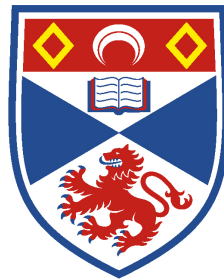# Courtship Communication in the Wild Chimpanzees of Budongo, Uganda

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St Andrews

This thesis is submitted in partial fulfilment for the degree of PhD
at the
University of St Andrews

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ABSTRACT

This thesis examines wild chimpanzee mating behaviour, and considers in particular the role of communication during mating. Previous studies have focused on compiling behavioural ethograms, or on a small subset of courtship signals. More generally, research on chimpanzee sexual behaviour has rarely looked at intentional communication, but instead focused on a handful of courtship tactics, such as male long-term aggression or female proceptive behaviour, despite every indication across great ape species that intentional communication is important in courtship. On these grounds, I undertook an examination of both male and female communication in the Sonso chimpanzee community in the Budongo forest, Uganda.

The chapters comprising this thesis examine female copulation calling, male gestural displays during opportunistic mating, male gestural displays during consortship, and the role of female preferences on male courtship displays. Parous and nulliparous females have different calling strategies based on high-ranking male audience, copulation duration, and level of female competition. Males use a small subset of their gestural repertoire to solicit for copulation, concentrating the majority of gesturing in 5 gesture types. Gestures were successful for both high- and low-ranking males, although high-ranking males employed more agonistic gestures than low-ranking males. All males showed high rates of persistence following failure, especially during consortship. Overall, the likelihood of copulation was not influenced by traditional courtship factors such as vigour, but rather was dependent on effective use of gestures.
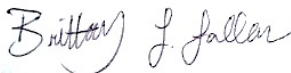
My research shows that both male and female chimpanzees use communication tactically during courtship: for females, this is evidenced by differing copulation call strategies in parous and nulliparous females. For males, social status plays less of a role than persistence for achieving copulation, although high-ranking males do use coercive gestures more frequently. Overall, I show that communication is an effective tool for answering questions about mating strategies in chimpanzees.

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I, Brittany Fallon, hereby certify that this thesis, which is approximately 36,000 words in length, has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in September 2012 and as a candidate for the degree of Doctor of Philosophy in September 2012; the higher study for which this is a record was carried out in the University of St Andrews between 2012 and 2016.

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ACKNOWLEDGEMENTS

This thesis is wholly dedicated to my late father, whose curiosity and spirit of adventure

spurred my own, and to my mother and grandmother, my unwavering pillars of support.

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LIST OF ABBREVIATIONS

ASO	Apparently satisfactory outcomes
GLMM	Generalised linear mixed model
LRT	Likelihood ratio test
OSR	Operational sex ratio
POP	Peri-ovulatory period
VIF	Variance inflation factors

Chapter 1: Sexual Behaviour Theory

INTRODUCTION

Sexual displays permeate the daily life of many species, whether demonstrations of strength (rhinoceros clashes: Goddard, 1966), ornamentation that indicates virility (bird plumage: Darwin, 1871), or any of the myriad forms of courtship that occur from single-celled organisms (*S. cerevisiae*: Jackson & Hartwell, 1990) to humans of many cultures (Eibl-Eibesfeldt, 2007). Courtship patterns across species are underpinned by the principles first described in Darwin's theory of sexual selection (Darwin, 1871). *Sexual selection* describes 'the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction' (Darwin, 1871). Put simply, sexual selection is the idea that traits evolve through competition for mates because they provide a mating advantage for individuals. This theory highlights the driving forces behind courtship and comprises the theoretical basis for my research on chimpanzee courtship communication.

Sexual selection

There are two principles of sexual selection: intra-sexual competition and inter-sexual competition. Intra-sexual competition describes competition within one sex for mates, and thus gives rise to characteristics such as aggressiveness and body size dimorphism (Darwin, 1871; Dixson, 2012). Inter-sexual competition, which occurs between the sexes, results in traits such as courtship songs or ornamentation (ibid). Both principles give rise to behaviour that is related to sexual selection at either an *ultimate* or *proximate* level.

Tinbergen described ultimate explanations as addressing the function of a given behaviour, or more plainly, why it exists and is a favoured trait (Tinbergen, 1963; Scott-Philips et al., 2011). Proximate explanations refer to the underlying mechanisms that explain how it works (Scott-Philips et al., 2011). Male meadow voles exposed to the odour of another

male, for example, increased their total sperm investment when mating with a female (*Microtus pennsylvanicus*: Ferkin, 2004). Here, olfactory cues mediate male meadow moles' behaviour on a proximate level, while the ultimate function is sperm competition. Both explanations are important for understanding behaviour.

Sex differences are the starting point for research on the mechanisms of sexual selection. Darwin predicted interplay between two main forces, male mate competition and female mate choice, as the primary manifestations of sexual selection, arguing that 'secondary sex traits' preferred by females often acted in opposition to natural selection (Darwin, 1871; Trivers, 1972). The parental investment theory, first discussed by Fisher (1930) and later developed by Trivers (1972), explains male and female differences as based on parental expenditure. Females are the limiting sex, due to the costs of reproduction, including fertilization, gestation, and a period of offspring dependency; male reproductive output is less constrained, especially in species with limited paternal investment. This leads to the idea of males as competitors and females as choosey. Darwin (1871) asserted that female preferences result in male showiness, both in physical appearance and in courtship displays; males engage in contests, scrambles, and endurance rivalry (Andersson, 1994). In primates, there has been a historical focus on obvious male traits (i.e. aggression and coercion) at the expense of the comparatively subtle female traits (Drea, 2005). Importantly, Darwin himself acknowledged that male competition and female choice were not exclusive, but complementary (Darwin, 1871). In the following sections, I briefly review the male and female behavioural manifestations of sexual selection, followed by a discussion of chimpanzee courtship communication.

Male competition and female counter-strategies

Intra-sexual male competition can be subtle, as in the case of sperm competition at the ultimate level. When competing outright for access to females, however, males tend to

compete using overtly aggressive strategies that coerce females at the proximate level, as found in taxa ranging from salamanders (*Plethodon cinereus*: Jaeger et al., 2002) to elephants (*Loxodonta africana:* Poole, 1989). Aggression can also be directed at sexually receptive females in the form of sexual coercion to achieve matings (Smuts & Smuts, 1993; reviewed by Clutton-Brock & Parker, 1995), as seen in such diverse species as waterfowl (reviewed by McKinney & Evarts, 1998), dolphins (*Tursiops sp.*: Scott et al., 2005), or primates (e.g. Japanese macaques, *Macaca fuscata*: Soltis et al., 1997). Among primates, male dominance and aggression seems to be the most common – and most effective – mating strategy.

The relationship between male aggression and precopulatory female choice is challenging to separate, as male competition can both help and hinder female choice (Qvarnstrom & Forsgren, 1998; Wong & Candolin, 2005). One theory suggests that male competition and female choice are mutually reinforced (Darwin, 1859; Wiley & Poston, 1996). For females, mating with competitive males can be ultimately beneficial, for example if competitive males monopolize resources (e.g. red-collared widowbirds, *Euplectes arden*s: Andersson et al., 2002) or provide genetic benefits by siring healthier offspring (Cox & Le Boeuf, 1977). In cases where females choose males that are likely to be genetically advantageous, it can behove females to actually incite competition rather than avoid it. Such is the case in species that produce copulation calls. Thus, females in many species prefer traits associated with dominance at the proximate level, such as bright colouration (rhesus macaques, *Macaca mulatta*: Waitt et al., 2003), frequent scent marking (pygmy loris, *Nycticebus pygmaeus*: Fisher et al., 2003), or high rank (chimpanzees: Goodall, 1986). Avian females, for example, prefer vigorous motor performance during courtship displays, presumably as an indication of males' health and virility (Byers et al., 2010).

While male aggression is often conspicuous and its benefits for reproductive fitness well documented in many species, females are not necessarily passive acceptors of aggressive

mates. Females sometimes evolve strategies to avoid or reduce male coercion (Clutton-Brock & Parker, 1995; Gavrilet & Arnqvist, 2001). Concealed ovulation may be an example of aggression avoidance at the ultimate level. Hanuman langurs have extended sexual receptivity that results in an increase paternity confusion and reduces the risk of infanticide (Hestermann et al., 2001). Human females who live in close proximity, i.e. roommates, can have synchronized menstrual cycles (McClintock, 1971); the same appears to be true for chimpanzee cage mates (Wallis, 1985). This tactic may allow both human and non-human primates to avoid aggression while still preferring dominant males: women in the fertile phase prefer males with ancestral traits of good quality such as facial/bodily masculinity and androgen-related odours (Gangestad &Thornhill, 2008).

Aggression avoidance also occurs at the proximate level. Japanese quail that witness male-male competition preferentially mate with the defeated individual, potentially avoiding injury since competitiveness correlates with aggressive mating (*Coturnix japonica*: Ophir & Galef, 2003). Females may also choose males who invest in offspring rather than male victors of combat (e.g. sand gobies, *Pomatoschistus minutus*: Forsgren, 1997). In non-human primates, subordinate males can thus sometimes increase their reproductive fitness through tactics such as socio-spatial relationships (chimpanzees, *Pan troglodytes*: Langergraber et al. 2013) or grooming (Japanese macaques, *Macaca mulatta*: Massen et al., 2012; chimpanzees, Kaburu & Newton-Fisher, 2015b).

Despite these female counter-strategies, in reality most roads lead to male coercion restricting or circumventing female choice. Indeed, Figure 1.1 outlines the possible pathways from female choice to mating success; in all but two cases, dominant males hold the advantage over subordinate males. In this representation, female preference for traits not associated with dominance - or negatively correlated with it - is the sole pathway toward subordinate male success.

Fig. 1. The possible ways in which male–male competition and female choice can interact in determining male mating success. Here, we assume that dominant males are successful at intimidating rivals. Pathway 'a' applies only when females prefer traits that are negatively correlated with dominance.
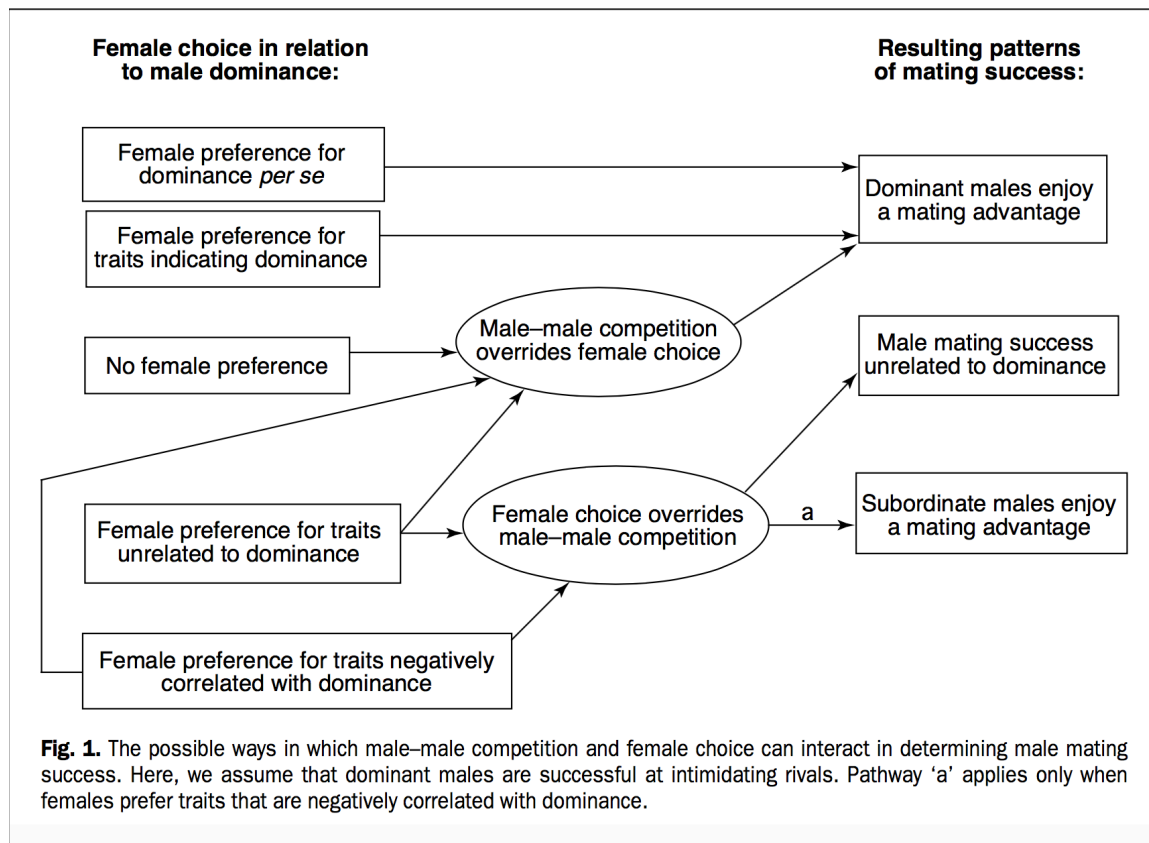
Fig. 1.1: Copied with permission from Qvarnstrom & Forsgren (1997)

Sexual selection and intentional communication

An extra layer of complexity is introduced into sexual strategy for great apes, from the discovery that their gestural communication is made intentionally. Apes are thus distinct from other primates because courtship needs to be studied as a communicative system, especially the choice of signals, when to use them, and signal evaluation by the opposite sex. In humans, for example, pick-up lines are one of the greatest tropes of modern courtship and seem to take on the fourth-order of Gricean intentionality – "I know that you know that I am joking when I use this phrase but I trust you understand that I want you to know I fancy you" – while also signalling humour, which has been shown to boost male mate value across cultures (for a review, see Kaufman et al., 2008).

Yet to date, research on great ape courtship has emphasized male-male mating competition (Muller et al., 2011), with less attention paid to subtler forms of courtship such

as vocal or gestural communication. Relatively little is known about male decision-making during gestural and vocal courtship displays, or how females evaluate male courtship displays. This is due in part to the recent understanding that great ape communication may be intentional, and in part due to the limited research on sexual behaviour in the wild, where courtship occurs within a natural context. Given the role courtship plays in sexual selection, ape courtship may be important to our understanding of the selectively favoured traits for males and females in each species. By way of background to this topic, I discuss chimpanzee sexual behaviour and communication in the following sections.

Chimpanzee sexual behaviour and competition

Chimpanzees live in communities of 10 to 200 individuals within a group-defended territory, typically comprised of a group of natal males and a larger number of females (Goodall, 1986). Females raise their offspring with no paternal investment (Wrangham & Smuts, 1980). Males have a linear dominance hierarchy with the two highest-ranking males – the alpha and beta males – siring the most offspring (Constable et al. 2001; Vigilant et al. 2001; Langergraber et al., 2010). Chimpanzee females have a concentrated period of sexual receptivity where they exhibit a large, pink swelling that remains inflated for 10-16 days (Deschner et al., 2004). Copulation occurs only during this swollen phase, with rare exceptions. The peri-ovulatory period (POP) is the three-to-four day window when ovulation is most likely to take place, and when males are most competitive for access to an oestrous female. Access to an ovulating female is vital for reproductive success, and competition between males gives rise to three mating tactics offering various levels of sexual exclusivity, as defined by Tutin (1979). *Opportunistic mating* is a relatively non-competitive mating strategy where all males have the opportunity to mate with a swollen female, as opposed to *possessiveness*, where one high-ranking male guards the female and prevents low-ranking

males from mating through aggression. During *consortship*, the most restrictive mating strategy, a male and female leave the group for her entire sexual cycle. Tutin (1979) hypothesizes that although males take the initiative to monopolize females in possessiveness and consortship, females must cooperate in order for the relationship to be successful. This hypothesis is challenging to test because possessiveness and consortship occur rarely and are difficult to observe.

As Figure 1.1 suggests, dominant males can co-opt many mating situations to be in their favour. It is clear that chimpanzee males prefer older, parous females and use sexual coercion as a means of enacting this preference (Muller et al., 2006; Muller et al., 2007; Muller et al., 2011; Feldblum et al., 2014). However, high-ranking males may be able to offer females more protection or resources than low-ranking males (Wrangham & Smuts, 1979; Smuts & Gubernick, 1992; Smuts & Smuts, 1993). Chimpanzee females thus occasionally tactically initiate sexual interactions with high-ranking males (Pieta, 2008), suggesting that they can modify their mating behaviour to some degree for their own reproductive benefit. Further, wild female chimpanzees experience asynchrony of the peri-ovulatory period (POP) and maximum swelling stage (Matsumoto-Oda & Ihara, 2010). Rather than acting as a counter-strategy to male aggression, here asynchrony is thought to encourage male mate guarding as a means of avoiding competition or aggression from other females.

Proactive sexual behaviour by females differs by community (Stumpf & Boesch, 2006; Pieta, 2008), possibly because of different counter-strategies to coercion. In some chimpanzee populations, female choice appears to be the dominant mating strategy (Matsumoto-Oda, 1999; Stumpf & Boesch 2005; Stumpf & Boesch, 2006; Stumpf & Boesch, 2010). It has been argued that in communities where males differ little in competitive power they are unable to exert direct coercion but instead attempt to bias female choice, for example through grooming (Kaburu & Newton-Fisher, 2015a; Kaburu & Newton-Fisher, 2015b).

Additionally, both males and females produce vocalizations and gestures strategically order to influence mate choice (Tutin & McGrew, 1973; Goodall, 1986; Nishida, 1997; Matsumoto-Oda & Tomonaga, 2005). Current research on chimpanzee communication examines the proximal function of such displays, i.e. the outcome or meaning of signals, with limited application to courtship displays. The ultimate function of chimpanzee communication during courtship has not explicitly been tested; however, data from other species suggests that courtship displays influence reproductive output.

Chimpanzee courtship communication

Early descriptions of male sexual displays (Tutin, 1979; Nishida, 1997) hint at the presence of intentional communication, and recent literature on gestural communication has identified several intentional gestures within the repertoire of sexual display behaviour (Liebal et al, 2004; Hobaiter & Byrne, 2011a; Hobaiter & Byrne, 2012). Kollar et al. (1968) wrote one of the earliest detailed descriptions of chimpanzee courtship, describing the Holloman Air Force chimpanzees, whom I later had the pleasure of working with at Save the Chimps, Incorporated. Kollar et al. (1968) describe typically male-initiated gestural displays that include open body postures highlighting the penile erection, exaggerated arm movements, and neutral facial expressions. He observed that males were frequently persistent in their solicitation of oestrous females, who screamed during copulation, and that males were sometimes threatening in manner when they approached females (ibid.). His descriptions nicely encapsulate, in broad strokes, courtship communication for chimpanzees.

Although the gestures described by Kollar et al. (1968) would not be termed intentional for several decades, observations by primatologists in the field corroborated the complexity of chimpanzee courtship displays. Goodall offers the first account of the social context under which courtship displays occur, describing the roles that males and females of different ages play, and female responses to solicitations. Her descriptions suggest that

chimpanzees adjust their sexual behaviour as they become more experienced. This maturation process seems intimately tied to communication, and she describes young females as occasionally misunderstanding male sexual solicitations as invitations to play (Goodall, 1986). Later research on gestural development confirmed that young individuals do learn to efficiently gesture with age and experience, although the exact means of development remain debated (Tomasello et al., 1985; Hobaiter & Byrne, 2011b). However, play has emerged as a gesture-rich context in which young individuals experiment with their communicative repertoire, sex play being no exception (Tutin & McGrew, 1973; Tomasello & Call, 1997).

Goodall's findings are confirmed by a survey of sexual behaviour in the Mahale chimpanzees (Nishida, 1997). Nishida records the use of apparent gestural sequences, as later found by Liebal et al. (2004) in captivity, and finds that some gestures lead to copulation less often than others. In other contexts, sequences seem to be a means by which individuals co-regulate and modify their gesture use (King, 2004; Tanner, 2004; Genty & Byrne, 2009). For young individuals in particular, sequences are a tool for learning which gestures are most effective within your group (Hobaiter & Byrne, 2011b). Gestural courtship sequences may likewise be a tool for males attempting to attract a female to mate. Nishida was the first to record in detail female response to male solicitations, describing both proceptive behaviour toward males and outright rejection (1997). Chimpanzee communication during consortship also hints at female choice: females who scream are able to thwart males' attempts at consortship (Tutin, 1979; Hobaiter & Byrne, 2012). Hobaiter and Byrne report that communication in this context was markedly different from all other contexts as males gestured more urgently than usual and only used gestures audible from short distances, apparently to avoid detection from the main group. Whether females exhibit preferences for certain courtship traits, as one would expect from literature on sexual selection in other species, is unknown. Females might, for example, prefer complex displays that reflect vigour,

variety, or dominance as underlying signals of male quality (Andersson, 1994). Alternatively, inexperienced and low-ranking males might produce displays consisting of gestural sequences as a means of narrowing in on the most effective solicitations. Effective communication may be one way in which low-ranking males avoid male-male competition and increase their reproductive success.

It should be noted that facial expressions are the least studied aspect of communication, including during courtship. Female chimpanzees produce a 'copulation grimace', to which males can lip smack in response (Tutin & McGinnis, 1981; Goodall, 1986). Both of these facial expressions are hypothesized to assist the male in coordinating copulatory activity (Savage & Bakeman, 1978; Dixson, 1998), but no sources indicate that they may be intentionally communicative. As such, in the following chapters I will concentrate on the vocalizations and gestures produced during sexual displays.

Aims of my thesis

Observations from both wild and captive chimpanzees reveal subtle dynamics in courtship displays that deserve further study. Although early descriptions of sexual displays are described as gestural, to the best of my knowledge no study has comprehensively examined sexual displays as intentional communication. Neither gesture combinations nor persistence, two key criteria for intentionality, have been systematically documented in solicitation attempts outside of chimpanzee consortship (Hobaiter & Byrne, 2012), although both are known to occur from general observations of reproductive behaviour and limited examples from captive studies. Critically, there has been no research on differences between males' courtship displays, and what traits (e.g. complexity, dominance of signaller) constitute a successful solicitation. It is not clear from the available data whether female preferences play a role in male courtship displays, or whether communication influences female response:

for example whether mating is more likely to occur following certain gesture combinations, or whether female parity status impacts mating likelihood. The pervasiveness of male sexual coercion implies that female choice may be overridden by aggression; comparing the displays of high- and low-ranking males, and female response to these displays, may provide insight into both male and female sexual strategies. In a further examination of female sexual strategies, I assess female copulation calls according to parity and audience effects.

Chapter 2: Methodology

STUDY SITE AND SUBJECTS

I conducted fieldwork at the Budongo Conservation Field Station (BCFS), located in the Budongo Forest Reserve in Masindi, Uganda, a protected area totalling 794 km^2 of primarily semi-deciduous forest (Eggeling, 1974; Plumptre, 1996). Fieldwork was conducted between the periods of June 2011-August 2011, May 2012-April 2013, and September 2013-March 2014, totalling approximately 2,688 hours of observation time.

Budongo Forest is home to an estimated population of 583 chimpanzees (Plumptre, Cox, and Mugume, 2003), including two research communities: Sonso (fully habituated) and Waibira (semi-habituated). Data were collected from the Sonso community, which included 66 individuals (19 males, 47 females) at the time of the study (Appendix I). Fourteen adult and sub-adult males (9 adults, 5 sub-adults) aged 10 to 35 were targeted for data collection as copulation partners. Of the females, 13 parous and 7 nulliparous females exhibited a swelling during the study period and were targeted as focal individuals.

Female-female competition

During my fieldwork season, there were an uncommon number of oestrous females, which led to an unusual level of female-female competition. This state resulted from several factors. Two new immigrants entered the community (Irene, Upesi), and three young natal females began their first sexual cycles (Helen, Monica, Tapura). At the same time, four cycling natal females (Anna, Katia, Kana, Rose) did not transfer communities, and three of them eventually had their first infants in their natal community (Anna, Katia, Rose). Finally, nine adult parous females stopped weaning their infants and came into swelling for the first time in 4-5 years (Gladys, Harriet, Janie, Kalema, Kewaya, Kwera, Kutu, Melissa, Tanja). All of the parous females were pregnant by the end of my study.

SAMPLING

I filmed interactions between males and oestrous females using a Panasonic HD V700 video camera and a Sennheiser MKE400 microphone. Data were collected in all-day focal follows of swollen females using all-occurrence sampling balanced across individuals (Altmann, 1974). In the event that multiple females were sexually receptive, focal follows were conducted of the female whose party contained the largest number of males. Effort was also made to follow males of all dominance rankings; therefore, where necessary, I targeted swollen females who were in a party with "uncommon" males in order to supplement limited data. Consortship was observed on an ad libitum basis, due to its rare occurrence.

During a focal follow, all interactions between males and oestrous females were filmed, including affiliation (grooming, food sharing, inspection of sexual swelling), aggression, and courtship displays either produced by or directed toward the female.

TERMS AND DEFINITIONS

An event was considered a *courtship display* if the signaller was either an oestrous female (of swelling size 1, 2, 3, or 4) or a male with a penile erection, where the outcome of the communication was sexual behaviour, such as inspection or copulation. Physical actions during courtship displays were considered a communicative act when discrete, intentional, and mechanically ineffective, following Hobaiter and Byrne (2011a). Such actions were considered intentional when directed toward a specific individual, and accompanied by response waiting, audience checking, and/or persistence (see Table 2.2 for definitions).

Video Coding

I used FileMaker Pro Advanced v. 11 for video analysis (Appendix II). Video data for courtship displays were first coded for contextual information including signaller, recipient, recipient attention state, swelling or erection size, recipient context, and party composition. A detailed explanation of these variables is found in Table 2.1. Video data on aggression and affiliation were entered into a database detailing the involved parties, length of the

interaction, and whether it occurred prior to or after a solicitation or copulation. Female

swelling size was decided by discussion between my field assistant, Monday Gideon, and

myself.

Table 2.1: Contextual variables

Variable	Definition
Signaller	Individual soliciting
Recipient	Target of communication
Recipient attention state	Attending (visible eye contact, head turning, or other behaviour indicating tracking of signaller's behaviour), full view (complete view of signaller), partial view (signaller visible peripherally), or out of view (recipient cannot see signaller or has back turned to recipient)
Swelling/Erection	Female swelling size was graded using degree of wrinkling (Furuichi 1987) on a scale of 0-4, as is routine on the site (Zuberbühler and Reynolds 2005), and male penile erections were noted as present or not.
Recipient context	The contextual behaviour of the recipient for example feeding, resting, or travelling.
Party composition	All individuals present.

Coding communication

Communication during courtship was coded for intentionality, goal, modality (i.e.

vocal or gestural), structure, response of the recipient to the solicitation, and success of

courtship display. Courtship displays were parsed into separate actions, including

communicative and non-communicative acts; thus, one courtship display might be comprised

of several actions (with some overlap, such as vocalizing while gesturing). For example, a

signaller may approach and sit before an oestrous female while erect (1), begin grooming the

female (2), gesture once unsuccessfully (3), and later gesture while vocalizing (4) before

successfully copulating – a four-part courtship display with one unimodal and one

multimodal communicative attempt. In turn, communicative attempts can be comprised of

multiple gestures or vocalizations. I parsed gestural communication into communicative

attempts according to three strategies: single gestures, sequences, and bouts (Table 2.2:

definitions previously used by Genty & Byrne 2009; Hobaiter & Byrne 2011b). These are

discussed in further detail in the relevant chapters on gestural communication.

Table 2.2: Communication variables

Variable	Definition
Audience check (Intentionality criteria)	Visibly monitoring the attentional state of audience
Response wait (Intentionality criteria)	Pause in communication, during which signaller continues to monitor recipient
Persistence (Intentionality criteria)	Continued attempt(s) after an unsuccessful communicative act
Goal	Apparent satisfactory outcome for the signaller, determined by response resulting in a cessation of communication attempts.
Communicative act modality	Vocal communication, gestural communication, or both
Vocalization	Vocalizations produced as part of courtship display: bark, hoo, grunt, pant hoot, pant grunt, scream, scream-copulation, laughter
Gesture	Gestures produced as part of courtship display.
Single gesture	A gesture isolated by a following pause lasting longer than 1 second
Gestural sequence	Several gestures in rapid succession, with a pause of less than 1 second between gestures
Gestural bout	Multiple single gestures or sequences, with intermittent pauses of more than 1 second. A bout is terminated by any response from the recipient that causes the signaller to cease gesturing.
Recipient behavioural change	Any non-communicative reaction: change in attentional state, approach or move away, groom, affiliate, aggress, copulate
Recipient communicative act	Vocalizations or gestures produced by recipient in response to courtship display.
Success	Goal met fully, partially, or not met.

Chapter 3: Female Copulation Calls and Competition[1]

ABSTRACT

Female chimpanzees, *Pan troglodytes*, are usually depicted as sexually submissive and bound by male coercion, because males are able to monopolize oestrous females, limiting a female's options for mate choice. I present behavioural data from a group of wild chimpanzees during a rare period in which up to 10 females cycled simultaneously, which prevented males from monopolizing oestrous females, thus changing the dynamic of male-female sexual interactions. Overall, I found that nulliparous and parous females employed different copulation calling strategies, reflecting their relative reproductive attractiveness and social standing within the community. Male partner rank, copulation duration and dominant male audience further influenced calling behaviour, and there was a non-significant trend for females to increase calling as the number of cycling females increased. Copulation calls did not influence the time to next copulation, nor did the rank of the subsequent consorting male. Additionally, male party size increased for parous females following a mating event, whether or not she produced copulation calls. I conclude that female chimpanzees are capable of adjusting their copulation calling flexibly, by taking into account their own sexual attractiveness, to incite male competition.

