
Conflict and Cooperation in Wild Chimpanzees

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I. INTRODUCTION

The twin themes of competition and cooperation have been the focus of many studies in animal behavior (Alcock, 2001; Dugatkin, 2004; Krebs and Davies, 1997). Competition receives prominent attention because it forms the basis for the unifying, organizing principle of biology. Darwin's (1859) theory of natural selection furnishes a powerful framework to understand the origin and maintenance of organic and behavioral diversity. Because the process of natural selection depends on reproductive competition, aggression, dominance, and competition for mates serve as important foci of ethological research. In contrast, cooperation in animals is less easily explained within a Darwinian framework. Why do animals cooperate and behave in ways that benefit others? Supplements to the theory of natural selection in the form of kin selection, reciprocal altruism, and mutualism provide mechanisms that transform the study of cooperative behavior in animals into a mode of inquiry compatible with our current understanding of the evolutionary process (Clutton-Brock, 2002; Hamilton, 1964; Trivers, 1971).

If cooperation can be analyzed via natural selection operating on individuals, a new way to conceptualize the process emerges. Instead of viewing cooperation as distinct from competition, it becomes productive to regard them together. Students of animal behavior have long recognized that an artificial dichotomy may exist insofar as animals frequently cooperate to compete with conspecifics. In taxa as diverse as insects, birds, and mammals, animals cooperate to obtain immediate or deferred fitness benefits.

Well-known examples include sterile castes of eusocial insects and cooperatively breeding birds and mammals (Koenig and Dickinson, 2004; Solomon and French, 1997; Wilson, 1971). In these cases, individuals cooperate with others and forego reproduction to gain direct or indirect fitness payoffs.

Chimpanzees and their behavior have been well studied in the wild. As one of our closest living relatives, chimpanzees generate considerable interest, given the insights they can provide to understanding human behavioral evolution (e.g., Moore, 1996; Wilson and Wrangham, 2003; Wrangham, 1999; Wrangham and Pilbeam, 2001). Chimpanzees also furnish a model system to investigate the manner in which animals compete and cooperate. Pioneering field research by Jane Goodall (Goodall *et al.*, 1979; Goodall, 1968) and Toshisada Nishida (Kawanaka and Nishida, 1975; Nishida, 1983; Nishida and Kawanaka, 1972) demonstrated that conflict plays a significant role in chimpanzee social relations, both within and between communities. Male chimpanzees compete for dominance status within communities and engage in lethal aggression between communities. Early observations of wild chimpanzees also highlighted their cooperative nature. Male chimpanzees spend a substantial amount of time grooming each other (Simpson, 1973) and form both short-term coalitions and long-term alliances that have important fitness consequences (Nishida, 1983; Riss and Goodall, 1977).

Considerable field research, totaling more than 180 years at seven sites, has been undertaken since Goodall and Nishida initiated their seminal studies (Table 1). As a result of new and continuing research, we now possess a rich body of information regarding competition and cooperation in chimpanzee society. Recent observations of aggressive behavior within and between communities are changing our views of the functional significance of chimpanzee aggression. Behavioral endocrinological studies are providing new insights into the physiological mechanisms underlying competitive relationships. New field observations are revealing unsuspected complexity in cooperative behavior, with chimpanzees reciprocally exchanging commodities that are both similar and different in kind. Finally, genetic data are being employed to explore the evolutionary mechanisms that might account for cooperation in chimpanzees.

In this chapter, we review our current knowledge of competition and cooperation in wild chimpanzees. We focus explicitly on recent field studies that shed new light on how chimpanzees compete, cooperate, and cooperate to compete. For part of this review, we rely on the results of our own research that bear on competition and cooperation. We make no attempt to summarize the extensive literature on the behavior of captive chimpanzees, as excellent reviews of this work can be found elsewhere (e.g., de Waal, 1998). We begin by outlining the social, demographic, and ecological contexts within which wild chimpanzees compete and cooperate.

TABLE I
LONG-TERM CHIMPANZEE FIELD STUDIES

Location	Community	Duration of study	Reference
Budongo Forest Reserve, Uganda	Sonso	1990–present	Reynolds, 1992
Bossou, Guinea	Bossou	1976–present	Sugiyama, 2004
Gombe National Park, Tanzania	Kasakela and Kahama	1960–present	Goodall, 1986
Kibale National Park, Uganda	Kanyawara	1987–present	Wrangham <i>et al.</i> , 1996
Kibale National Park, Uganda	Ngogo	1995–present	Mitani <i>et al.</i> , 2002b
Mahale Mountains National Park, Tanzania	Kajabala and Mimikiri	1965–present	Nishida, 1990
Tai National Park, Ivory Coast	North	1979–present	Boesch and Boesch-Achermann, 2000

II. CHIMPANZEE SOCIETY, DEMOGRAPHY, AND ECOLOGY

Chimpanzees live in fission-fusion communities that vary considerably in size, ranging from 20 to 150 individuals (Boesch and Boesch-Achermann, 2000; Goodall, 1986; Nishida, 1968; Nishida *et al.*, 2003; Sugiyama, 2004). Within communities, chimpanzees form temporary subgroups or parties that fluctuate in size, composition, and duration. Parties include 4–10 individuals on average, and usually contain more males than females (Boesch, 1996; Chapman *et al.*, 1995; Matsumoto-Oda *et al.*, 1998; Mitani *et al.*, 2002a; Newton-Fisher *et al.*, 2000; Sakura, 1994; Wrangham, 2000).

