was present were obtained by creating spectral slices (Amplitude plotted against frequency; figure 5.2) at the relevant points indicated in figure 5.1.

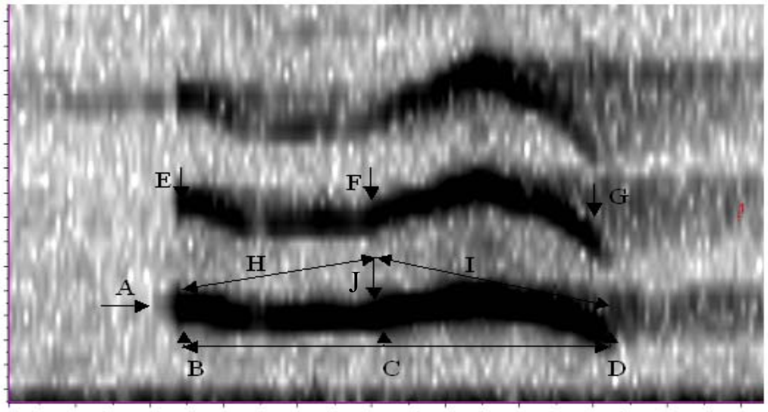

Figure 5.1: Illustration of how spectral parameters were taken: A: Fundamental frequency band. B: Call beginning C: Call middle D: Call end. Peak frequency measures in the fundamental were taken initially at the beginning, middle and end of call, to facilitate transition onset/offset determination, though only call middle remained in the final model (J, see figure 5.2). E: Peak Frequency of call at call beginning F: Peak Frequency of call at call middle G: Peak frequency of call at call end (see figure 5.2) H: Transition onset I: Transition offset. Mean pitch is not illustrated (see appendix I for identical procedure).

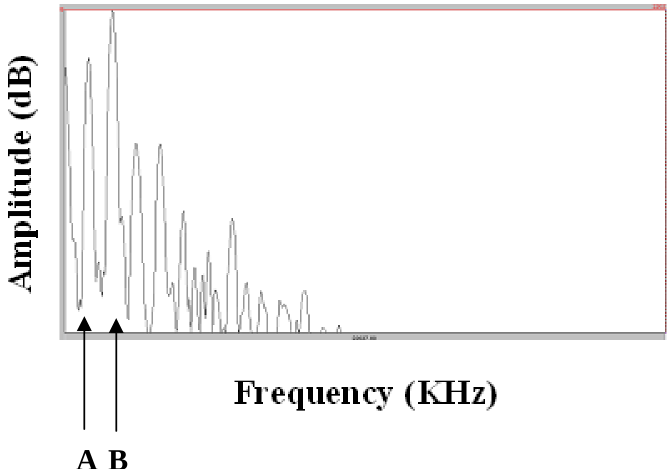

Figure 5.2: Illustration showing how peak frequency of the fundamental (J) and of the call (E,FG) were measured at each call stage (beginning, middle, end; figure 5.1). The first spike (A) denotes the peak frequency of the fundamental and the second spike (B) denotes the peak frequency of the call.

Statistical analyses

I performed co-linearity checks for the 10 parameters and found that all had satisfactory variance inflation factors of less than 8.0 (Slocombe and Zuberbuhler, 2007). Variance inflation factors (VIF) 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. I analysed all calls given during a bout and calculated a median value for each parameter, which was then subjected to statistical analyses. I ran MANOVAs and two-way univariate GLMs to explore the effect of categorical variables on the acoustic structure of copulation calls, e.g. male rank and cycle period. Univariate GLMs account for multiple contributions from the same individual by incorporating female ID as a random factor in the model (Pinheiro and Bates, 2000; Deschner et al., 2003). If appropriate, I then used a Discriminant Function Analysis (DFA) to verify whether acoustic structure could be quantitatively assigned to particular variables. All ten acoustic parameters were used to generate the discriminant function. Since the acoustic data for male rank were two-factorial (female ID; male rank), it has been argued that conventional DFA does not allow for a valid estimation of the overall significance of discriminability (Mundry and Sommer, 2007). If the original DFA achieved significance, I used a permutated Discriminant Function Analysis (pDFA) to estimate the significance of the number of correctly classified calls (cross-validated). To determine the effect of location on calling probability I conducted a binary logistic regression (see chapter four). All tests were carried out using SPSS version 15.0 and R version 2.5.1 (R core development team). Alpha levels were set at 0.05.

Results

Female Identity

To determine if female chimpanzees gave individually distinctive copulation calls, I analysed 256 calls, constituting 71 calling bouts from 6 cycling females (LL: N=23; MK: N=11; NB: N=9; WL: N=19, JL: N=4; KY: N=5). A between-subjects MANOVA showed that female identity significantly affected the acoustic structure of copulation calls (F(5,60)=2.288, Wilks Lambda=0.47, P=<0.001). 5 of the 10 acoustic parameters varied significantly amongst individuals throughout the cycle. The acoustic parameters that accounted for most of the variance were all frequency measures: peak frequency in F_0 (F(5,42)=7.350, P<0.001, peak frequency at call beginning (F(5,42)=3.176, P=0.016), peak frequency at call end (F(5,42)=3.808, P=0.006), transition onset (F(5,42)=4.431, P=0.002), and mean pitch (F(5,42)=4.879, P=0.001). Discriminant Function Analysis revealed that the 10 acoustic variables explained a significant amount of variation amongst the individual female callers (Wilks' lambda = 0.085, $\chi^2_{(55)}$: 141.41, P <0.001). Calls could be classified to individual females with 56% accuracy (cross-validated), a rate significantly above chance expectation (Binomial (0.167), P<0.001, 2-tailed).

Female Ovulatory Status

To investigate whether females provided reliable information about their fertility state, I compared the acoustic structure of copulation calls given during their POP (N_{calls}=16) and Post-POP (N_{calls}=10) from five complete maximally tumescent oestrus cycles (LL: N=1; NB: N=2; WL: N=2). A two-way between-subjects ANOVA (with female identity as a random factor) indicated that the female's fertile phase had no effect on any of the 10 temporal or spectral acoustic parameters (all p-values > 0.1 see table 5.1), suggesting that fertility was not acoustically marked in chimpanzee copulation calls. Because I found no differences, or even trends, in any of the acoustic variables, I refrained from conducting further discriminant function analyses.

Table 5.1: Results of Univariate ANOVA's, comparing each acoustic parameter measured, during POP and Post-POP.

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Acoustic parameter	F-Value	P Value
Call duration	$(F_{1,20})$ 0.139	**0.74**
Call unit duration	$(F_{1,20})$ 0.829	**0.439**
Interval duration	$(F_{1,14})$ 0.861	**0.435**
Peak frequency in fundamental middle	$(F_{1,20})$ 0.026	**0.887**
Peak frequency at call beginning	$(F_{1,20})$ 0.154	**0.73**
Peak frequency at call middle	$(F_{1,20})$ 0.313	**0.624**
Peak frequency at call end	$(F_{1,20})$ 0.055	**0.833**
Transition onset	$(F_{1,19})$ 0.528	**0.525**
Transition offset	$(F_{1,19})$ 0.485	**0.54**
Mean pitch	$(F_{1,18})$ 0.316	**0.624**

Male dominance rank

To determine if female copulation calls vary acoustically with male rank, I analysed calls from five females whilst copulating with high and low-ranked males. A between-subject univariate ANOVA, with female identify as a random factor, revealed that peak frequency at call beginning was significantly higher when females mated with high-ranked than with low-ranked males (Sidak corrected for multiple comparisons F(1,54)=24.064, P=0.006; see figure 5.3 and 5.4).

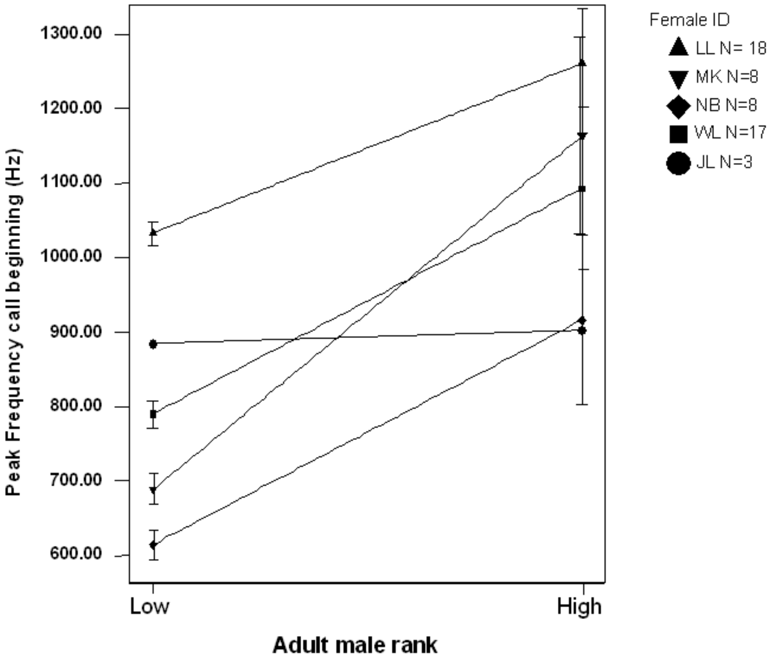

Figure 5.3: Mean peak frequency at copulation call beginning (Hz) for each female when copulating with high and low-ranked adult males. Error bars represent mean +-1SE. Differences are mainly caused by shifts in the location of acoustic energy from the fundamental frequency to one of the harmonics at call onset.

When taking all 10 acoustic parameters into account, a DFA failed to explain a significant amount of variation in the acoustic structure of copulation calls given with low and high-ranked males (Wilks' lambda =0.682, $\chi^2_{(12)}$=12.615, P=0.398). Only 46.3% of copulation calls were correctly classified (cross validated) according to the rank of the mating male, a level below that expected by chance. Given that only one acoustic variable differs between male ranks, this last DFA finding was to be expected. Therefore on a more crude, all parameter level, copulation calls do not seem to differ with partner rank, though at a more fine scale there are subtle and striking differences.