INTRODUCTION

Chimpanzee copulation calls are rhythmic, high frequency, and acoustically distinct screams produced by females (Townsend et al., 2011). Females typically produce copulation calls during intromission, but occasionally emit calls before or after copulation; young females even call during swelling inspection, albeit rarely (Fallon, pers. obs.). Since copulation calls do not seem tied to the event itself, they are thought to have a purpose beyond simple mechanistic responses to copulation (Pradhan et al., 2006).

Copulation calls commonly occur among mammals, from brown bats (*Myotis lucifugus*: Thomas, 1979) to elephant seals (*Mirounga angustirostris*: Cox & LeBoeuf, 1977), although they differ in acoustic structure. For example, brown bat males give a low-frequency call with rising frequency modulation (Thomas, 1979), while elephant seal females give a loud, threatening 'belch-roars' (Bartholomew & Collias, 1962). Due to their near-ubiquitous occurrence and often-complex acoustic structure, much research has focused on

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[1] Some of the data of this chapter were used in: Fallon, B. L., Neumann, C., Byrne, R. W., & Zuberbuhler, K. (2016). Female chimpanzees adjust copulation calls according to reproductive status and level of female competition. *Animal Behaviour*.

copulation call function in the primate taxa (Hauser, 1990). The majority of the hypotheses explaining the adaptive significance of primate copulation calls have originated from research on monkey species, a surprising fact given the crucial role that apes play in understanding the evolution of human behaviour from a phylogenetic perspective (Tomasello, 2010). To date, 14 different hypotheses have been put forward to explain the function of copulation calls, most of which share a common theme: copulation calls are sexually selected traits that benefit the calling individual's reproductive success (Pradhan et al., 2006).

Proposed function of copulation calls

Pradhan et al. (2006) provide an overarching review of copulation call findings across 10 species of Old World primates, narrowing in on two functional explanations: sperm competition and infanticide risk. Proximately, copulation calls lead to these functions by inciting competition among males and encourage mate guarding from the consort male. Two general calling patterns emerge from their careful review: Females are both more likely to call when mating with dominant males, and more likely to call at the end of copulation (ibid).

Male partner rank influences copulation call rates in several primate species (i.e. yellow baboon: Semple et al. 2002; chimpanzees: Townsend et al. 2008; bonobos: Clay & Zuberbuhler, 2011). By alerting males to copulations with high-ranking individuals, females promote indirect male choice by inciting male-male competition, ideally between high-ranking males (Hauser, 1990; O'Connell & Cowlishaw; 1994; Henzi, 1996; Semple, 2001; Semple et al., 2002). Ultimately the female benefits by getting the best sperm. Copulation calls encourage mate guarding behaviour by attracting the attention of the alpha male and encouraging him to guard the female caller until conception is possible (Henzi, 1996). In cases where females' calls provide reliable cues to male dominance rank, females encourage guarding from high-ranking males, which can incur genetic advantages as well as future protection. Since females in many primate species are vulnerable to infanticide (Van Schaik,

2000; Muller et al., 2007), there seem to be strong selective pressure acting on females to evolve behavioural counter-strategies to protect offspring (Steenbeeck et al., 1999; Sterck et al., 2005; van Schaik, 2000).

Central to Pradhan et al.'s (2006) review is the assumption that all females should share the same motivation for calling, even though males in many species have clear female mate preferences. Few studies take into account female social status, despite the fact that male rank is a factor in nearly all of the studies cited by Pradhan et al. (2006). Further, females without offspring may be subject to different calling pressures than mothers. Indeed, subsequent research on *Pan* has indicated that female social status and parity is an important component of calling and other social behaviour (Townsend et al., 2008; Clay & Zuberbuhler, 2011).

Chimpanzee copulation calls

The acoustic structure of a chimpanzee copulation call is unique to each individual and provides an approximate, but imprecise, cue to fertility (Townsend et al., 2011). Calls are exclusively produced during the period of sexual swelling, a combination of visual, olfactory, and audible signals that may assist males in determining the exact day of ovulation (Semple, 2001). It is not known whether chimpanzee calls include information regarding ejaculation or the rank of the signaller, as is found in other species; nor is it clear what influence such calls have on potential mates. In general, *Pan* species produce copulation calls at a much lower rate than other primates (Pradhan et al., 2006), suggesting calls reflect strategies other than paternity confusion.

Research from long-term field studies has demonstrated that chimpanzee females are exposed to intense social pressure from other group members, primarily when resources are constrained (Pusey, et al., 2008; Pusey & Schroepfer-Walker, 2013). Accordingly, social audience – especially the presence of dominant individuals – influences female calling

behaviour. In a brief study of 64 copulations, Hauser (1990) found that captive chimpanzee females called more with established adult males than young adult males. Females in the Budongo forest likewise called more when mating with high-ranking males as compared to low-ranking males (Townsend et al., 2008).

Female chimpanzees can suffer heavily from infanticide by both males and females (Townsend et al., 2007; Wilson et al., 2014). In Budongo, a site where infanticides are perpetrated by females as well as males, both social status of the calling individual and social audience seem to influence calling patterns. Low-ranking females refrained from calling when mating with high-ranking males if high-ranking females were nearby, potentially hiding their sexual activity in these circumstances (Townsend et al., 2008). Females were also less likely to vocalize when surrounded by other females of equal or higher rank to themselves. This effect interacted with the rank of the copulating male, suggesting that low-ranking females became more sensitive to the presence of higher-ranking conspecifics when mating with a high-ranking male (Townsend et al., 2008). Bonobos also take into account female audience, copulation calling more in the presence of the alpha female as a tactic to reduce female-female competition (Clay et al., 2011). Generally, it seems likely that female chimpanzees – like many primates – use copulation calls as a vocal counter-strategy to minimize infanticide threats and reduce female-female competition, where the benefits of calling ultimately outweigh risking aggression from more dominant individuals. However, support for this hypothesis largely resides on studies of female audience, with less known about the influence of males on females of different ranks.

Male aggressors clearly influence female copulatory presents (Muller et al., 2006; Muller et al. 2007; Muller et al., 2011), but there has been no comprehensive research on the influence of male audience on female callers. For example, males preferentially aggress

parous females (Muller et al., 2011), which might in turn influence parous females' calling behaviour. Female chimpanzees call more with high-ranking males (Hauser, 1990; Townsend et al., 2008), but it is not clear whether the underlying strategy aims to subvert male preferences, to promote paternity confusion, or both. In other species, copulation calls can be clearly tied to a function (e.g. promoting paternity confusion) or at least an outcome (e.g. causing an increase in male audience). One outcome for captive female chimpanzees is that they tend to receive more aggression following vocal copulations with young adult males than established adult males (Hauser, 1990). Other than this tentative finding, little research examines the outcome of copulation calling in chimpanzees, for example whether it results in increased mating competition. Additionally, despite social status influencing female calling behaviour in the presence of female audiences, there is no analogous research on whether low-status (i.e. young, nulliparous) females have different calling strategies based on male audience.

Hypotheses & predictions

Based on the findings and theories discussed above, I hypothesized that chimpanzee females might modify their copulation calls according to i) their own social status, and ii) the social status of individuals in the audience. Competition among females is likely to be highest during periods when several females cycle simultaneously, leading to competition for sexual access to males. This may be particularly taxing on nulliparous females who are generally found less attractive than parous females (Muller & Mitani, 2005; Muller et al., 2006; Muller et al., 2007). Thus, I tested the hypothesis that copulation calling strategies differ for parous and nulliparous females, taking into account previous evidence that parity reflects sexual attractiveness. In particular, I predicted nulliparous females should exhibit a more aggressive calling strategy, i.e. calling at higher rates, given their need to compete against more attractive parous females (See comparable data from

the Kanyawara community: Thompson et al., 2013). I also predicted that strategic calling

be especially evident during periods when many females are in oestrus and competition is

high.

If, as the literature suggests, females call as a means of inciting male competition,

then calls should result in increased male competition. Since male competition for matings

with parous females is likely to be higher than for nulliparous females, I predicted that parous

female calls would result in the clearest evidence of increased male competition. Barbary

macaque females, for example, were mated sooner, and by the higher-ranking of two males,

following the playback of her copulation call (*Macaca sylvanus*: Semple, 1998). Based on

this finding, I tested whether male party size increased following female copulation calls and

whether subsequent partners were of higher rank than the initial copulation partner. I also

hypothesized, given evidence that calls increase sperm competition, that females who called

were likely to be mated faster than silent females.

METHODS

Data collection and study subjects

I filmed 1,157 copulations between males and oestrous females using a Panasonic

HD V700 video camera, recording vocalizations with a Sennheiser MKE400 microphone.

FileMaker Pro Advanced v. 11 was used to code filmed data for swelling stage,

presence/absence of copulation call, partner identity and rank, audience, duration of

copulation, and the number of females with swellings in the community at the time of

copulation. Determining the dominance relations between chimpanzee females is

notoriously difficult, mainly because some females rarely interact with each other.

Therefore I did not include female rank because it was not possible to carry out a reliable

rank assessment during the time of the study. The analyses in this chapter include data

from fourteen males (9 adults, 5 sub-adults) and 20 females (13 parous and 7 nulliparous).

Only one nulliparous female gave birth during the study; this female lost her first two infants in consecutive pregnancies (one to infanticide, one to unknown causes), and was thus excluded from analysis on the grounds that her parity status changed during the study period and her attractiveness as a fit mother was unclear.

Copulation calls are acoustically distinct from other vocalizations, and do not occur outside of the oestrus period. I limited the definition of copulation call to calls produced during a sexual act, although nulliparous females occasionally produce calls during male inspection of their swellings (Fallon, pers. obs.). Swelling stage was estimated by the degree of wrinkling on a scale of 0-4, where size 4 indicates a fully inflated swelling (Furuichi, 1987; Zuberbühler & Reynolds, 2005). Length of copulation was measured from the start of intromission to its cessation. Audience was defined as any individual present in the travelling party, i.e. within 50m of the focal female at the time of copulation. As copulation calls are readily audible to the human ear within this range, I am confident that calls were audible to individuals within the party. Male dominance rank was assessed using pant-grunt data, which is regularly used as a reliable indication of submission in male chimpanzees (Goodall, 1986). Males were considered high-ranking if they were ranked 4 or above in the dominance hierarchy.

Statistical analysis

All statistical analyses were conducted using R (version 3.1.2; R Core Team, 2014) and the lme 4 package (version 1.0-7; Bates et al., 2014). Christof Neumann, a postdoctoral fellow at the University of Neuchatel, provided statistical guidance.

Model 1: Female copulation calls and competition

I tested the factors that affected the probability of female copulation calling with a generalized linear mixed model (GLMM) with binomial error structure and logit link function (Bolker et al., 2009). Age and parity were related in this sample. In an earlier study, a

distinction was made between young and old parous females (Muller et al., 2006), but this was not possible here since the sample only contained two young parous females. Given the prior evidence that parity is a strong determinant of attractiveness in chimpanzees, and that aggression toward parous females yields a higher copulation rate (Muller et al., 2007; Feldblum et al., 2014), I chose to exclude age as a factor in this analyses in favour of including parity.

I assessed the following predictor variables: partner rank (1-14, where 1 is high-ranking and 14 is low-ranking), copulation length (continuous, seconds), female parity (binary, parous/nulliparous), number of high-ranking male in the audience (continuous, 1-4), presence of a parous female in the audience (continuous, 1-4), number of nulliparous females in maximum swelling (continuous), and number of parous females in maximum oestrus (continuous). Female identity and male identity were set as random effect variables. There were 16 instances in which multiple copulations occurred consecutively with identical audiences. I therefore fitted an additional random effect 'event' to account for repeated data points under identical conditions with reference to audience. However, the variance attributable to 'event' was negligible (<0.0001) and I therefore decided to remove this term from the full model.

I initially tested the two-way interactions between parity and all other variables, to address whether factors affected mothers and non-mothers differently. I transformed numeric variables where necessary to achieve symmetric distributions and standardised them to mean=0 and SD=1 (Schielzeth, 2010). To confirm model validity, I used variance inflation factors (VIF: Fox & Weisberg, 2011), which verified that collinearity was not an issue (maximum VIF = 2.2). I checked for influential cases by calculating Cook's distances (c.f. Nieuwenhuis et al., 2012): I identified one influential female and male, reflecting a total of 13 copulations. Removing these cases resulted in only minor changes of parameter estimates and

did not affect my conclusions. Results are presented for the complete data set. Using a

likelihood ratio test (LRT: Quinn & Keough, 2002), I tested the full model against a null

model comprised of the intercept and random effects. I removed four interaction terms out of

six tested because they did not improve model fit (LRT: all $\chi^2_1 < 2.6$, all $P > 0.1$) and to be able

to assess the importance of main effects comprised in interaction terms (Hector, et al., 2010).

Model 2: Outcome of copulation calling

In a linear mixed model, I tested whether the interval of time between copulations was

shorter following copulations where the female called, and whether calling resulted in

attracting a male of higher rank. Factors included copulation call (binary, yes/no), same male

in the subsequent copulation or not (binary, yes/no), female parity (binary,

parous/nulliparous), rank of male in first copulation (1-14, where 1 is high-ranking), and rank

difference between male partners in first and second copulation (factor with three levels:

negative rank difference, positive rank difference, or same rank). Male and female identities

were set as random effect variables. The model included the two-way interaction between

calling and female parity, to assess whether the time interval between copulations was

different for parous and nulliparous females; additionally, I included the two-way interaction

between calling and whether or not the male in the subsequent copulation was the same male

as in the first copulation. I removed both interaction terms because they did not improve

model fit. All numeric variables were standardised and centred.

Model 3: Male party size following a copulation call

I ran a GLMM with binomial error structure and logit link function to assess whether

male party size increased following a copulation call. I excluded copulation events for which

all community males were present. I included four factors: in party size (response variable:

binary, yes/no), copulation call (binary, yes/no), parity (binary, parous/nulliparous), and partner rank (1-14, where 1 is high-ranking). The size of the audience in the first copulation was set as an offset variable to control for the fact that an increase in audience is more likely for small parties. Male and female identities were set as random effect variables. Initially, the model included the two-way interaction between copulation call and parity but this was removed from the final model, as it did not improve model fit (LRT: $\chi^2 = 0.22$, df = 1, p = 0.6394). Numeric variables were standardised and centred.

RESULTS

Model 1: Female copulation calls and competition

Females produced copulation calls for 48.1% (557 calls) of 1,157 copulations, slightly more than has been reported previously (Hauser 1990; Townsend et al., 2011). The full model was significantly different from the null model (LRT: χ^2_{13}=48.71, $P < 0.001$; Table 3.1).

Table 3.1: Results of the GLMM testing factors affecting calling likelihood of female chimpanzees during copulation[1].

	Estimate	SE	Z	CI	P
Intercept	-0.752	0.341			
Parity (nulliparous)	1.962	0.619		0.749 to 3.174	
Parous in audience	-0.046	0.106	-0.435	-0.253 to 0.161	0.6639
Nulliparous in maximum oestrus	-0.017	0.084	-0.202	-0.181 to 0.147	0.8399
Parous in maximum oestrus	0.166	0.092	1.811	-0.014 to 0.346	0.0701
Number of high-ranking males in audience	0.121	0.116		-0.106 to 0.348	
Male partner dominance rank	-0.370	0.106	-3.501	-0.577 to -0.163	0.0005
Duration	0.073	0.084		-0.092 to 0.237	
IA parity : number of high-ranking males in audience	-0.389	0.161	-2.411	-0.705 to -0.073	0.0159
IA parity : duration	0.516	0.172	2.993	0.178 to 0.853	0.0028

[1]The reference level for parity is "parous" and is comprised in the intercept. *Z,* CI and *P* values are omitted for intercept and main effects comprised in interactions. IA = interaction. CI = 95% confidence interval.
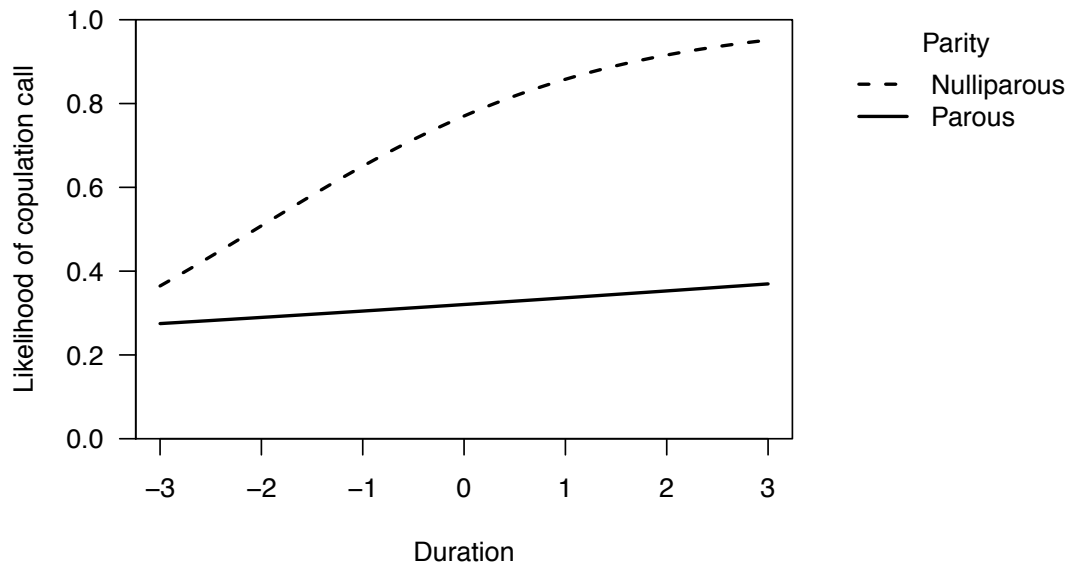
Fig. 3.1: The interaction between parity and copulation duration in the probability of copulation call production. Parous females show a slight increase in likelihood of calling as duration increases. Nulliparous females show a larger increase in likelihood of calling as duration increases. Presented are model estimates based on centred and standardised data.

Females, irrespective of their parity status, were more likely to give copulation calls when mating with high-ranking than low-ranking male partners (estimate=-0.37, SE=0.11, z = -3.50, *P*= 0.0005, Fig. 3.2).
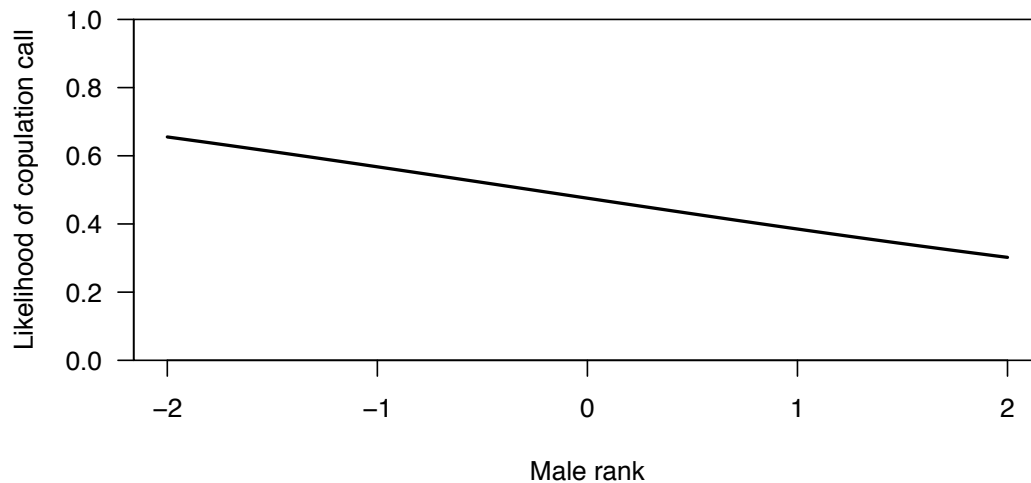
Fig. 3.2: The effect of partner rank on the probability of copulation call production. Females who mate with high-ranking males (left) are more likely to call than females who mate with low-ranking males (right). Presented are model estimates based on centred and standardised data.

Audience

Male audience, but not female audience, predicted female calling behaviour. There was a significant interaction between parity and dominant male audience in the probability of call utterance (LRT: χ^2_1=5.84, *P*=0.0157; Fig. 3.3). This interaction reflects the fact that, as the number of dominant males in the audience increased, nulliparous females were less likely to call, and parous females more likely to call. The number of parous females in the audience did not have a significant effect on female calling for either parous or nulliparous females (estimate=-0.05, SE=0.11, z=-0.44, *P*=0.6639).
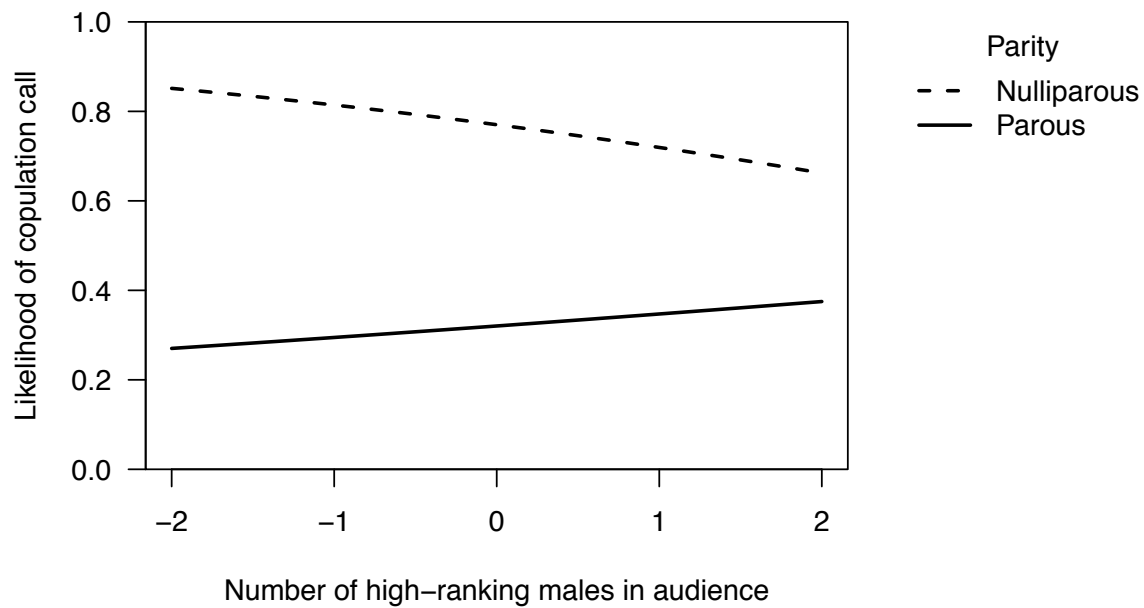
Fig. 3.3: The interaction between parity and dominant male audience. As the number of dominant males increases (left), parous females show an increase in likelihood of calling, and nulliparous females show a decrease. I applied a logarithmic transformation to 'male audience'. Presented are model estimates based on centred and standardised data.

Female competition

The minimum number of maximally swollen (stage 4) females on a given day was 0, and the maximum was 10, with an average of 3 fully swollen females per day. As the number of parous females in maximum oestrus increased, there was a non-significant trend for the probability of calling to rise (estimate=0.17, SE=0.09, $z = 1.81$, *P*=0.0701; I applied a logarithmic transformation to 'number of parous females in oestrus'). In contrast, the number of nulliparous females in full oestrus had no effect on either nulliparous or parous calling behaviour (estimate=-0.02, SE=0.08, *z*=-0.20, *P*=0.8399).

Model 2: Outcome of copulation calling

Model 2 addressed male behaviour toward an oestrous female following a copulation in which she emitted a call, by testing whether females, in their next mating event, were mated sooner or by a higher-ranking male following a call than a silent copulation. The final

model was not significant (LRT: χ2 = 7.50, df = 5, p = 0.1864, Table 3.2).

Table 3.2: Results of the liner mixed model testing the outcome of copulation calling[1]

	Estimate	SE	*t* value
Intercept	-0.11	0.10	
Copulation call (yes)	0.15	0.08	1.817
Same male (yes)	0.18	0.14	1.270
Parity (Parous)	0.05	0.10	0.513
Partner rank difference	-0.05	0.05	-0.984
Partner rank	-0.03	0.06	-0.454

[1]P values are not included here because the full model was not significant.

Model 3: Male party size following mating with a copulation call

Here, I tested whether male party size increased following a copulation call. The

model trended toward significance (LRT: χ^2 = 6.48, df = 3, p = 0.0906, Table 3.3). There

was a significant effect on party size, with parous females associated with larger parties than

nulliparous females; however, this occurred regardless of whether the parous female gave a

copulation called or not.

Table 3.3: Results of the GLMM testing factors affecting party size increases[1].

	Estimate	SE	*z* value	*p* value
Intercept	-1.86	0.20		
Copulation call (yes)	0.18	0.20	0.891	0.373
Parity (Parous)	0.47	0.20	2.343	0.019
Partner rank	-0.07	0.09	-0.756	0.449

[1]Increase in party size is comprised in the intercept.

DISCUSSION

Female chimpanzees employed different copulation calling strategies depending on

their own attractiveness and social standing within the community, most likely as an

adaptation functioning to maximise their reproductive success. All females were more likely to call when mating with males of high rank, confirming previous findings (Townsend et al., 2008). Nulliparous females were more likely to call than parous females, regardless of copulation duration or the number of high-ranking males in the audience. As the number of parous oestrous females increased in the community, all females were more likely to call, though this trend was non-significant. However, a dominant male audience affected parous and nulliparous females differently. While parous females were more likely to call as the number of high-ranking males in the audience increased, nulliparous females were *less* likely to call. Female calling behaviour was thus affected by four factors: female parity, copulation duration, dominant male audience, and (marginally) number of other cycling females. Surprisingly, I found no evidence for an increase in male competition following a copulation call; male party size was larger for parous females regardless of their calling behaviour.

It has been argued that females call to incite sperm competition (O'Connell & Cowlishaw, 1994), a strategy that presumably becomes more effective during longer copulations - which are more likely to lead to ejaculation and to be noticed by other individuals, most importantly males of higher rank than the current partner. In my study, although all females were more likely to call during long than short copulations, this effect was largely driven by nulliparous females, while parous females only showed a slight increase in the probability of calling. One possibility is that nulliparous females, generally less attractive for the males, are more motivated to draw attention to themselves by calling to incite male-male competition. This may be especially true given the trend for male parties to increase in number around parous females even when they do not give copulation calls. With this in mind, it seems that parous females, who are more attractive for high-ranking males (Muller et al., 2006) and more likely to be mate-guarded, may have fewer incentives to advertise their sexual status – either because male coercion prevents them from doing so, or

because their desirable status means they have less need to compete with other females. Consistent with the latter hypothesis, I found that parous females increased their calling when the potential payoff was high, for example when multiple high-ranking males were present: thereby generating sperm competition and increasing paternal uncertainty, which is likely to reduce future infanticide risk. However, I was unable to measure any outcome of calling that suggested an increase in competition. It is possible that the high number of swollen females at the time of study meant that males had less need to be competitive in seeking out calling females.

Nulliparous females' call rates were negatively affected by the number of high-ranking males in the audience, but nonetheless their overall calling rates were higher than those of parous females no matter the audience. Based on these findings, I regard fear of dominant males, leading to suppression, to be the most likely proximal explanation for this male audience-driven reduction in calling, but other interpretations are possible. For example, nulliparous females call less in the presence of multiple high-ranking males, perhaps because calling further will not increase male party size, as seen in the third model. In Budongo, several older females have a history of violence toward other females (Townsend et al., 2007; Townsend et al., 2008), so it is also possible that dominant female audience plays a role in nulliparous call suppression. A previous study with the same population found that low-ranking adult females suppressed copulation calls in the presence of equal- or higher-ranking females, and that this effect was stronger when they were mating with high-ranking males (Townsend et al., 2008). Because of the difficulty of establishing a reliable female dominance hierarchy in this study, I used parous female audience instead of dominant female audience; using this measure I was unable to replicate the previous result, although key social factors were very different during the two studies. In the Townsend et al. (2007) study, few females were cycling simultaneously and female-led infanticide risk was a high; in my study, many

females were cycling and thus male-led infanticide risk was high (Wilson et al., 2014). Given that females seem to modify their calling strategically based on social factors, it is likely that the difference in threat level from females may explain the previously found sensitivity to female audience. Townsend et al. (2008) found no effect of dominant male audience on female calls. However, their data were largely on older females, and I have shown here that nulliparous females are more strongly influenced by dominant male audience than parous females.

