



Female chimpanzees adjust copulation calls according to reproductive status and level of female competition



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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. We 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, we 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 nonsignificant trend for females to increase calling as the number of cycling females increased. We conclude that female chimpanzees are capable of adjusting their copulation calling flexibly, by taking into account their own sexual attractiveness, to incite male competition.

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Sexual selection theory predicts an interplay between two main forces, mate competition and mate choice (Darwin, 1871; Trivers, 1972). In most systems, females are the limiting sex, which results in males becoming competitors and females being able to choose. Males tend to compete using overt aggressive strategies, as found in many taxa from salamanders, *Plethodon cinereus* (Jaeger, Gillette, & Cooper, 2002) to elephants, *Loxodonta africana* (Poole, 1989). Aggression can also be directed at oestrous 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 & Everts, 1998), dolphins, *Tursiops* sp. (Scott, Mann, Watson-Capps, Sargeant, & Connor, 2005) or primates (e.g. Japanese macaques, *Macaca fuscata*; Soltis, Mitsunaga, Shimizu, Yanagihara, & Nozaki, 1997). Chimpanzee males, *Pan troglodytes*, use sexual coercion as a means of enacting their preference for older, parous females (Feldblum et al., 2014; Muller, Kahlenberg, Thompson, & Wrangham, 2007; Muller, Thompson, Kahlenberg, & Wrangham, 2011; Muller, Thompson, & Wrangham, 2006; Wrangham & Muller, 2009). As a counter-strategy to coercion, chimpanzee females sometimes 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. In some chimpanzee populations, female choice appears to be the dominant mating strategy (Matsumoto-Oda, 1999; Stumpf & Boesch, 2005, 2006, 2010), which may be related to the steepness of the male dominance hierarchy (Kaburu & Newton-Fisher, 2015a). Here, it has been argued that in communities in which 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, 2015b).

Generally, however, female chimpanzees are widely viewed as the more solitary and passive sex. In contrast to the extensive data on male-male mating competition, relatively little is known on how female chimpanzees, or indeed any female primates, take other female competitors into account during mating (Stumpf & Boesch, 2006; Townsend, Deschner, & Zuberbühler, 2008). Competition from other females may be especially grave for nulliparous females in the face of male preference for older, parous females. Female-female competition is generally hard to detect as it tends to manifest in ways not directly associated with mating success: for example, through physical aggression, resource manipulation, infanticide or reproductive suppression of others (reviewed by Stockley & Bro-Jørgensen, 2011). In great apes and humans, for

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example, such indirect female competition has been documented repeatedly (chimpanzees, *P. troglodytes*, and bonobos, *Pan paniscus*: Pusey, Williams, & Goodall, 1997; Kano, 1992; Townsend, Slocombe, Thompson, & Zuberbühler, 2007; humans: Benenson, 2013; Campbell, 2013). Human females in particular are noteworthy for indirect aggression towards female competitors, such as social exclusion (Benenson, Markovits, Thompson, & Wrangham, 2011) or punishing perceived social superiors (Winstead & Griffin, 2001). In chimpanzees, immigrant females compete in many day-to-day interactions with resident females over access to resources (Pusey & Schroepfer-Walker, 2013), which causes immigrants to avoid high-ranking females in their daily ranging behaviour (Murray, Mane, & Pusey, 2007). While physical aggression between adult females is rare, there are multiple reports of selective aggression towards immigrant females, presumably because they pose a threat to resident females' resources (Boesch & Boesch-Achermann, 2000; Kahlenberg, Thompson, Muller, & Wrangham, 2008; Pusey et al., 2008). Such aggression can be severe, preventing young females from immigrating (Pusey et al., 2008) and possibly resulting in female-led infanticidal behaviour, as documented in at least one community (Townsend et al., 2007). Perhaps for this reason, immigrant females in both gorillas, *Gorilla gorilla beringei* (Watts, 1992) and chimpanzees (Boesch & Boesch-Achermann, 2000; Kahlenberg et al., 2008; Nishida, 1979) have been observed to rely on male protection and occasionally to ally with each other against resident females. In contrast to this general type of female competition, however, there are no comparable studies of direct female-female competition over sexual partners, apart from isolated anecdotes (e.g. Nishida, 1979). There is some evidence for indirect effects of intrasexual competition, in that the stress of immigration appears to delay conception in immigrant females by several years despite the fact that they have regular sexual cycles (Nishida et al., 2003; Pusey & Schroepfer-Walker, 2013).