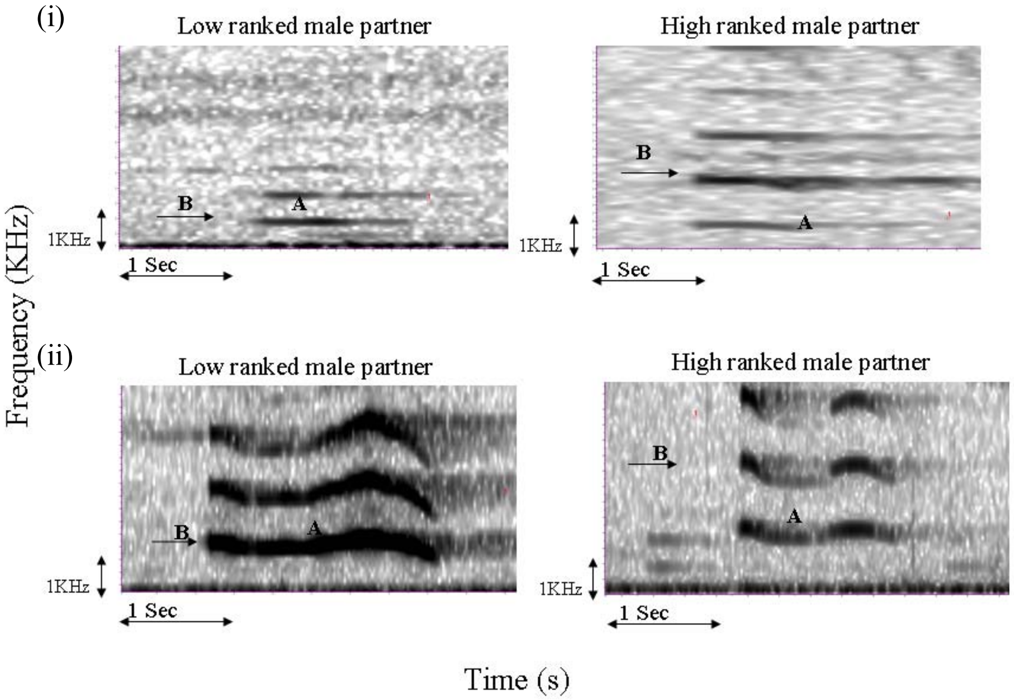

Figure 5.4: Time-frequency spectrogram for female chimpanzees (i) LL and (ii) WL when copulating with high and low-ranked adult males. Filter bandwidth: 159Hz, Frequency resolution: 86.1Hz. Visible are the fundamental frequency (A) and the first two harmonic bands. (B) indicates the frequency at the beginning of the call where maximum energy occurs (peak frequency of the call).

Finally, in cases when females mated with low-ranking males (N=98), their vocal behaviour was affected by location. When at least one high-ranking male was present (N=80), calling females copulating with a low-ranking male called significantly more if they were exposed in a tree than on the ground in more dense vegetation (controlled for copulation number, binomial logistic regression B=-2.148, P<0.001). An identical analysis with high-ranking males found no such difference between tree and ground (B=0.575, P>0.1).

Discussion

In the previous chapter, I have shown that female chimpanzees use copulation calls in flexible and potentially strategic ways, probably to confuse paternity and to gain the future support of adult community males (see chapter four). My results here further support the paternity confusion hypothesis but also highlight that natural selection appears to have favoured acoustic variation within these calls. In particular, calls may encode caller identity and very subtly, the relative social position of the male mating partner.Whether other chimpanzees perceive these acoustic differences will have to be further investigated.

I interpret these findings as follows: Firstly, although chimpanzee females appear to be motivated to advertise their receptive state through calling, they do not provide accurate information about the timing of ovulation, a pattern also found in barbary macaques (Pfefferle et al., 2008a). By concealing ovulation, females prevent monopolisation by a socially dominant male and hereby increase paternity confusion (Pradhan and van Schaik, 2008), a strategy that is likely to secure them with future protective support. Whilst females are probably primarily interested in copulating with high-ranking males, young low ranking males will play an important role in the intermediate future (Boesch and Boesch Achermann, 2000; Stumpf and Boesch, 2005; Pradhan et al., 2006). It is therefore possible that ovulation concealment has evolved under the selection pressure of paternity confusion amongst high-ranking and to some extent lower ranking males (Tutin, 1979; Goodall, 1986; Boesch and Boesch Achermann, 2000; Reynolds, 2005).

It has been shown that chimpanzee males exhibit mating preferences for older females (Muller et al., 2006), possibly because they require fewer cycles before conception (Deschner and Boesch, 2007). Given that concurrently cycling oestrous females may compete with each other over access to males (see chapter four) the ability to convey identity becomes a useful tool, keeping potential listening male mating partners informed as to the whereabouts of certain females.

Finally, most surprisingly, this study has also indicated that the dominance rank of the mating male has a subtle effect on the acoustic structure of primate copulation calls. Whilst it has previously been shown in yellow baboons that temporal acoustic parameters differ with the rank of the male mating partner (Semple et al., 2002), no difference was found in frequency-based call measures. Only one acoustic variable out of ten measured, varied with male rank, and because of this, discriminant function analysis failed to separate the calls overall. However, it is not unlikely that chimpanzees are able to use these acoustic cues, when attending to calls, and that even very subtle changes in the acoustic structure are salient to listeners.

From a more functional standpoint, what advantages could there be to copulating females signalling the rank of the mating male in their copulation calls?

I found that female chimpanzees generally prefer to remain silent when copulating with low-ranking males, usually after taking active steps to ensure furtive mating (Pers. observations). However, females sometimes do still produce copulation calls in these circumstances, and this was one aspect of calling behaviour that remained unexplained. My results here suggest this may be related to the likelihood of detection by other group members, in these instances, high ranking males. When mating with a low-ranking male, females produced copulation calls significantly more often if mating took place in a tree where the female is visually exposed and has little control over a male’s solicitation. Indeed, a recent instance of attempted solicitation by a male in a tree resulted in a 40m fall, which ultimately ended with the female’s death (BCFS long term data). Not only are tree matings more precarious but females are generally prevented from furtive mating, in contrast to when they are in the dense vegetation on the ground.

Mating with a low-ranking male is socially risky. High-ranking males have been seen to attack females for copulating with low-ranking males and it is thought that such sexual coercion helps improve high-ranking male access to preferred females (Van Schaik et al., 2004; Kahlenberg, 2006). Interestingly, high-ranking males appear to avoid confrontations with other males, even the low-ranking ones, and thus it is normally the females that receive the brunt of such male aggression (Goodall, 1986; Hauser, 1990; Matsumoto-Oda, 1999). I tentatively propose that, with an acoustically distinctive copulation call, females are providing some form of honest information regarding the rank of her copulating partner, and it is possible that this decreases male aggression. In other words, owning up to their dealings, rather than continuing to mate surreptitiously, may allow females to control the potential for aggression from high-ranking males in these risky situations.

In line with the results presented in chapter four, these data suggest that the primary function of chimpanzee copulation calls is to spread the probability of paternity more evenly amongst adult male group members enlisting their future protective support. Whilst high-ranking adult males represent the most efficient short-term protectors, low-ranking males can become high-ranking in the future, hence mating and paternity confusion amongst these males may also be part of a female’s long term sexual strategy. Furthermore, my analyses suggest that the identity of the female is encoded within copulation calls and so potentially available to listening males. Given that multiple females can cycle simultaneously and that with increasing age some females become preferred over others (Tutin, 1979; Muller et al., 2006) labelling one's own identity may increase overall fitness levels. Taken together, these findings suggest that female competition, and the aggression that accompanies it, may be more of a signifant social pressure than previously recognised, shaping not only call production, but also the fine acoustic structure of copulation calls.

However, it would be naïve to think that female competition is the only relevant social pressure female chimpanzees are exposed to in the reproductive context. Female and male sexual strategies rarely complement each other and strong conflict of interest is often the result (Van Schaik et al., 2004). Females chimpanzees should be interested in paternity confusion, reducing the risk of male and female infanticide, whilst males should be interested in maximising paternity certainty (Hrdy, 1977; Van Schaik et al., 2004; Pradhan et al., 2006). Although my results on copulation calling frequency (chapter four) did not seem to indicate this, more detailed acoustic and location analyses did to some extent: copulation calls acoustically label the rank class of the male partner. Honestly indicating the rank of the mating partner may be an additional vocal strategy employed by female chimpanzees to moderate the aggressive potential of nearby high-ranking males.

It should be stressed that this is just a working hypothesis and one potential explanation of many. To test this last theory more thoroughly, long-term data analyses on calling behaviour, aggression and habitat location need to be implemented, in addition to including more copulation calls from high and low ranked mating partners. Possibly due to the unusual male:female sex ratio at Budongo (1:3) (chapter three, see also Stumpf and Boesch, 2005) male-female aggression was rarely observed over the 10-month study period (35/287 copulation events). However, records from previous years with more representative sex-ratios indicate that this is not the norm and female-directed male aggression does indeed occur (BCFS long term data, Newton-Fisher, 2005, Pers. comm.) However, until such data are available, these results should be viewed cautiously. The logical next step will be to experimentally verify whether these calls are meaningful in this way to other group members and to what degree males, or indeed females, are guided in their behavioural decisions by these acoustic cues.

To date, no close range playback has been conducted with wild chimpanzees to test what they understand from calls and how they can use this information to their social advantage. Because chimpanzee copulation calls are likely to play a crucial role in a female's reproductive success it would be unwise to attempt the first comprehension playback with such an important vocal signal.

In chapter six I sought to overcome this problem by experimentally testing the meaning of victim screams. Like copulation calls, these vocalisations play an important role in the social lives of wild chimpanzees, but because of their ubiquitous occurrence, are less likely to adversely affect the future success of these animals. Victim screams therefore provide the perfect oppurtunity to test how females chimpanzees comprehend vocalisations and what potential social benefit this affords them.

Chapter Six: Wild chimpanzees distinguish between different scream types: evidence from a playback study

Summary

When experiencing aggression from group members, chimpanzee females commonly produce screams. These agonistic screams vary acoustically as a function of the severity of aggression the caller is facing. To determine whether individuals could meaningfully distinguish between screams given in different agonistic contexts, I conducted a series of field playback experiments with a community of wild chimpanzees in the Budongo Forest, Uganda. Possibly due to the challenging nature of their vocal repertoires and social systems, no previous attempts have been made to experimentally test call comprehension in any wild great ape species. In this study, I compared subjects' responses to screams given in severe and mild aggression. Subjects consistently discriminated between the two scream types in ways that suggested they assigned meaning to these calls. In order to control for the possibility that response differences were a product of the screams' peripheral acoustic features, rather than any encoded social meaning, I employed a control condition. I used tantrum screams, given by individuals that experienced extreme social frustration, but no physical threat. Acoustically, tantrum screams matched severe agonistic screams in their peripheral acoustic features, although they conveyed very different information. Accordingly subjects showed little interest in these calls. Together, these results demonstrate that chimpanzees are able to meaningfully distinguish between these graded scream variants. Recent research has indicated that females can compete aggressively and even lethally for resources. I therefore suggest that by attending to conspecifics' calls, chimpanzees can understand the nature of social events they cannot see and potentially use this information to make future evasive behavioural decisions.

The results from this chapter have been submitted for publication

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Introduction

Discriminating between signallers and receivers and investigating the associated behavioural and cognitive processes separately, is one particularly useful approach to studying animal communication (Seyfarth and Cheney, 2003). In the previous chapters I have focused on copulation calling in wild chimpanzees and how the use and acoustic structure of this vocalisation has been potentially shaped by social pressures. This work has begun to address the question of chimpanzee vocal counter-strategies to female competition, but primarily from the producer's perspective. If we are to get the full picture as to the role vocalisations play in mediating female competition, it is necessary to understand what the receivers can extract from vocalisations. In this chapter I attempt to address this question for the first time in any wild ape species, focusing specifically on what female chimpanzees understand from agonistic screams.

Once considered a solely male affair, intense aggression is now known to be an important feature of both male and female chimpanzee social lives (Kahlenberg et al., in press (a); Pusey et al., in press; see also chapter three). In females, such aggression is thought to be a result of competition for resources such as food, or even male mating partners and can have considerable fitness consequences, sometimes culminating in lethal infanticidal attacks (chapter three).