I found a non-significant trend for females to produce more copulation calls when there were multiple females in oestrus, which may function to attract males in times of high female-female competition. This effect was only found when multiple parous females were in maximum oestrus, suggesting that females differentiate the threat level of potential competitors. Both findings are consistent with the hypothesis that advertising becomes more relevant when female-female competition is high. One potential confound is female age, which I was unable to include due to its overlap with parity status: I did not have a sufficiently high number of young parous females to investigate both factors independently. The combination of old age and parous status has proven important at other sites (Muller et al., 2006; Feldblum et al., 2014). Future studies should attempt to disentangle the separate effects of age and parity.

Also, although I treated all copulation calls equally, females occasionally exhibit 'deceptive' swellings unaccompanied by ovulation (Goodall, 1986), and it is possible that I inadvertently included calls produced during anovulatory swellings. Since females do not adjust their calling during the peri-ovulatory period for cycles where they do ovulate (Townsend et al., 2011), I do not expect the possible inclusion of such calls to influence these results.

CONCLUSION

My findings on the copulation calling of nulliparous females are consistent with their social standing: young, low-ranking, and often new immigrants to the community. Female oestrus cycles have been described as a 'social passport' with which young females gain sexual partners and increase their social status (Boesch & Boesch-Ackermann, 2000). My data extend this metaphor to include copulation calling as a tool with which new females integrate by advertising their sexual state to males in the community. The differences between parous and nulliparous calling indicate a shift in tactics for reproductively successful females that reflects the male interest that is demonstrated in the party size surrounding a parous female. I suggest that frequent calling may be the optimal strategy for nulliparous females, as a tactic to attract mates and increase their chance for reproductive success. With no offspring, and with little threat of male coercion, nulliparous females have more freedom to advertise their sexual receptivity and instigate sperm competition. Nonetheless, I found that that some suppression occurs where male coercion is a high risk because more dominant males are present.

In contrast, parous females call less overall, and only slightly increase calling with increasing copulation duration and dominant male audience. This marked departure from nulliparous calling indicates that parous females have a different optimal strategy in how to use calling strategically, a need that might be due to several factors, including overall call suppression associated with an increased risk of male coercion and the need to protect offspring. Alternatively, the low likelihood of calling could merely reflect the fact that parous females have less need to advertise, since males flock to parties with parous females in oestrus. These two explanations are challenging to separate given that parous females are also more prone to coercion. Both parous and nulliparous females had a tendency to increase calling as a function of the number of other parous females in oestrus, suggesting that females

might be able to assess the level of female competition and modify their calling strategy accordingly.

Overall, my findings confirm the hypothesis that females of different reproductive status produce copulation calls flexibly using different strategies, which I argue reflect their attractiveness. This does not necessarily imply that females consciously assess their attractiveness. For instance, females might alter their calling behaviour in response to male interest, a reliable proxy of attractiveness. Strategic advertisement appears to be one way in which females indirectly compete with each other, echoing findings of indirect mate competition in human females. For both female humans and chimpanzees, drastic times call for drastic measures; in the next chapter, I examine whether male chimpanzees likewise adjust their courtship communication tactically based on their social standing.

Chapter 4: Coercion and Gestural Courtship during Opportunistic Mating

ABSTRACT

Sexual coercion is one strategy male chimpanzees use to increase their access to mating, but such coercion is only evident in the long-term. For example, females present to the males who aggress them most frequently over time, and males sire the most offspring with females they aggress long-term. In the short-term, however, several studies demonstrate that females exercise choice in whom they mate with, preferentially mating with males who frequently groom them or males with whom they have an established friendship. In the short-term, further, aggressive behaviour almost never leads directly to copulation. This contrast is puzzling: females might be expected to mate more frequently with aggressive males, as aggressiveness is an honest signal of mate quality. Yet how can males signal quality in the short-term, where aggression is not effective? Male courtship displays are one area that has been ignored thus far in this debate. In this chapter, I consider whether male gestural courtship reflects long-term sexual coercion, and whether females use courtship displays to discriminate between potential mates.

INTRODUCTION

In her seminal work *The Chimpanzees of Gombe*, Jane Goodall describes a scene in which a popular female, Flo, is followed by an entourage of over fourteen adult and adolescent males (1986). The males attentively follow Flo's every movement, and within the course of her oestrous cycle most will have mated with her. This account depicts opportunistic mating, the most common mating strategy, which Tutin defines as "non-competitive mating, when a receptive female may be mated by all of the adult males in the group" (1979). Although males and females commonly mate with multiple individuals as part of this strategy, depicting opportunistic mating as 'non-competitive' may be an oversimplification of mate competition for both sexes.

Chimpanzee males typically initiate sexual interactions using gestural mating displays accompanied by a penile erection (Tutin & McGrew 1973; Goodall, 1986). Although cycling females occasionally initiate courtship by producing gestural displays toward males (Nishida, 1997), this strategy is primarily used by adolescent females, whom Goodall describes as 'insatiable' (1986). Instead, adult females display non-gestural proceptive behaviour toward males as an indication of interest, such as approaching and sitting by the male (Stumpf & Boesch 2005; Stumpf & Boesch, 2006; Pieta, 2008). By contrast, males of all ages and

rankings produce overt courtship displays, which are persistent in nature and can escalate in frustration (Goodall, 1986). This difference between sexes has led to a burgeoning body of literature on the role of female choice and male coercion in mating.

Opportunistic mating and female choice

In addition to gestural courtship displays, males use other means to improve their standing with potential mates. Females exhibit a mating preference for males who frequently groom them (Stumpf & Boesch, 2005), and males target high-value parous females as grooming partners, presumably to curry favour (Proctor et al., 2011). Some evidence suggests that females mate more frequently with males who share meat with them (Gomes & Boesch, 2009). Females also show different rates of proceptivity and resistance for certain males, and alter their proceptive behaviour toward preferred males during the peri-ovulatory period (Stumpf & Boesch, 2006). In large communities, a close male-female socio-spatial relationship predicts paternity as accurately as male dominance (Langergraber et al., 2013). These findings point toward the influence of affiliation on female choice, with Pieta (2008) concluding "…males attempted to implement their preferences toward females via solicitation, but not aggression". Indeed, aggression of an oestrous female rarely leads directly to copulation (Goodall et al. 1986; Nishida, 1997; Pieta, 2008; Stumpf & Boesch, 2010).

Opportunistic mating and sexual coercion by males

In many cases, however, male coercion seems to trump female choice. Certainly females may rebuff unwanted male advances (Stumpf & Boesch 2005; Stumpf & Boesch, 2006), and often do so by appealing to other dominant males for protection (Nishida, 1997). However, male chimpanzees use long-term aggression toward females as a means of

achieving their mate preference for older, parous females (Muller et al., 2006), and this directly influences their reproductive success (Feldblum et al., 2014). Such aggression is not limited to the oestrous period, but occurs throughout the course of a female's life, with the effect that females in the peri-ovulatory period present more frequently to males who regularly target them for aggression (Muller et al., 2011). These findings suggest that chimpanzees experience a constant state of mating competition, where females continue to be influenced by long-term male coercion during non-competitive strategies like opportunistic mating. Such coercion can also be a choice for females – by cosying up to dominant males, females presumably respond to honest signals of fitness that will be beneficial for their offspring (Nunn, 1999). As discussed above, studies of choice during opportunistic mating do find evidence of female choice, but Muller et al. (2011) argue that long-term male aggression is the real reason for the female preferences, since none of the studies on female choice accounted for long-term male aggression.

While the data on long-term male coercion indicates that female choice is based on a history of successful violent aggression (Muller et al., 2011; Feldblum et al., 2014), the effect of this coercion is not apparent in the short-term. The absence of evidence for short-term male coercion toward cycling females may therefore be an inaccurate reflection of coercion tactics. Thus far, the study of male coercion has been limited to female-directed aggression. Few studies on coercion discuss the composition of male courtship, despite evidence from other species that the content of mating displays influences success. One reason for this oversight may be the general lack of literature on the content and relative aggressiveness of male solicitations. However, males' determination to enact their mating preferences using courtship displays, which often share elements similar to agonistic displays (Goodall, 1986), certainly suggests that gestural coercion is worth exploring; in the following sections, I review the available evidence on gestural courtship.

Gestural courtship

Yerkes (1939) was among the first to document gestures occurring during chimpanzee courtship, writing "…(Males) may solicit (female) cooperation by gestures whose meaning is unmistakable". He described three categories of gesture:

> *"The genital gesture of exhibitionism; the hand gesture of appeal; or, instead*
>
> *of such gestures of request, the male may slap or stamp the ground or floor in*
>
> *a gesture of command"(p. 83).*

With this description, Yerkes presumed that chimpanzee gestures reflected different goals ('appeal'/'request' or 'command') and included some element of coercion. Although his intuition was well-grounded, the concept of goal-directed, intentional communication in ape gestures has only recently been addressed empirically. As the breadth of research on intentional communication has expanded in recent years, courtship remains a neglected area given the difficulties of studying sexual behaviour in captivity, where females are often given contraceptives and the ratio of males to available females is typically lower than occurs naturally. Likewise, studies on male coercion have primarily ignored gestural courtship displays in favour of overt behaviour like aggression.

Tutin and Nishida offer the most detailed descriptions of courtship to date, describing between them 18 potential gestures (Tutin & McGrew, 1973; Nishida, 1997). Of these gestures, seven are also described during agonistic interactions (Goodall, 1986). Male chimpanzees produce these gestures concurrently or consecutively, creating displays that comprise between one and four gestures (Nishida, 1997). Little is mentioned regarding the structure of courtship displays, or how males choose which gestures to use. Nishida (1997) examined the structure of 89 courtship displays, noting that displays with multiple gestures were not more successful than displays with one gesture. This may reflect that females mate

with males regardless of the courtship display, but it is not clear whether this is by choice (based on other factors such as rank or social relationship) or coercion. However, displays comprised of multiple gestures were seldom repeated exactly: the same combination of gestures was recorded only twice, indicating that novelty may be important to females. There is no discussion of the signaller rank or identity for the remaining courtship displays, or the role these factors might play in females' preferences. The most frequent gestures used in successful courtship displays were *sitting-hunch* and *leaf clip*, while the most frequent gestures used in unsuccessful displays were *leaf clip*, *punch object/ground*, and *object shake*. On the topic of male dominance and aggression, Nishida (1997) describes rejected males kicking or hitting resistant females – although such direct aggression did not lead to copulation – and there is no discussion of courtship displays as aggressive in nature. By contrast, he describes one older female who successfully solicited males using a "sex dance" comprised of the gestural sequence 'present + branch shake + bipedal run' (Nishida, 1997).

Tutin and McGrew (1973) address male dominance and its relation to sexual aggression and idiosyncratic behaviour in Shadow, their subject. Since Shadow was the only male in the captive community, Tutin and McGrew were not able to comment on female choice. Shadow initially exhibited a number of uncommon solicitations, including 'flip lip' and 'sex display', a bipedal position with hands above the head so as to maximally expose the erection. Although this behaviour is described as idiosyncratic, a similar sexual invitation ('bipedal sex dance') is described in Mahale, indicating that it is simply rare (Nishida, 1997). Toward the end of the eight-month study, Shadow used this unusual behaviour less frequently, instead relying upon behaviour also used during agonistic interactions, such as bipedal display, pilo-erection, *branch shake*, and *rock*, which Tutin and McGrew (1973) observed in tandem with Shadow's increasing assertiveness over the females in the group. Shadow's rising dominance was also accompanied by more frequent use of courtship tactics

such as 'glance and follow', where the female response is elicited merely from the gaze of the male. Tutin and McGrew (1973) hypothesize that the shift in repertoire was largely due to Shadow's dominance toward the end of the study, such that he felt comfortable producing displays that could be viewed as threatening, as well as possessing the rank needed to use subtle courtship cues. Aggressive courtship displays were also produced only by dominant males in the ARL Colony chimpanzees, who are described as producing a "threat body gesture" (Kollar et al., 1968). In sum, courtship displays clearly vary greatly in content, item order, and aggressiveness, which may be related to dominance rank of the signaller.

Intentionality, meaning, and aggression

The debate surrounding whether language is rooted in vocal or gestural origins came to a head around the turn of the 21st century with a number of seminal papers (Armstrong et al., 1994; Corballis, 2002; Rendall et al., 2009), bringing with it a renewed interest in the possibility of intentionality in ape communication. It is now clear that chimpanzee gestures are intentional, and that signallers use gestures with purpose and intent (Tomasello et al., 1985). Moreover, it has recently been shown that chimpanzee gestures have meaning (Hobaiter & Byrne, 2014), offering a possible explanation for Yerkes' (1939) separate categories of courtship 'requests' versus 'commands'. Indeed, the available evidence on gesture use does suggest a partial overlap between intentional gestures used during aggression and those used during courtship.

For example, one captive study on intentional communication in chimpanzees describes 12 courtship gestures, nine of which were also used during aggression; yet the most common solicitation, *genital offer,* was never used during aggression (Liebal et al., 2004). This research also replicates Nishida's (1997) finding that courtship displays are most often single gestures, rather than sequences, but likewise does not account for age and rank of the

signaller (Liebal et al., 2004). Critically, it is not known whether females respond differently to courtship gestures that are also used during aggression, or whether using such gestures might be a short-term coercive tactic for males.

In a study of meaning in wild chimpanzee communication, four gestures (*leaf clip, object move, present sexual, stomp*) have been identified as having a primary meaning of 'give (me) sexual attention' to either a male or female, and three gestures (*leaf clip, object shake, punch object/ground*) as having a secondary meaning of 'sexual attention' to either a male or female (Hobaiter & Byrne, 2014). Three courtship gestures had alternate meanings of 'stop that' (primary meaning for *stomp*) and 'move away' (primary meaning for *punch object*; secondary meaning for *object move*). Additionally, *object shake, punch object/ground*, and *stomp* have been described in aggression displays. Males can also reinforce gestures with assertive behaviour; one study on gestural communication during consortship found that males couple urgent, high frequency use of gestures with high rates of female-directed aggression (Hobaiter & Byrne, 2012).

Hypotheses & predictions

The foregoing section reviews a number of compelling reasons to further explore opportunistic mating, particularly to address the use of intentional communication during courtship and possible use of short-term male coercion via gestural communication. Much of the current evidence on both sides of the debate on female decision-making and male coercion ignores gestural courtship, despite some indications that this behaviour may mediate mating success in certain circumstances. The primary aim of this chapter is to investigate whether sexual coercion of females is apparent in gestural courtship, reflecting well-established patterns of male dominance in the long-term, or whether courtship displays offer females an opportunity to be selective about their mates. Overall, I expect male rank to influence both the content and composition of a successful display, since it is well established

that high-ranked males are also the most aggressive toward females (Muller et al., 2011; Feldblum et al., 2014). I discuss my specific hypotheses and predictions below.

Based on the hypothesis that young chimpanzees use rapid sequences and a large repertoire as a means of 'trial and error' when learning gesture meanings (Hobaiter & Byrne, 2011b), I suggest that courtship is likely to be a novel context for low-ranking, sub-adult males, and if so, rank and repertoire size should be related such that younger, inexperienced individuals will have a larger courtship repertoire (Hypothesis 1).

When dominant males produce displays, the available empirical evidence (Tutin, 1979) suggests they use aggressive gestures more commonly that low-ranking males. Thus, I expect gestural coercion to be a tactic primarily employed by high-ranking males, such that high-ranking males have more agonistic gestures in their repertoire and employ them more frequently (Hypothesis 2).

Another theory posits that long-term male aggression influences the likelihood of female copulatory presents, especially for parous females (Muller et al., 2011). In this case, dominant males have less need to produce courtship displays than low-ranking males. I discuss high- and low-ranking males non-gestural initiating behaviour descriptively, followed by a test of the hypothesis that parous and nulliparous females respond to non-gestural initiation (defined on p. 38, Methods) differently, given findings that female response to males differs by parity (Stumpf & Boesch, 2005; Pieta 2008) (Hypothesis 3). Given the finding that parous female copulatory presents are related to a history of coercion (Muller et al., 2011), I predict that non-gestural initiations will be more successful with parous females. Further, in line with Muller et al., I predict that high-ranking males will initiate copulation by approaching females at a higher rate than low-ranking males (Hypothesis 4), and will also be more successful than low-ranking males in initiating copulation solely by approaching the female (Hypothesis 5).

When males use courtship gestures, I hypothesize that some gestures will be more successful than others based on the finding that chimpanzee gestures are associated with specific contextual meaning (Hobaiter & Byrne, 2014; Hypothesis 6). I also suggest high-ranking males will be more successful than low-ranking males in eliciting a response from the female. I test the hypothesis that coercive gestures might be more effective for some males, predicting that high-ranking males should be more frequently successful when using coercive gestural displays, while low-ranking males, for whom coercion is likely to be ineffectual, should avoid coercive behaviour. I expect this to vary for parous and nulliparous females, given they are exposed to different levels of coercion (Muller et al., 2011; Hypothesis 7).

The typical high-ranking males strategy of long-term coercion may influence how males respond to failure: I predict that high-ranking males will be more likely to persist following failure as a means of coercion (Hypothesis 8). High-ranking males' experience should thus yield more effective gesturing, for example by gesturing solely toward attending females (Hypothesis 9). Finally, I test the hypothesis that silent and audible gestures have different success rates, predicting that audible gestures are more effective based on previous findings that threat behaviour is often audible (Hypothesis 10).

METHODS

Data were collected in all-day focal follows of swollen females using all-occurrence sampling balanced across individuals (Altmann, 1974). I followed 20 females (13 parous, 7 nulliparous) and 14 males (9 adults, 5 sub-adults). All adults and sub-adults were included in analyses unless otherwise stated; infants and juveniles were excluded. Fieldwork was conducted between the periods of June 2011-August 2011, May 2012-April 2013, and September 2013-March 2014, totalling approximately 2,688 hours of

observation time. I filmed sexual interactions between males and cycling females using a Panasonic HD V700 video camera, recording vocalizations with a Sennheiser MKE400 microphone. FileMaker Pro Advanced v. 11 was used to code filmed data for gestural communication.

Definitions and operational criteria

I defined *gesture* following Hobaiter and Byrne (2011a) as "discrete, mechanically ineffective physical movements of the body observed during periods of intentional communication". Gestures were considered intentional when accompanied by *gaze checking* (indicating a direct recipient), *response waiting*, or *persistence*. Although some definitions of gesture distinguish between gesture and bodily postures (e.g. *genital offer*; Genty & Zuberbuhler, 2015), for simplicity's sake I consider all intentional postures as gestures. An individual's *core repertoire* was defined as the gestures that comprised at least 70% of a male's total gesturing. An *agonistic* courtship gesture is a gesture that has been described in the literature as part of aggressive displays by adult individuals in the wild (Goodall, 1986, Hobaiter & Byrne, 2011a; Hobaiter & Byrne, 2014). These include *arm fling, arm raise, bipedal swagger, drum object, gallop, object move, object shake, punch object, rock, slap object, stiff stance,* and *stomp object*. Gestures were also noted as audible or silent.

I follow Tutin's definition of *opportunistic mating* as "non-competitive mating, when a receptive female may be mated by all of the adult males in the group" (1979). Gestures were considered part of a courtship display when produced by a male with a penile erection and directed toward a female in oestrus, or vice versa. Gestures were considered *completely successful* when the signaller ceases gesturing in apparent satisfaction with the response of the recipient. A gesture was *partially successful* when the recipient's response partially satisfies the signaller's goal (Hobaiter & Byrne, 2014) – for example, a female moving closer

to a soliciting male, but not yet presenting for copulation. *Unsuccessful* gestures did not result

in signaller satisfaction, and were typically accompanied by persistent gesturing by the

signaller in response to a negative response from the recipient, such as walking away from

the signaller.

Chimpanzees occasionally preceded or accompanied displays with non-gestural

behaviour, which I categorized into six types (Table 4.1). I also noted whether displays were

male or female initiated. Male coercion was defined as physical aggression toward an

oestrous female or use of agonistic gestures and persistence following female resistance.

Female choice was defined following Halliday (1983): copulation after female proceptive

behaviour, or no copulation after female resistance behaviour. Female swelling size was

determined on a 0-4 scale according to degree of wrinkling following the protocol of the field

site, where 4 indicates a female is maximally swollen (Furuichi, 1987; Zuberbuehler &

Reynolds, 2005).

Table 4.1: Non-gestural courtship behaviour

Behaviour	Definition
Aggressive display	Male chases or physically harms the female.
Approach	Male approaches female in a direct path while erect, visible within a radius of 10m.
Eye contact	Male meets the female's eyes while erect.
Groom	Male grooms female
Inspect swelling	Male touches or sniffs a female's swelling.
Lead away	Erect male makes eye contact with the female, then turns and moves to a secluded area (Nishida 1997)
Masturbate	Erect male self-stimulates while looking at a female

Statistical analysis

All statistical analyses were conducted using R (version 3.1.2; R Core Team, 2014)

and the lme 4 package (version 1.0-7; Bates et al., 2014). I analysed the courtship gestures of

fourteen male individuals. Zefa was observed producing 13 courtship displays during

opportunistic mating, and is excluded from analyses where noted on the basis of small sample size. The sample size of courtship displays for all other males was >20. In the mixed models, male and female identities are set as a random effect; other statistical analyses were conducted with the means per individual to account for pseudoreplication, and all assumptions were met unless otherwise noted. No data were transformed for the analyses in this chapter. Statistical tests were considered significant at $\alpha = 0.05$.

Correlations and Chi-squared tests

I used partial correlations to test the relationship between rank and repertoire size. Partial correlations controlled for observation time per individual, and their use is noted in the text. I performed Pearson's Chi-square Test for Independence to assess the relationship between female parity (parous, nulliparous) and gesture success (success, failure). I performed Pearson's Chi-square Test for Independence to test the probability that success (success, failure) and gesture type (*leaf clip, object shake, genital offer, rock*) are related. I repeat the same analysis in a 3x2 Chi-square after removing *genital offer*, the only gesture with a clear visual clue toward copulation (erection).

T-test and ANOVA

I used three independent samples t-tests to assess differences between high- and low-ranking males in regards to 1) approach rates prior to courtship, 2) the count of gestural persistence following failure (yes/no), and 3) the count of gestural persistence following a partially successful gesture (yes/no). All assumptions were met for each test.

I conducted a one-way ANOVA to test whether gesture success was influenced by modality (silent/audible) against the null that the modalities were equally successful. To test the influence of modality on partial and complete success combined, I conducted a one-way ANOVA of modality on combined success against the null that the modalities were equally successful.

Linear models: Rank and use of agonistic gestures

I conducted three linear models to assess the relationship between rank and use of agonistic gestures. First, I tested whether the number of agonistic gestures in an individual's repertoire was predicted by rank (continuous, 1-14), controlling for observation time (number of observed events). I used a likelihood ratio test (LRT: Quinn & Keough, 2002) to compare the full model against a null model consisting of the intercept and observation time. I used the same model design to test whether the number of agonistic gestures within an individual's core repertoire was predicted by rank, as compared to a null model comprised of the intercept and observation time. Finally, I tested a linear model that assessed whether rank predicted the total proportion of agonistic gestures produced by each individual, controlling for observation time. I compared this model against a null model consisting of the intercept and observation time.

Mixed model: Rank and success of agonistic gestures

Using a generalized linear mixed model with binomial error structure and logit link function (Bolker et al., 2009), I tested the factors that affected the probability of success for agonistic gestures. Here, an agonistic gesture was considered successful if it led to copulation, and unsuccessful if it did not. The model included the following variables: male rank (1-14, continuous), whether or not a gesture was agonistic (binomial, yes/no), and the interactions between parity (binomial, yes/no) and all other variables. I removed one interaction term because it did not improve model fit (LRT: $p > 0.1$). Male identity and female identity were set as random effects. Collinearity was not an issue, as the maximum VIF (Fox & Weisberg, 2011) was 1.06. I used an LRT to compare the full model against a null model consisting of random effects.

Mixed model: Rank and success of approach

I conducted a generalized linear mixed model to test the factors that affected the

probability of success for the non-gestural initiation approach. An approach was considered successful if the female copulated with the male, and unsuccessful if a female did not copulate with the male. The model had a binomial error structure and logit link function (Bolker et al., 2009). I assessed two predictor variables, whether or not a gesture occurred in tandem with approach (binomial, yes/no; reference level =no), and male rank (continuous, 1-14). Female identity and male identity were set as random effects. The maximum VIF (Fox & Weisberg, 2011) was 1.016, indicating no collinearity. I used an LRT to compare the full model against a null model consisting of random effects.

3.2 | RESULTS

In this section, I discuss the repertoire of courtship gestures in Sonso chimpanzees and how males employ their repertoire to achieve matings. I focus on possible differences between high- and low-ranking males, based on previous evidence that rank influences mating strategies (Muller et al., 2006; Wroblewski et al., 2009). When possible, I consider the effect of female social status on signaller success.

Description: The courtship gestural repertoire

I recorded 1,673 gestures used during opportunistic courtship in 321 courtship displays, including 26 gesture types (Table 4.2) produced by 14 males (9 adults and 5 sub-adults), ages 10 to 34. *Arm raise, leaf clip, object shake, genital offer*, and *rock* were the most commonly used gestures, accounting for more than 78% of courtship gestures produced. Fifteen gestures recorded during opportunistic courtship are gestures also commonly used during agonistic encounters, totalling 44% of gestures produced (Table 4.2). Of the five most common gestures, two (*object shake* and *rock*) were agonistic.

The average repertoire size for males was 18 gestures, with individual repertoires ranging from 15 to 22 gestures (Appendix I). Individual repertoire size was dependent on the

number of courtship displays for that individual, $r=0.968$, n=14, $p=0.042$. There was a trend for repertoire size to increase with age using a partial correlation that controlled for observations per male, $r=0.4929$, n=14, $p=0.0869$. Nick, the alpha male, had the largest repertoire of gestures used during courtship, as well as the largest proportion of agonistic gestures used in courtship.

Males did not regularly employ all gestures within their courtship repertoire; instead, males utilized a *core repertoire* of a few frequently used gestures. Individuals' core repertoires were between three and seven gestures, with a median of four gestures. Nick had the highest number of gestures in his core repertoire, and was therefore the least consistent in gesture choice. There was considerable overlap between gestures in males' core repertoire, with the most common gestures being *leaf clip* (7 males), *object shake* (10 males), *genital offer* (9 males) and *rock* (6 males).

Hypothesis 1: Rank and repertoire size are related

Rank and repertoire size were not related using a partial correlation that controlled for sample size, $r=0.47$, n=14, $p=0.09$, but rank and core repertoire size were related, $r=0.77$, n=14, $p<0.01$. Since rank and age are related, I was not able to test both variables together.

Hypothesis 2: High- and low-ranking males use agonistic gestures at different rates

To assess whether rank predicted the number of agonistic gestures within individual repertoires, I used a likelihood ratio test to compare a linear model with a fixed effect of rank to a model without it. The model with rank had a better fit (LRT: $\chi^2 (12)=27.3$, $p < 0.05$), and there was a positive relationship between rank and number og agonistic gestures, indicating that high-ranking males have more agonistic gestures in their repertoire. Likewise, I tested whether rank predicted the number of agonistic gestures within each male's *core repertoire*

using a likelihood ratio test. The model including rank was a better fit (LRT: χ^2 (12)=0.18, p

< 0.02); high-ranking males had more agonistic gestures in their core repertoire. Finally, I

tested whether rank predicted the proportion of agonistic gestures produced by each

individual; the model including rank was a better fit (LRT: χ^2 (12)=4.505, p =0.05), with

high-ranking males producing agonistic gestures more often than low-ranking males.

Table 4.2: Gestural repertoire for opportunistic mating

Gesture	Audible	No. Recorded
Arm fling*	No	8
Arm raise*	No	236
Arm shake	No	2
Arm swing*	No	43
Beckon	No	4
Big Loud Scratch	Yes	60
Bipedal run*	Yes	8
Bipedal swagger*	Yes	22
Bump rump	No	7
Chest beat	Yes	1
Drum object*	Yes	11
Gallop*	Yes	9
Leaf clip	Yes	242
Leaf strip	Yes	2
Lunge	No	4
Object move*	Yes	4
Object shake*	Yes	381
Pelvic thrust	No	6
Genital offer	No	200
Punch object/ground*	Yes	61
Rocking*	No	140
Slap object*	Yes	10
Stiff stance*	No	25
Stomp*	Yes	67
Tap other*	No	120
Total		**1673**

*Indicates agonistic gesture

Description: Non-gestural courtship initiation

Prior to copulation, males often engage females without using gestures, for example

by grooming or aggressing the female (See Table 4.2 in Methods). Occasionally, this type of

non-gestural initiation behaviour results directly in copulation, with no further courtship

needed. I identified six types of non-gestural initiation during mating contexts, which could

occur either on their own or accompanied by gestures (Table 4.2). High- and low-ranking males overall used non-gestural tactics at similar rates; 43.6% of courtship displays produced by high-ranking males utilized non-gestural courtship initiation, while 41% of displays produced by low-ranking male displays used non-gestural initiation, with no individual male laying outside two standard deviations from the mean for their rank (high-ranking $\mu = 0.499$, $\sigma=0.198$; low-ranking $\mu = 0.436$, $\sigma =0.097$). Males produced gestures in tandem with initiating behaviour in 117 cases, most often while approaching females (77 cases, 65%).