In many species, including chimpanzees, females generate signals of sexual receptivity, such as visually salient sexual swellings, olfactory cues or copulation calls (Deschner, Heistermann, Hodges, & Boesch, 2004; Townsend et al., 2008). Copulation calling is thought to incite sperm competition between males while affording females protection from infanticide (Engelhardt, Fischer, Neumann, Pfeifer, & Heistermann, 2012; O'Connell & Cowlshaw, 1994; Oda & Masataka, 1995; Pradhan, Engelhardt, van Schaik, & Maestriperi, 2006; Semple, 1998). Call production appears to be partially strategic, as evidenced by reports of call repression and furtive behaviour in chimpanzees and geladas, *Theropithecus gelada*, which allow females to promote paternity confusion while avoiding aggression from dominant males (Le Roux, Snyder-Mackler, Roberts, Beehner, & Bergman, 2013; Matsumoto-Oda & Tomonaga, 2005). Similarly, chimpanzee females can suppress copulation calls in the presence of equal- or higher-ranking females (Townsend et al., 2008), suggesting that they have some measure of vocal control to mitigate infanticide risk (Townsend et al., 2008; Townsend et al., 2007). Among bonobos, in which high-ranking allies are important to reduce female-female competition, females give copulation calls more frequently in the presence of the alpha female (Clay, Pika, Gruber, & Zuberbühler, 2011).

Based on these findings, it is likely that female competition in the context of reproduction plays a role in the calling behaviour of *Pan*, the extent of which requires further investigation. We reasoned that copulation calls allow females to compete indirectly with other cycling females by inciting competition among males. Chimpanzee copulation calls are individually distinct, but do not alter in acoustic structure across the ovarian cycle (Townsend, Deschner, & Zuberbühler, 2011). Competition is likely to be highest during periods when several females cycle simultaneously, which is then likely to lead to competition for sexual access to

males. This may be particularly taxing on nulliparous females who are generally found to be less attractive than parous females (Muller & Mitani, 2005; Muller et al., 2006; Muller et al., 2007).

In this study, we tested the hypothesis that copulation calling strategies differ for parous and nulliparous females, based on previous evidence that parity reflects sexual attractiveness. In particular, we 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, Machanda, Muller, Kahlenberg, & Wrangham, 2013). We also predicted that strategic calling would be especially evident during periods when many females are in oestrus and competition is high.

METHODS

Study Site and Subjects

The study was conducted at the Budongo Conservation Field Station (BCFS), located in the Budongo Forest Reserve in Masindi, Uganda, a protected area totalling 794 km² of primarily semi-deciduous forest (Eggeling, 1947; Plumptre & Reynolds, 1996). Budongo Forest is home to an estimated population of 583 chimpanzees (Plumptre, Cox, & Mugume, 2003), including two habituated communities, Sonso and Waibira. Data were collected from the Sonso community, which included 66 individuals (19 males, 47 females) at the time of the study. Fourteen adult and subadult males (nine adults, five subadults) aged 10–35 years were targeted for data collection as copulation partners, and all males were included in our analysis. Of the females, 13 parous and seven nulliparous females experienced an oestrous cycle during the study period and were targeted as focal individuals. 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.

Data Collection

Data were collected in all-day focal follows of cycling females using all-occurrence sampling balanced across individuals (Altmann, 1974). Fieldwork was conducted between June and August 2011, between May 2012 and April 2013 and between September 2013 and March 2014, totalling approximately 2688 h of observation time. We filmed 1157 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 (www.filemaker.com) 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 undergoing oestrus 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 we did not include female rank because it was not possible to carry out a reliable rank assessment during the time of the study.

Chimpanzee copulation calls are rhythmic, high-frequency and acoustically distinct screams (Townsend et al., 2011). We limited our definition of copulation call to calls produced during a sexual act, although females occasionally produce calls during male inspection of their swellings. Swelling stage was estimated by the degree of wrinkling on a scale of 0–4, where 4 indicates a fully inflated swelling (Furuichi, 1987; Zuberbühler & Reynolds, 2005). Length of copulation was measured from the start of intromission

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