Due to the dense nature of the chimpanzee natural habitat and the fission-fusion nature of their social system however, female chimpanzees cannot always directly observe ongoing conflicts. Therefore, the ability to make references about the nature of events would be clearly adaptive, allowing individuals to make a number of important decisions, such as whether or not to intervene, or to avoid the ongoing interaction. Furthermore, the ability to monitor out-of-sight agonistic interactions will greatly increase the amount of social knowledge about third party relationships an individual female can accumulate. Compiling of social knowledge is likely to have direct fitness benefits and may have even driven the evolution of large brains in primates (Humphrey, 1976).

Previous research has indicated that non-human primates appear to be capable of extracting meaning from calls given during agonistic interactions. The agonistic screams of rhesus macaque monkeys for example, have been shown to vary with the severity of the attack and the rank of the opponent (Gouzoules et a., 1984). Subsequent playbacks showed mother macaques were sensitive to this information conveyed in their offspring's screams. Females responded most to screams consistent with high risk of physical harm to the infant or a threat to the matrilineal dominance by a lower ranking individual (Gouzoules et al., 1984).

Similarly to macaque monkeys, chimpanzees also produce context-specific screams. Slocombe and Zuberbuhler (2007) have recently shown victim screams can vary with the severity of attack an individual is experiencing (reviewed in chapter one). However, whether listening individuals can meaningfully differentiate between these graded call types still remains unknown.

In collaboration with Katie Slocombe, I conducted a playback experiment to test if listeners could distinguish between victim screams elicited by different types of aggression. We conducted the study with a habituated group of wild chimpanzees in the Budongo Forest, Uganda. To date, only two previous studies have used playbacks with wild communities. As discussed in chapter one, in both cases the focus was on how chimpanzees responded to the presence of extra-community individuals. If we are to understand subtle social cognition, it is crucial to playback calls from recognisable group members. Numerous studies with free-ranging baboons have already provided vital insights into the meaning and function of intra-group social signals (e.g. Bergman et al., 2003; Wittig et al., 2007), but comparable efforts have never been attempted with any wild ape species.

This lack of effort in any of the great apes is most likely due to two factors. To begin with, most great apes, including chimpanzees, have extremely graded vocal systems that are inherently difficult to examine (Marler and Tenaza, 1977). Secondly, in general, fieldworkers have refrained from applying experimental techniques to wild apes, despite the well-known power of playback experiments as tools in the investigation of call comprehension (Seyfarth et al., 1980). So far, only a single captive playback experiment has been performed with great apes to probe their understanding of conspecific calls (Slocombe and Zuberbühler, 2005b),

An additional aim of this final chapter therefore is to devise an ethically and methodologically sound protocol for conducting playbacks with free-ranging chimpanzees.

I predicted that if chimpanzees distinguished between different types of agonistic screams, they would show more interest in screams linked with significant social consequences. That is, cases in which the aggression was most severe and thus potentially likely to pose a threat to surrounding chimpanzees, what is sometimes termed “snowballing”. In line with previous research (e.g. Cheney et al., 1995; Gouzoules et al., 1984) I expected the chimpanzees to demonstrate this with a longer looking duration in the direction of the calls and a faster latency to orientate towards them. Several recent monkey playback studies have simply compared responses to the acoustically distinct signals of interest (e.g. Pfefferle et al., 2008b), however, this leaves the possibility that subject responses are being driven purely by the low level acoustic features of the calls. In this case, as screams given to severe aggression are longer in duration and higher in pitch than screams given to mild aggression (Slocombe and Zuberbuhler, 2007), differential responses to these calls could be directly driven by the saliency and the physical features of the two call variants (Owren and Rendell, 1997). To control for this possibility we included a control condition, where we presented subjects with tantrum screams given by group members. Tantrum screams are approximately matched in acoustic structure to the severe screams, but, to the human ear, they are even more intense signals than the screams given during conflicts. If subjects processed the informational content or meaning of the screams, then tantrum screams should be fairly irrelevant to them, despite their overt acoustic features. To summarise, if chimpanzees were extracting information about the likely eliciting event from the call, they should react most to severe victim screams, and a less so to mild victim and tantrum screams. Alternatively, if they are responding to the most salient and intense vocal signals in their environment, with no regard for the underlying informational content, they should show the greatest reaction to tantrum and severe screams and a weaker response to mild screams.

Methods

Study area and Subjects

The playback study was conducted on the Sonso community of chimpanzees, in the Budongo Forest, Uganda (Reynolds, 2005). During the period of study (Jan-November 2007) the group comprised 78 individuals including 8 adult males, 25 adult females, 6 sub-adult males and 3 sub-adult females, all of which were individually known, but with varying degrees of habituation (for more details see chapter two).

Playback stimuli

Playback stimuli consisted of victim screams given in response to severe and mild aggression. The stimuli came from five sub-adult males, who provided several exemplars of screams to both severe and mild aggression. Sub-adult males are generally considered as more innocuous members of the group and therefore their screams provided the perfect way to test call comprehension without inducing high arousal responses. I was able to confirm the pattern of acoustic differences between mild and severe victim screams reported by Slocombe and Zuberbühler (2007) by measuring each call in each stimulus along four parameters (duration, mean pitch, mean frequency of the first formant and peak frequency in the fundamental, see appendix I). I then calculated a median value of each acoustic parameter for each stimulus. Subsequently, I averaged the values for the stimuli in each stimulus class (severe, mild and tantrum; see table 6.1). This acoustic analysis was performed using Praat version 4.3.37 and scripts written by M. Owren.

Chimpanzees of this community are known to react to screams occurring within about 30m by looking towards the sound source and sometimes by becoming pilo-erect, displaying or approaching. We did not want the chimpanzees to approach the source of the noise, as their suspicions would have been aroused upon finding no chimpanzee at the corresponding location. We therefore limited the playback stimulus to a short bout of screaming of approximately 3 seconds. Pilot observations (conducted by Katie Slocombe) indicated this duration was long enough to elicit interest in the stimulus without inciting approach. As reactions could also be affected by relatedness of subject to stimuli-provider I only played screams of unrelated individuals to subjects.

To control for responses being driven by the saliency of the acoustic features of the signal, I also tested subjects' responses to tantrum screams, provided by two infants, which were comparable in acoustic fine structure with that of severe aggression screams (see table 6.1)

Table 6.1: The mean values and SD of 4 acoustic measures for each scream condition**.** N refers to the number of scream bouts (used as stimuli) that contributed to the mean values reported in each category. Mann Whitney U tests revealed no significant differences between the acoustic measurements of the tantrum screams and severe screams.

	1st Formant (hz)	SD	**Peak freq of fundamental (hz)**	SD	**Duration (s)**	SD	**Mean Pitch (hz)**	SD
Tantrum (N=5)	**1451**	92.8	**1574**	103.9	**0.44**	0.1	**1450**	113
Severe (N=6)	**1435**	38.4	**1436**	62	**0.54**	0.17	**1404**	58.6
Mild (N=7)	**1261**	201	**1276**	189.3	**0.31**	0.15	**1064**	215
Mann Whitney U value	12 (p=0.662)		4 (p=0.052)		10 (p=0.429)		10 (p=0.429)	

Calls used as playback stimuli were recorded opportunistically from known individuals by KS and ST using a Sennheiser ME66 microphone and a Sony TCD-D8 portable DAT recorder (KS) or a MARANTZ PMD 660 solid-state recorder (ST). Recordings of vocalizations were transferred directly from the solid state memory card or digitally from the DAT recorder, onto a PC (Toshiba: Celeron, Fujitsu Siemens: Amilo). Calls were digitised at a sampling rate of 44.1 kHz, 16 bits accuracy, using Cool Edit Pro LE. Raven (Version 1.2) was used to cut the stimuli and to fade the background noise in and out at the start and end of each stimulus, to avoid the playback having an abrupt onset and offset. Stimuli contained only one chimpanzee calling and relatively low levels of background noise (cicadas, wind). Each playback stimulus was approximately equal in bout length (3 seconds) and I used Raven 1.2 to equate the stimuli in terms of RMS amplitude (see table 6.2). We checked that all stimuli sounded natural to an experienced human listener at a distance of 30m and could not be heard clearly behind the speaker at 100m. Stimuli were stored and played in WAV format on an Ipod Nano and broadcast using a NAGRA DSM speaker/amplifier. The speaker was concealed in a modified rucksack throughout the experimental period so the chimpanzees never saw the equipment in operation (see figure 6.1)

Figure 6.1: Photograph illustrating the speaker used to conduct playbacks, concealed in a rucksack.

Table 6.2: The mean duration and RMS amplitude of stimuli in each condition.

	Severe (N=6)	Mild (N=7)	Tantrum (N=5)
Mean duration	3.04 (0.20)	3.01 (0.11)	2.90 (0.21)
Mean RMS Amplitude	8423 (239)	8367 (160)	8433 (325)

Protocol

The experimental phase consisted of test (severe scream, mild scream) and control (tantrum scream) trials that followed a within subject design, with each subject receiving all three trial types in a counterbalanced order. The protocol followed the same principles as traditional playback experiments conducted with monkey species (Seyfarth et al., 1980), but had some additional features to maximise the suitability of this paradigm for this fission-fusion great ape species. A minimum of three operators were required to run the experiment in a fashion that maximised the realism of the playbacks: one to stay with the experimental subject – the receiver of the vocalisation (always ST), one to stay with the 'scream provider' (the individual whose calls we played from the speaker) and one to play the stimulus from the speaker. We used Motorola GP340 radios or Nokia 2600 mobile phones to maintain contact between all three operators throughout the duration of the experiment. Each operator collected data on a number of behaviours prior to and following a playback.

(1) 'Focal' operators, who followed the experimental subject, recorded all occurrence aggression, specifically the number of aggression bouts the subject was involved in or witnessed and the duration and number of screaming bouts the subject heard. All observations of grooming and pant-grunting (a social greeting vocalisation given by subordinates to dominants) received and given by the subject were also recorded. Once a playback was completed operators noted the identity of all individuals in the party to ensure that future playback subjects would not receive a stimulus they may have previously overheard.

(2) Operators with the scream provider recorded the time and nature of all loud vocalisations made by members of the scream provider's party and the identity of the vocaliser. In addition, the general behaviour of the scream provider (e.g. grooming, resting, feeding) and the time at which it changed was also recorded. They particularly looked for behavioural changes at the time of the playback.

(3) Operators with the speaker recorded all individuals within a 50m vicinity of the speaker at the time of playback.

To prevent the scream provider from hearing his own vocalisation he, or she, had to be >100m away from the speaker (see figure 6.2). In order to maximise realism, the distance and direction of the playback had to be plausible. It was therefore vital that the scream provider did not vocalise within 10 minutes prior to the playback, announcing his true presence in a different location of the forest to the subsequent playback.