Hypothesis 3: Female parity influences the success of non-gestural initiation

Males attempted copulation using only non-gestural initiation, and no gestures, in 120 cases (Table 4.3). I excluded 8 cases because the success was unknown (for example, visibility was poor). Only 51 cases resulted in copulation with no further action needed from the male (Table 4.3). These cases are not independent samples, as several individuals contributed multiple times to the dataset. High-ranking males produced 59% of the completely successful cases (30/51), but there was no effect of female parity status on initiation success using a 2x2 chi-square test, $\chi^2 (1) = 12.97$, $p = 0.302$.

In 120 cases where males initiated courtship without gestures, they persisted following failure by subsequently producing a gestural courtship display in the majority of cases (95/112, 84%), relying on gestures when other means of attracting females were unsuccessful; high-ranking males accounted for 71% of such persistence (79/112). Thus, females were able to reject males outright in only 17 cases.

Table 4.3: Success of non-gestural solicitations produced without gestures

Behaviour	Successful	Unsuccessful	Total
Aggress	4 (25%)	12 (75%)	16
Approach	44 (58%)	32 (42%)	76
Eye contact	1 (20%)	4 (80%)	5
Groom	1 (100%)	0	1
Inspect swelling	0	1 (100%)	1
Lead away	0	11 (100%)	11
Masturbate	1 (100%)	0	1
Total	**51**	**61**	**112**

Hypothesis 4: High- and low-ranking males approach females at different rates

The most common non-gestural initiation tactic for males was to approach the female. I recorded 200 cases of approach prior to copulation, 42 of which were initiated by females. Three cases for low-ranking males are excluded because the success was unknown. There was no significant difference between approach rates for high- and low-ranking males, $t(10)=1.157, p=0.2783$. Males used 'approach' accompanied by gestures a total of 77 times (out of 155 uses of approach).

Hypothesis 5: High- and low-ranking males differ in success when approaching females

I conducted a logistical GLMM assessing the likelihood of a successful approach (N=155) according to male rank and gesture use. The full model was significant against the null model (LRT: $\chi^2_{13} = 16.114, p < 0.01$; Table 4.4). Male rank did not predict the success of an approach using a GLMM. Gestures tended to make an approach less successful (Fig. 4.1).

Table 4.4: Results of the GLMM testing the factors affecting approach success

	E	SE	Z	P
Intercept	0.031	0.671		
Gesture	-1.734	-0.460	-3.767	-0.000
Male Rank	0.059	0.095	0.622	0.534

E= effect, SE = Standard deviation, Z = z-score, P= significance value

Effect of Gestures on Approach Success
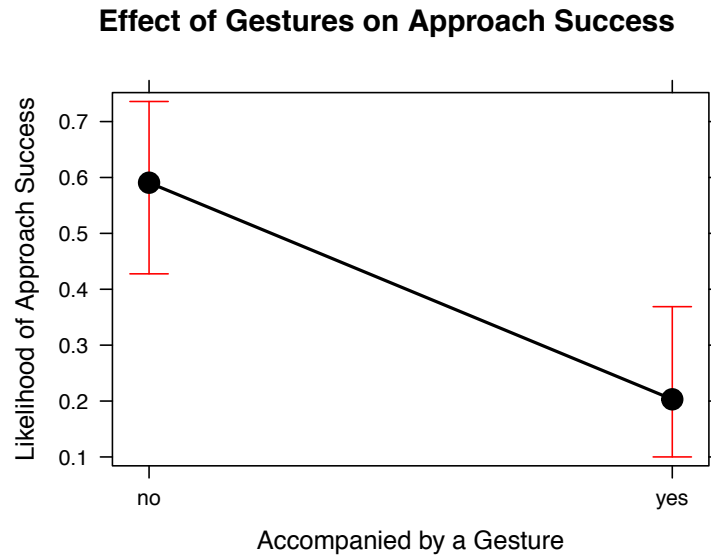
Fig. 4.1: The effect of gestures on the likelihood of success for an approach. *In logistic models, the response variable is constrained between 0 and 1, resulting in asymmetrical error bars; the closer to 0.5 the estimate occurs, the more symmetrical the error bars.*

Hypothesis 6: Gestures are not equally successful, and their success differs by male rank

The large, varied repertoire and the frequency with which males produce gestural displays suggests that gestures are an important part of effectively communicating sexual interest. Table 4.5 includes the five gestures most commonly used as the first gesture of a courtship display, and the success of these gestures for both high- and low-ranking males when used as the first gesture in a display.

A 4x2 chi-squared analysis of the four most common gestures (*leaf clip, object shake, genital offer, rock*) gives a significant difference between success rates, $\chi^2(3) = 5.90$, $p < .001$. After removing *genital offer*, the most successful gesture, there was no significant difference between the success of *leaf clip, object shake*, and *rock* in a 3x2 chi-squared analysis, $\chi^2(2) = 4.357$, $p = 0.7$. Surprisingly, signaller rank did not influence the success rate of a gesture: as is clear from the raw data in Table 4.5, an effective gesture is successful regardless of the rank of the signaller.

Table 4.5: The success of the most common first gestures in a display for high-and-low-ranking males

Gesture Type	Total number of times used first	Success rate	Number of times used first (high-ranking male)	Number of times used first (low-ranking male)	Success for high rank	Success for low-rank
Arm raise*	23	74% (17/23)	11	12	63% (7/11)	83% (10/12)
Leaf clip	37	30% (11/37)	10	27	30% (3/10)	29% (8/27)
Object shake*	69	45% (31/69)	40	29	42.5% (17/40)	48% (14/29)
Genital offer	56	82% (46/56)	29	27	79% (23/29)	85% (23/27)
Rocking*	30	56% (17/30)	11	19	54% (6/11)	58% (11/19)

*Indicates agonistic gesture.

Hypothesis 7: Agonistic gestures differ in success for high- and low-ranking males in relation to female parity

I conducted a GLMM to assess whether agonistic gestures were more successful for high- or low-ranking males. The full model was significant from the null model (LRT: χ^2 (4) = 15.31, $p < .001$; Table 4.6). There was a non-significant trend in the interaction between parity and agonistic gestures: while all gestures were more likely to be successful with parous females, agonistic gestures were more successful with parous females than nulliparous (Fig. 4.2).

Table 4.6: Results of the GLMM testing success of agonistic gestures.

	E	SE	Z	P
Intercept	1.185	0.486		
Parity	0.162	0.326	0.498	0.619
Male Rank	0.032	0.057	0.558	0.577
Agonistic	1.007	0.336		
IAParity:Agonistic	0.749	0.451	1.663	0.096*

The reference level for parity is 'parous' and is included in the intercept. Z and P values are omitted for intercept and main effects included in interaction. IA = interaction.

Interaction Between Parity and Agonistic
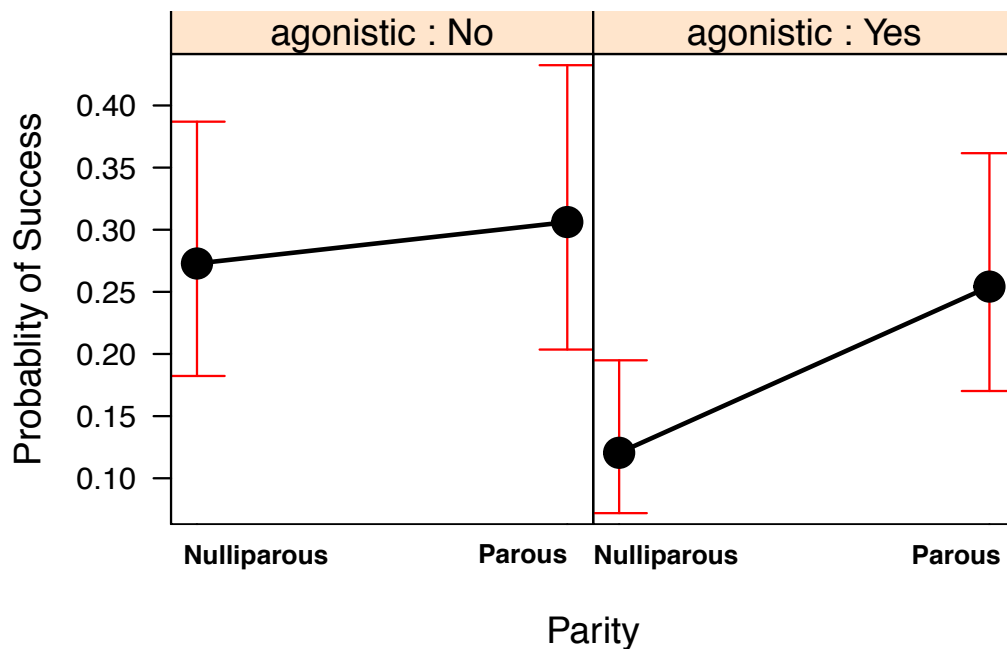
Fig. 4.2: The interaction between parity and agonistic gestures in the likelihood of gesture success. *In logistic models, the response variable is constrained between 0 and 1, resulting in asymmetrical error bars; the closer to 0.5 the estimate occurs, the more symmetrical the error bars.*

Hypothesis 8: High- and low-ranking males react differently to initial failure

Following the failure of a first gesture, males are likely to persist, especially if they have received a positive sign from the female ('partial success'). Persistence following a failed gesture is not sufficiently different between high and low-ranking males, $t(29.11)=0.361$, $p=0.72$. Rank likewise did not influence persistence following a partially successful gesture, $t(31.870)=-0.44$, $p = 0.67$.

Table 4.7 includes males' persistence following their first gesture. If the first gesture is unsuccessful, males persist in 81% of cases, and if the gesture is partially successful, they persist in 93% of cases. Females rejected males outright in 19 cases (Table 4.7).

Males persisting following a failure tended to use audible gestures (87% of persistent gestures were audible whereas only 33% of first gestures were audible). Following a partial

success, where the female is already attending and responding in a favourable manner, males

were more likely to use a silent gesture (52% of gestures).

Table 4.7: Persistence following first gesture

Successful	Persistence		Total
	No	Yes	
No	14.4% (19)	85.6% (113)	132
Partial	5.2% (5)	94.8% (93)	98
Yes	99% (104)	1% (1)	105
Total	128	207	**335**

Following a failed first gesture, males often persist using additional gestures. Three of

the five most common 'second gestures' are agonistic, (Table 4.8). *Object shake* was the

most common second gesture, meeting with success in 81% of cases, as compared to a 42.5%

success rate when used as a first gesture. In total, agonistic gestures resulted in complete

success in 17% of cases, while non-agonistic gestures resulted in complete success in 50% of

cases. The sample size per individual was too small to test this statistically without

pseudoreplication.

Table 4.8: Gesture following failed gesture

Gesture	Times occurring as second gesture	Success rate as second gesture
Arm raise*	13	69% (9/13)
Leaf clip	14	43% (6/14)
Object shake*	43	81% (35/43)
Genital offer	25	76% (19/25)
Rocking*	15	53% (8/15)

*Indicates agonistic gesture

Genital offer: a case study of gesture combinations

Genital offer is one of the most common gestures, and also one of the most effective.

When used as the first gesture in a bout, *genital offer* is more often used as a single gesture

(45/72) than as part of a sequence (27/72). High-ranking males did not *genital offer* to

females more than low-ranking males, with males of all ranks using *genital offer* at virtually

the same rate (Table 4.9).

Table 4.9: Success of 'genital offer' when used as first gesture in a bout

	High-ranking male success	Low-ranking male success	Total
Unsuccessful	8	5	13
Partially successful	11	16	27
Successful	12	20	32
Total use of genital offer as first gesture in bout	**31**	**41**	**72**

When genital offer is used in a two-gesture sequence, males most often pair it with

arm raise, object shake, or *rock* – all agonistic gestures (Table 4.10). Indeed, all but four of

the gestures used in combination with *genital offer* are agonistic gestures. Three gestures –

object shake, slap object, and *punch object* – are audible gestures, but only *object shake* is

used frequently in combination with *genital offer*.

Table 4.10: Gestures used in combination with genital offer in two-gesture sequence

Gesture preceding or following genital offer	Genital offer is first in sequence	Genital offer is second in sequence	Total
Arm raise*	4	6	10
Arm swing*	4	1	5
Object shake*	8	4	12
Genital offer	2	2	4
Rocking*	5	3	8
Reach	1	-	1
Thrust	1	-	1
Slap object*	-	1	1
Punch object*	-	1	1
Leaf clip	-	1	1

*Indicates agonistic gestures

Hypothesis 9: High- and low-ranking males differ in gesturing with attending females

In cases where the attentiveness of the female was known, the majority of solicitations

began with the female visibly attending the male, or else facing in his direction. This appears

to be a scenario orchestrated by the male; only 22/183 cases of a first gesture where female

attentiveness was known were produced when the female was not attending, and all but two

of these gestures were audible (for example, *object shake* or *leaf clip*) perhaps intended to

grab the female's attention. Low- to-mid-ranking males were responsible for the majority of

solicitations toward non-attending females; sub-adult males solicited females in 9 of the 22 cases, while a single mid-to-high-ranking male – Kato – produced 10 of the 22 gestures.

Hypothesis 10: Silent and audible gestures differ in success

Silent and audible gestures were produced nearly equally as the first gesture in a display, occurring 89 and 91 times respectively. Modality predicted the success of a gesture such that silent gestures were completely successful more often than audible gestures using an ANOVA, $F(1, 24)=7.78$, $p=.009$. Combining partial success and complete success, there was a non-significant trend for silent gestures to be more successful than audible gestures using an ANOVA, $F(1, 24)=3.87$, $p=.059$. This may be biased by the fact that some silent gestures have an extremely high success rate (e.g. *genital offer*), whereas some audible gestures are very unsuccessful (e.g. *leaf clip*).

DISCUSSION

Opportunistic mating is the sexual strategy most commonly used by male chimpanzees, both high and low ranking. This strategy does not seem to be preferred by males of any particular rank; all males at Budongo used it more or less equally. The chance for sexual coercion is thus high, with multiple males in direct competition for access to cycling females. Perhaps for this reason, the courtship repertoire of 26 gestures includes 15 gestures that are also used in agonistic contexts such dominance displays. High-ranking males had a higher number of agonistic gestures within their repertoire, as well as their core repertoire, and were significantly more likely than low-ranking males to employ agonistic gestures (Hypothesis 2). There was also a trend for agonistic gestures to be more successful, especially with parous females (Hypothesis 7). Males frequently persisted following female resistance behaviour, with females successfully rejecting males following non-gestural initiation in only 17 cases, and following the first gesture in 19 cases.

Males begin courtship by simply approaching the female, a tactic that has equal levels of success for high- and low-ranking males (Hypothesis 4). Female parity did not influence the success of non-gestural initiation (Hypothesis 5). It seems that high-ranking males have no less need than low-ranking males to produce gestural courtship displays. This was unexpected given that male sexual coercion increased the likelihood of female copulatory presents, especially for parous females at other sites (Muller et al. 2011, Feldblum et al. 2014). In fact, combining an approach with gestures was less successful than simply approaching a female, but this is difficult to interpret due to a small sample size (Hypothesis 5). It is possible that the low rate of combining approach with gestures demonstrates that approaching may be a tactic where success is largely determined by male dominance or coercion. Despite this, males of all ranks attempted this strategy at equal rates with and without gestures (p.43), leaving open questions regarding the influence of gestures and rank on courtship.

The success of the first gesture in a display did not significantly vary according to the rank of the signaller, implying that effective gestures are successful regardless of who produces them (Table 4.5). As might be expected given this finding, males of all ranks persisted at equal rates following failure or partial success (Hypothesis 8). One interpretation of this result is that female choice is what leads to copulation, not gesturing; this is supported by the fact that gesturing was associated with unsuccessful approaches. Yet, males used different strategies when persisting, increasing their success by switching the modality of the gesture or by using gesture combinations (Table 4.7). The modality of a gesture has clear implications for the success of a display. In the rare case where a female is not already attending to an erect male, he will employ a noisy gesture to attract her attention. When a female is attending, silent gestures are more successful than audible gestures in leading to mating, and yet males seem to prefer using audible gestures. I suggest that these are coercive

tactics employed by rebuffed or ignored males, and that males' preference for agonistic audible gestures reflects growing sexual frustration as they meet repeated failure. In this scenario, agonistic audible gestures might serve as an emphatic request, akin to an angry judge's gavel banging for silence. This is supported by the high rate of success for *object shake* as a second gesture (Table 4.8). In the case of *genital offer*, it seems audibility is not a primary concern, possibly because this gesture is frequently used toward the end of a display, when the female is already attending to the male.

Males' use of gesture combinations supports the interpretation that males tactically use agonistic gestures to coerce females. Of the five most common gestures, only non-agonistic gestures – *leaf clip* and *genital offer* – were typically used as single gestures toward the beginning of a display, while agonistic gestures – *arm raise, object shake*, and *rock* – were more likely to be used in combination with other gestures, or toward the end of a display. By using emphatic, agonistic gestures after failure to reach their goal, males of all ranks are clearly communicating their frustration in a threatening manner.

This study is somewhat limited due to the difficulties of sampling gestural communication in a wild population. Nonetheless, the data presented here are an asset compared to captive studies that say little about natural communication.

CONCLUSION

These findings offer insight into the strategy behind opportunistic courtship, where success is not necessarily rank-dependent, offering males a relatively low-cost mating tactic as compared to long-term sexual coercion. Effective communication can influence the outcome of a display as males adroitly manipulate their chosen gestures, level of coercion, modality, and sequence order in order to reach success. The increased use of agonistic gestures following repeated failure indicates that males do use gestures to intimidate females, and are successful in doing so. Contrary to previous studies suggesting that female choice is

an option in the short-term, the results here demonstrate that, in Sonso chimpanzees, high-ranking males who meet with female resistance persist with agonistic behaviour until the female acquiesces. This is particularly successful with parous females, who respond more favourably to agonistic gestures regardless of signaller rank. Female choice likely still occurs if females mate more frequently with males they prefer, as in Kibale (Pieta, 2008), but seemingly unwanted males use gestural coercion in the face of rejection. Future studies should compare high-ranking males' use of agonistic gestures with their aggressive behaviour in the long-term, to determine whether these coercive means complement each other by increasing female copulatory presents.

Chapter 5: Coercion and Gestural Courtship during Consortship

ABSTRACT

Consortship is a mating strategy in which a male and female chimpanzee pair leaves the community for the duration of a female's sexual cycle. The possibility of paternal certainty makes this strategy valuable for males, while females in some communities may benefit from inbreeding avoidance by going on consortship. Yet, consortship is risky and can result in death if a consorting pair is caught. Thus, males are somewhat beholden to a female's willingness to comply in silence as a given pair travels away from the community. On the other hand, some accounts of consortship describe severe female beatings, indicating that long-term aggression might suppress or influence female choice. In Budongo, consortship might be a favourable strategy when there is a surplus of oestrous females (measured by Operational Sex Ratio). In this chapter, I explore gestural and vocal communication during three successful and one attempted consortships. Males and females engaged in a seemingly constant negotiation where males gestured to persuade females to follow them, with a high rate of failure, as females ignored their requests, while whimpering and requesting reassurance or affiliation. There was no evidence of gestural coercion other than repeated persistence, which was only rarely accompanied by aggressive behaviour. Further, two of four consorting females risked inbreeding by their choice of consort, contrary to the hypothesis that inbreeding avoidance is primary cause for consortship. I conclude that communication during consortship reflects the balancing of male and female mating interests, and that both female choice and male preference are at play.

INTRODUCTION

The least common mating strategy for chimpanzees, consortship (or safari), is also the most risky for both males and females (Tutin, 1979). Consortship is defined as 'when a single male escorts a female away from the group and maintains exclusive copulatory access to her, as both of them take positive steps to avoid other chimpanzees' (Tutin, 1979). Consorting couples tend to travel to the outskirts of the community's range, and occasionally into neighbouring territory (Tutin, 1979; Nishida, 1983; Hobaiter & Byrne, 2012). The risk of encountering neighbouring males, as well as the risk of being discovered by community males, can result in harm (McGinnis, 1973; Goodall 1986) and in extreme cases, death (Hobaiter, 2010).

One of the most intriguing aspects of consortship is variation across different sites, which has been little addressed and remains unresolved. Consortship is used frequently at some sites, and rarely at others (Goodall, 1986; Boesch & Boesch-Ackermann, 2000); in some communities, high-ranking males use consortship as a mating strategy, but in others it

is a strategy for low-ranking males (Tutin, 1979; Wroblewski et al., 2009). Perhaps as a result

of this variability, whether coercion or female choice drives consortship is a source of

disagreement in current literature, with few data supporting either hypothesis (Tutin, 1979;

Goodall, 1986; Boesch & Boesch-Ackermann, 2000; Constable et al., 2001; Hobaiter &

Byrne, 2012). Further, little attention has been paid to the identity, rank, or parity of females

taken on courtship, and whether this too varies by site. If so, female status may explain at

least part of the differences in coercion, as older, parous females are more likely to be the

victims of male aggression (Muller et al., 2006). It is unknown whether consortship pairings

might sometimes reflect a long-term, underlying relationship between two individuals, and

whether this might be coercive or friendly in nature.

In this chapter, I review the available literature across sites under the theme of

coercion and female choice, in particular any evidence for or against long-term consorting

relationships. I discuss the history of consortship in Budongo, including the social standing of

both individuals in a consorting pair. Finally, I use gestural communication during four

consortships to test the hypothesis that males coerce females on consortship against the

hypothesis that females willingly take part, while also exploring the social situations that lead

to a successful consortship.

Consortship: A common occurrence or a rare risk?

Consortship is not the predominant mating strategy at any known field site (Muller &

Wrangham, 2001), yet the frequency of consortships does vary, reported regularly at Gombe

(Wroblewski et al., 2009), but rarely in Ngogo, Kanyawara, or Tai (Watts, 1998; Boesch &

Boesch-Ackermann, 2000; Wrangham, 2002). Interestingly, although consortship was

initially uncommon in Budongo (Reynolds, 2005), recent years have seen an apparent

increase in consorting behaviour, although this may be due simply to observer sampling bias

(Hobaiter & Byrne, 2012; Fallon, pers. obs.). One plausible explanation for the differences within and between communities may be shifts in the operational sex ratio (OSR), as observed in Gombe, where use of consortship varied as the number of reproductively mature males and the number of swelling periods exhibited by females increased (Goodall, 1986).

The priority of access model posits that male dominance ranking is the primary factor influencing access to females (Cowlishaw & Dunbar, 1991). It also predicts that as the male to female ratio reduces, high-ranking males are more able to monopolize females (Altmann, 1962), and this appears to hold true for chimpanzees (Constable, et al. 2001; Vigilant et al., 2001). Nonetheless, in Gombe, where there are low rates of female transfer, low-ranking males are able to increase their paternity by taking females, often of a similar rank, on consortship. Thus, dominant males become less able to monopolize females when receptive females are abundant, leading to alternative strategies, such as consortship, as a viable strategy for 'non-winning' males. High-ranking males are likewise unable to monopolize paternity when there are many males in a group (Boesch, 2009). A similar phenomenon is found in lemurs (*Lemur catta*), where variance in the OSR both between and within groups resulted in low-ranking males trying alternative mating strategies, such as earning tolerance from high-ranking males (Mertl-Millhollen et al., 2014).

Although the evidence is sparse, it is possible that changes to the OSR may account for differences in consortship frequency between groups, given that OSR influences the prevalence of alternative mating strategies and high-ranking males' monopoly of females. Alternatively, it has been proposed that consortship is a strategy to avoid inbreeding, given the low rate of female transfer at Gombe (Constable et al. 2001; Muller & Mitani, 2005). Constable et al. (2001) noted that females with high-ranking male relatives would often consort with low-ranking males; if this is the case across sites, then consortship becomes an

ideal strategy for natal females at risk of inbreeding, and should be accompanied by little coercion.

Female choice and coercion during consortship

In Tai, consortship "reflects the females' willingness to follow males that have superior social potentialities than others" (Boesch & Boesch-Ackermannn, 2000); male sexual coercion is less frequent at Tai than other sites, leading to more opportunity for female choice as compared to other communities (Stumpf & Boesch, 2010). In Gombe, Goodall portrayed considerable amounts of coercion, describing "punishing assaults" for females who refuse consortship (1986), while at the same site Tutin (1979) hypothesized that consortship is "mediated by female choice". In Budongo, females who screamed during consortship, thereby risking discovery, have sometimes been severely punished, even to the point of death; yet it has been argued that females may end consortship if they so choose by vocalizing (Tutin, 1979; Hobaiter, 2010; Hobaiter & Byrne, 2012). Similarly, Kollar et al. (1968) describe males on consortship as "punishing a companion for being too far away [from him]". The disparity between consortship descriptions at different sites is puzzling, but not necessarily contradictory; as discussed in previous chapters, females may choose males based on their history of long-term coercion (Muller et al., 2007). Still, this hypothesis has not been considered in the literature in regards to consortship.

The viability of sexual coercion may vary with the style of male dominance, for example 'despotic' versus 'egalitarian' dominance hierarchies (hierarchy steepness as measured by David scores: Kaburu & Newton-Fisher, 2015a). In egalitarian communities, males are more evenly matched in strength and dominance, and coercive tactics become secondary in favour of biasing females through grooming (Kaburu & Newton-Fisher, 2015b). In contrast, the steep dominance hierarchies of despotic communities allow individual males, who have no near equals, to use coercion unchecked. Under this explanation, the prevalence

of coercion is explained by combining the Operational Sex Ratio with an understanding of the male hierarchy.

Applying this concept to consortship might explain some of the variation in female choice across sites; coercive consortship should be less frequent in an egalitarian community, as a given male should be unable to monopolize a female. A community with a steep dominance hierarchy, however, should be more prone to coercion, and possibly also coercive consortship. One problem with this hypothesis is that it rests upon the priority of access model, assuming that the highest-ranked males receive the most access to females, whether by coercion or cooperation. However, consortship in Gombe allows low-ranking males to thwart the priority of access model and increase their reproductive success (Wroblewski et al., 2009). Consequently, examining the variance in who successfully initiates consortship across sites is critical to our understanding of coercion or choice in this strategy.

A strategy for all?

The rank of male consorts is strikingly different in Gombe as compared to other sites. Although all Gombe males participate in consortship, low-ranking males are the more frequent consorters (Tutin, 1979; Wroblewski et al., 2009). In both Budongo and Tai, only alpha males or future alpha males have been seen to use consortship (Boesch & Boesch-Ackermann, 2000; Hobaiter & Byrne, 2012). Matsuzawa et al. (2011) briefly describe the beta male as regularly consorting with a specific female, suggesting that high-ranking males are typically those who resort to consortship in Bossou. Only a single case of consortship, initiated by a high-ranking male, has been reported in Kanyawara (Wrangham, 2002). At most sites, consortship is an alternate strategy rather than a primary means of achieving copulations, which begs the question why alpha males sometimes choose consortship over possessive or opportunistic behaviour.

Consortship is a risky strategy in that males must leave the community for an extended period of time, thereby gambling their place in the dominance hierarchy upon their return, in addition to the risk of encountering neighbouring groups (Goodall, 1986). In communities with steep dominance hierarchies, consortship may be limited to alpha males who have little to fear from leaving the community for weeks on end. Alpha males typically also use the possessive mating strategy, which nonetheless allows for so-called sneaky copulations from other males (Goodall, 1986; Matsumoto-Oda & Tomonaga, 2005). Presumably, alpha males only choose consortship when the potential for paternity certainty is highest (i.e. during a conceptive cycle), or when other males are unlikely to usurp the alpha's rank while he is away. Several factors converge to favour consortship as a strategy for low-ranking males in Gombe: first, the low transfer rate of natal females yields a comparatively high chance for inbreeding, which seems to make females willing partners for consortship as a means of distancing themselves from male relatives (Constable et al., 2001; Wroblewski et al., 2009). This has led some to suggest that female choice drives consortships (Tutin, 1979; Hobaiter & Byrne, 2012). Following findings that males prefer older, parous females (Muller et al., 2006), high-ranking males in Gombe father more offspring with older females, leaving young, natal females available for consortship with low-ranking males (Constable et al., 2001;Wroblewski et al., 2009). In this scenario, the benefit of exclusive female access during consortship apparently outweighs the risk of falling in rank – or, as is more likely for low-ranking males, losing the chance to rise in rank.

Although much attention has been paid to consorting males, less scrutiny has been applied to consorting females. In most communities, only a small proportion of females go on consortship (Table 5.1). This may simply be a reflection of rarity of researchers recording consortship, which is difficult to observe, or it may reflect some females' willingness to engage in this mating strategy more so than other females. Consortships seem to be instigated

with parous females in Kanyawara and Budongo (Wrangham, 2002; Hobaiter & Byrne, 2012), whereas consortship occurs regardless of parity in Tai (Boesch & Boesch-Ackermann, 2000). In Gombe, consorting pairs tend to reflect the priority of access model in that low-ranking males typically take less desirable nulliparous females on consortship (Wroblewski et al., 2009). There is also some evidence for females being taken on consortship following the loss of an infant (e.g. Boesch & Boesch-Ackermann, 2000; Fallon, pers. obs.), which is also when the likelihood of conception is higher (Nishida et al., 1990).

