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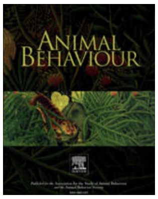

Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*

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Competition for fertile females determines male reproductive success in many species. The priority of access model predicts that male dominance rank determines access to females, but this model has been difficult to test in wild populations, particularly in promiscuous mating systems. Tests of the model have produced variable results, probably because of the differing socioecological circumstances of individual species and populations. We tested the predictions of the priority of access model in the chimpanzees of Gombe National Park, Tanzania. Chimpanzees are an interesting species in which to test the model because of their fission–fusion grouping patterns, promiscuous mating system and alternative male mating strategies. We determined paternity for 34 offspring over a 22-year period and found that the priority of access model was generally predictive of male reproductive success. However, we found that younger males had higher success per male than older males, and low-ranking males sired more offspring than predicted. Low-ranking males sired offspring with younger, less desirable females and by engaging in consortships more often than high-ranking fathers. Although alpha males never sired offspring with related females, inbreeding avoidance of high-ranking male relatives did not completely explain the success of low-ranking males. While our work confirms that male rank typically predicts male chimpanzee reproductive success, other factors are also important; mate choice and alternative male strategies can give low-ranking males access to females more often than would be predicted by the model. Furthermore, the success of younger males suggests that they are more successful in sperm competition.

Among mammals, males usually compete over access to fertile females (Trivers 1972; Cunningham & Birkhead 1998). Accordingly, there is a well-documented relationship between male dominance rank and reproductive success in many group-living species (e.g. red deer, *Cervus elaphus*: Pemberton et al. 1992; northern elephant seals, *Mirounga angustirostris*: Haley et al. 1994; African wild dogs, *Lycaon pictus*: Girman et al. 1997). In these species and numerous others, high-ranking males have higher reproductive success than their lower-ranking counterparts.

Many primates likewise show a positive correlation between male rank and reproductive success (e.g. bonobos, *Pan paniscus*: Gerloff et al. 1999; Hanuman langurs, *Semnopithecus entellus*: Launhardt et al. 2001; rhesus macaques, *Macaca mulatta*: Widdig et al. 2004; multimale gorilla, *Gorilla gorilla*, groups: Bradley et al. 2005). However, the relationship is complex, and there is variation in the strength of the association (Ellis 1995). The relationship between rank and reproductive success was formalized into the 'priority of access' model, which predicts how many offspring should be sired by each male based on each male's rank and two demographic factors: the number of male competitors and the number of receptive females present for each conception (Altmann 1962). For example, if five males are in a group with two receptive females, priority of access predicts that the two highest-ranking males will each gain access to one female. Several studies have found support for this model (e.g. Japanese macaques, *Macaca fuscata*: Soltis et al. 2001; mandrills, *Mandrillus sphinx*: Setchell et al. 2005; savannah baboon, *Papio cynocephalus*: Alberts et al. 2006) while another study in grey mouse lemurs, *Microcebus murinus*, did not (Radespeil et al. 2002). However, lemurs breed synchronously and have a dispersed social system that may make it difficult for males to successfully monitor and defend mates. The influence of breeding synchrony has been observed in other species

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as well; dominant male domestic cats, *Felis catus* L., were more successful when females had asynchronous oestrus (Say et al. 2001).

Despite the general correlation between dominance rank and reproductive success, several factors may alter the influence of rank and explain deviations from the priority of access model. Male coalitions, female choice and alternative male mating strategies can alter male access to females (Smuts 1987) and decrease the correlation between rank and reproductive success in primates. Some females may prefer middle- or lower-ranking males, thereby enabling those males to bypass their place in the queue (e.g. rhesus macaques: Chapais 1983; ringtailed lemur, *Lemur catta*: Pereira & Weiss 1991; Japanese macaques: Soltis et al. 2001; Hayakawa 2007; chimpanzees: Stumpf & Boesch 2005, 2006). Furthermore, low-ranking males can sometimes avoid direct competition with dominant individuals by sneaking copulations, as occurs in Japanese and rhesus macaques (Berard et al. 1994; Soltis et al. 2001). The degree to which these factors are important is probably contingent upon the socioecology of the species or population.

Chimpanzees represent a particularly interesting system in which to investigate the applicability of the priority of access model. Unlike the primate species referenced above, chimpanzees live in a fission–fusion social system in which subgroups, known as parties, are temporary within a permanent community (Nishida 1968; Goodall 1986; Boesch & Boesch-Achermann 2000). Thus, even though males can be ranked in a linear dominance hierarchy (e.g. Boesch & Boesch-Achermann 2000; Mitani & Amsler 2003; Muehlenbein et al. 2004), access to females may be dependent on party composition. For example, lower-ranking males have higher courtship success when higher-ranking males are absent (Matsumoto-Oda 1999). Access to females could also vary across populations given differences in gregariousness and dispersal. Compared to East African chimpanzees, *P. t. schweinfurthii* (Gombe: Wrangham & Smuts 1980; Williams et al. 2002; Murray et al. 2007), West African female chimpanzees, *P. t. verus*, are more gregarious and show comparable levels of gregariousness and similar home ranges to males (Bossou, Guinea: Sugiyama 1988; Sakura 1994; Taï National Park, Cote d'Ivoire: Boesch 1996; Boesch & Boesch-Achermann 2000; Lehmann & Boesch 2005). Additionally, while chimpanzee females generally disperse at sexual maturity (Goodall 1986; Nishida et al. 1990; Boesch & Boesch-Achermann 2000), approximately 50% of females in the main study community at Gombe National Park, Tanzania remain in their natal community with related males (Pusey et al. 1997).