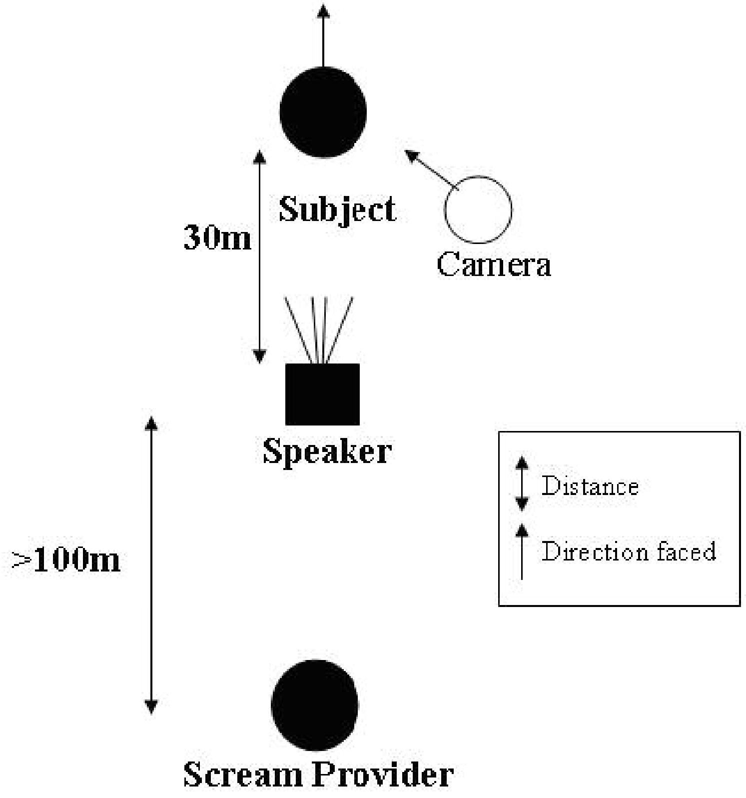

Figure 6.2: Schematic representation of experimental set-up.

As soon as the subject was resting on the ground (without feeding or grooming, which may distract him from the stimulus or to make his response ambiguous) and alone (to exclude the possibility that any subsequent response to the stimulus was a result of social referencing), the speaker operator took the loudspeaker 30m away from the subject in the direction of the scream provider and concealed himself. In order to prevent unwillingly exposing any chimpanzee to an intense stimulus, I meticulously ensured no other chimpanzees were within 30m of the speaker before the screams were played back. In the absence of the scream provider's vocalisations this experimental set-up realistically simulated the presence of another chimpanzee 30m away, involved in either an agonistic interaction of severe or mild intensity or a tantrum.

Another prerequisite was that the subject had to be facing away from the speaker so any orientation response was unambiguous. When this condition was met the focal operator used a Panasonic NV-GS 250 digital video camera to film the subject for 30 seconds before and 1 minute after playback. Due to low visibility at this site, the focal operator usually had to be within 10m of the subject and only the very well-habituated individuals of this community would tolerate this, when alone on the ground. The focal operator was responsible for checking with the other operators that all conditions had been met before telling the speaker operator to play the stimulus. Focal subjects were then followed for as long as possible after each trial and data collection continued.

To avoid order effects I counterbalanced trials, ensuring subjects did not hear conditions in the same order. I also waited at least 1 day in between trials and the same focal subject never appeared in consecutive experiments. Screams occur naturally at a high daily rate (approximately 6 scream bouts/hour) in this chimpanzee community (Townsend and Slocombe, unpublished data), however playbacks were conducted at a very low rate over 10 months (mean =3 /month, Range = 0-7/month). I also ensured that no chimpanzee heard the same stimulus twice. If a subject had been in the vicinity of a playback I conducted with another focal, I played a different exemplar to that individual, rather than repeat the same stimulus they may have overheard.

Playback trials and data analysis

A total of six, very well habituated, subjects were tested in all three conditions. Unfortunately only four females in the Sonso community would tolerate the degree of following needed to conduct these experiments. Because with within-subject designs it is virtually impossible to find significant effects with samples smaller than six (Mundry and Fischer, 1998), I had to supplement these adult females with two adult male subjects from the community. Males and females are unlikely to differ in their call comprehension skills (Cheney and Seyfarth, 1990) and thus substituting one sex for another should not detract from the overall aims of this experiment.

Five subjects were tested only once for each condition. One subject heard stimuli from two different individuals (severe N=2; mild N=2) and she showed the same pattern of response to both sets of stimuli. To avoid pseudoreplication I averaged her responses for each test condition. Two trials were excluded due to problems with the experimental set-up confounding the subject's response. In one trial, the subject's reaction was consistent with the predicted direction and in the other trial the reaction went in the opposite direction to that predicted. Two further females only received the control condition and were not included in the analyses. However, their responses to this condition were very similar to the responses of the other six subjects tested.

I coded videotapes frame by frame using Adobe Premier Pro C53 software. The following three behavioural responses were measured: **(1)** Latency: Time from stimulus onset to the subject orientating its head towards the speaker. **(2)** Looking duration: Time for which the subject orientated its head towards the speaker in the minute after the playback**. (3)** Number of looks: Number of consecutive looks towards the speaker in the minute after the playback

To ensure accurate coding of videotapes, a second coder (KS), blind to the trial type, was asked to analyse 25% of trials (5 trials). We compared the measures taken by each coder and found very high levels of agreement (Pearson's correlation for latency = 0.974 (2-tailed, $p<0.001$), duration = 0.93 (2-tailed, $p=0.002$), number of looks = 1.00 (2-tailed, $p<0.001$)**,** which indicates the trials had been accurately coded.

Statistical analysis

Non-parametric tests were used for comparisons (SPSS version 12.0). All tests were two-tailed. As we were dealing with low sample sizes, we calculated exact p-values, as opposed to asymptotic ones, as recommended by Mundry and Fischer (1998).

Results

Playbacks occurred between 8am and 4pm, typically at around 11am ($\text{Mean}_{\text{time of day}}$ =11.08, SD +/- 2.12hrs). Prior to playbacks subjects were followed for on average 188 minutes (SD+/- 131) and after playbacks I continued to follow subjects for a mean duration of 69 minutes (SD+/- 30). To prevent the scream provider from hearing his own vocalisation, he was required to be a minimum distance of 100m from the speaker, however during some playbacks the scream provider could be further, up to 1000m away ($\text{Mean}_{\text{scream provider distance}}$ = 355, SD+/-262).

Behavioural responses

Severe versus mild screams

I predicted that if subjects processed the information conveyed by screams, they should respond more strongly to severe than mild screams. My prediction was supported: during the minute following playback subjects looked towards the speaker for longer in response to severe screams than mild screams (Exact Wilcoxon matched-pairs-signed-rank-test: Z=-2.20, N=6, *P*=0.031; see table 6.3, figure 6.3). There was also a trend to look at the speaker more times and more quickly in response to severe screams than mild screams (number of looks: Z=-2.06, N=6, *P*=0.06; latency to look: Z=-1.57, N=6, *P*=0.156; see table 6.3; figure 6.3 and figure 6.4).

Table 6.3: Behavioural responses of subjects to each of the three playback conditions. Mean values across the 6 subjects and the standard deviations are shown.

	Severe (n=6)	**Mild (n=6)**	**Tantrum (n=6)**
Mean Latency (s)	**1.19 (0.35)**	**1.72 (0.72)**	**2.64 (0.91)**
Mean Duration of Looking (s)	**14.66 (6.87)**	**6.99 (4.12)**	**6.79 (5.11)**
Mean Number of Looks	**2.58 (1.20)**	**1.16 (0.41)**	**1 (0.63)**

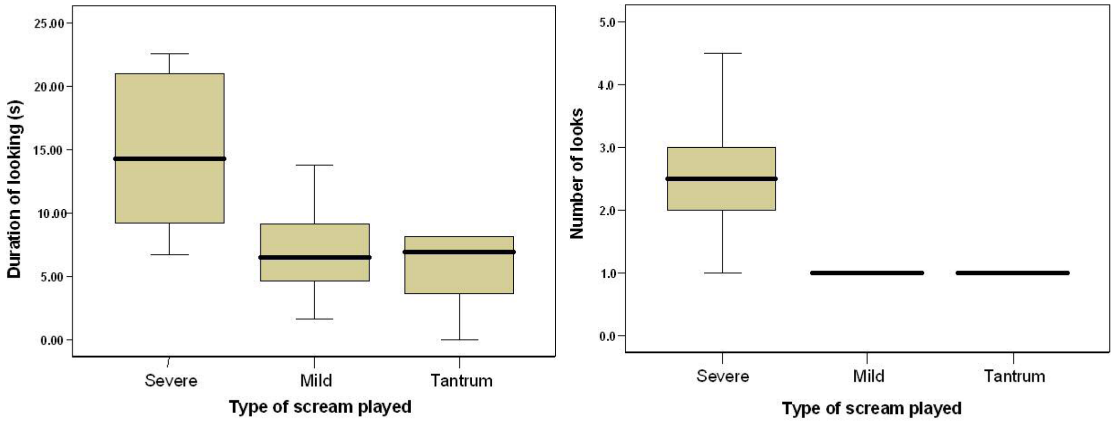

Figure 6.3: Boxplots illustrating the total duration spent looking at the speaker and the total number of looks in the minute after playback in response to three types of playback stimuli. Boxplots illustrate medians, interquartile ranges and highest and lowest values.

Severe screams versus tantrum screams

To address the more parsimonious explanation that subjects were simply responding to the more intense acoustic features of the severe screams I compared subjects' responses to screams given in severe conflicts with tantrum screams. If responses were driven by the saliency of the sound and its 'attention grabbing' acoustic features, I would expect subjects to show roughly equal interest in both the severe and tantrum screams. In contrast to this prediction, during the minute following playback subjects looked towards the speaker for longer (Exact Wilcoxon matched-pairs-signed-rank-test: Z= -2.23, N=6, *P*=0.031; see table 6.3, figure 6.3), more times (Z= -2.20, N=6, *P*=0.031; see table 6.3, figure 6.3) and more quickly (Z= -2.20, N=6, *P*=0.031; see table 6.3 and figure 6.4) in response to severe compared to tantrum screams. In one control trial, the subject (NB) did not orientate to the speaker at all. I allocated her a "ceiling latency" which was the maximum latency observed from the analysed trials to allow her inclusion in latency analyses.

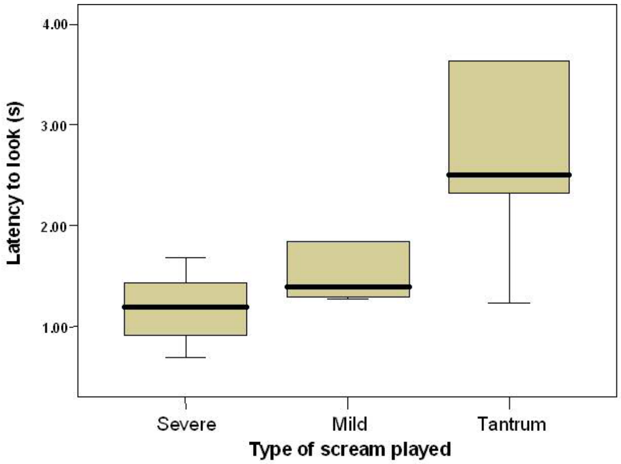

Figure 6.4: Boxplots illustrating the latency to look in response to playbacks in each condition. Boxplots illustrate medians, inter-quartile ranges and highest and lowest values.

Effect of prior exposure to screams

As aggression and screaming also occurred naturally during the study period, a subject's responses could have been modulated by these events, e.g. by how much aggression the subject had perceived prior to playback.

In order to examine the effect of prior exposure to naturally occurring screams I calculated the number of screaming bouts focal subjects could have seen or heard in the hours before a playback trial. Mean duration of screaming witnessed and heard did not differ significantly between conditions (severe versus mild: Mann Whitney exact: $U=22$, $Z=-0.319$, $N_{severe}=7$, $N_{mild}=7$, $P=0.805$; severe versus tantrum: Mann Whitney exact $U=18$, $Z=-0.429$, $N_{severe}=7$, $N_{tantrum}=6$, $P=0.731$, see table 6.4). This suggests that previous exposure to conflict did not explain any of the observed response differences.