Table 5.1: Summary of consortship behaviour across sites[1]

Field Site	Approx. community size	Typical male rank	Percent of females known to go on consortship	Percent of conceptions during consortship	References
Budongo	81 (7 males, 25 adult females)	High	Unknown	Unknown	Hobaiter & Byrne, 2012
Gombe	45 (11 adult males, 14 females)	All males	100%	19-21%	Constable et al. 2001; Wroblewski et al., 2009
Mahale	86 (12 adult males, 40 adult females)	High	3%	8-20%	Hasegawa &Hiraiwa-Hasegawa, 1990
Tai North	32 individuals (3 adult males, 11 females);	High	44%	31%	Boesch & Boesch-Ackermann 2000; Stumpf & Boesch, 2010
Tai South[2]	62 individuals (4 adult males, 25 adult females)	High	44%	31%	-

[1]Adapted and updated from Table 4.7 (Boesch & Boesch-Ackermannn 2000).
[2]Numbers for consortship are lumped for Tai North/South groups

Timing of consortship in relation to ovulation also varies; forty-four percent of Gombe consortships included females within the peri-ovulatory period, but the swelling stage of female at the time of initiation varied (Table 5.2; Goodall, 1986). Tutin suggests female swelling variance is a function of male opportunity, such that males will initiate consortship

with a nearly ovulating female when they have the chance, regardless of swelling size (1979). This is especially true for low-ranking males, who are likely unable to steal an ovulating female during the highly competitive peri-ovulatory period (POP) (Goodall, 1986). Gombe is the only site to report data on the peri-ovulatory period and swelling size.

Table 5.2: Female swelling stage during consortship initiation in Gombe

Female status	Approx. swelling size*	Percent Consortship initiation**
Maximally swollen	4	39.5%
Tumescent (non-max swelling)	2-3	16%
"Flabby"	1	12%
No swelling	0	20.5%
Pregnant	0	12%

*Approximate numeric swelling sized based on verbal descriptions from Goodall, 1986
**Data from Goodall, 1986, p. 459

Although complete consortships are rarely observed, it seems that the rate of copulation is relatively low. The highest number of matings between a consorting pair recorded in Gombe was four in one day (Goodall, 1986). This is surprising given that females copulate upwards of 20 times per day during opportunistic mating, and begs the question whether consortship yields the desired results for reproductive success and if so, for whom.

Reproductive success

For males, a successful consortship theoretically ensures paternal certainty, with exclusive access to an ovulating female, often for the duration of her menstrual cycle. Few data are available on the likelihood of paternal success during consortship. Some evidence suggests that the paternal return from consortship may vary by male (Boesch & Boesch-Achermann, 2000; but see Constable et al., 2001 for a critique of DNA sequencing techniques). This variance may be explained by the males' ability to detect ovulation, as high-ranking males are thought to be more adept at detecting female fecundity (Boesch &

Boesch-Ackermann, 2000; Deschner et al., 2004; Boesch, 2009). In Gombe, the pattern is clear: although all males participate in consortship, low-ranking males achieve the most conceptions in this strategy, more so than dominant males, by targeting low-ranking, nulliparous females (Wroblewski et al., 2009). In another study of three observed consortships in Gombe, all resulted in conception for the consort male (Constable et al., 2001). The seeming differences in paternity between communities suggest that consortship is not a successful strategy for a particular type of male, but rather is dependent on other factors such as social status of the desired female. One influential factor missing from the current literature (but see Hobaiter & Byrne, 2012) is evidence documenting what constitutes a successful request for consortship, as well as females' means of accepting or rejecting consortship requests.

Gestures

Consortship initiation appears similar to other mating strategies, although males initiating a consortship typically do not display a penile erection. Goodall (1986) describes consorting males gazing toward a female while pilo-erect, using *branch shake, rock, bipedal swagger*, and *arm stretch* (hereafter referred to as *arm raise* from description) in a "summons", and takes care to note the potential for violence should the female not respond favourably to gestural initiations. In Bossou, *heel tap* is described as a frequent consortship gesture, along with *object shake, stomp*, and *leaf clip* (Matsuzawa et al., 2011). Budongo males used 21 gesture types during consortship, most prominently *object shake* and *object move*; consortship also accounted for the majority (26/29 cases) of the rare *rub rump* gesture (Hobaiter & Byrne, 2012).

Males on consortship avoided using long-distance audible gestures, such as *drum object*, in favour of short distance audible gestures, presumably to avoid detection from both

neighbouring groups and community males (Hobaiter & Byrne, 2012). Of the gestures described during consortship, many are gestures also used in aggressive displays (*object shake, object move, rock, bipedal swagger, heel tap, stomp*), possibly an indication of high rates of coercion. Indeed, males gesture more urgently during consortship than other contexts, and direct severe aggression toward females when their vocalizations risk attracting attention (Hobaiter & Byrne, 2012). At the same time, the prevalence of reassuring behaviour such as intermittent grooming, embraces, and *rub rump* gestures showcases males' effort to appease females, and more research is needed to determine the full extent of coercion or female choice during consortship.

Hypotheses and predictions

The aim of this chapter is to discuss why individuals participate in consortships despite the high risk of injury from community males and neighbouring groups if caught. Based on the finding that Gombe females who frequently go on consortship are natal females at risk of inbreeding, I discuss the background and incentives for the three female subjects to consider whether consortship is a strategy to avoid inbreeding (Hypothesis 1). Given the large number of receptive males and females in Budongo, as compared to Gombe, I predict that Budongo females at risk of inbreeding are not more likely to go on consortship than other females. I also describe female consortship behaviour, including communication and likelihood of ovulation occurring during consortship.

I then examine whether gestures and aggression during four consortships reflect the coercion seen during opportunistic mating, in order to test the hypothesis that males coerce females on consortship (Hypothesis 2). This hypothesis is grounded in the finding that males in Budongo heavily aggress consorting females, even to the point of death (Hobaiter & Byrne, 2012). I use males' gestural communication to test whether the high-ranking male consort used agonistic gestures more than the low-ranking male consort, predicting that both

males use coercive gestures equally. As the use of frequent single gestures (as compared to gesture sequences) has been considered part of the 'urgency' of consortship communication (Hobaiter & Byrne, 2012), I explore this idea in more detail, testing whether single gestures or sequences are more effective in eliciting a female response. I predict that single gestures will be more effective given the necessity for males to herd females away from the community (Tutin, 1979). To that end, I briefly describe males' success and persistence when gesturing, their goals (ASOs), and the rate of female rejection.

Finally, I examine Operational Sex Ratio during consortships to assess whether competition level has an effect on mating strategy (Hypothesis 3). I do this by testing whether the sex ratio on consortship start days is higher than on other days, predicting that competition (as measured by OSR) is higher on consortship start days than other days.

METHODS

Fieldwork was conducted between the periods of June 2011-August 2011, May 2012-April 2013, and September 2013-March 2014, totalling approximately 2,688 hours of observation time. I use Tutin's (1979) definition of consortship, "when a single male escorts a female away from the group and maintains exclusive copulatory access to her, as both of them take positive steps to avoid other chimpanzees". A courtship event was considered consortship if the consorting pair remained apart from the community for a period of at least 48 hours (Hobaiter & Byrne, 2012). Consortship observations were collected while conducting focal follows of oestrous females; occasionally, males produced displays that resulted in consortship rather than opportunistic mating, and I recorded these on an ad-hoc basis.

In total, 20 females exhibited a sexual swelling during the study period, 13 parous and 7 nulliparous. Infant and juvenile males were excluded from data collection, leaving 9 adult males and 5 sub-adult males as possible mates. I recorded four attempts at

consortship, which involved two adult males and three adult females, using a Panasonic

HD V700 video camera, recording vocalizations with a Sennheiser MKE400 microphone.

FileMaker Pro Advanced v. 11 was used to code filmed data for gestural communication.

As in Chapter 4, I defined *gesture* following Hobaiter & Byrne (2011a) as "discrete,

mechanically ineffective physical movements of the body observed during periods of

intentional communication". Gestures were considered intentional when accompanied by

gaze checking (indicating a direct recipient), *response waiting*, or *persistence*. Although some

definitions of gesture distinguish between gesture and bodily postures (e.g. genital offer;

Genty & Zuberbuhler, 2015), for simplicity's sake I consider all intentional postures as

gestures. A gesture was considered 'agonistic' if it was previously documented in the

literature as occurring during aggression (See Chapter 4 on opportunistic mating).

I also recorded non-gestural behaviour that preceded or accompanied displays, as in

Chapter 4, and have copied the definitions below (Table 5.3) noting whether displays were

male or female initiated. Male coercion was defined as physical aggression toward an

oestrous female or use of agonistic gestures and persistence following female resistance.

Female choice was defined following Halliday (1983): copulation after female proceptive

behaviour, or no copulation after female resistance behaviour.

Sexual swellings and peri-ovulatory period

Swelling stage was estimated by the degree of wrinkling on a scale of 0-4, where 4

indicated a fully inflated swelling (Furuichi, 1987; Zuberbühler & Reynolds, 2005). The peri-

ovulatory period (POP) was defined as 3-7 days prior to de-tumescence of the female sexual

swelling (Deschner et al. 2004; Emery Thompson & Wrangham, 2008). Following Emery

Thompson and Wrangham (2008), I defined the first day of de-tumescence as D0, counting

backward to D3-D7. This measurement includes swelling days with the highest likelihood of

ovulation, but is not exact. In cases where the first day of de-tumescence was not observable

(e.g. the pair remained apart from the community for the duration of a female's cycle), I inferred a possible range based on the first known date of de-tumescence.

Table 5.3: Non-gestural courtship behaviour

Behaviour	Definition
Aggressive display	Male chases or physically harms the female.
Approach	Male approaches female in a direct path while erect, visible within a radius of 10m.
Eye contact	Male meets the female's eyes while erect.
Groom	Male grooms female
Inspect swelling	Male touches or sniffs a female's swelling.
Lead away	Erect male makes eye contact with the female, then turns and moves to a secluded area (Nishida, 1997)
Masturbate	Erect male self-stimulates while looking at a female

Operational sex ratio

To account for the level of male-male competition during consortship, I used the Operational Sex Ratio (OSR) of sexually available males to sexually available females (i.e. females not pregnant or in lactational amenorrhea) using the formula set forth by Mitani et al. (1996). The number of reproductively available females varied by year, reflecting conception and immigration. In addition, I calculated two separate ratios for each consortship: adult Operational Sex Ratio, and OSR including fecund sub-adult as well as adult individuals. Mitani et al.'s (1996) Operational Sex Ratio accounts for the number of fertile days per individual in a given year. The formula estimates an average of the total time an individual could be sexually active using the following formula, where m = number of reproductively available males, B = duration of inter-birth interval in years, 365 = number of days in a year, f

is the number of reproductively available females, n = the sum of the number of oestrous

cycles until conception for each individual, and c= is the length of oestrus in days:

$$\frac{m * B * 365}{f * \sum_{i=1}^{n} c}$$

This formula results in a ratio of "the number of male-days per female-days in which

potentially procreative copulations occur" (Marlowe & Berbesque, 2012). I used community

statistics for inter-birth intervals (average 3.11 years), number of cycles to conception

(average 5.9), and the average length of oestrus (average 12.5 days). If a female was within

the first three months of pregnancy, I classified her as ostensibly 'reproductively available' as

females continue to exhibit sexual swellings and males, who appear unable to detect early

pregnancy, continue to mate with them (Goodall, 1986; Deschner et al., 2004). OSR results in

a theoretical number of 'sexually receptive days', but does not account for the actual number

of swollen females on a given day. Therefore, I also calculated a Daily Sex Ratio on the first

day of consortship to assess competition in real time; for this, I used the ratio of

reproductively available males to the number of females in swelling stages 3 or 4 on a given

day, as a means of assessing the level of male-male competition on the start day of a

consortship.

Statistical analysis

All statistical analyses were conducted using R (version 3.1.2; R Core Team, 2014)

and the lme 4 package (version 1.0-7; Bates et al., 2014). The sample size of consortships

was N=4, with two males and three females participating. No data were transformed for the

analyses in this chapter. Statistical tests were considered significant at $\alpha = 0.05$.

Hypothesis 1: Incest risk

To test Hypothesis 1, I performed Pearson's Chi-square Test for Independence to assess whether swollen females at risk of incest (yes, no) were observed participating in a consortship (yes, no) at a rate higher than expected.

Hypothesis 2: Male coercion

I conducted several statistical tests to explore male gesturing during consortship. First, I compared the two males' observed use of agonistic gestures using a 2x2 Pearson's Chi-square test to explore whether an individual employed agonistic gestures (yes, no) differently between mating strategies (consortship, opportunistic mating). I used the same test, with Yates' continuity correction for non-independence, to compare whether the observed cases of single gestures or sequences were different than expected during consortship/opportunistic mating. I then used a 2x2 Chi-square test to compare the association between success (success, failure), and gesture combinations (single, sequence). Finally, I performed a 4x2 Pearson's Chi-square Test for Independence to test the probability that success (success, failure) and gesture type (*big loud scratch, object shake, leaf clip, leaf strip*) are related.

Hypothesis 3: Operational Sex Ratio

To consider whether reproductively available sub-adults affect the level of sexual competition, I used an independent samples t-test to assess whether there is a difference between two measures of OSR (one with reproductively available sub-adults included, one without). A difference might suggest that sub-adults do play a role in the level of sexual competition and that a measure of including sub-adults may be a more accurate predictor of social circumstances.

To assess whether OSR influenced the occurrence of consortships, I compared the concrete measure of competition (Daily Sex Ratio) and the theoretical measure of competition (Operational Sex Ratio) on consortship days. A difference might suggest that DSR, the measure of competition between swollen females, better predicts OSR, the theoretical competition between reproductively available, but not necessarily swollen, females.

RESULTS

In this section, I describe three cases of successful consortship and one case of attempted consortship. I compare data on male consorts' rank history, consortship initiation, gestural repertoire, use of aggression, and whether they successfully took the female on consortship. For female consorts, I compare data on their parity, swelling stage, history of consortship participation, risk of inbreeding, and willingness to participate in consortship, as measured by response to male solicitations. Finally, I compare data on the Operational Sex Ratio and Daily Sex Ratio at the time of consortship initiation.

Hypothesis 1: Inbreeding risk (and life history of consorting pairs)

I recorded four consortships for two adult males, Kato and Zefa, and three females, Harriet, Janie, and Ruhara (Table 5.4). The research period also included unobserved consortships between Kato with both Harriet and Ruhara, while Zefa took a parous female Kutu on three consecutive consortships. Two of the three females had a risk of incest due to a high-ranking son (Table 5.4); however, swollen females with high-ranking sons were not more likely to go on consortship than swollen females without high-ranking sons in a 2x2 chi-squared analysis, $\chi^2(1)=2.62$, $p>0.1$.

Table 5.4: Observed consortships

Consorting Pair	Consortship start date	Female incest risk	Female parity and rank	Male rank (1-14)	Male incest risk	Successful (longer than 48 hours)
Kato and Harriet	March 14, 2013	Yes (adult son Hawa, rank 3)	Parous, high	7 (Middle)	Yes (mother Kutu)	No
Kato and Ruhara	January 13, 2014	Yes (adult son Nick, rank 1)	Parous, high	7 (Middle)	Yes (mother Kutu)	Yes
Kato and Janie	March 12, 2013	No	Parous, middle	7 (Middle)	Yes (mother Kutu)	Yes
Zefa and Ruhara	December 18, 2012	Yes (adult son Nick, rank 1)	Parous, high	2 (High)	No	Yes

Zefa acted as beta male until the overthrow of the alpha male, Nick, in December 2013, which sparked a stalemate period of over one year where the Sonso community had no clear alpha male, and where male relations were in constant flux. Following Nick's loss of the alpha position, Zefa commenced on multiple consecutive consortships that typically lasted around three weeks each; Zefa's exact rank at the time of his consortships is difficult to determine due to lack of pant-grunt data. However, it was clear from the behaviour of others in the group that he remained high-ranking.

Kato, on the other hand, was middle-ranking in position 7 out of 14 males, and is the first middle-ranking male known to go on consortship in Budongo. Each of his three consortships also occurred following the overthrow of the alpha male. Interestingly, during this time Kato was observed in frequent alliance with other high-ranking males (Fallon, pers. obs.), and by December 2015 (2 years following the overthrow of the alpha), Kato was ranked third out of all males (Fedurek, pers. comm.).

Description: Female communication

Janie, Harriet, and Ruhara responded infrequently to male gesturing with either vocalizations or gestures. Females produced three gesture types during consortship: *bump*

rump (4 cases), *present* (10 cases), and *tap other* (4 cases), all as single gestures. Only *bump*

rump and *tap other* were initiated by females, while *present* was produced in response to

male gesturing. All female initiated gestures had an ASO of affiliation, and were largely

successful. Only one case of *tap other* required persistence, while a second case resulted in

outright failure with no persistence.

I recorded a total of 25 vocalizations produced by females, which were occasionally

accompanied by affiliative behaviour (Table 5.11). Nineteen of the vocalizations (Seven

pant-grunts, six screams, and six whimpers) were produced by Harriet during Kato's failed

attempt at consortship, and likely contributed to its eventual failure. The majority of female

consortship vocalizations were produced following pant-hoots from the larger community,

after which both individuals exhibited signs of nervousness.

Table 5.11: Female vocalizations during consortship

Vocalization	Total produced	Accompanying gestures
Pant-grunt	10	Tap other (3 cases)
Scream	9	Bump rump (4 cases), genital offer (1 case)
Whimper	6	Tap other (2 cases)

Description: Female swelling stage and ovulation status

Males initiated courtship with females at various swelling stages. Kato initiated

consortships with one maximally swollen female, one female with a swelling size of one, and

one female with no swelling, while Zefa initiated consortship with one maximally swollen

female. All of the females were emerging from lactational amenorrhoea following the

weaning of their infants.
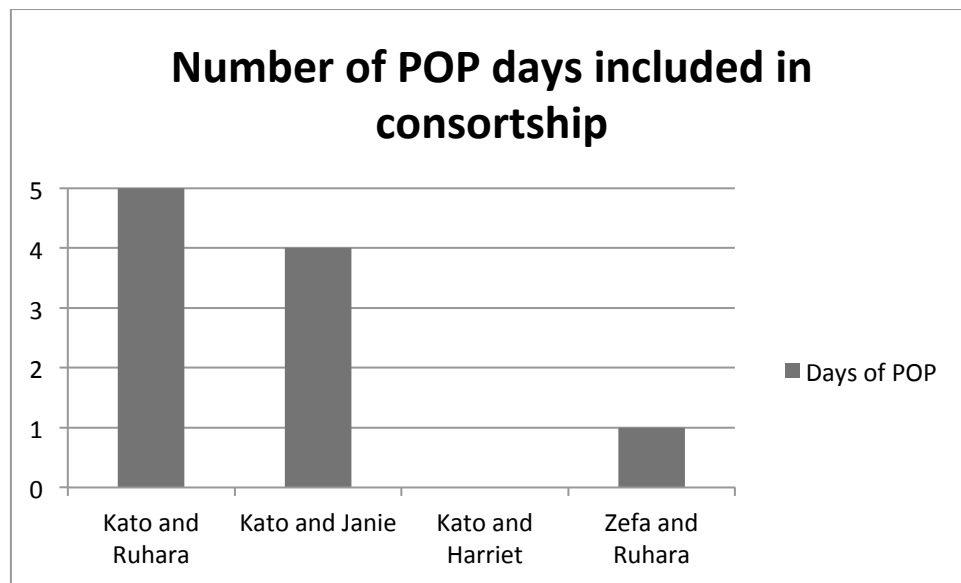
Fig. 5.2: Possible days of the POP including in consortship.

As conception is most likely during the peri-ovulatory period, I calculated the number of likely ovulation days included in consortships (from a range of 0-5 days; Fig. 5.2). Kato solicited Ruhara for consortship at the beginning of her swelling, with a swelling size of one. The period of consortship lasted for one month, and therefore presumably included the entirety of the peri-ovulatory period (POP). Kato and Janie left on consortship when she was maximally swollen and on the second day of the POP. The two remained together off-grid for two full days, returning the afternoon of the third consortship day, which was Janie's fifth day of the POP. Harriet had just finished a sexual cycle and had no swelling when Kato unsuccessfully initiated consortship. Zefa and Ruhara left for consortship when Ruhara was maximally swollen, and returned four days later when Ruhara had no swelling. Presuming Ruhara's day of de-tumescence occurred within the span of these four days, their consortship included between 0 and 2 days of the POP (averaged as one day in Fig. 5.2). None of these four consortships resulted in pregnancy; however, Harriet conceived in her next cycle, roughly 13 days following Kato's attempt (paternity unknown), while Janie also conceived 18 days later, but lost her infant (paternity unknown) to infanticide.

Hypothesis 2: Male gesturing, aggression, and consortship initiation

Males initiated consortship both with courtship gestures and other initiating signals (non-gestural courtship initiation), without the accompanying visual signal of a penile erection. I recorded 253 gestures used during consortship, including 12 gesture types (Table 5.5), of which seven were agonistic. Zefa employed agonistic gestures more often than Kato, $\chi^2(1)=7.06$, $p<0.01$. *Leaf clip* and *object shake* were the most commonly used gestures, accounting for 64% of courtship gestures. I have added one gesture to the consortship gestural repertoire that was not in my opportunistic mating repertoire, but which has been reported previously in the community: *bump rump*, where two individuals briefly touch bottoms, accompanied by a rapid up and down movement (Hobaiter & Byrne, 2012). I did not record any examples of *heel tap*, which has been described in consortship in Bossou, but which does not appear to be in the Sonso repertoire (Hobaiter & Byrne, 2011a).

Table 5.5: Gestural repertoire for consortship

Gesture	Kato	Zefa	No. Recorded
Arm raise*		*	3
Big Loud Scratch*	*	*	20
Bump rump	*		12
Leaf clip	*	*	80
Leaf strip	*	*	10
Object move*		*	17
Object shake*	*	*	82
Genital offer		*	2
Punch object/ground*	*		10
Rocking*	*	*	6
Slap object*		*	3
Stiff stance*	*		6
Tap other		*	2
Total	**211**	**42**	**253**

*Indicates agonistic gesture

Description: Non-gestural consortship initiation

During consortship, I recorded 58 cases of communication initiated using non-gestural courtship behavior (Table 5.6). Prolonged eye contact (five seconds or longer) and

leading away were the most common non-gestural initiations, comprising 77% of observations. In fifteen cases, non-gestural initiations were produced without any accompanying gestures, nine of which were 'leading away' the female by making eye contact accompanied by travelling a short distance away from the female and then response waiting for her to follow. The remaining 43 cases were produced in tandem with gestures, with *object shake* as the most common gesture, accounting for 37% of cases. Eight of the twelve gestures recorded in tandem with non-gestural initiation were agonistic gestures; these gestures accounted for 58% of all combinations with initiation behaviour.

Table 5.6: Non-gestural initiation during consortship

Initiation	Times observed
Aggress	2
Approach	6
Approach pilo-erect	5
Eye Contact	21
Grooming	3
Lead Away	24
Total	**58**

Single gestures and sequences

I recorded 134 single gestures and 62 sequences in 196 bouts. *Object shake* (N=61) and *leaf clip* (N=20) were the most common single gestures. Sequences were largely two-gesture sequences (N=40 cases); *big loud scratch, object shake, leaf clip*, and *stomp* were the most common gestures used in sequences. Consorting males were more likely to use a single gesture than a sequence, rather than use sequences and single gestures equally, using Pearson's Chi-squared test with Yates' continuity correction (due to non-independence), $\chi^2(1)=93.43$, $p<0.001$ (Fig. 5.1).
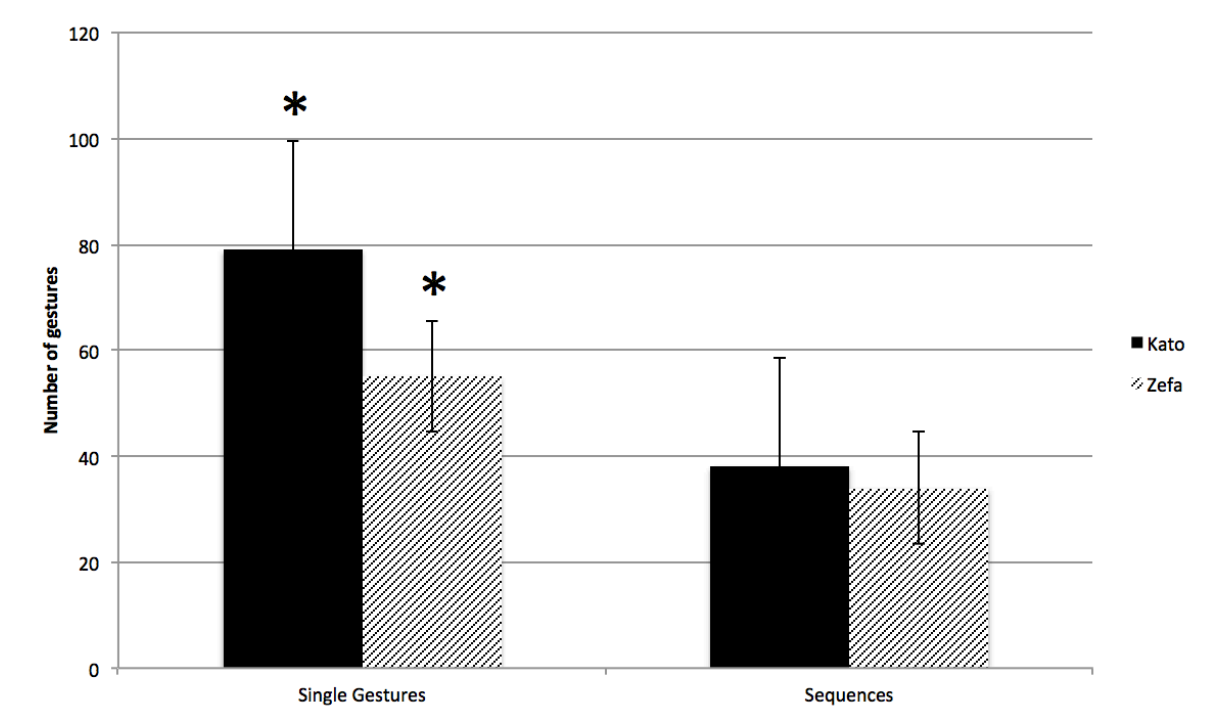
Fig. 5.1: Consorting males Zefa and Kato both use single gestures significantly more than sequences.

Success

Gestures met with outright failure in 56% (141/253) of cases, partial success in 22% (54/253) of cases, and immediate success in 22% (54/253) of cases. I could not determine success or failure in the remaining four cases. Single gestures and sequences did not differ in success or failure using a 2x2 Chi-squared test, $\chi^2(1)=3.709$, $p=0.295$. There was no significant difference in the success rate between the four most common gestures – *big loud scratch, object shake, leaf clip*, and *leaf strip* – when using a 4x2 Chi-squared test, $\chi^2(3)=12$, $p=0.213$.

Persistence

Consorting males persisted following 90% of failures and 85% of partial successes. Thus, in 24 cases total (10%), females were able to resist males without male persistence. However, when the first gesture in a bout was met with failure, males persisted - ignoring female resistance - in all but three cases (106/109 failed bouts). *Object shake* accounted for the majority (37%, 73/199) of persistent gestures. In 60 instances of persistence, males

accompanied persisting with non-gestural behaviour (Table 5.7). Persisting behaviour was

apparently coercive (aggression, pilo-erect) in 13% (8/60) of cases.

Table 5.7: Non-gestural behaviour accompanying persistence

Non-Gestural Behaviour	Count of Persistence
Aggress*	3
Approach	7
Approach Pilo-erect*	3
Eye Contact	21
Lead Away	24
Stand Pilo-erect*	2

*Indicates possibly coercive behaviour

What do gesturing males aim to achieve?

I recorded five apparently satisfactory outcomes (ASOs) during consortship:

affiliation, follow me, groom me, stop behaviour, and sexual attention (to male) (Table 5.8).

The vast majority of gestures (140/196) fit the definition for the ASO 'follow me'. The ASO

'stop behaviour' was requested solely in response to females vocalizing; when a male

intimidated a vocalizing female, she stopped vocalizing immediately in every case. I recorded

three instances of copulation, one between Zefa and Ruhara, one between Kato and Ruhara,

and one between Kato and Janie.

There was a substantial overlap in gestures used for each ASO. For example, *object

shake* was used to request all five ASOs during consortship, and nearly every gesture was

used to request the ASO 'follow me'. Table 5.9 includes the gestures for each ASO here with

those defined as primary and secondary meanings by Hobaiter & Byrne (2014).