Females have conspicuous sexual swellings when they are sexually receptive, and they mate promiscuously (Goodall 1986; Nishida & Hiraiwa-Hasegawa 1987). Hormonal patterns indicate that they ovulate when they are maximally tumescent (Deschner et al. 2003; Emery Thompson 2005). Males can therefore monitor female receptivity and should theoretically concentrate their mating efforts during key periovulatory periods. In fact, males show higher rates of mating during the most fertile days within a cycle, and during conceptive cycles than during nonconceptive cycles (Deschner et al. 2004; Emery Thompson 2005; Emery Thompson & Wrangham 2008). Males also preferentially focus their mating efforts on certain individuals. A recent study from the Kanyawara community in Kibale National Park, Uganda, reported that males preferred older females and suggested that the preference for older females is selected for since they have more maternal experience and their survival may indicate higher genetic quality (Muller et al. 2007).

Male chimpanzees show three different mating strategies: (1) opportunistic, (2) possessiveness or mate guarding and (3) consortship (Tutin 1979). Consortship occurs when a male–female dyad travels alone and mates away from other members of the community. When a male has a successful consortship with a female during the fertile period of a conceptive cycle, he benefits from increased paternity certainty by eliminating competition. However, consortships are also costly since pairs often travel to the edge of the community range where they risk attack by neighbouring chimpanzee communities (Goodall 1986; Gombe Stream Research Centre, unpublished data), and males involved in consortship cannot monitor other females in the group.

Consortships seem to occur more frequently at Gombe (Goodall 1986) than at other study sites (Mahale: Hasegawa & Hiraiwa-Hasegawa 1990; Kibale: Watts 1998; Taï: Boesch & Boesch-Achermann 2000; Budongo: Reynolds 2005). Only 10% of offspring are conceived through consortship at Taï (Boesch & Boesch-Achermann 2000) while 21% of offspring are conceived through consortship at Gombe (Constable et al. 2001). Interestingly, only the alpha male at Taï achieved success through consortship in Boesch & Boesch-Achermann's (2000) study, while low- to middle-ranking fathers achieved success through consortship at Gombe (Constable et al. 2001). Therefore, at Gombe, where females are less gregarious, low-ranking males may have more opportunity to lead females away on consortships.

Besides competing for fertile females through aggression and social dominance, males can also compete via sperm competition. When females copulate with multiple males, the male that produces the most sperm gains an increased chance of fertilizing a receptive female (Parker 1970). Bercovitch & Nürnberg (1996) found that rhesus macaque sires have significantly larger testes than nonsires. Sperm production generally correlates with testes size, and in diverse taxa there is a strong correlation between relative testes size and mating system, with the most polyandrous species having the largest testes (reviewed in Gomendio et al. 1998). Chimpanzees, with their highly promiscuous mating system, have particularly large relative testes size, suggesting that they experience intense sperm competition (Harcourt et al. 1981; Møller 1988; Harcourt et al. 1995). As well as individual differences in testes size, another likely factor influencing a male's success in sperm competition is age. In humans and other primates, various measures of male fertility and physiology decline with age (reviewed in: Kidd et al. 2001; Eskenazi et al. 2003; Bribiescas 2006). The promiscuously mating common lizard, *Lacerta vivipara*, also shows age-related decline in reproductive success (Richard et al. 2005), and younger bulb mite, *Rhizoglyphus robini*, males outcompete older males, siring a larger proportion of the females' eggs (Radwan et al. 2005). Thus, as long as young, even low-ranking, males secure copulations during periods of opportunistic mating with fertile females, we might expect them to outcompete older males in sperm competition and achieve fertilization.

Here, we analyse 22 years of data to test whether male chimpanzees at Gombe National Park conform to the priority of access model. Prior work from Taï chimpanzees found that paternity patterns fit well with the model (Boesch et al. 2006). Although we also expected it to hold at Gombe, we predicted that it would not conform as closely since females are less easily monitored in this population than in more socially cohesive groups, such as the Taï population. We further predicted that deviations from the model would result from inbreeding avoidance, whereby females that remained in their natal community would mate with unrelated males that would not necessarily be predicted to have access according to the model parameters. We also expected that low-ranking males would successfully sire offspring with younger, less desirable females and through consortships, and that younger males would be more successful than older males.