Table 6.4: The mean and SD of screaming bout duration witnessed and heard, before playback, in each condition.

	Severe (N=7)	Mild (N=7)	Tantrum (N=6)
Mean duration of screaming bouts witnessed and heard (s)	168 (189)	189 (227)	232 (195)

Short-term behavioural changes in response to playback experiments

Playback experiments with wild chimpanzees raise some ethical concerns. For example, the possibility exists that simulating agonistic encounters with playbacks artificially increases subsequent levels of aggression in the community. To ensure that never took place, I performed a number of additional post-hoc analyses. Firstly, I investigated whether our playbacks caused any immediate effects by analysing levels of aggression in the hour preceding and following playbacks. I predicted that if playbacks intensified levels of aggression, then more aggression should be observed in the hour following experiments. I found no evidence to support this prediction. In fact, I found a trend towards more aggression occurring in the hour before playback compared to the hour after, although this trend was not significant (Mean scream duration$_{\text{hour before}}$ = 46.7 sec (SD= 61.7), mean scream duration $_{\text{hour after}}$ = 18.8 sec (SD= 29.5); Wilcoxon signed rank test: Z=-1.829, N=20, p=0.067; mean scream bouts $_{\text{hour before}}$ =2.95 (SD= 2.7), mean scream bouts $_{\text{hour after}}$ =1.7 (SD=2.0), Wilcoxon test: Z=-1.498, N=20, p=0.134). As aggression levels vary throughout the day, with less fighting generally occurring in the heat of the day, I also analysed exactly the same time periods on ‘matching control’ days when no playback occurred. I found a similar trend for there to be less aggression later in the day on non playback days (Mean scream duration$_{\text{hour before}}$ = 70.8 sec (SD= 112.0), mean scream duration $_{\text{hour after}}$ = 44.7 sec (SD= 66.4); Wilcoxon test: Z=-1.790, N=20, p=0.073; mean scream bouts $_{\text{hour before}}$ =4.4 (SD= 5.6), mean scream bouts $_{\text{hour after}}$ =2.9 (SD=3.9), Wilcoxon test: Z=-1.039, N=20, P=0.299). It is apparent there was generally less aggression on days when I performed a playback experiment (probably because it was more difficult to meet all conditions necessary to perform a playback on days when aggression levels were high), but the pattern of aggression was stable across days with and without playbacks. Taken together, these results indicate that playbacks had no immediate effects on the daily pattern of aggressive incidents in this community.

Long-term effects of playback experiments

In a final analysis, I looked for longer-term effects by comparing aggression levels across years. Of the 20 playbacks considered, 7 occurred within one month (January 2007) when conditions were optimal. I compared all occurrences of aggressive interactions that took place in January 2007 and compared them with the matched period in the previous year (Slocombe, unpublished data). In January 2006, there were on average 0.97 aggression bouts per hour (48 bouts observed over 49 hours focal time) and in January 2007, there were on average 0.93 aggression bouts per hour (73 bouts observed over 79 hours). Based on these data, I concluded that scream playbacks did not adversely affect general levels of aggression in the Sonso community.

Finally, to see if other social behaviours were affected, I recorded grooming and pant-grunt vocalisations prior to and after playbacks. Grooming and pant-grunting only occurred once before a playback and twice following a playback. I therefore could not conduct any meaningful analyses, but my impression was that playbacks did not appear to influence the usage of these behaviours. In addition, the scream provider was never observed to show any orientation or approach to the speaker or a change in broad behavioural category (rest, travel, feeding) at the time of playback. This indicated that, as demanded by the experimental protocol, the individuals whose screams I played back could not hear them and were not adversely affected by playbacks.

Discussion

This study has found that chimpanzees show more interest in screams given during severe rather than mild aggression. When listening to a short bout of screaming from an unrelated individual in response to severe aggression, subjects looked at the speaker for longer and tended to look more times, and with shorter latency than to the same individual’s screams given to a case of mild aggression. This shows that chimpanzees are capable of extracting information about the severity of the attack from the scream; that is, they appeared to process the calls’ meaning. I found no evidence for the hypothesis that responses were driven directly by the acoustic features or physical saliency of the stimulus presented to them. Whilst tantrum screams matched or even surpassed severe victim screams in a number of acoustic features, individuals showed little interest in this call type, showing they were not simply orienting to the most acoustically salient sounds. Chimpanzees looked at the speaker more slowly, for less time and less often to tantrum compared to severe screams. Tantrum screams are largely irrelevant to most community members and the lack of response indicated subjects were processing these calls, potentially at a semantic level. My study is consistent with the idea that chimpanzees attend to the meaning of screams and can infer the severity of an attack from listening to the screams alone.

The aim of this chapter was to determine what information female chimpanzees can extract from victim screams. As explained earlier, only four females could be tested and I had to supplement these females with two male subjects. These were a well-established, though older male (MA), and a low ranking young male (MS). Of all the males, they were the most female-like in their behaviour, spending time away from the core main group, foraging alone and generally avoiding male-male conflict (Townsend, Pers. obsv). Whilst this is a potential drawback, males and females are unlikely to differ in their comprehension skills of socially important acoustic signals (Cheney and Seyfarth, 1990).

When a female is resting on the ground she is vulnerable to attack, most especially if the aggression escalates, snowballing out of control (Goodall, 1986). As a consequence evasive action may be needed. The potential risk to the listener can be extrapolated from the type of aggression being experienced by the caller and therefore it makes sense for resting individuals to attend more to events that may signal greater danger for them. Ultimately females may be able to use these screams to make informed future behavioural decisions that increase their overall fitness.

Up until now the only work to experimentally address call comprehension in any ape species has been performed in captivity (Slocombe and Zuberbuhler 2005b), raising issues of ecological validity. Field playbacks using social signals have led to great advances in our understanding of what information calls convey and the social-cognitive skills of other primate species (e.g. Cheney et al., 1995; Bergman et al., 2003). The current study has demonstrated that field playbacks are a feasible method for work with wild chimpanzees. Moreover the customised protocol outlined will hopefully stimulate further research on chimpanzee vocal communication and social cognition. Although the number of protocol prerequisites is onerous, with a correspondingly slow rate of data collection, they are essential to generate a realistic scenario with animals of heightened social awareness, such as the chimpanzee. As with all playback experiments, this is critical to obtaining meaningful results and minimising the chances of disturbing the animals by presenting them with implausible or impossible events. For ethical reasons, I consider it essential that measures of aggression and other social behaviours continue to be collected ensuring that these field experiments do not negatively impact on the natural behaviour of these animals.

To conclude, this study has demonstrated that intra-group playback experiments using social signals can be successfully conducted with wild chimpanzees. I found that individuals distinguish between different types of screams, which form part of a larger graded call system. They also extract the corresponding social information from the screams they hear, consistent with the notion chimpanzees process the meaning of the call, rather than just responding to salient acoustic features. By attending to these screams, females can potentially avoid escalating female aggression and hence this may be one viable strategy employed by female chimpanzees to dissipate the risks associated with their competitive social lives.

In the previous chapters, I have focused more on call production, specifically how females use their vocalisations in potentially tactical ways. However, the signaller constitutes only one half of the story. Here I demonstrated that vocalisations do play a crucial role in the lives of female chimpanzees, shedding light on such communication from the receiver’s perspective.

Chapter Seven: General Discussion

Summary

In this chapter I will reflect on the findings from the previous empirical chapters, bringing them together to address the original questions, particularly: how significant a threat is competition to wild female chimpanzees and how can they use their vocalisations to mediate this social pressure? I will also focus on what further information these results can provide us with for understanding chimpanzee vocal communication and the cognitive processes that underpin it. I will conclude by looking further ahead, suggesting potential future studies to address this topic more systematically.

Female competition in chimpanzees – a social threat?

From over 50 years of wild research, it is now known that chimpanzees lead complex social lives. They reside in fluid social groups, the size and composition of which are constantly changing. Males dominate one another, but rank is transient and can be altered through a variety of strategies such as aggression or tactical affiliation (Goodall, 1986; Newton-Fisher, 1997). Males are also the philopatic sex and cooperate together to defend territories against incursions by hostile neighbouring communities. As is clearly evident, a great deal of our knowledge regarding chimpanzee social complexity stems from research on male chimpanzees. Historically, in evolutionary studies of animal behaviour, male mammals have always been portrayed as the more socially intricate of the two sexes, particularly the more competitive one (reviewed in Hrdy, 1981), and this has often led to the female sex becoming neglected. In comparison to the competitive, tactical and lethally aggressive male chimpanzee, females are often depicted as peaceful and passive individuals, attentive purely to the upbringing of offspring. This crude stereotyping has resulted in the assumption that females have to deal with fewer social pressures than males.

Whilst, of course, there are inevitable differences between the sexes, it is unlikely that the female chimpanzee’s social world is more easily navigable than the male’s. A growing body of research over the last ten years on female competition is finally beginning to dispel this commonly held myth.

Direct contest competition pervades the lives of many female primates. Through aggression, philopatry and female alliances, dominants consistently outperform subordinates. For a while, female great apes, particularly the chimpanzee, appeared to conform to their passive role, leading many to assume female competition was not a significant social process in the lives of chimpanzees (Wrangham, 1997). However through combining behavioural data from multiple years, Pusey et al., (1997) challenged the notion of the passive female pawn, showing that females vary in their reproductive success and highlighting contest competition for resources as a potential mechanism driving this variance.

I provided further evidence for competition amongst females, in Budongo chimpanzees (chapter three). Over a period of 28-months three instances of lethal coalitionary female aggression in the form of infanticide occurred in the Sonso community. These attacks simultaneously coincided with a dramatic demographic shift in the community. Between 2001-2006, 13 new females immigrated, thereby increasing the number of resident females and skewing the sex ratio. Such a high influx of new females is likely to have put pressure on community resources and females responded aggressively to this increased demand. A similar relationship has been documented in the Kanyawara community of chimpanzees, Uganda, with females also showing heightened levels of aggression during times of immigration. These observations therefore provide crucial evidence in support of Pusey et al.,'s (1997) original hypothesis: competition for resources can have a significant contest component.

Exactly what the females in the Sonso community are competing over is not completely clear. In most studies of female competition in primates, the main focus is on competition over food, primarily because it is more easily quantifiable (Wrangham, 1980; Koenig, 2002). In primate groups where the male:female sex ratio is skewed, or where males differ in their quality, mating partners and their sperm can also become a resource that is competed over (Bergland et al., 1993; Palombit et al., 2001; Rosvall, 2008). At Sonso, food competition is one obvious explanation. Although the community is known to have a high food density relative to other studied communities (Newton-Fisher, 2003; Bates, 2005; Emery Thompson et al., 2007), the high rate of female immigration, combined with too few adult males to expand the community home range, means that food availability may become limiting amongst resident females.

In this community, such a highly female skewed sex ratio also highlights males as a resource worth competing over. Over the14 month study period, there were almost three females for every male. Because multiple promiscuous females can cycle at any one time (Deschner et al., 2003; Stumpf and Boesch, 2005) and male sperm quantity is known to decrease with consecutive ejaculations, the sperm of males may be one resource females are interested in securing.