Table 5.8: Apparently Satisfactory Outcomes during Consortship

ASO	Definition	Gestures Used During Consortship
Affiliation	The signaller is satisfied by affiliating with the female, such as inspecting or tapping the female's swelling	Big loud scratch, bump rump, leaf clip, object shake, tap other
Follow me	The signaller is satisfied when the female follows him	Arm raise, big loud scratch, bump rump, leaf clip, leaf strip, object move, object shake, punch object, **slap object**, stiff stance, **stomp,** rock
Groom me	The signaller is satisfied when the recipient engages in grooming	Leaf clip, object move*, object shake*, stomp*, punch ground*
Sexual attention (to male)	The signaller is satisfied following copulation	Genital offer forward, **object shake***
Stop behaviour	The signaller is satisfied when the recipient stops behaviour (typically vocalizing)	Object shake*, rock, stiff stance*

*Indicates agonistic gestures; bold gestures are those previously reported by Hobaiter & Byrne (2014) during consortship

Table 5.9: Apparently Satisfactory Outcomes for All Contexts

ASO	Primary meaning gestures	Secondary meaning gestures
Affiliation	-	-
Follow me	Jump; **slap object**; throw object	Foot present; rub rump; **stomp two feet**
Groom me	Big loud scratch	Bite; present grooming
Sexual attention (to male)	Leaf-clipping; object move; stomp	**Object shake**; punch object or ground
Stop behaviour	Grab; hand on; jump; push; side roulade; slap other; somersault; stomp two feet; tap other	Arm swing; bite; foot present; hand fling; punch other; shake hands; slap object

Data taken from Hobaiter & Byrne (2014)

How do consorting pairs combine ASOs?

Here, I have limited the analysis to gestural sequences comprised of 2 or 3 gestures. I recorded three sequences for 'Affiliation', ten for 'Follow me,' and two for 'Groom me' (Table 5.10).

Table 5.10: Gestural sequences for each ASO

ASO	Sequences
Affiliation	Big Loud Scratch + Object shake
	Object shake + Leaf clip
Follow Me	Big Loud Scratch + Object shake
	Leaf clip + Leaf clip (2)
	Leaf clip + Big Loud Scatch
	Object shake +Leaf clip (3)
	Object shake + Punch
	Object shake + Stomp
	Leaf clip + Big Loud Scratch + Leaf Clip
Groom Me	Object shake + Object shake
	Object shake + Stomp

Object shake was produced in ten of the fifteen sequences. The most common two-gesture sequence was *object shake + leaf clip*, which occurred four times – once for ASO 'affiliation' and three times for ASO 'follow me'. Other sequence repetitions include *object shake + stomp* for ASOs 'groom me' and 'follow me', and *Big Loud Scratch + object shake* for ASOs 'affiliation' and 'follow me'. Within a sequence, *leaf clip* was the most often repeated gesture, occurring twice in three separate sequences. All sequences were audible with the single exception of the sequence produced by a female (*tap other + present sexual*).

Hypothesis 3: Operational sex ratio and consortship

The Sonso population average Operational Sex Ratio across the study period was 4.67, close to the species average OSR of 4.54 (Mitani et al. 1996). There was little variation in OSR on different consortship days, with no value laying more than two standard deviations outside the mean (μ=13.97, σ= 1.17). There was a non-significant trend for a lower OSR when including both adults and reproductively active sub-adults (i.e. cycling nulliparous females and males above 10 years, the age of male fecundity) using Welch's t-test, t(5.89)=2.072, p=0.08.

There was also a significant difference between the Daily Sex Ratio on consortship

days and the OSR on consortship days when using Welch's t-test, $t(3.89) = 19.92$, $p < 0.001$

(Table 5.12). This is clear from the raw data: over the course of the study period, the average

number of females in oestrus per day was N=3 and the average daily sex ratio was 4.67. On

days where a consortship began, the average number of females in oestrus was N=6.67, and

the average daily sex ratio was 2.18.

Table 5.12: Consortship Operational Sex Ratio and Daily Sex Ratio

Consorting Pair	Consortship start date	Num. of cycling females	OSR (all sexually active individuals)	OSR (adults only)	# of females in 3/4 swelling	Daily Sex Ratio
Kato and Harriet	March 14, 2013	16 (11 adults)	14.37	12.31	8 (6 parous)	1.75
Kato and Ruhara	January 13, 2014	14 (9 adults)	15.39	13.68	6 (2 parous)	2.3
Kato and Janie	March 12, 2013	16 (11 adults)	13.47	11.19	5 (4 parous)	2.8
Zefa and Ruhara	December 18, 2012	17 (12 adults)	12.68	12.31	7 (4 parous)	2

DISCUSSION

The above results find the most support for Hypothesis 3, consortship occurring

during periods of high competition. In the cases presented here, consortship in Budongo

occurred during a surplus of females: the Daily Sex Ratio during consortship indicated a low

level of male-male competition for females, with an average OSR of 2.18 as compared to the

population average OSR of 4.54 reported by Mitani et al. (1996). There was more than twice

the number of oestrous females on consortship days than on non-consortship days (See

Chapter 4 on opportunistic mating). As shown by copulation calling during this period in

Chapter 3, oestrous females are susceptible to female-female competition and adjust their

calling strategies accordingly; here, females likewise seem more willing to engage in

consortship during a time of high female-female competition as a means of ensuring a high-quality mate. I found no support for Hypothesis 1, as females at risk for incest were not more likely to go on consortship than other swollen females. Although females resisted male gesturing more often during consortship than during opportunistic mating, hinting at the possibility for female choice to play a role in consortship, this did not prevent male coercion. In support of Hypothesis 2, male coercion leading to consortship, consorting males were prone to persuasive gesturing by persisting at high rates and employing aggressive behaviour when faced with possible failure.

Of the three females solicited for consortship, all were multiparous and all were resuming sexual cycles following weaning. Half of consorting females in Budongo had high-ranking sons in the community (3/6, including individuals from Hobaiter & Byrne 2012), and so may be avoiding inbreeding (Constable et al., 2001). In my study, swollen females at risk of incest were not more likely to consort than other swollen females (Hypothesis 1). Some females seemed more willing to go on consortship than others and followed the male with little overt resistance, although this was difficult to quantify due to few data on female behaviour during consortship. Overall, female communication during consortship was rare, with vocalizations expressing nervousness and gestures seeking affiliation. Harriet was the only female to cause a complete disruption by vocalizing, but she was also the female furthest away from the peri-ovulatory period, and the only female not in sexual swelling. In contrast, communication by Janie and Ruhara reflected nervousness and a need for affiliative reassurance, but little resistance. This could be explained either as compliance or as a vocalization suppression effect of long-term coercion. However, when females vocalized as though to end the consortship, Zefa and Kato both aggressed their partners and gestured for the ASO 'stop behaviour' using the agonistic gestures *object shake* and *stiff stance* in a clear warning (Hypothesis 2).

Consorting females seemed to go on consortship with high-quality males, specifically males of current or future high rank. Although I report the first known case in Budongo of a mid-ranked male going on consortship, Kato quickly rose in rank thereafter, while Zefa was the community's beta male; further, Hobaiter & Byrne (2012) reported four consortships, two each from the community's alpha male and future alpha male. Neither Zefa nor Kato were observed to go on consortship previously, and their consorting behaviour during my study was temporally associated with upheaval in the male hierarchy following an alpha male turnover: in the absence of a possessive alpha male, it seems males were free to pursue alternative mating tactics. Additionally, the unusual number of females in oestrus likely made it difficult for any alpha male contender to monopolize a given female (Hypothesis 3).

In all cases, males initiated consortship by making prolonged eye contact or leading away a female by gesturing from some distance away, as though to convince her to follow; this has also been described in Mahale (Nishida, 1997). Males gestured primarily to request females to follow them, and only rarely for sexual attention, which was the most common request during opportunistic mating. There was no evidence that males preferred to begin a display with a certain gesture, but all first gestures had an Apparently Satisfactory Outcome of 'follow me'. This reflects the primary goal of the male to get the female away from the group as quickly as possible before being discovered, and this was also the ASO in the majority of cases.

Zefa and Kato used 12 gesture types to initiate consortship, including seven agonistic gestures; Zefa used a higher proportion of agonistic gestures (Hypothesis 2, coercion). Females were successfully resistant, with no male persistence, in 24 (10%) of cases; however, females did not respond to 56% of all gestures. Still, for a male on consortship, a failed gesture (e.g. the female does not follow when asked) is still a success for the consortship on the whole if the female maintains her willingness to accompany the male on consortship. A

low rate of success might be expected of a costly mating strategy, especially as the majority of my dataset occurred as males attempted to persuade females to leave the main group.

Unlike gesturing during opportunistic mating, agonistic gestures were not more likely to be used than non-agonistic gestures; this is possibly due to small sample size as two gestures, *object shake* (agonistic) and *leaf clip* (non-agonistic), accounted for 64% of all consortship gestures. Both males were more likely to use single gestures rather than sequences, as during opportunistic mating; when using sequences, they tended to be comprised of only two gestures. *Object shake* was the most common gesture used in sequences, followed by *leaf clip* (Table 5.10). During consortship, males must continuously (albeit briefly) request females to follow; although there was a low rate of success in gesturing, males persisted regularly, typically with *object shake.* Non-gestural persistence was only aggressive (e.g. pilo-erection) in 13% of cases, indicating coercion is not as prominent during consortship as I predicted (Hypothesis 2). Although grooming as consortship initiation has been reported previously (Hobaiter & Byrne, 2012), I recorded few cases of grooming (Table 5.6), likely because most of my data were recorded during the crucial beginning stages where travelling away from the group was paramount, as opposed to later in consortship once the couple were safely out of range of the community. The urgency of this scenario is exemplified by Kato's failed consortship with Harriet, which was disrupted when Harriet repeatedly screamed and attracted the high-ranking Musa, who proceeded to aggress Harriet while Kato fled. Later in the day, Kato was severely aggressed by three dominant males, Musa, Squibs, and Hawa. It is also of note that Zefa had previously sired one of Ruhara's offspring, and that she subsequently accompanied him on multiple consecutive consortships, possibly reflecting a long-term association. Ruhara was also the only female to go on consortship for the duration of her peri-ovulatory period, which could indicate either her willingness to go on consortship or her susceptibility to long-term

coercion. None of the consortships reported here resulted in conception, although Janie and Harriet both conceived within 18 days of the consortship initiation.

CONCLUSION

In this chapter, I explored three possible motivations behind consortship. Although these hypotheses were not mutually exclusive, I found the strongest support for Hypothesis 3, consortship occurring during periods of high competition, as measured by OSR, a proxy for competition. In Budongo, consortship is best described as a rare mating strategy that occurs under unusual circumstances – in this case, during a surplus of oestrus females and upheaval of the male hierarchy. These conditions offered freedom for both males and females. Parous females, who under normal circumstances would typically be guarded by alpha males, were not actively prevented from consortship, whereas males had the opportunity to consort with high-value females. Thus, consortship communication can be summarized as a constant negotiation between two parties, where males repeatedly assert their dominance (Hypothesis 2) and females are able to thwart consortship entirely by vocalizing. Although these findings may on the surface seem contradictory, I argue that consortship reflects both the dynamic nature of competition and the balance of male and female interests that drives sexual selection. Male coercion does not exclude the possibility of female choice, and in primates the two are irrevocably entwined. Consortship demonstrates this give-and-take very nicely, as males and females negotiate the way through a risky mating strategy through the combination of gestures and vocalizations. In the end, both benefit: males ensure paternal certainty in the case of conception, while females get high-quality males – even if coercion is the indicator of quality. In the next chapter, I explore sexual selection in chimpanzee courtship displays further through a direct comparison of gestures and Operational Sex Ratio during opportunistic mating and consortship, examining whether females demonstrate a preference for certain gestures, gesture combinations, or attributes such as audibility or repetition.

Chapter 6: Male Courtship and Female Preferences

ABSTRACT

Sexual selection acts upon courtship displays in many species, but this has not been tested for in chimpanzee courtship. For instance, female preferences frequently influence male displays via inter-sexual competition, leading males across several species to demonstrate honest qualities during displays: examples include signal duration, signal rapidity, audibility, and novelty. In this chapter, I tested the hypothesis that the success of a gesture is influenced by species-general female preferences for courtship display characteristics using a GLMM. The likelihood of gesture success was predicted by whether or not a gesture was in a sequence, the interaction between parity and audibility, and the interaction between parity and bout position of the gesture. Gesture success increased when single gestures were used rather than sequences, and decreased when males used displays of multiple bouts. The use of audible gestures increased the likelihood of success with parous females, but decreased success with nulliparous females. Gesture success was not influenced by signaller rank, repetition or novelty, or whether or not a gesture was agonistic. I conclude that male chimpanzee gestural displays do not reflect species-general signals of mate quality. Instead, gesture success was predicted by effective use of intentional, meaning-based communication.

INTRODUCTION

In the previous chapters, I presented evidence that chimpanzees of both sexes use communication strategically during courtship. This claim is demonstrated by females adjusting copulation calls according to their attractiveness and male audience; males switching gesture modality following failure; males using agonistic gesture combinations to coerce uninterested females; and by males opting to pursue consortship when the ratio of males to oestrus females is in their favour. Key to all of these findings is that chimpanzee mate displays, whether male or female, exhibit considerable variability that appears to stem from an inherent flexibility in their communicative repertoire.

Communicative flexibility can be considerable. For example, across behavioural contexts (e.g. travel, play, courtship) chimpanzee gestures are reliably associated with apparently satisfactory outcomes that suggest intrinsic meaning in the gesture itself; but gestures can also be employed outside of their primary contextual meaning. Such flexibility is not well understood: in particular, it is not always clear what cues signallers use to inform their gesture choice. I previously demonstrated that males persist following failure by using

audible gestures in 87% of cases (Chapter 4, page 42). Males could then choose between 13 audible gestures from their courtship repertoire of 27 gesture types, a considerable amount of choice that remains thus far unaccounted for.

Since courtship displays in most animal species are sexually selected as outcomes of female choice (Darwin, 1859), variation in chimpanzee displays may likewise reflect female preferences in addition to being intentional signals. Females across taxa select males on the basis of honest signals of fitness, a preference that determines courtship displays in males of many species via sexual selection (Darwin ,1859). When males invest little in their offspring, as in chimpanzees, courtship displays might reflect similar female preferences. To test this hypothesis, I first review the literature on animal courtship to determine which display characteristics have been selected as honest indicators of male quality in response to female choice in other species. Following, I test whether chimpanzee courtship gesture success is likewise dependent upon these traits.

Physical vigour

One unifying theory proposes that male motor performance during courtship, indicative of physical vigour and skill, consistently provides females with a reliable measure of mate quality (Byers et al., 2010). Many human cultures, for example, incorporate dancing into their courtship rituals (Hendrie et al., 2009), and to that end dancing has been posited as a signal of high-quality traits like physical strength (Hugill, et al., 2009) and sensation-seeking (Hugill et al., 2011). One experimental study found that human females prefer male dance moves that exhibit variability and amplitude of the head and torso, and speed of the knee, which the authors interpreted as a preference for big, vigorous bodily movements that reflect male skill, health, and fitness (Neave et al., 2010); in short, dance appears to be a sexually selected trait (Kaeppler, 1978).

Physical vigour as courtship is also common throughout the animal kingdom, as is reflective in the successful courtship for many species. Male wolf spiders, *Hygrolycosa rubrofasciata*, 'drum' their abdomen on dry leaves to court females, who prefer drums of longer duration as well as a higher drum rate. For another species of wolf spider, *Schizocoza sp.*, the rate and duration of courtship signalling influences female choice (Shamble et al., 2009). The same is true both for fireflies, *Photinus consimilis*, in which females choose males with higher flash pulse rates and duration of signalling (Demary et al., 2006; Lewis & Cratsley, 2008), as well as flashes of mean length at higher rates (Branham & Greenfield, 1996). Male fiddler crabs, *Uca perplexa*, wave their dominant pincer more rapidly and with shorter intervals between waves in the presence of females, but not other males (Murai & Backwell, 2006). To my knowledge, only one study has specifically noted anything similar in primate courtship display: Hobaiter & Byrne (2012) found that chimpanzee males gestured more urgently, with frequent persistence and use of short-term audible gestures, while on consortship. As a general principle, in many species rapidity and duration of courtship displays seem to be reflective of a vigour that reflects good genetic quality.

Audibility

Audibility is another common theme in successful courtship displays, both to attract and to hold a female's attention. In insects, cicadas produce courtship songs that are preceded by a bouts of audible wing-flicks, followed by groups of 1-3 audible abdomen pulses (Sueur & Aubin, 2004). As mentioned previously, wolf spiders use both visual and audible signals during courtship (Hebets & Uetz, 1999). Many bird species also opt to combine leaps and jumps with loud displays, e.g. wing flaps or sounds produced by tail vibrations, thus including both audible and visible components (reviewed by Byers et al., 2010). For example, in addition to constructing highly decorated bowers, male satin bowerbirds, *Ptilonorhynchus*

violaceus, perform dancing displays that incorporate acoustics such as wing flaps (Borgia, 1985a; Borgia, 1985b). Among primates, female tufted capuchins, *Sapajus apella*, combine vocalizations with eyebrow raises, touch and runs, head cocking, and nuzzling (Janson, 1985; Carosi et al., 2005). Proboscis monkeys, *Nasalis larvatus*, likewise vocalize while pouting their lips in courtship (Yeager, 1990; Murai, 2006).

Novelty and repetition

The degree to which repetition is evident in chimpanzee courtship gestures is puzzling. In a review of animal courtship, Byers et al. (2010) offers a possible explanation:

> *"Indeed, one of the most striking aspects of many male mating displays is their repetitive nature. Certainly, the vigorous repetition of a display can serve other functions, such as repelling rivals, or simply increasing the likelihood of attracting a female, but to the extent that repetition is energetically costly, or to the extent that repetition exposes the signaller to danger or risk of retaliation, it becomes a way in which the quality of males can be compared."*

Thus, the energetic cost of courtship, including repetition, is thought to be the primary means by which females assess physical vigour, and to that end courtship is demonstrably costly in species such as salamanders, *Desmognathus ochrophaeus* (Bennett & Houck, 1983), and sage grouse, *Centrocercus urophasianus* (Vehrencamp et al., 1989). It seems unlikely that courtship displays of rapid, repeated signals are as reflective of physical vigour for a chimpanzee as for a salamander; after all, chimpanzees engage in many activities that are more physically strenuous than gestural courtship displays, some of which also influence their reproductive success. Although there has been no research on the energetic cost of gestural courtship displays in primates, chimpanzees engage in costly long-term aggression displays (for example: running, throwing branches, physical assault of females) as an alternate means of increasing copulation rate and paternity (Muller et al., 2011; Feldblum et al., 2014).

Females in many species also prefer varied, complex displays, suggesting that larger repertoire sizes may indeed be beneficial to males (Andersson, 1994). Female jumping

spiders, *Habronattus pugillis,* systematically prefer males who exhibit complex/novel seismic signals (Elias et al., 2006), and *Rabidosa rabida* wolf spiders adjust the complexity of their displays according to visual/seismic signalling conditions (Wilgers & Hebets, 2011). A comprehensive analysis of innovation in primates found that males exhibit a higher incidence of innovation during courtship than females (Reader & Laland, 2001). Given the general female preference for complex displays, presumably males in many species attempt to find the optimal balance between the female preference for novelty and the use of repetition as a signal of physical vigour. Although I do not focus solely on vocalization here, given chimpanzees' propensity for bodily courtship displays, it is worth noting that females in some bird species prefer males with larger vocal repertoires (Searcy, 1983; Podos et al., 1992). To my knowledge, there is no evidence that females of any species prefer larger gestural repertoires.

Coercion and parity

Threatening behaviour can be an important component of mating displays, including in chimpanzees (Goodall, 1986; Hobaiter & Byrne, 2012). Bowerbirds have notably elaborate courtship displays which can sometimes be threatening, and young females have a lower level of toleration for threatening displays than older females (Patricelli et al., 2004); strikingly, males seem to adjust the threat level of their display based on females' 'startle' reactions (Patricelli et al., 2002). Male cowbirds actually avoid high-intensity 'threat' wing displays, which have been shown experimentally to elicit less response in females than low-intensity displays (O'Loghlen & Rothstein, 2012), suggesting that threat level can thwart courtship success. It is unclear whether a similar interaction between threat level and female age/parity might be found in chimpanzees. However, as I have shown in the previous

chapters, sexual coercion does seem to play a role in courtship displays, and thus it may also influence gesture outcome.

Summary

Across taxa, a number of common themes emerge as an effective courtship display: a high frequency of signalling and signal duration; audibility; repetition; a level of threat; and to some degree, variety. Additionally, signals sometimes indicate the signaller's rank or vary with the social status of the recipient. Based on these findings, I propose that chimpanzee courtship displays, in addition to being effective, intentional requests for copulation, might incorporate some of the same principles of sexually selected communication seen in the courtship of other species. As such, courtship gesture success might potentially be influenced by species-general female preferences for indications of vigour, audibility, variety, and repetition. Female social standing, i.e. parity, may also influence female preferences.

Hypotheses and predictions

Here, I test whether gesture success is influenced by audibility, repetition, signal duration, threat level, and variety. As these factors are shown to be important in other species (discussed above), I predict that they will also influence the likelihood of gesture success in chimpanzee courtship (Hypothesis 1).

Given my finding in Chapter 3 that parous and nulliparous females can have different mating strategies, I posit that parous females' higher social status affords more choice during courtship than is possible for nulliparous females. As such, I hypothesize that the above variables (audibility, repetition, signal duration, threat level, and variety) will affect parous and nulliparous females differently (Hypothesis 2). I test both Hypothesis 1 and 2 using a GLMM of gesture success with parity set as an interaction variable.

METHODS

The data for this model comprises the gestural repertoire for courtship set forth in Chapter 4 (Opportunistic Mating), and follows the same methodology of all-day focal follows of oestrous females with all-occurrence sampling of male courtship displays (Altmann, 1974). Fourteen male signallers (Ages 10-23) and seventeen female recipients (10 parous, 7 nulliparous) were included in the model.

Terms

As in the previous chapters, a gesture is defined as a "discrete, mechanically ineffective movement" (Hobaiter & Byrne, 2011a). A *courtship display* is any behaviour toward directed toward an oestrous female, and accompanied by a penile erection. A *sequence* is a series of gestures with <1 second between them, while a *bout* is multiple gestures separated by >1 second. I defined gestures as *long duration* if they occurred in a sequence (i.e. rapid signalling) or if the display consisted of multiple bouts. Gestures were *audible* if the action produced a sound, as in *leaf clip*. Following the first use of a gesture, I marked subsequent uses of that gesture within the same display as *repetition*; if not a repeated gesture, gestures were considered *novel* to the display. I included both male rank and whether or not a gesture was *agonistic* to represent coercion. In this chapter, I did not consider any gestures to be partially successful; here, successful gestures lead to copulation and unsuccessful gestures did not.

Statistical analysis

Using a generalized linear mixed model with binomial error structure and logit link function (Bolker et al., 2009), I tested the factors that affected the probability of a male courtship gesture leading to copulation. Predictor variables included: male signaller rank (1-14, where 1 is high-ranking), female recipient parity (binary, parous/nulliparous), whether a

gesture occurred as part of a sequence (binary, yes/no), the position of a gesture within a bout (continuous, 1-6), repetition (binary, yes/no), audible (binary, yes/no), and agonistic (binary, yes/no). I set gesture type, signaller identity, and recipient identity as random effect variables. Parity was set as a two-way interaction with all other variables, given prior evidence that females respond to different motivations during courtship (Chapter 3). Four interaction terms were removed from the final model because they did not improve model fit (LRT, all p >0.1).

No variables were transformed and the results comprise the complete data set. The highest variance inflation factor was 1.17, indicating no collinearity (VIF: Fox & Weisberg, 2011). I tested the full model against a null model comprising the intercept and random effects of gesture type, signaller identity, and recipient identity (LRT: Quinn & Keough, 2002). All statistical analyses were conducted using R (version 3.1.2; R Core Team, 2014) and the lme 4 package (version 1.0-7; Bates et al., 2014).

RESULTS

The full model was significant compared to the null model (LRT: χ^2_{11}=32.00, p <0.001; Table 5.1). Three factors significantly influenced the outcome of a gesture: whether the gesture occurred in a sequence, the interaction between parity and audibility, and the interaction between parity and bout position. No other factors approached significance, and parity did not significantly interact with any other variable.

Hypothesis 1: What influences gesture success?

Sequence and bout position

Males used single gestures rather than sequences in 357/847 gestures. For all male signallers, single gestures were more successful than gestures in sequences (Fig. 6.1). Single gestures had a success likelihood of 25%, which dropped to just 13% for gestures in

sequences. This was true for both parous and nulliparous females. There was also a significant interaction between parity and bout position on the probability of success: gestures occurring late in a display (e.g. in the fifth bout of a display) were less likely to be successful, particularly when directed at parous females, for whom the likelihood of success was nearly zero (Fig. 6.2). Comparatively, gestures directed toward nulliparous females were much less successful, with only a slight decrease in the probability of success for later bouts as compared to parous females.
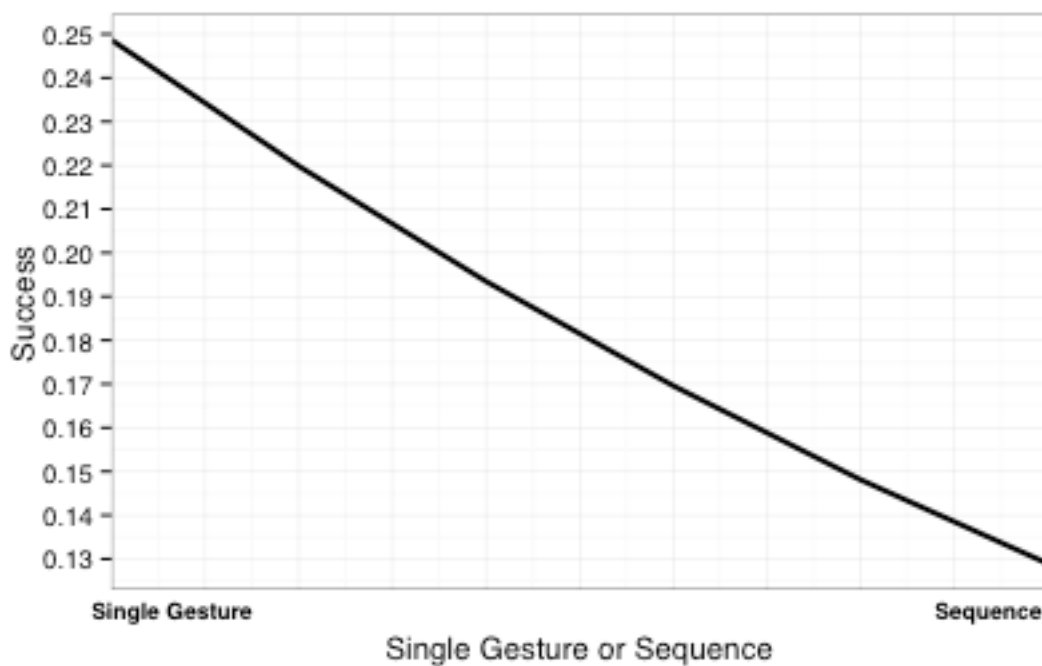
Fig. 6.1: The rate of success for single gestures or sequences
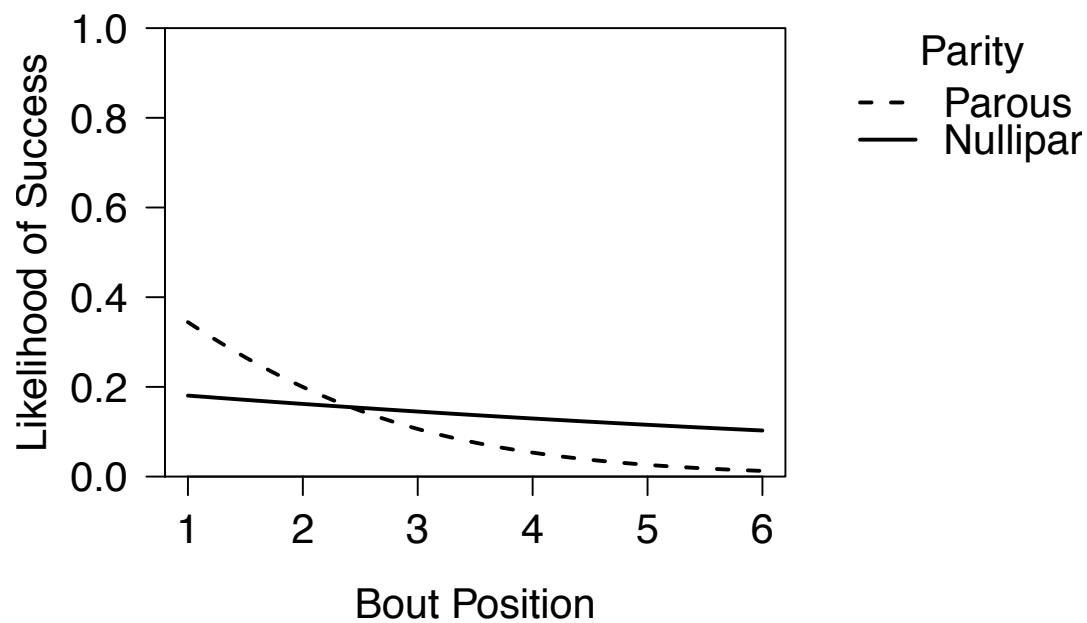
Fig. 6.2: The interaction between parity and bout position in the likelihood of success.