Additionally, I showed that high-ranking males intervened during the female-led infanticides, probably due to their previous mating history (chapter three). High-ranking males are also the most efficient protectors and perpertrators of male initiated infanticide, which is true for a number of primate species (Van Schaik, 2000; Pradhan et al., 2006). Given that chimpanzee males differ in their ability to provide a sufficient protective service for females and their offspring, and that infanticide represents a significant threat to female fitness, it is very plausible that residents are also competing over the males for the potential post-natal services they can offer (Palombit et al., 1997; 2001; Palombit, 2000). This may be particularly true at Sonso where, due to the death of the previous alpha male (DN), there remain only four high-ranking males.

It should be noted that these female-led infanticides are not the first to be documented in chimpanzees. Goodall (1986) also observed such female-initiated attacks in the 1970's; however, many dismissed these cases as "pathological" behaviours because of the relatedness of the female perpetrators (mother and daughter dyad) and the observations that they always consumed the victims. My results do not support this explanation. In these instances at Sonso, multiple females were involved and the infant bodies were never seen to be consumed. Together these observations suggest that lethal female aggression is probably part of the wider female behavioural repertoire. They also suggest that females are capable of working together and forming aggressive coalitions against other females; a behaviour previously thought only to be employed by males (Goodall, 1986; Wilson and Wrangham, 2003). A further important outcome of these observations is therefore that males and females may not differ in their aggressive propensities and tactics as much as previously thought: lethal coalitionary aggression is not necessarily a gender specific trait in apes.

Whilst, in general, females do lead more subtle and secluded lives than males (Goodall, 1986), this does not necessarily translate into social simplicity. In conjunction with research from other chimpanzee field sites (Kahlenberg, in press a;b; Pusey et al., 1997; in press; Emery Thompson et al., in press), my findings provide clear evidence that under certain socio-ecological conditions female chimpanzees are subject to significant social pressures and threats that, at times, carry substantial fitness consequences.

Calls as social tools

The idea that the social fabric of female chimpanzee lives is complex, competitive and potentially dangerous is a relatively new concept. Because of this, at present, we know very little regarding how females cope with these demands. In chapters 4-6, I specifically investigated this gap in understanding and proposed that vocalisations play an integral role in mediating female competition and the aggression that accompanies it. Vocalisations are known to function as crucial tools in the social lives of many mammals, particularly primates.

One commonly held theory suggests that vocalisations facilitated the evolution of complex primate social living (Dunbar, 1993; McComb and Semple, 2005).

To address how females may use vocalisations to deal with female competition, I chose to focus on more commonly produced and evolutionarily relevant vocalisations: copulation calls and victim screams. In the face of female competition and its accompanying aggression, there seemed to be an advantage to the strategic use or comprehension of these vocalisations.

Copulation calls

In chapter four, I showed that most traditional explanations cannot be invoked to explain why female chimpanzees produce copulation calls. Instead, I found that social factors, particularly the threat of female social conflict, seemed to better explain call production in female chimpanzees.

To this end, I analysed calling behaviour from a dual perspective: why females produced copulation calls and importantly, why they did not. This was primarily driven by the observations that chimpanzees call at much lower rates than other primate species (Pradhan et al., 2006). Thus, it seemed that not calling was the default behaviour. Furthermore, if we are to fully understand the function of copulation calling, both production and withholding of the behaviour needs to be understood, an often neglected aspect in previous studies.

I found that females were probably calling to confuse paternity amongst the high-ranking males of the community. Females were calling more in situations when they could advertise their receptivity to more high-ranking males, but at the same time they were concealing their proximity to ovulation. Fertility concealment has been addressed both empirically and theoretically (Semple, 1998a; Semple et al., 2002; Van Schaik et al., 2000; Van Schaik et al., 2004; Pradhan et al., 2006; Pfefferle et al., 2008a) and is generally considered as a strategy to enhance paternity confusion amongst males. By not advertising fertility, females are likely to prevent occupation by the most dominant male and increase paternity confusion amongst other males. But why would Sonso females be interested in paternity confusion amongst the high-ranking males? Protection against male infanticide is of course one possibility, though at Sonso female chimpanzees are the primary perpetrators, being involved in three out of five documented instances. As previously described, these female infanticides are a direct result of increased competition amongst residents for resources, and represent a real threat to fitness for any female chimpanzee.

In at least one of these three instances, high-ranking male chimpanzees were directly observed trying to prevent the ensuing attack. At Gombe, similar behaviours have been documented. High-ranking males have been observed attempting to intervene during female-led attempted infanticidal attacks (Pusey et al., in press). I propose that confusing paternity with copulation calls may therefore be one short-term vocal strategy to enlist the protective support of high-ranking males.

This is not the first time infanticide has been implicated in explaining the adaptive significance of copulation calls. O'Connell and Cowlishaw (1994) hypothesised that whilst copulation calls of baboons primarily function to incite sperm competition, one potential by-product of such competition is paternity confusion amongst males. Male infanticide is a particularly pervasive feature of baboon life (Palombit et al., 1997; 2001; Cheney and Seyfarth, 2007), hence females that employ behaviours to minimise this risk will possess a selective advantage over others. Although protection from male infanticide has been highlighted, this is the first work to invoke female-led infanticide, a very different threat, in understanding the function of primate copulation calls.

The second aim of chapter four was to understand the other side of the problem: why chimpanzee females often refrain from producing copulation calls. I found that when low-ranking females copulated with high-ranking males and refrained from calling, there were always more high-ranking adult females in the nearby audience. This suggests that the "decision" to call is also mediated by the likelihood of being detected by other more competitive female conspecifics. By flexibly modifying call production based on who can hear them, female chimpanzees may be strategically avoiding potential female initiated aggression. At times, females that did not employ this vocal strategy experienced substantial aggressive consequences from nearby females of higher rank (Townsend, Pers. observations, see chapter four). Though the sample was low, eight instances in total, these aggression data provide some of the first evidence for males being a competed-over resource. Whether it is their sperm or their post-natal protective services females are interested in securing is not yet clear, though later I address what additional studies could be conducted to further test these preliminary findings.

Interestingly call flexibility was only observed in the low-ranking adult females; high-ranking females showed no obvious patterns. This is possibly because high-ranking females are more competitively-able and thus less likely to be as sensitive to the presence of conspecifics, compared to the more vulnerable lower ranking females. Unfortunately, my sample of high ranking females was too small (N=2) to address this question systematically. This is certainly one aspect which could be focused on in future research. Specifically, how does female competition affect females of different ranks and do high and low ranked females employ similar vocal counter-strategies?

In combination, these results suggest that female chimpanzees are capable of using copulation calls in flexible and seemingly strategic ways, and that one potential selective pressure driving the tactical use of these calls has been competitive female social relationships. Chapter four also provides an additional strand of research to the question of copulation calling in primates. Most studies to date have focused primarily on these calls as signals of receptivity to nearby males (Pradhan et al., 2006). Whilst this is probably one important aspect of copulation calling, the fact that the copulating female is part of a complex social network comprising of, most importantly, social competitors, must also be factored in and accounted for. Only then will we get a clearer picture of what function these vocalisations have in primates and indeed other mammals.

In chapter five, I continued with the question of copulation calls as social tools, but focused less on their production and more on what information they may additionally convey to listening individuals. I found that the acoustic structure of copulation calls do not indicate the female's proximity to ovulation. Therefore, neither call occurrence nor acoustic fine structure can be used by males to assess a female's fertility. These results provide further evidence for the hypothesis that chimpanzee copulation calls function to confuse paternity amongst males. Recent research suggests Barbary macaques behave in similar ways. Pfefferle et al., (2008b) collected over 1400 copulation events, noting the timing and occurrence of calls in addition to recording them acoustically. Their results show that, whilst calls do signal the occurrence of ejaculation, they provide no evidence regarding fertility and proximity to ovulation. Similarly to chimpanzees, such ovulation concealment is predicted to create paternity confusion amongst mating males. In Barbary macaques, male or female infanticide is not a relevant risk and thus paternity confusion is unlikely to enlist male protection. Instead, males are thought to provide a post-natal service in the form of paternal care and investment, a behaviour that is known to be common in this macaque species (Heistermann et al., 2007; Brauch et al., 2007; Pfefferle et al., 2008a).

Previously, I argued that paternity confusion amongst the high-ranking males, aided by copulation calling, is probably the most effective strategy if females are to avoid female-female competition and its consequences (chapter four). However, through employing further analyses on the acoustic structure of copulation calls and the locations (i.e. on the ground, in the trees) in which they were produced, it became clear that males have also played a role in the evolution of this call in one way or another. I found that females may acoustically signal the rank of the male in their copulation calls. Yellow baboons are also known to encode such social information in their copulation calls (Semple et al., 2002), and this is thought to help other males judge the competitive ability of the mating partner. In chimpanzees, however, I found no evidence for the idea that copulation calls induce male-male competition (chapter four) thus, why exactly females should signal the male partner was not completely clear.

The reason only became evident when also taking into account the location in which these calls were produced. Location did not seem to effect a female's production of copulation calls when with a high-ranked male, but it had a significant impact when with a low-ranked male. I found that females would be more likely to produce them with low-ranked males if they were more exposed and if furtive mating was impossible. Although copulation calls per se may not incite competition, high-ranking males do still tend to aggressively exclude lower ranking males from mating, usually by challenging the female (Goodall, 1986; Hauser, 1990; Watts, 1998; Boesch and Boesch-Achermann, 2000; Van Schaik et al., 2004; Kahlenberg, 2006; Duffy et al., 2007). Perhaps due to this additional social threat, matings with low-ranking males are ostensibly cryptic and females often refrain from producing copulation calls. However, in instances when furtive mating is not possible, such as in exposed trees, one additional vocal strategy for females is to produce a copulation call, but one that reliably indicates the rank of the partner.

Vocal communication is known to play a crucial role in settling agonistic contests (Anderson, 1994) and it has been suggested that honest signalling in vocalisations is one mechanism through which such settling occurs (e.g Red Deer, <u>Cervus elaphus</u> (Clutton-Brock and Albon, 1979; Reby and McComb, 2003); Elephant Seals (Sanvito et al., 2007); Baboons (Kitchen et al., 2004)). With their copulation calls, female chimpanzees may be honestly signalling the rank of their mating partner and it is possible such acoustic labelling, and conforming to social "norms", could minimise the propensity for male aggression.

An additional implication of these results is that, when in socially risky situations (such as mating with low-ranked males), females are sensitive to how exposed they are, and potentially what high-ranking males can and cannot see. This provides a further layer to our understanding of, not only the social pressures females are exposed to and the kind of vocal strategies employed to deal with these effectively, but also the cognitive processes that might underpin these behaviours. This is a topic I will address later.

Chapters four and five, provide the first evidence for female-specific vocal counter-strategies to social pressures, namely that of female-female competition. At the same time, my results have indirectly elucidated that males, and the social pressures they impose, may have additionally shaped the evolution of these acoustic signals, most obviously their fine acoustic structure. This highlights the very important point that, only with in-depth analyses is it possible to begin to understand the function of animal vocalisations, how they are used and what selective pressures they have evolved under. For example, the majority of copulation call studies have solely focused on calling frequency and the contexts eliciting their production (Pradhan et al., 2006). Very few have attempted to additionally take into account the fine acoustic structure of these calls (Semple et al., 2002), as well as the instances when females do not call. Unless such an integrated approach is taken, it is very difficult to draw conclusions regarding the role these calls play in the lives of primates, or indeed other mammal species.

To what degree similar forces determine female calling behaviour in other communities needs to be addressed. Due to various socio-ecological factors, chimpanzees differ remarkably in their behaviours between communities. Systematic investigation into these variations has led some to suggest chimpanzees possess their own forms of culture (Whiten et al., 2004; Whiten et al., 2005). Given the unique social and demographic structure at Budongo, it is possible that my findings regarding the function of female copulation calls are community specific, though recent research on the Ngogo community of chimpanzees suggests this may not be the case. From a long-term data set comprising almost 6500 copulations, no evidence was found for copulation calls inciting male-male competition, confirming my results. Hormonal analyses additionally showed their copulation call production was not correlated with proximity to ovulation, again results in line with my findings (Gunther Pers.comm). Whilst additional studies still need to be conducted at more contrasting chimpanzee research sites (Ngogo is roughly 250km from Budongo), such similar findings from a much larger sample size implies that my results are not necessarily Budongo-specific, but consistent across at least two east-African communities.

Additional studies could also involve experimentally verifying the observational results presented in chapters four and five. Again, this is an aspect that I will come to later when discussing future directions.

Agonistic Screams

In chapter six, I moved away from how females use vocalisations as social tools, in the production context, to try and understand how females can comprehend vocalisations and what social advantage such comprehension could give them.

I found that chimpanzees can meaningfully distinguish between screams labelling differing aggression severity. Within this experimental design, I also included an infant tantrum control condition. To date, most monkey playback studies have focussed on comparing responses given only to the acoustically distinct signals of interest (e.g. Cheney and Seyfarth, 1990; Pfefferle et al., 2008b). Because calls can often differ in their acoustic features, it is entirely possible that differential responses are obtained because one call type is more salient than the other. This is a confounding factor that is rarely tested.

In this respect, chimpanzee victim screams are no different. The tantrum control condition worked because tantrum screams matched severe screams in their acoustic parameters, yet were elicited under very different conditions (e.g. when infants were not fed or carried). If chimpanzees were just responding to the saliency of the acoustic signal and not the informational content, I predicted they should respond equally to both severe and tantrum screams. This is the first time that acoustic intensity has been controlled for in a call comprehension playback experiment, and my results showed that tantrum screams were responded to least of all conditions. From this, I suggested chimpanzees are not just responding to the peripheral acoustic features, but processing the semantic content of victim screams at some level.

Comprehension of agonistic severity through vocalisations is advantageous for female chimpanzees, as it allows them to keep track of changes in their surrounding social environment and to make appropriate behavioural decisions. Observations of third party, bystander females becoming involved in female aggression are not uncommon at Budongo. For example on the 23rd July 2007 at 11.58am, adult female WL had just copulated with adult male MS. After descending the tree WL was subjected to a coalitionary attack by alpha female NB and mid-ranking female KL. WL began producing victim screams and as the aggression escalated, an uninvolved female KU, who was in the process of moving away, became included into the aggression (11.59am). KU then also began producing victim screams until the fight was dispersed by MS and high-ranking male BB. Whilst this is only one anecdote, it well illustrates the point that vocal signals can serve as carriers of vital information with non-trivial fitness consequences. Comprehension of victim screams is a good illustration of this more general capacity.

Of course, there may be other explanations, for example, subjects may be responding more to victim screams to assess whether to intervene. Similar studies on Rhesus macaques found that mothers responded more to severe screams than mild screams (Gouzoules et al., 1984). Because the screams played back were from offspring, Gouzoules et al., (1984) hypothesised that overt reactions to severe screams arose because it represented the greatest threat to these individuals. Unfortunately, due to the arduous methodological pre-requisites required when conducting these experiments with chimpanzees, it was only possible to test unrelated individuals over the 10 month time period. Hence, at this point it is not possible to make similar claims, at least in chimpanzees, though future studies could address this question more thoroughly.

As the first experiment of its kind, there were some inevitable design and protocol problems that need to be rectified if future studies are to become more efficient. Firstly, because I was interested in what information females can extract from victim screams, I was automatically restricted in my sample size, as only a small number of adult females at Budongo are sufficiently habituated for continued following. Even after lengthy attempts, (45 non-playback days in the forest, 14 straight days without one experiment), it was still only possible to test four adult females in each condition. Two further females (KY, KU) received the tantrum control trial, but under test conditions these females refrained from travelling or resting on the ground (critical playback pre-conditions) and thus could not be completed. Consequently, I had to supplement these four females with two adult males. As described in chapter six, I purposefully picked males that were most “female-like” in their behaviour, at that time, particularly in their avoidance behaviour during fights. Whilst I understand this was not ideal, it was the only available option I had if I was to systematically address chimpanzee comprehension skill from the female’s perspective. In the future, if the focus of a playback study is again females, active steps should be taken towards pre-experimental habituation. Only with this measure will it be possible to test a sufficient number of female subjects.

An additional problem with the experimental methodology relates to the control condition and the stimuli used for this. In the test conditions, we were playing back unrelated sub-adult male screams. Therefore, ideally, I should have used tantrum screams from the same individuals, ensuring uniformity across all conditions. Unfortunately, sub-adult males rarely give such vocalisations, making it impossible to get a large enough library of calls from different individuals. The fact that we saw little response to tantrum screams could be because subjects generally ignore infant calls, despite their acoustic intensity. Although this is a valid point, the fact remains that acoustic structures alone are insufficient to explain the observed behavioural responses

Despite these methodological issues, chapter six provided the first evidence for call comprehension of a graded signal in any wild ape species. Female chimpanzees may use these calls to judge ongoing social events, particularly the intensity and potential danger of ensuing agonistic interactions, and subsequently employ this information to make social decisions. This chapter also showed that playbacks with wild apes are possible, even those that exhibit fission fusion social systems, such as the chimpanzee. With this protocol, I hope to pave the way for future experimental studies into understanding how females, and indeed males, use their vocalisations as social tools in their complex daily lives.

Additional cross taxa examples

Primates are a useful model for understanding how animals use vocalisations in socially calculated ways, primarily because they are known to lead complex social lives (Byrne and Whiten, 1988), and vocalisations often represent an important communicative medium. The latter point is particularly true for chimpanzees, due to their fission fusion social system and the dense nature of their surrounding habitat.

So far, only a small number of studies have addressed the social functions of chimpanzee vocalisations, though, unsurprisingly, these are mainly viewed from the male perspective. For example, Mitani and Gros Louis (1998) showed that chimpanzee males were capable of acoustically converging their pant hoots. Whilst it was initially unclear as to the function of this vocally learnt behaviour, with more detailed analyses it became apparent that such convergence occurred primarily between close allies. Mitani and Gros Louis (1998) proposed that the active modification of pant hoot structure was an important vocal strategy to enhance social bonds between males. More recently, Slocombe and Zuberbuhler (2007) investigated the potential function of chimpanzee victim screams. These agonistic vocalisations have long been thought to recruit aid (Goodall, 1986) and Slocombe and Zuberbuhler found that such recruitment could be done in tactical ways. Chimpanzees were found to exaggerate their victim screams only if there was an individual of higher rank who could potentially intervene on their behalf. These results combined are particularly intriguing because they show that, in addition to the production of calls, the acoustic structure of vocalisations can be used in socially manipulative ways.

Baboons are another socially and vocally well-studied primate group. As mentioned in chapter one, Chacma baboons are now known to use vocalisations to reconcile and repair social bonds, not only themselves, but also on behalf of kin (Wittig et al., 2007). Their long-distance “Wahoo” calls are also crucial, settling dominance rifts between males of differing status (Kitchen et al., 2003). In Gelada baboons, with an entirely different harem-based social system, males use “yelping calls” to dissuade other prospective males from attempting a take over – a strategy thought to enhance male tenure (Dunbar, 1984). Females are also thought to use vocalisations in tactical ways producing “solicitation calls” to incite recently aggressive (and hence successful) nearby males to approach and inspect her sexual swelling.

Primates are not the only animals to employ vocalisations in socially complex ways. Dolphins (Tursiops truncates), for example, produce acoustically and individually distinctive signature whistles. These whistles are more generally thought to maintain social cohesion and facilitate the prevailing fission-fusion social system (Janik and Slater, 1998). However, similarly to chimpanzees, allied male dolphins have been found to acoustically modify their signature whistles into an “alliance signature” that serves to identify the caller as a member of the alliance (Smolker and Pepper, 1999). Exactly who these alliance signatures are aimed at and what social function they have is not clear, though a number of possibilities have been suggested. Signatures could be directed at other males. Given that male units often compete with one another (Connor et al., 1992), sharing a common vocal label might make it easier for the members of an alliance to signal that they are allied and therefore represent a formidable competitive force. Alternatively, alliance signatures could be directed towards receptive females. These whistles could indicate the males’ ability to herd cooperatively and effectively and hence decrease the likelihood females will attempt to escape (Smolker and Pepper, 1999). Whatever the explanation, it is clear that dolphins utilize their distinctive signature whistles in interesting and potentially socially adaptive ways.

Outside of the mammals, chickens (Gallus gallus) provide some of the best evidence for seemingly strategic call use. When encountering food, chickens produce stereotypical pulsatile food calls. A cockerel’s tendency to utter food calls is strongly affected by the presence and nature of the receiver (Marler et al., 1986b). Food calling was typically given in the presence of strange or familiar female hens, but completely withheld in the presence of a male. It is thought that such flexible, socially context specific calling, operates to attract receptive females to the presence of available food and hence increases mating opportunities for the caller. Interestingly, males were also found to produce food calls even when there was no food available. This study has been interpreted as evidence for tactical deception in animal communication (Hauser, 1997) suggesting that even chickens are capable of socially calculated vocal behaviour.

A common theme that seems to be lacking from these studies is how social context effects female vocal behaviour. My results from chapters 3-6 might begin to address this gap in understanding. The world through which female chimpanzees navigate is socially multifaceted, even dangerous, and one way for females to maneuver successfully within this world is through the skilled use of vocalizations. I hope that this research will stimulate further, much needed focus, on female chimpanzees and other mammal species. Only with more research effort will we truly begin to understand the complexities underlying female social behaviour and the accompanying vocalisations.

Chimpanzee communication and cognition

My findings also provide a crucial insight into the cognitive mechanisms that might underlie chimpanzee behaviour. Here, in this penultimate part of the discussion, I will briefly outline what we already know regarding chimpanzee cognition and how my findings from this thesis contribute to our overall understanding of this long-debated topic.

From a number of primarily captive-based studies, we now know that chimpanzees are particularly skilled in the cognitive domain (e.g. Tomasello et al., 2003). In the social realm chimpanzees appear to be capable of differentiating self from others, passing the mark test on a number of occasions (Gallup, 1970). They are also capable of tracking lines of gaze geometrically (Tomasello et al., 1999), perspective taking (Hare et al., 2000), and even potentially understanding what others know (Hare et al., 2001).