Hypothesis 1 & 2: Parous and nulliparous females respond differently to audibility

There was a significant interaction between parity and audibility in the probability of success, (LRT: $\chi^2_1=32.00$, $p <0.04$). The interaction reflects the fact that audibility had a different effect on success for parous and nulliparous females. For nulliparous females, the likelihood of success decreased with audible gestures, while the likelihood of success increased with audibility for parous females (Fig. 6.3).
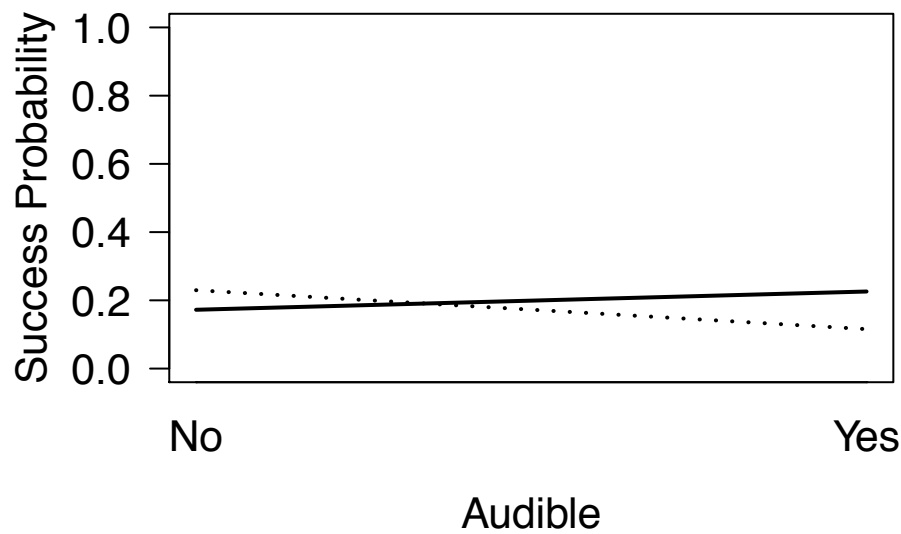
Fig. 6.3: The interaction between parity and audibility in the probability of success. Dotted line = nulliparous, solid line = parous. Silent gestures = 0, audible gestures = 1.

Table 6.1: Results of GLMM model testing factors affecting the likelihood of gesture success during courtship

	Estimate	**SE**	**Z**	**P**
Parity	-0.358	0.421		
Male rank	0.019	0.047	0.408	0.684
Repetition	0.342	0.329	1.039	0.299
Agonistic	0.096	0.528	0.182	0.856
Audible	-0.825	0.403		
Bout position	-0.131	0.169		
Sequence	-0.804	0.295	-2.724	**0.006**
IA parity:audible	1.162	0.568	2.044	**0.041**
IA parity:boutposition	-0.612	0.303	-2.019	**0.043**

IA = interaction.

DISCUSSION

Chimpanzee courtship gestures do not seem to reflect female preferences for honest indicators of male quality, as in many animal displays. The factors that predicted whether gestures led to copulation were instead characteristics of effective gesturing, supporting Hypothesis 1: use of single gestures rather than series, effective use of bouts, and use of audible gestures. Thus it is evidently the intended meaning of the gestural communication

itself, when effectively conveyed, that convinces females to accept males as mating partners, rather than proximal cues to male quality. However, parous and nulliparous females did respond differently to bout position and audibility of a gesture, providing support to Hypothesis 2. Parous females were more likely to respond favourably within the first bout of a display, while the likelihood of success after four bouts was nearly zero. By contrast, gestures were similarly successful for nulliparous females no matter the bout position, and only slightly less likely to be successful in a later bout. Audible gestures increased the likelihood of success for parous females, but decreased the likelihood of success for nulliparous females.

As discussed previously, gestural courtship displays are unlikely to be a physically costly for chimpanzees, and therefore do not fit the traditional definition of an honest signal. Here, I hypothesized that courtship displays may nonetheless be acted upon by inter-sexual selection, for example with varied, lengthy displays that demonstrate cognitive complexity and directly influence mating opportunities. What seems to be the case, as was hinted in previous chapters, is that simple, effective gesturing is what leads to courtship success. In some cases, the intentional, meaning-based communication of chimpanzees means that some common themes of signalling in other species – e.g. rapid signalling – are not reflective of skill or effectiveness, but rather ineptitude. Young chimpanzees in particular use rapid gestural sequences as a means of trial and error (Hobaiter & Byrne, 2011b). Thus in courtship, single gestures were far more effective than sequences for all females (Fig. 6.1).

Effective gesturing may also explain the interactions with parity. Parous females, who are more desirable for males, were nearly twice as likely to copulate within the first bout, regardless of the male signaller (Fig. 3.1). This suggests that if males do not successfully communicate their interest within the first few gestures, parous females are unlikely to respond favourably. This may also reflect male long-term coercion such that parous females,

eager to avoid aggression, respond more quickly than nulliparous females. Nulliparous females, who have less opportunity to discriminate between male suitors due to their lower mate value, and who are less likely to be victims of sexual coercion, exhibit roughly the same favourable response rate across all bouts. Further, the use of audible gestures increased males' success with parous females, likely reflecting signallers' use of audible gestures when recipients are not attending (Hobaiter & Byrne, 2011a). Audible gestures were less successful with nulliparous females. Although this is difficult to interpret, it is possible this is a fear effect indicative of the overlap between agonistic and audible gestures (Chapter 4). Alternatively, this may reflect immigrants' lower level of acquaintance with signallers.

Neither rank nor threat in the form of agonistic gestures predicted the likelihood of gestural displays leading to copulation. This is surprising, given ample evidence that high-ranking males sire more offspring than low-ranking males (Constable et al., 2001; Newton-Fisher et al., 2010), and that coercion leads directly to increased paternity (Feldblum et al., 2014). In Chapter 4, I demonstrated that high-ranking males had a higher proportion of agonistic gestures in their repertoire, and that they employed agonistic gestures more often than low-ranking males. Since intra-sexual selection relies upon the hypothesis that some individuals incur a reproductive advantage by producing certain honest signals, I predicted that high-ranking males' use of agonistic gestures might influence gesture success overall. This was not the case: instead, effective gesturing met with success regardless of the signaller rank. Still, the idea of a 'cognitively costly' display is one worth further exploring. While the model here examined the traits held constant across signallers, individual variation between males may illuminate the pressures of sexual selection further. For example, gesture success is likely influenced by long-term sexual coercion within pairs. Were that the case, I would expect sequences of agonistic gestures to lead to copulation, especially given the trend for agonistic gestures directed toward parous females to lead to copulation.

CONCLUSION

The model in this chapter illuminated the extent to which communication skills influence gestural courtship success over rank or coercion. Males succeeded in copulating with a female when they produced the appropriate gestures as a single gesture, an audible gesture, or within the first few bouts of a display. In contrast, long displays consisting of sequences and multiple bouts were unsuccessful. Parous females were generally more discriminatory than nulliparous females; this is both indicative of their social standing and attractiveness, and indicative of the level of coercion they experience. Overall, it is clear that successful communication during courtship influences male mating success, but the degree to which it mediates variance in reproductive success between males remains unclear.

Chapter 7: General Discussion

INTRODUCTION

My primary aim in this thesis was to investigate wild chimpanzee communicative strategies during courtship. Previous studies have focused on compiling behavioural ethograms (Tutin & McGrew, 1973; Nishida 1997), or on a small subset of courtship signals (Hobaiter & Byrne, 2014; Roberts & Roberts 2015). More generally, research on chimpanzee sexual behaviour has rarely looked at intentional communication, but instead focused on a handful of courtship tactics, such as male long-term aggression (Muller et al., 2006; Muller et al., 2011) or female proceptive behaviour (Stumpf et al., 2005; Stumpf et al. 2006), despite every indication across great ape species that intentional communication is important in courtship (Tutin, 1979; Nishida, 1997; Townsend et al. 2008; Clay et al. 2011; Hobaiter & Byrne, 2012; Genty & Zuberbühler 2014). On these grounds, I undertook an examination of both male and female communication in the Sonso chimpanzee community in the Budongo forest, Uganda.

SUMMARY OF FINDINGS

Female communication

Females rarely gestured during courtship, and their communication was largely limited to vocalizations during copulation. Calling reflected males' preference for parous females, in that nulliparous females called more frequently. All females had a higher likelihood of calling when mating with a high-ranked partner, a distance that increased with high-ranking males, and nulliparous females were more than twice as likely as parous females to call during long copulations (Figure 3.1). There was an interaction between parity and male audience that reflected an underlying difference in biological strategy: parous females called more frequently in the presence of more high-ranking males, while nulliparous females called less. I interpreted the causal mechanism of this difference as suppression:

based on fear or nervousness of high-ranking males, but it could also reflect a suppression effect in the presence of a number of high-ranking females, which has previously been found in this community, but which I was unable to test. All females were slightly more likely to call when there were other oestrous females in the community. I found no evidence that copulation calling resulted in the female being mated by a higher-ranking male in the subsequent copulation, or that copulation calling increased male party size. Party size was larger for parous females, regardless of whether they called or not, possibly explaining their low rate of calling. Intriguingly, both effects are counter to the well-established interpretation of copulation as inciting sperm competition.

Male communication during opportunistic mating

Opportunistic mating is a mating tactic by which males of all ranks are able to mate with oestrous females. Males did not use vocal behaviour during opportunistic mating, instead relying upon frequent gesturing and other signals, such as gaze. Prior to gestural displays, males sometimes purposefully approach a female with a penile erection and engage in non-gestural behaviour, such as making prolonged eye contact. I found that at Budongo this was equally successful for high- and low-ranking males. If this tactic did not entice a female, males typically continued to solicit the female using gestures.

Males used 26 gesture types to signal their interest in swollen females, none of which were idiosyncratic to particular individuals. However, males employed only a small subset of their courtship repertoire regularly, with *leaf clip*, *genital offer*, *object shake*, and *rock* accounting for nearly 80% of all gesturing. Fifteen gestures in the courtship repertoire are gestures also used during aggression displays. Gestures were successful in leading to copulation regardless of the signaller's rank; and gestures were successful whether the female recipient was parous or nulliparous.

Courtship displays were characterized by a high rate of persistence, with high- and low-ranking males persisted at equal rates. Following an unsuccessful gesture, males persisted in 84% of cases. All males were more likely to use audible gestures as persistence, even though silent gestures were more successful overall; presumably this functioned to attract the attention of a non-attending female. Male strategies differed, however, when it came to the use of agonistic gestures. High-ranking males had a higher proportion of agonistic gestures in their repertoire, and also employed agonistic gestures more often than low-ranking males. Regardless of a male's strategy, however, females were only able to reject males following an approach in less than 20% of cases, and following the first gesture in 5% of cases.

Male gesture during consortship

In Budongo, consortship is an uncommon and highly risky mating strategy (Hobaiter & Byrne, 2012). I recorded three successful consortships and one unsuccessful attempt at consortship by two males, Kato and Zefa, involving three females, Janie, Harriet, and Ruhara who went on consortship twice. All three consorting females were parous, and all were recently cycling following lactational amenorrhoea. Males initiated consortship at various stages of female swelling; three consortships included part of the peri-ovulatory period, and the fourth consortship likely included at least one day of the peri-ovulatory period. Although none resulted in pregnancy, both Janie and Harriet conceived in the cycle following their consortship. All consortships occurred when there were a high number of swollen females in the community.

Males used 12 gesture types to solicit females for consortship, including seven agonistic gestures; gestures were frequently unsuccessful (56%; 141/243). Zefa, the higher-ranking of the two males, had a higher proportion of agonistic gestures in his repertoire. Despite this, agonistic and non-agonistic gestures were used at equal rates. However, males

persisted following a failed gesture in nearly 100% of cases, occasionally accompanying their persistence with aggressive behaviour (pilo-erection, charging display).

Leaf clip and *object shake* were the most common gestures, accounting for over 60% of gesturing. Kato and Zefa used single gestures more than sequences, particularly when their intended meaning (ASO) was 'follow me' (140/196 cases). In an analysis of fifteen gesture sequences, all sequences included object manipulation in the form of *object shake* or *leaf clip*. All female gestures had an outcome of 'affiliation'. Female vocalizations, which included pant-grunts, whimpers, and screams, were typically produced in apparent fear following the pant-hoots of the larger community. Harriet produced the majority of these vocalizations, eventually causing other males to interrupt the consortship and severely aggress both consorting individuals.

Female preferences and courtship displays

Contrary to courtship in many species, females showed no sign of mating with males based on signals that were proximate cues of male quality. Instead, gestures led to copulation when they possessed characteristics that have been found associated with effectiveness of communication: for example, the use of single gestures and audible gestures. There were some differences in likelihood of copulation based on the parity of the female recipient. Single gestures were more likely to lead to copulation than sequences regardless of female parity. For parous females, audible gestures increased the likelihood of success, while the opposite was true for nulliparous females. Further, while parous females were nearly twice as likely to copulate with a male within the first bout, nulliparous females were only slightly more likely to copulate within the first bout.

INTERPRETATION OF FINDINGS

From the above results, I now address three overarching themes: female courtship strategies, male courtship strategies, and what courtship tells us about chimpanzee communication and the role of sexual selection.

What strategies do females use during courtship?

There are two predominant theories of female chimpanzee mating strategies. The first argues that females are not victims of male coercion, but assert their own mate choice for preferred males and successfully reject unwanted males (Stumpf & Boesch, 2005; Stumpf & Boesch, 2006; Pieta, 2008). The second states that females have no choice, and are bound by male coercion; and further, that mating with coercive males represents the optimal outcome for females (Muller et al., 2006; Muller et al., 2011; Feldblum et al., 2014). Whether females have choice or are bound by coercion seems to vary by community. A recent hypothesis that distinguishes between 'egalitarian' and 'despotic' hierarchies suggests that mate choice may be determined by the steepness of power differentials between males: in egalitarian communities, a single male cannot monopolize resources because other males are powerful enough to keep him in check (Kaburu & Newton-Fisher 2015a, 2015b). In despotic communities, such as Budongo, one male can monopolize resources and other males have less power to challenge him (Kaburu & Newton-Fisher, 2015a). My work shows that, in a similar manner, courting females in Budongo have different mating strategies based on parity status and the level of female competition.

Parous females

Males prefer to mate with older, parous females, a behaviour that seems to be adaptive because such females are proven mothers and are demonstrably fecund (Muller et al., 2006). I found that, while all females were more likely to copulation call when mating

with a high-ranking male, parous females were especially likely to call in the presence of multiple high-ranking males. One ultimate explanation for this behaviour is that the parous females incite sperm competition when the potential genetic payoff is high. Moreover, advertising in the presence of high-ranking males increases the likelihood of paternity confusion as high-ranking males father more offspring (Constable et al., 2001), and potentially reduces the risk of infanticide (Townsend et al., 2007).

In this study, parous females were the only females to be taken on consortships, which all took place during a period of high female competition (p. 67, Table 5.12). In eight consortships recorded at Budongo, including those presented here, only one female was nulliparous, and she later died from injuries associated with resisting consortship (female Lola: Hobaiter, 2010; Hobaiter & Byrne, 2012). Parous females, on the other hand, seem more willing to participate in consortship. Although male gesturing was less successful during consortship than during opportunistic mating, parous females nonetheless remained with their consort. The notable exception to this was Harriet, who screamed until nearby males interrupted the consortship, attacking both her and the consorting male Kato. Harriet was not swollen at the time Kato had initiated consortship; whether that can account for her resistance, or whether she found Kato an unsuitable mate in some way, is not certain. However, given that Harriet conceived 18 days later, it seems likely that she was rejecting Kato, a mid-ranked male at the time. Although consorting females did not always respond to males' gestural requests for the outcome 'follow me', they did gesture and vocalize seeking affiliation. However, this occurred because males in both studies attacked females who vocalized loudly, thereby risking discovery from other individuals. The sum of these findings suggests that for consorting females in Budongo, high-ranking, coercive males are the most likely partners.

Parous females also differed from nulliparous females in their response to male gestural displays. They were most likely to respond to males in the first bout of a display; following that, there was little likelihood of mating. Parous females may respond more quickly to males in order to avoid coercion, as indicated by the trend for agonistic gestures to be more successful with parous females than with nulliparous females. Alternatively, parous females may simply be responding to effective gesturing. Since there was not an interaction between parity and rank in the likelihood of gesture success, responses by parous females does seem primarily governed by the effectiveness of gesturing. Consistent with this hypothesis, males who used audible gestures rather than silent gestures were more likely to be successful with parous females, likely because they were responding appropriately to the recipient's attention state. However, females were rarely able to reject males outright, and were met with repeated persistence during both opportunistic mating and consortship.

Overall, parous females do seem to have some choice. Females actively incite competition among high-ranking males by copulation calling; although they seem generally willing to go on consortships, they are able to reject a mid-ranked male, as in the case of Harriet and Kato; finally, parous females respond to effective gesturing, regardless of signaller rank.

Nulliparous females

Nulliparous females are less preferred than parous females because they have long periods of sub-fecundity after menarche, are not yet proven mothers, and have high rates of infant mortality (Muller et al., 2006). Lack of male interest leads to nulliparous females being "insatiable" in their attempts to mate (Goodall, 1986). Accordingly, I found that nulliparous females called with high-ranking males, called more frequently than parous females overall, and called at an especially high rate during copulations of long duration, thereby inciting sperm competition. However, nulliparous females decreased their likelihood of calling in the

presence of multiple high-ranking males, which may be due to fear of dominant males, or possibly a fear of dominant females when in large parties, as has been found previously (Townsend et al., 2008).

Similarly, nulliparous females responded favourably to gesturing males across all bouts, and were only slightly less likely to copulate following a gesture in a later bout. Again, this appears likely to reflect the ultimate explanation of inciting sperm competition. They were also more likely to respond to silent gestures rather than audible gestures. The ultimate reason for this is less clear, but a proximal explanation may be fear of the signaller, especially in the case of unfamiliarity males, as in the case of immigrant females.

Nulliparous females seem to exert less choice than parous females. This is true not because they are bound by male coercion, but because they have fewer options for suitors due to high-ranking males seeking out parous females. Since nulliparous females cannot afford to discriminate between suitable mates, inciting competition is their primary mating strategy.

What strategies do males use during courtship?

The literature on male mating strategy centres on male coerciveness and the importance of rank. For example, high-ranking males father more offspring (Constable et al. 2001; Newton-Fisher et al., 2010); females present more to coercive males (Muller et al., 2006); and long-term coercion increases male paternity (Feldblum et al., 2014). Early behavioural observations of courtship hint that males may use coercion during courtship itself, a tactic that increases with rank and experience (Tutin, 1979; Goodall, 1986; Nishida, 1997). Further, communication tactics seems to differ between different opportunistic mating and consortship (Hobaiter & Byrne, 2012).

Opportunistic mating

In my study, male rank did not influence whether a gesture led to copulation, but did influence gesture choice. High-ranking males had a higher proportion of agonistic gestures in their core repertoire, and employed agonistic gestures more than low-ranking males overall. There was a high rate of persistence for all males, and the majority of persistent gestures were agonistic. That males are both persistent and prone to apparent frustration when producing displays is an indication that gestural courtship is yet another venue where males coerce females, but coercion did not seem to be males' sole strategy.

Male gestural courtship also reflected previous findings on efficient, intentional chimpanzee gestural communication. For example, single gestures were more effective than sequences. Males adjusted their bodily state according to a female's attention state prior to beginning a courtship display, and used audible gestures when recipients were not attending.

Males also used non-gestural initiation tactics, such as purposefully approaching a female, aggression, or grooming. However, these tactics were rarely successful in leading to copulation, and males frequently followed up such a lack of success by gesturing. Approach was the most common non-gestural tactic used, and both low- and high-ranking males approached females equally, with no difference in the success rate of approach between males of different ranks.

Consortship

It is difficult to draw broad conclusions on consortship based on a sample size of four observed consortships. Combining my findings with those of Hobaiter & Byrne (2012), it is clear that Budongo males predominantly solicit parous females for consortship. Only one nulliparous female has been recorded on consortship, in stark contrast to Gombe, where

nulliparous females regularly go on consortship (Wroblewski et al., 2009). None of the eight observed consortships resulted in conception.

Gesturing during consortship is notably persistent. As Hobaiter & Byrne (2012) documented, males gesture frequently and urgently, most often for the ASO 'follow me'. This repeated, persistent request is made most often by the gestures *object shake* and *leaf clip*. Rather than wait attentively for females to respond to a request, males typically gesture for the ASO 'follow me', continue moving, and then gesture 'follow me' again. Importantly, the primary meaning of *leaf clip* is 'sexual attention', suggesting that a combination of gesture meaning and leading away may offer a contextual clue to females indicating male interest in consortship.

In both studies, males attacked females who vocalized too loudly, but frequently followed aggression with the ASO 'affiliate me', for example by employing *bump rump*, a mutual affiliation gesture where both individuals touch rumps. I interpreted the cycle of aggression and affiliation as a negotiation between males and females. Females can and do completely interrupt a consortship by screaming and attracting the attention of other males, implying an element of female choice. This occurred for Kato and Harriet's consortship, and Kato was chased and beaten by the interrupting males. On the other hand, there is also a real risk for females who attempt to terminate consortship. A consorting nulliparous female, Lola, repeatedly screamed but failed to attract other males, and eventually died from the injuries caused by her male consort (Hobaiter & Byrne, 2012).

What does courtship tells us about chimpanzee communication?

This study is the first systematic examination of wild chimpanzee intentional gestural communication in courtship, and the first to distinguish between parous and nulliparous

female mating tactics. Here, I discuss the importance of my findings to the broader topic of communication.

Vocal communication

Females produced vocalizations during courtship in the form of copulation calls, screams, pant-grunts, and whimpers. Males, on the other hand, never vocalized during consortship. This may be a consequence of the benefit to a male in concealing possible paternity from other males. Female copulation calls and screams may be due to the benefits of advertising their sexual receptivity and thereby inciting sperm competition: in this study, both parous and nulliparous females used copulation calls. Additionally, I recorded one case of a parous female screaming and thus thwarting a consortship between her and a single male by attracting other males.

The findings presented in Chapter 3 are the first demonstration that females adjust their copulation calling strategies according to their parity. Based on this finding, future studies should consider the influence of parity on other vocalizations, such as pant-hoots, which may also reflect parous and nulliparous females' differing strategies. Further, chimpanzees adjust victim screams strategically based on male audience (Slocombe & Zuberbühler, 2007); it is likewise possible that this may differ for parous and nulliparous females.

Gestural communication

Great apes are the only animals known to gesture intentionally, making their communication systems critical to our understanding of the evolution of language. Chimpanzee gesture is particularly important because males use gestural courtship displays to influence their reproductive success.

A key finding of my thesis is that gestures are successful in leading to copulation regardless of signaller rank, and that such success is dependent upon effective use of bouts, sequences, and audible gestures. Whether a gesture leads to copulation is not tied to proximate traits of male quality, but rather to female attractiveness; males can thus directly influence their probability of mating with a parous female by succinctly and audibly soliciting copulation. This is important for low-ranking males, as it has been amply demonstrated that parous females otherwise assess male quality through rank (Goodall, 1986) and present more frequently to males who coerce them in the long-term (Muller et al., 2006; Feldblum et al., 2014). Gestural courtship therefore offers an opportunity for low-ranking males to improve their chances for reproductive success with valued females.

The recent finding that chimpanzee gestures typically have more than one meaning, in the sense of apparently satisfactory outcomes for signallers, raised the question of how chimpanzees make a specific meaning clear. I have shown that males utilized 27 gesture types of their entire repertoire of 66 gestures (Hobaiter & Byrne, 2011a) solely to request sexual attention, but that four gesture types made up the majority of solicitations. In opportunistic courtship, the meaning of a gesture was clear from contextual cues: a male with a penile erection solicited a swollen female, two visual cues indicating courtship. However, this was not the case for consortship, where a male without an erection could solicit a female with or without a swelling to follow him. The majority of consortship sequences included *leaf clip*, which has a primary meaning of 'sexual attention', or *object shake*, which has a primary meaning of 'move away' and a secondary meaning of 'sexual attention' (Hobaiter & Byrne, 2014). The most common sequence in consortship was *object shake + leaf clip*, which might be considered therefore to have a combined meaning of 'move away/sexual attention + sexual attention'. It may thus be possible that females surmise a request for sexual attention from

males' frequent use of *leaf clip* during consortship, and that the lack of erection may cue them into the consortship context.

CONCLUSION

Despite the importance of courtship for reproductive success in many species, research on chimpanzee courtship communication has been limited to two studies on copulation calls (Hauser, 1990; Townsend et al., 2007) and one on intentional gesturing during consortship (Hobaiter & Byrne, 2012). I addressed this issue by undertaking the study of female and male courtship in a wild chimpanzee population, the Sonso community of the Budongo Forest. Using the predominant theories of female choice and male coercion, I explored (1) whether male and female courtship strategies differed according to social status, (2) which vocal and gestural courtship tactics were successful, and (3) how communication differed by mating strategy.

My results reveal that male and female chimpanzees adjust their communication tactically to attract high-value mates. Females do so according to parity. While nulliparous females are somewhat bound to any mating opportunities that arise, parous females show a clear preference for effective gesturers, and target their copulation calls when the payoff is high. Male gesturing is less divided by social status, because effective persistence seems to be the primary strategy for males of all ranks, leaving little room for female rejection. However, high-ranking males employ more agonistic gestures than low-ranking males during opportunistic mating. In Budongo, female choice is possible, in the rare cases of rejecting consortship or preferring effective gesturers, but in general it seems likely that mating with the most effectively coercive males is the optimum for parous females, because females called in such a way as to incite sperm competition. In addition to providing a novel perspective on the role social status plays in mediating courtship success, I have also shown

that male chimpanzees utilize a large portion of their gestural repertoire to effectively communicate a single meaning. Courtship communication is, and can continue to be, a rich context for the study of signaller motivations, including the proximate and ultimate explanations underlying chimpanzee mating strategy.