In the physical world chimpanzees exhibit equally skilled cognitive behaviour. Captive work has recently suggested that they possess causal understanding of various problems (Horner and Whiten, 2005; Hanus and Call 2008), which complements evidence from the wild showing that they are skilled tool-users. Tools may be used to extract food sources (such as nuts (Boesch and Boesch Achermann, 2000), honey and termites (Goodall, 1986)), or to attend to themselves (e.g dabbing bleeding wounds, cure stomach ailments (Goodall, 1986)). Furthermore, because of the intricacies associated with these skills, many require active learning (Lonsdorf et al., 2004). The exact mechanism underlying such learning is a particularly contentious issue. Though teaching has been suggested (Boesch, 1991a), these observations are anecdotal and no study has, as yet, produced systematic evidence for this method of skill acquisition (Slocombe, 2005). Trial-and-error learning is one alternative, as is learning skills through social observations (Whiten et al., 2004). The ability for chimpanzees to learn by copying others is thought to be a particularly useful strategy as it improves the number of novel complex behaviours they can gain over a lifetime (Whiten et al., 2005).

The results from this thesis provide further evidence for the growing point that chimpanzees are skilled cognitive animals, but primarily from the vocal realm. This is a commonly ignored avenue when assessing ape cognition (Slocombe, 2005). Firstly, my findings indicate that copulation call production is affected by the female listening audience (chapter four). To date, most audience effects have been identified concerning the mere presence or absence of conspecifics (Le Roux et al., 2007) and its influence on calling behaviour. In addition to this, female chimpanzees are also sensitive to the specific composition of the audience, from a rank-based and numerical point of view. Constantly keeping track of ever-changing audience composition, and its social implications, is no simple task (Wilson et al., 2001). It requires that females monitor their surrounding conspecifics and use this information to make vocal "decisions". Chapter five provides an additional layer of cognitive complexity showing that females may also take into account what males can see. Whilst perspective taking has been previously shown in captivity (Hare et al., 2000), these results provide an extra ecological dimension – indicating one possible advantage to this skill in the wild. Findings of this sort provide some evidence against the widely held model of primate calls as hardwired response predispositions (see Zuberbuhler, 2007; Tomasello, in press) in favour of explaining call production in terms of complex social cognitive processes.

I additionally showed that chimpanzees are capable of processing the informational content of victim screams and possibly using this to make informed future behavioural decisions. These results contradict the traditional assumption that chimpanzees are purely attentive to the most salient signals in their environment and that their comprehension of vocalisations is cognitively simplistic (Owren and Rendall, 1997). Instead, chimpanzees may be capable of drawing inferences about their social world they cannot see from listening to and processing vocalisations. Through focusing on the more parsimonious explanations, its very likely we have overlooked the role information about out-of-sight events, gained from vocalisations, has on the behaviour of chimpanzees.

This thesis proposes that females can use vocalisations in potentially tactical ways. Tactical behavioural strategies, such as deception have, in the past, been highlighted as potential indicators of cognitive sophistication in primates (Hauser, 1997, Byrne and Whiten, 1988). If this is indeed the case, my results contribute importantly to previous findings. Such developments provide a much-needed ecologically relevant approach for future work investigating the cognitive sophistication of our closest living relative, the chimpanzee.

Future directions

What are the next steps in understanding female competition and the accompanying vocal counter-strategies? Because female competition in chimpanzees was initially disputed, we still have little detail regarding this social process, particularly the underpinning mechanisms. In this thesis, I have proposed that one resource females may compete over is males, specifically their sperm or the protective post-natal services they may provide. I showed that high-ranking females can display severe aggression to low-ranking females when advertising successful copulations - possibly as a form of competitive exclusion. Evidence for such direct competition over males has been found in a number of primate and mammal species (Rosvall, 2008), however, it would also be very interesting to isolate potentially more subtle means through which females compete over this resource. For example, male primates mate guard females through a number of behavioural mechanisms, including direct aggression towards soliciting males, maintaining close proximity to the cycling female, or post-coital grooming with the female (Semple, 1998b). It is also very plausible that females may employ similar behaviours in order to maximise their access to high-ranking males. This is one hypothesis that could be directly tested with more observational data from Budongo. Furthermore, it would be important to address similar questions at other field sites, to ensure the effects we are detecting are not site-specific, but instead part of the wider socio-ecology of the chimpanzee.

My findings suggest that in response to female competition and the aggression that can accompany it, females can use their copulation calls in a flexible manner. Albeit interesting, these results are purely observational and it is therefore crucial to systematically verify them with a playback experiment. As previously explained in chapter five, we were initially wary to attempt the first wild ape playback experiment with such a reproductively important vocalisation as the copulation call. However, as we have now managed to devise a methodologically and ethically sound protocol for conducting playback experiments, the possibility of testing the function of chimpanzee copulation calls has become increasingly more possible.

One of the most surprising results from chapter four was that the presence of high-ranking females affects the female's decision to give a copulation call. I will now outline a potential experiment that could rigorously test this novel result.

"Do oestrus female chimpanzees modify copulation call production in a tactical manner?"
In this study I would aim to experimentally test whether females have voluntary control over their copulation calls and whether they produce the calls in a tactical fashion. During oestrus periods, female chimpanzees mate promiscuously and copulation is often preceded by male and female courtship behaviour. Within this pre-copulatory time window, I will simulate the arrival of a high-ranking female into the party, through playing a frequently-occurring 'greeting' vocalisation; the pant-grunt. If females have voluntary control over their vocal production and are sensitive to the presence of higher-ranking females, I predict that they should suppress the production of copulation calls when hearing pant-grunts of higher-ranking females. As a control, pant-grunts from a socially less relevant, low-ranking female are played back and the prediction is that this should not affect copulation call production. I would employ the playback protocol outlined in chapter six to maximise realism, reduce the chances of extinction behaviour and minimise social disturbance.

This is just one example of a number of different experiments that could be undertaken to test the function of chimpanzee copulation calls. Obvious additional studies include testing what information males can extract from copulation calls, particularly whether they can extrapolate female identity or the rank of the mating partner. Similar playbacks have been employed with other monkey species and have yielded very interesting results (Barbary Macaques: Semple, 1998b; Semple and McComb, 2000; Pfefferle et al., 2008b; Yellow Baboons: Semple, 2001). A further subject that is likely to receive a lot of future interest, is what female conspecifics can understand from copulation calls. In a system where females theoretically compete for access to males, one very logical prediction is that information regarding ongoing mating activity is also relevant to females (Pfefferle et al., 2008b). Chimpanzees are no exception and I would be interested to see how they use such information to make informed social and sexual decisions. Such questions are likely to provide a whole new dimension to understanding the evolutionary function of primate copulation calls and indeed other socially relevant vocal signals

Conclusion

Only recently has the myth of the passive female chimpanzee been dispelled. For a long time females were considered as solitary, peaceful individuals, their lives periodically turned upside down by sexually-excited, aggressive males. The mere concept that they may compete with one another over resources and exhibit male-like aggressive tendencies when doing so, would have been immediately ruled out. Slowly but surely, our portrait of the female chimpanzee is changing. In this thesis, I have attempted to help paint a new emerging picture. This portrait depicts females as living in a complex and volatile social world, capable of using and comprehending their vocalisations in strategic ways allowing safe navigation through this, at times hostile, environment. These results, from the vocal domain, complement very recent findings that suggest females employ subtle yet complex behavioural strategies to avoid conflict with each other (see Emery Thompson et al., 2008). Together this highlights that even where females interact infrequently, “female initiative” (Wrangham, 1980) can be a powerful force in the evolution of social and vocal systems. Selective impact does not necessarily correspond with social power. I hope these findings will stimulate further research into the social lives, behaviours and ultimately the minds of female primates.

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Appendix I

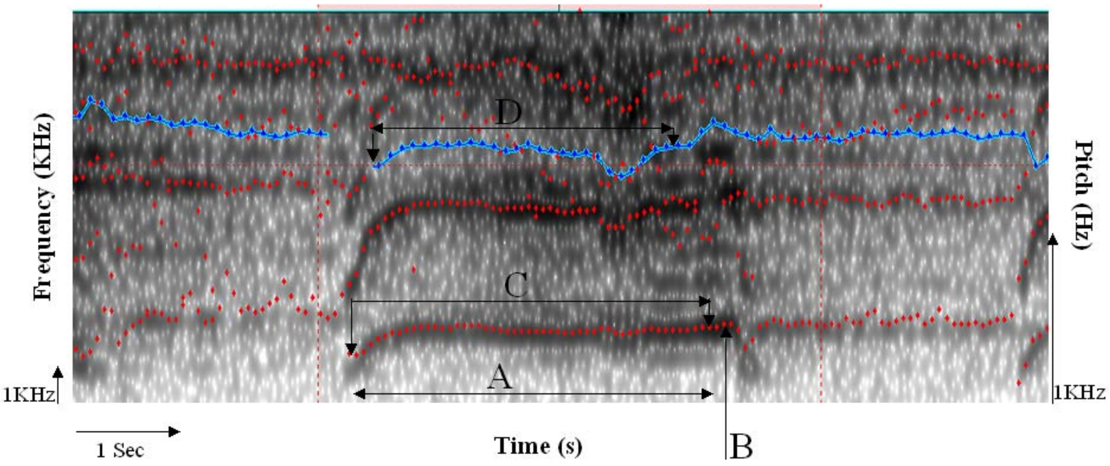
Severe, mild and tantrum scream acoustic analysis

In chapter four I was able to able to replicate the pattern of acoustic differences between mild and severe screams reported by Slocombe and Zuberbuhler (2007). Furthermore I showed that severe screams and tantrum screams are matched in their acoustic structure. Here I will briefly outline the acoustic analysis protocol undertaken and the results obtained (see appendix figure 1 and appendix table 1).

Methods

I measured victim and tantrum screams along four independent parameters using PRAAT version 4.3.37 and scripts written by M. Owren (see appendix figure 1):

1) Duration: the length of the individual screams constituting a scream bout (s).
2) Mean pitch of the scream: the scream's average pitch (indicated by blue line) (Hz).
3) Mean frequency of the 1st formant: the average frequency of the screams 1st formant band (Hz).
4) Peak frequency in the call: highest frequency in the fundamental (Hz).



Appendix Figure 1: A tantrum scream produced by infant Karo of the Sonso community, Budongo Forest, Uganda, illustrating how the four temporal and spectral parameters were measured from each scream. A: the duration of the scream (s); B: the peak frequency of the scream (Hz); C: the first red dotted line indicates the tracking of the 1st formant. A script written by M. Owren calculates the average frequency over this formant (Hz); D: the blue line indicates the tracking of the pitch of the scream. From this, a script written by M. Owren calculates the mean frequency, or "pitch" of the fundamental (Hz). An identical method is used to calculate pitch in copulation calls (chapter five).

Results

Trial type	**1st formant**	SD	**Peak frequency of fundamental**	SD	**Mean pitch**	SD	**Duration**	SD
Severe (N=5)	**1435.45**	38.4	**1435.54**	62	**0.54**	0.17	**1404.25**	58.6
Mild (N=7)	**1260.8**	201	**1276**	189.3	**0.31**	0.15	**1064**	215
t value	**2.149**		**1.933**		**0.543**		**2.619***	

Appendix table 1: The mean values and SD of four acoustic measures for mild and severe scream conditions. N refers to the number of scream bouts (used as stimuli) that contributed to the mean values reported in each catergory. Mean values of parameters matched the desriptive statistics reported in Slocombe and Zuberbuhler (2007). T-values revealed a significant difference (indicated by *) only in duration, though this is highly likely due to the small sample sizes used (N=7 Vs N=5).