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APPENDIX I: SONSO COMMUNITY CHIMPANZEES

FEMALES & THEIR OFFSPRING

AN   **Anna** (90 ± 1 yr): crooked swelling, thin-bodied, resembles PS (first seen early 2003, named March 2006,   formerly Stranger F)
>*??*   *Unnamed/unsexed infant (23 Oct 13 ± 2 weeks – 31 Oct 13 AN seen without baby)*

BH   Bahati (Dec 94 ± 1 wk): *last seen in August 2009 (emigrated to the Waibira community)* upturned nose, pointy head   like mother, puckered lips, small swelling when in estrous

BN   *Banura (in or before 68): Last seen in June 07* .club right foot, balding, pointed ears (~ 38 yrs or older) (first identified Oct 20th 1993)
>*ZF*   **Zefa** ♂ (82 ± 6 mo) adult, see below
>*SH*   *Shida ♀ (90 ± 1 yr): disappeared Sep 04*
>*BT*   Beti ♀ (1 Oct 96 ± 3 days): juvenile (*most likely emigrated, last   seen around 2009*
>*BE*   *Ben ♂ (13 Sep 01 ± 3 days – 01)*
>*BD*   *Banda ♀ (23 Oct 04 – 7 Nov 05)*

BC   **Beatrice** (76 ± 5 yrs): right hand missing, broad ears, slit in left ear, short fingers (3rd and 4th on left hand) (first seen May 21st 2004, named   April 2006, formerly Stranger H)
>SQ   **Squibs** ♂ (91 ± 1 yr) son of Beatrice (confirmation DNA sequencing March 2011), see below
>BG   **Birungi** ♀(March 04 ± 4 months)
>*BA*   Bakata ♂ *(30 Apr 13± 2 weeks –06 Sept 13 BC seen without BA)*

BW   *Bwera (in or before 75)* (first identified April 28th 1992) (last seen with infant Biso August 9th 1994)
>*BI*   *Biso ♂ (90 ± 1 yr – 94)*

CL   Clea (86 ± 2 yrs): dark brown face w/ black circles under the eyes, slim, small head (~ 20 yrs) (first identified March 21st   1997 and named August 28th 1997). *Not seen since 2006.*
>*CT*   Clint ♂(27 Apr 02 ± 2 days)

CC   **Coco** (00 ± 1 yr): dark face, resembling KN, index toe of the left foot is short (first seen January 17th 2014, named October 2nd 2014, formerly Stranger 1)

EM   *Emma (Sep 91 ± 2 yrs):* light spotty face, immigrated in 97, disappeared Jan 03

FL   **Flora** (in or before 79): missing RH from wrist, slit in right ear, splayed toes on right foot (first seen Jan 03 with FD and FK, formerly Stranger C))
>*FD*   **Fred** ♂ (94 ± 1 yr), adult, see below
>*FK*   **Frank** ♂ (99 ± 1 yr): subadult, see below
>??   *Unnamed/unsexed infant (04 Jun 05 ± 2 weeks – 25 July 05)*
>*FA*   **Faida** ♀ (Oct 06 ± 1 month)
>*FH*   **Faith** ♀ (27 Feb 13 ± 1 day)

GL   **Gladys** (76 ± 5 yrs): long body, size of Janie, wide vagina when swollen, white beard around the mouth, nervous. (~35 yrs) (first seen in Easter 2004 with juvenile GN, named in June 2006, formerly Stranger G)
>*GN*   **Gina** ♀ (96 ± 2 yrs), subadult
>GR   **Goria** ♀ (06 ± *1 yr*)
>GF   **Geoffrey** ♂ (09 June 13 ± 3 weeks)

HT   **Harriet** (in or before 78): black face, left ear slit, wrinkled cheeks, small bald patch, nervous, (first seen with infant HW Sept. 11th 1996)

        HW   **Hawa** ♂ (93 ± 1 yr), adult, see below

        HL   **Helen** ♀ (Feb 01 ± 3 wks), subadult, hooked left hand (snare) last seen April 13: probably migrated

        HY   **Honey** ♀ (4 Oct 05 ± 3 days), juvenile

        HR   **Heri** ♀ (7 Nov 09 ± ? wks)

        HI   **Harmoni** ♀ (26 Oct 13 ± 1 day)

IN   **Irene** (99± 1 yr): black spots on the edge of the swelling when in estrous, dark and wrinkled face (like Juliet), crew cut" hairstyle (like Kwera) (first seen May 2012, named May 2013, formerly Stranger 3)

JN   **Janie** (84 ± 1 yr): black face, crescent-cut in right ear, long tufts of hairs on lower jaw, droopy eyes (immigrated Sept. 28th 1995)

        JT   Janet ♀ (1 Oct 99 ± 3 days): sub-adult, bold

        ??   *Unnamed ♂ infant (12 Jan 05 ± 1 week – 24 Jan 05)*

        JS   **James** ♂ (4 May 06 ± 1 month), juvenile, brown long face with spots, black around the eyes, lost 4 fingers on right hand (only thumb left)

        ??   *Unnamed ♀ infant (03 Nov 12 ± 1 day – 09-10 Nov 12, infanticide)*

        ??   *Unnamed/unsexed infant (02 Jan 14 ± 4 days – 04 Jan 14 JN seen without baby)*

JL   **Juliet** (90 ± 1 yr): left hand in permanent fist (snare injury), very large swelling when in full estrous (first seen Jan 02, named Jan 03, formerly Stranger D2)

        ??   *Unnamed ♂ infant (13 Aug 09 ± 2 weeks – 13 Aug 09) Infanticide by NK, NB and NR*

        JB   **Jacob** ♂ *(2 March 2011 ± 10 days)*

KL   **Kalema** (79 ± 1 yr): hooked right hand w/o hair, pointy head, brown hairs below bald patch, grey beard (first identified April 28th 1992)

        ??   *Unnamed/unsexed infant (20 Dec 1993 ± 1 week – Jan 1994)*

        BH   Bahati ♀ (Dec 94 ± 1 wk): upturned nose, pointy heads like   mother; *(emigrated toWaibira)*

        KM   Kumi ♀ (17 Sep 00 ± 2 days): pointy head, small for age, subadult

        ??   *Unnamed/unsexed infant (22 Sept 05 ± 7 days – 30 Sept 05)*

           KC   **Klauce** ♂ (5 Sept 06 ± 2 days), juvenile, very broad ears, clear eyes

        ??   *Unnamed ♀ infant (11-12 Sept 12 exact – 13 Sept 12)*

        ??   *Unnamed ♂infant (26 Jul 13 ± 1 day –killed by FK on the 30th Sept 13, infanticide)*

        ??   Unnamed ♂ infant (07 Sept 14, exact)

KY   **Kewaya** (83 ± 1 yr): totally twisted right hand, close set eyes, big brow ridge (first identified April 28th, 1992)

        KA   **Katia** ♀ (30 Dec 98, exact): big ears, confident; brown face, subadult

        ??   *Unnamed/unsexed infant (July 05 ± 2 weeks – 25 Nov ± 3 weeks)*

        KX   **Kox** ♀ (7 April 07, +/- 2 months)

        ??   *Unnamed ♀ infant (19 Sept 13 ± 1day – 12 Oct 13 KY seen without baby)*

        ??   *Unnamed/unsexed infant (26 Nov ± 5 days)*

KG   **Kigere** (in or before 1976): missing right foot (first identified March 11th, 1992), slit on middle of left ear

        KD   *Kadogo ♂ (90 ± 6mo – 99)*

        ??   *Un-named infant (97, born prematurely and dead)*

KE   **Keti** ♀ (1 Sep 98 ± 1 wk) , subadult

KI   **Kuki** ♀(16 Sep 03 ± 3 days), juvenile

KP   **Kaspa** ♀ (28 Oct 08 ± 1 wk)

KU   **Kutu** (in or before 79): top of left ear slit horizontally, high up (first identified August 8th, 1992)

        KT   **Kato** ♂ (Sep 93 ± 1 mo): adult, see below

        KN   **Kana** ♀ (29 Oct 98 ± 1 day): oval-shaped eyes, black marking under left eye, hooked left hand (snare injury), right heel does not touch the ground (stiff after snare injury), subadult

        KS   **Kasigwa** ♂(15 Aug 03 ± 2 wks): prominent bald patch, juvenile

        KH   **Kathy** ♀ (28 Jul 08 ± 3 days)

        ??   *unnamed/unsexed infant (14-15 Feb 2013 exact – 17-18 Feb 2013)*

        KF   **Kefa** ♂ (26th march 2014 exact)

KW   **Kwera** (in or before 81): long face, "crew cut" hair style, slim, large ears (first identified August 5th, 1992)

        KZ   **Kwezi** ♂ (14 Jan 95 ± 2 wks): adult, see below

        KR   **Karo** ♀ (1 Nov 01 ± 1 day), black face, bold behavior, juvenile

        KB   **Karibu** ♀ (9-10 Jan 07)

        KJ   **Kaija** ♂ (06-07 Jul 13 exact)

LL   *Lola (88 ± 1 yr – 15 Jan 08 ± 1 week): dark face, face is squeezed like Mukwano, skinny (~18 yrs) (first seen 2003, named on 9 May 2005)*

MM   *Mamma (in or before 1970 – 99): large body size, hairy (first seen June 1995 with MH, last seen August 13th, 1998)*

        MH   *Muhara ♀ (85 ± 1 yr – 01) (last seen Aug 01)*

MT   *Matoke (62 ± 5 yrs – 93)*

        TT   *Toto ♂ (88 ± 1 yr)*

ML   **Melissa** (1975±5 *years*): wrinkled face, white scars, brown back/legs, ear tufts, big body (first seen Sept. 26th 2001 with MR)

        MR   *Mark ♂ (97 ± 1 yr – 2007): white beard, juvenile (~9 yrs) [Non-Sonso father]*

        ??   *Un-named (02, still-born)*

        MN   **Monika** ♀ (13 July 03 ± 2 wks), round body, white beard, juvenile

        MB   **Mbotella** ♂ (14 Jan 09 ± 3 wks)

        ??   *unnamed ♀infant (15 Nov 14 ± 1 day, her carcass carried by ML on the 21st of Nov 14))*

MK   **Mukwano** (80 ± 3 yrs): small brown face w/ black spots, tufted hairs on back of neck, balding head, two middle fingers short on left hand (first identified April 28th, 1992)

        MD   *Monday ♂ (Nov 02 ± 1 mo – 03) (last seen May 2nd 2003)*

        ??   *Unnamed/unsexed infant (2 July 06 ± 1 day: killed on 2 July 06 infanticide)*

        MI   **Marion** ♀ (11 Nov 07 ± 1 month), small for her age

NB   **Nambi** (in or before 62): Buddha belly, balding, small slit on left ear, white beard, pointed mouth (first identified June 21st 1994)

        MU   *Muga ♂ (77 ± 1 yr – 00)*

        AY   *Andy ♂ (82 ± 6 mo – 00)*

        MS   **Musa** ♂ (91 ± 6 mo), adult, see below

        NR   Nora ♀ (Feb 96 ± 3 wks): subadult, right hand snare injured: *emigrated to Northeast community around*

July 2010: seen in Northeast (Waibira) March 2011.

NT   **Night** ♀ (6 Feb 03, exact), bold behavior, long face, juvenile

OK   **Oakland** (96 ± *1 year*). Immigrated February 2010, long black face with pink ears, pointed cone-like head, long, thin bodied,
index finger LH is bent.

??   *Unnamed ♀ infant (24-25 Jul 12 exact – killed on the 25th of Jul, infanticide)*

??   *Unnamed ♂ infant (5-6 Sept 13 – killed on the 6th of Sept 13 by unknown individual - infanticide)*

??   Unnamed ♂ infant (16 Sept 14, exact)

PL   *Polly (in or before 84): white scar on right arm; (~ 22 yrs or older) (first seen Jan 2003 with PS, formerly Stranger A, last seen Aug 2008 in weak conditions)*

PS   **Pascal** ♂ (98 ± 1 yr): subadult, see below

PN   Polina ♀ (22 Oct 04 ± 1 month, most likely the 'lost baby' seen first on 25/10/2008): *disappeared:*
possibly last seen July 2010; also named Lost Baby 1 (LB1) from that point

RD   *Ruda (in or before 76 – 01)* (first identified Nov 1992, died January 29th 2001)

BO   *Bob ♂ (90 ± 6 mo- Last seen July 07):* big ears, long face [Non-Sonso father]

RE   Rachel ♀ (Jun 97 ± 1 mo): white beard, pointy ears, subadult: last seen May 2011: likely emigrated to East/Southeast

RE   Rachel (Jun 97 ± 1 mo): white beard, pointy ears, ('aged elf') travels with BO since orphaned, subadult: last seen May 2011: likely emigrated to East/Southeast

RH   **Ruhara** (1965 ± 5 years): completely bald head, large grey body (first identified April 14th 1992)

NK   **Nick** ♂ (82 ± 1 yr), adult (alpha since end 2006), see below

GT   *Grinta ♀ (90 ± 1 yr – 99)*

RS   **Rose** ♀ (15 Nov 97 ± 1 day): tanned face w/ pale lips, adult

RM   **Ramula** ♀ (6 Sep 02 ± 1 wk), juvenile

RF   **Rafia** ♀ (4th July 07 ± 2 wks)

RS   **Rose** (15 Nov 97 ± 1 day): tanned face w/ pale lips, pointy head, adult (seen with a baby in July 2011)

RK   *Rafiki ♀ (25 Feb 2011 ± 5 days); baby disappeared in August 2011*

RY   **Reynolds** ♂ infant (8 Oct 13 ± 2 days)

SB   *Sabrina (in or before 81) (first seen with SL 2001 and named in April 2001): trapped in mantrap Nyakafunjo*
August 2010

SA   Sally ♀ (96 ♂1 yr): *last seen end 2009*

SN   *Sean ♂ (Sept 02 ± 1 mo – 2007)*

ST   **Sharlot** ♀ (Jan 6th 07 ± 1 week): from September 2010, she was also called Lost Baby 2, as she
appeared alone in the community after SB died in August 2010. DNA sequencing confirmed LB2 to
be ST (March 2011). August 2011: ST seen trying to suckle from WL, who she stays with now.

SL   *Salama (81 ± 2 yrs – ??, seen briefly 95 & 01)*

SR   *Sara (?? – 00)* (first seen November 27th 1995, last seen February 29th 2000)

SE   *Sarine (71 ± 5 yrs): formerly Stranger I, brown legs like RH, hairy black arms, big ears pointing to the side, brown hairs in front of ears, looks like TK around the eyes,*

missing hairs on the wrists (first seen May 2004 with SM, named April 2006, formerly Stranger I) (last seen very weak 10th of May 13)

> SM **Simon** ♂ (93 ♂ 1 yr), adult
> ?? *Unnamed/unsexed infant (May 04 ± 1 month – Sept 05 ± 8 months)*
> SK *Sokomoko ♂ (Oct 06 ± 2 weeks) (last seen with SE 10th of May 13)*

SH *Shida (90 ± 1 yr): missing left hand, right ankle snared, shy, disappeared Sep 04*

TJ **Tanja** (84 ± 5 yrs) formerly stranger E. Big slit in upper part left ear, wart on left cheek (first seen Dec 1st, 2003, named March 1st, 2009)

> TP **Tapura** ♀ (99 ± 2 yrs), subadult
> TM **Tamara** ♀ (04 ± 2 yrs), juvenile
> TW **Twenty** ♀ (March 11± 2 months)

UP **Upesi** (99 ± 1 yr) named on the 12/11/2012) formerly S1 (first seen 23/05/2012). pale and narrow face, fluffy body with 2 layers of hairs .

VR **Verena** (97 ± 1 yr: named on 30/11/08): formerly juvenile female moving with HT: now subadult. She has fluffy side cheek beard, very dark face, formerly known as the 'juvenile female that is with Harriet' (she was seen occasionally in the west part of the home range since 2006).

VT *Vita (90 ± 1 yr – 98)*

WL **Wilma** (in or before 81): right hand missing, black wart under right eye, big body (first seen Oct 16th, 2001 with WS, named Nov 2001), now travelling with Sharlot (see above)

> WS *Willis ♂ (96 ± 1 yr – 01) (last seen Dec. 2001)*

ZN *Zana (in or before 81-2007- 03 Aug 07):* both hands deformed, droopy lips (first identified Sept. 1992).

> ZL **Zalu** ♂ (29 Jun 95 ± 3 days): adult, [Non-Sonso father?], see below
> ZD **Zed** ♂ (May 01 ± 1 mo): subadult

ZM *Zimba (in or before 68): broad ears, brown face, scrunched face(first identified August 11th, 1993). Disappeared in the week following an intergroup encounter that left her severely injured on 6 May 2011*

> KY **Kewaya** ♀(83 ± 1 yr) [Non-Sonso father]
> GZ *Gonza ♀ (90 ± 1 yr – 02) (last seen 2002, possible emigration)*
> ZP *Zip ? (15 June 96 ± 2 wks – 96)*
> ZG **Zig** ♂ (24 Jun 97 ± 2 wks): large sticking out ears, thin limbs, snare injury on RH, subadult
> ZK *Zak ♂: (21 Nov 02 ± 1 day- 6 May 2011), juvenile: died after attack during intergroup encounter*
> ?? *Unnamed ♂ infant (08 Mar 09 ± 1 day – 19 Mar 09)*

MALES & THEIR OFFSPRING

AY *Andy (82 ± 6 mo – 00) (body recovered July 20th 2000)*

BK *Black (74 ± 2 yrs – 20 Jan 05): long black hairs covering body, small bald patch, white forehead scar (died after   falling out of tree Jan 20th, 2005).*

> BH Bahati ♀ (Dec 94 ± 1 wk)
> NR Nora ♀ (Feb 96 ± 3 wks)
> KN **Kana** ♀(29 Oct 98 ± 1 day)
> CT *Clint ♂(27 Apr 02 ± 2 days)*
> RM **Ramula** ♀ (6 Sep 02 ± 1 wk), juvenile
> ZK *Zak ♂: (21 Nov 02 ± 1 day- 6 May 2011)*

KI   **Kuki** ♀(16 Sep 03 ± 3 days), juvenile

BO   *Bob (90 ± 6 mos - 07):* long, light face, big forward facing ears, hunched body. Snare around middle finger right hand. Disappeared May 2007. [Mother = RD |

        TP   **Tapura** ♀ (99 ± 2 yrs), subadult

BB   *Bwoba (87 ± 1 yr – Feb 09):* brown skin (most noticeable on face), large jaw, bald patch, stocky.

        KS   **Kasigwa** ♂(15 Aug 03 ± 2 wks)

        KX   **Kox** ♀ (7 April 07, +/- 2 months)

BY   *Bwoya (65 ± 5 yrs – 01) (last seen Dec. 8th 2001)*

        KL   **Kalema** (79 ± 1 yr)

CH   *Chris (67 ± 3 yrs – 97) (last seen Aug. 9th 1997)*

        AY   *Andy (82 ± 6 mo – 00) (body recovered July 20th 2000)*

        KY   **Kewaya** (83 ± 1 yr)

        KT   **Kato** (Sep 93 ± 1 month)

        ZL   **Zalu** (29 Jun 95 ± 3 days)

        AN   **Anna** (90 ± 1 yr)

        EM   *Emma (Sep 91 ± 2 yrs):*

        PS   **Pascal** (98 ± 1 yr)

DN   *Duane (66 ± 2 yrs – 26/02/08): prominent brow ridge, grey back hair, pronounced dimples, slit in right ear, alpha until 2006. Died a sudden death (within 20 min) on 26/02/2008*

        SH   **Shida** ♀ (90 ± 1 yr)

        RS   **Rose** ♀ (15 Nov 97 ± 1 day)

        KE   **Keti** ♀(1 Sep 98 ± 1 wk)

        JT   **Janet** ♀ (1 Oct 99 ± 3 days)

        KM   **Kumi** ♀ (30 Dec 98, exact)

        MI   **Marion** ♀ (11 Nov 07 ± 1 month)

FD   *Fred (94 ± 1 yr): large pale face, hands and feet are brown, white patch at the bottom of the back, stout body, still a bit shy. Adult. [Mother = FL] [father=almost certainly from Sonso] (last seen 17th of July 14, a dead body very similar to FD was found in Nyakafunjo on the 22nd of July 2014)*

        BG   **Birungi** ♀(March 04 ± 4 months)

FK   **Frank** ♂ (99 ± 1 yr):, pale face and large ears, stout body, smaller than Fred, subadult [Mother = FL] [father=almost certainly from Sonso]

GS   *Gashom (87 ± 1 yr – 26/02/08): brown face, small testicles, missing third finger, hairs on lower jaw (first seen 7/94, last seen 26/02/08 at dead body of Duane).*

HW   **Hawa** (93 ± 1 yr): very dark face, small slit on left ear, ridges around nose, long and black body, adult [Mother = HT]

JK   *Jake (88 ± 1 yr – 95) (first seen 9/94, immigrant with no mother, last seen Feb 4th, 1995)*

JM   *Jambo (78 ± 2 yr – 03) (found murdered in sugar cane May 6th 2003)*

        HW   **Hawa** ♂ (93 ± 1 yr)

        HL   **Helen** ♀ (Feb 01 ± 3 wks)

JG   *Jogo (88 – 94) (first seen 11/92, last seen April 23rd 1994)*

KK   *Kikunku (76 ± 1 yr – 98) (last seen July 6th 1998)*

        BO   *Bob (90 ± 6 mos - 07)*

        KA   **Katia** ♀(30 Dec 98, exact)

        ZT   *Zesta (1980 ± 3 yrs – 98)*

KT **Kato** (Sep 93 ± 1 month): close set eyes, large brow ridge, black around nose, broad shoulders, right foot 4th and 5th toes fused together, probably due to snare injury, adult [Mother = KU]

KZ **Kwezi** (14 Jan 95 ± 2 weeks): sharp eyes, long face, long hairs on sides of face, dark muzzle, adult [Mother = KW]

MA *Maani (1965 ± 5 yrs – Aug 08) long narrow face and body, grey back hair, white around nipples, chest scar (last seen Aug 08 in very weak conditions)*
        KR   **Karo** ♀ (1 Nov 01 ± 1 day)
        MN   **Monika** ♀ (13 July 03 ± 2 wks)

MG *Magosi (alpha until 94; died 99, approx. age: 50s??) (body found July 4th, 1999)*
        MU   *Muga ♂(77 ± 1 yr – 00)*
        NK   **Nick** ♂ (82 ± 1 yr), alpha
        GZ   *Gonza ♀(90 ± 1 yr – 02)*
        MS   **Musa** ♂ (91 ± 6 mo), adult
        ZG   **Zig** ♂ (24 Jun 97 ± 2 wks), subadult

MO *Mukono (1967 – 94) (last seen Feb 12th 1994). First seen 1992.*

MR *Mark (97 ± 1 yr – 07): white beard, still with tuft, spots on face [Mother = ML] [father=almost certainly from Sonso]*

MS **Musa** (91 ± 6 mo): dark face, tufts of hairs stick out from face, adult [Mother = NB]
        GR   **Goria** ♀ (06 ± *1 yr*)
        ST   **Sharlot** ♀ (Jan 6th 07 ± 1 week)

MU *Muga (77 ± 1 yr – 00) (disappeared and presumed dead 2000)*
        KZ   **Kwezi** ♂ (7 Jan 95 ± 3 wks), adult

NJ *Nkojo (1968 ± 5 yrs) (last seen Sept 29th, 2001)*
        ZF   **Zefa** ♂ (82 ± 6 mo), adult
        GS   *Gashom ♂(87 ± 1 yr), died February 2008*
        SM   **Simon** ♂ (93 ♂ 1 yr), adult
        RE   Rachel ♀ (Jun 97 ± 1 mo), subadult

NK **Nick** (82 ± 1 yr): long hairs on lower jaw, 'Elvis-style sideburns', brown/grey and muscular body, current alpha since end 2006 [Mother = RH]
        HY   **Honey** ♀ (4 Oct 05 ± 3 days)
        FA   **Faida** ♀ (Oct 06 ± 1 month)
        SK   **Sokomoko** ♂ (Oct 06 ± 2 weeks)
        KB   **Karibu** ♀ (9-10 Jan 07)
        KH   **Kathy** ♀ (28 Jul 08 ± 3 days)

PS **Pascal** (98 ± 1 yr): large ears, spotted face, lower lip often dropping, long body, ,subadult [Mother = PL]

SM **Simon** (93 ± 1 yr): folds in both ears, long and very dark face, still shy, adult [Mother = SE]

SQ **Squibs** (91 ± 1 yr): protruding bottom lip, bald patch developing, turgid testicles, brownish face and body, adult [Mother = BC] [father=almost certainly from Sonso]

TK *Tinka (1960 ± 5 yrs) : hooked/wasted left hand, hooked right hand w/ hairs loss, slow moving. Died 11.01.2010, Nyakafunjo*

VN *Vernon (1965 ± 2 yrs – 99) (last seen June 29th 1999)*
        GN   **Gina** ♀ (96 ± 2 yrs), subadult
        VR   **Verena** (97 ± 1 yr: named on 30/11/08)

ZT *Zesta (1980 ± 3 yrs – 98). (First seen 1993). Killed by BK and DN.*

ZF **Zefa** (82 ± 6 mo): stout build, black face, cheek dimples, big triangular bald patch, short 4th and 5th fingers, no hairs on the back thin hair, adult [Mother = BN]
        ZD   **Zed** ♂ (May 01 ± 1 mo): subadult

KC   **Klauce** ♂ (5 Sept 06 ± 2 days), juvenile

JS   **James** ♂ (4 May 06 ± 1 month), juvenile

RF   **Rafia** ♀ (4th July 07 ± 2 wks)

KP   **Kaspa** ♂ (28 Oct 08 ± 1 wk)

ZG   **Zig** (24 Jun 97 ± 2 wks) pale face, long bodied, thin hairs on body. large sticking out ears, thin limbs, pronounced snare injury on RH, wrist bent. Lost the use of his right eye in January 2010 after a fight with an unknown individual. Extremely well habituated, subadult

ZL   **Zalu** (29 Jun 95 ± 3 days): left ear is damaged, very black face and body, long hairs around face and on body, adult [Mother = ZN]

APPENDIX II: VIDEO ANALYSIS CODING SHEET

Clip Number [ ]   **Solicitation** [ ]
Name [ ]   **Length** [ ]
          Date [ ]

Signaller [ ]   **Recipient** [ ]
Sig Age [ ]   **Rec Age** [ ]   **Erection** ☐ Yes ☐ No ☐ Unk
Sig Context [ ]   **Rec context** [ ]   **Location** ☐ Ground ☐ Tree
Goal [ ]   **Rec State** [ ]   **Swelling** ☐ 0 ☐ 1 ☐ 2 ☐ 3 ☐ 4 ☐ 4P

Precopulatory Behaviour:

Check atn? ☐ Yes ☐ No ☐ Unk   **Gesture** [ ]   **Seq <1** [ ]
Action [ ]   **Body Part** [ ]   **Bout** [ ]
Vocal [ ]   **Object Used** [ ]   **Aud?** [ ]
Facial Exp [ ]

Response gesture [ ]   **Wait** ☐ Yes ☐ No ☐ Unk
Response vocal [ ]   **Persist** [ ]
Response facial [ ]   **Goal Met** ☐ Yes ☐ No ☐ Partial ☐ Unk
Response action [ ]   **From previous** ☐ Bigger ☐ Smaller ☐ Same ☐ NA

Copulation Behaviour:

Dom Male [ ]   **Dom Male State** [ ]
Dom Fem [ ]   **Dom Fem State** [ ]
Interference? [ ]   **Copulation Vocal** [ ]
Intromission [ ]   **Copulation Exp** [ ]

Postcopulatory Behaviour:

Dart? ☐ Yes ☐ No ☐ Unknown   [ ]
Last Solicitation [ ]

APPENDIX III: MALE GESTURAL REPERTOIRES

Frank Arm fling*, Arm raise*, Arm swing*, Beckon, Big Loud Scratch, Bipedal run*, Bipedal swagger*, Drum object*, Gallop*, Leaf clip, Leaf strip, Object move*, Object shake*, Genital offer, Punch object/ground*, Rocking*, Stiff stance*, Stomp* ,Tap other*

Fred Arm raise*, Arm shake, Arm swing*, Beckon, Big Loud Scratch, Drum object*, Leaf clip, Leaf strip, Lunge, Object move*, Object shake*, Pelvic thrust, Genital offer, Punch object/ground*, Rocking*, Slap object*, Stomp* ,Tap other*

James Arm raise*, Big Loud Scratch, Bipedal run*, Bipedal swagger*, Bump rump, Chest beat, Drum object*, Gallop*, Leaf clip, Leaf strip, Lunge, Object move*, Object shake*, Genital offer, Punch object/ground*, Rocking*, Slap object*, Stiff stance*, Stomp*

Kato Arm fling*, Arm raise*, Arm shake, Arm swing*, Big Loud Scratch, Bipedal run*, Bipedal swagger*,Bump Rump, Drum object*, Leaf clip, Leaf strip, Lunge, Object move*, Object shake*, Genital offer, Punch object/ground*, Rocking*, Slap object*, Stiff stance*, Stomp* ,Tap other*

Klauce Arm raise*, Beckon, Bipedal run*, Bipedal swagger*,Chest beat, Drum object*, Gallop*, Leaf clip, Object move*, Object shake*, Pelvic thrust, Genital offer, Punch object/ground*, Slap object*, Stiff stance*, Stomp*

Kwezi Arm fling*, Arm raise*, Arm swing*, Gallop*, Leaf clip, Leaf strip, Lunge, Object move*, Object shake*, Genital offer, Punch object/ground*, Rocking*, Slap object*, Stiff stance*, Stomp* ,Tap other*

Musa Arm fling*, Arm raise*, Arm shake, Arm swing*, Beckon, Big Loud Scratch, Bipedal run*, Bipedal swagger*, Drum object*, Leaf clip, Object move*, Object shake*, Pelvic thrust, Genital offer, Punch object/ground*, Rocking*, Slap object*, Stiff stance*, Stomp* ,Tap other*

Nick Arm fling*, Arm raise*, Arm shake, Arm swing*, Beckon, Big Loud Scratch, Bipedal run*, Bipedal swagger*, Drum object*, Gallop*, Leaf clip, Leaf strip, Lunge, Object move*, Object shake*, Genital offer, Punch object/ground*, Rocking*, Slap object*, Stiff stance*, Stomp* ,Tap other*

Pascal Arm raise*, Arm swing*, Big Loud Scratch, Bipedal run*, Bipedal swagger*, Gallop*, Leaf clip, Lunge, Object move*, Object shake*, Genital offer, Punch object/ground*, Rocking*, Slap object*, Stiff stance*, Stomp* ,Tap other*

Simon Arm fling*, Arm raise*, Big Loud Scratch, Gallop*, Leaf clip, Leaf strip, Lunge, Object move*, Object shake*, Genital offer, Punch object/ground*, Rocking*, Slap object*, Stiff stance*, Stomp* ,Tap other*

Squibs Arm fling*, Arm raise*, Arm shake, Arm swing*, Big Loud Scratch, Bipedal run*, Bipedal swagger*, Drum object*, Object move*, Object shake*, Genital offer, Punch object/ground*, Rocking*, Slap object*, Stiff stance*, Stomp* ,Tap other*

Zalu Arm swing*, Beckon, Big Loud Scratch, Bipedal run*, Bipedal swagger*, Drum object*, Gallop*, Leaf clip, Object move*, Object shake*, Genital offer, Punch object/ground*, Rocking*, Slap object*, Stiff stance*, Stomp* ,Tap other*

Zed Arm fling*, Arm swing*, Beckon, Big Loud Scratch, Drum object*, Gallop*, Leaf clip, Lunge, Object move*, Object shake*, Pelvic thrust, Genital offer, Punch object/ground*, Rocking*, Slap object*, Stiff stance*, Stomp* ,Tap other*

Zefa Arm raise*, Arm swing*, Beckon, Big Loud Scratch, Bipedal run*, Bipedal swagger*, Bump rump, Drum object*, Leaf clip, Leaf strip, Lunge, Object move*, Object shake*, Genital offer, Punch object/ground*, Rocking*, Slap object*, Stiff stance*, Stomp* ,Tap other*