Membership in chimpanzee communities is open due to dispersal. Female chimpanzees, typically, but not always, disperse from their natal groups after reaching sexual maturity at an age of about 11 years (Boesch and Boesch-Achermann, 2000; Nishida *et al.*, 2003; Sugiyama, 2004; Williams *et al.*, 2002b). In contrast, males are philopatric and remain on their natal territories for life. After dispersing, and following a 2- to 3-year period of adolescent subfecundity, female chimpanzees begin to reproduce, with an average interbirth interval of 5 to 6 years for offspring who survive to weaning (Boesch and Boesch-Achermann, 2000; Nishida *et al.*, 2003; Sugiyama, 2004; Wallis, 1997).

Chimpanzees feed principally on ripe fruit, although at most sites they also consume insects and hunt vertebrate prey (Newton-Fisher, 1999a; Nishida and Uehara, 1983; Wrangham, 1977; Wrangham *et al.*, 1998; Yamakoshi, 1998). As large-bodied frugivores (female median weight at

Gombe = 31 kg; Pusey *et al.*, 2005), chimpanzees move over extensive areas in search of seasonally scarce fruit resources. Territory sizes average between 5–30 km² depending on habitat type and quality (Chapman and Wrangham, 1993; Hasegawa, 1990; Herbinger *et al.*, 2001; Lehmann and Boesch, 2003; Newton-Fisher, 2003; Williams *et al.*, 2002b). Male chimpanzees defend their territories vigorously against neighbors (Boesch and Boesch-Achermann, 2000; Goodall *et al.*, 1979; Watts and Mitani, 2001; Williams *et al.*, 2004). Intercommunity interactions are extremely hostile and occasionally result in fatalities (Wilson and Wrangham, 2003; Wrangham, 1999).

This social, demographic, and ecological setting forms the background for investigating conflict and cooperation in chimpanzees. Competition for scarce fruit resources sets the stage for conflict between female chimpanzees. Long birth intervals produce a skewed operational sex ratio, leading to intense male-male competition. Territoriality adds conflict between communities to the already high levels that exist within communities. Despite the labile nature of chimpanzee parties, male chimpanzees are typically more social than females (Boesch, 1996; Halperin, 1979; Newton-Fisher, 1999b; Nishida, 1968; Pepper *et al.*, 1999; Sakura, 1994; Wrangham, 2000; Wrangham *et al.*, 1992). Male sociality predisposes them to affiliate and cooperate in several behavioral contexts. As noted previously, male chimpanzees spend considerable time grooming each other and are well known for forming short-term coalitions in which two individuals join forces to direct aggression toward third parties. Males also hunt together, share meat, develop long-term alliances to improve their dominance rank, and communally defend their territories during boundary patrols.

In what follows, we will show that cooperation and competition are inexorably intertwined in the lives of chimpanzees, and that attempts to characterize their behavior as either one or the other are neither valid nor useful. Competition nevertheless frequently represents the driving force behind chimpanzee cooperation. We therefore consider patterns of conflict between chimpanzees before turning to the manner in which they cooperate.

III. CONFLICT

Wild chimpanzees can spend hours resting and grooming peacefully in mixed social groups, and affiliative interactions among them are frequent and varied. Nevertheless, conflict over food, females, and dominance status

is a regular occurrence in chimpanzee society, and this can lead to intense aggression both within and between groups.

Data on rates of aggression in chimpanzees are surprisingly rare, given the behavior's conspicuous expression and years of systematic observation in the wild. However, clear sex differences have emerged from long-term research. First, males are aggressive much more frequently than females (Bygott, 1979; Goodall, 1986; Muller, 2002). Second, males employ aggression in different contexts than females. Most female aggression is related to competition over food or defense of offspring, whereas male aggression tends to result from competition over dominance status (Goodall, 1986; Muller, 2002; Nishida, 1989; Wittig and Boesch, 2003a).

Males are also aggressive to individuals from neighboring communities in the context of territorial defense. The most forceful displays of chimpanzee aggression occur during intercommunity encounters, as males sometimes cooperate to inflict lethal wounds on strangers. Although females occasionally accompany males on territorial patrols, they do not generally play an active role in such encounters (Goodall, 1986; Nishida, 1979; Watts *et al.*, in press). An exception to this is at Tai, where females frequently join in aggressive calls directed at neighbors, but nonetheless refrain from participating in physical attacks (Boesch, 2003; Boesch and Boesch-Achermann, 2000).

Sex differences in chimpanzee aggression are best understood with reference to the different factors that affect male and female reproduction. Female reproduction is limited primarily by environmental resources such as food, whereas male reproduction is limited primarily by access to females (Bradbury and Vehrencamp, 1977; Emlen and Oring, 1977; Trivers, 1972). Patterns of aggression, their proximate mechanisms, and their relationships to underlying reproductive strategies, are discussed in detail in following sections. We consider males first because aggression between them is currently better understood.

A. WITHIN-GROUP COMPETITION AMONG MALES

Chimpanzees exhibit an extreme female bias in parental investment and pronounced male skews in the operational sex ratio and potential reproductive rate. Consequently, sexual selection theory predicts that mating competition among males should be relatively intense (Clutton-Brock and Parker, 1992; Trivers, 1972). Observations from long-term field studies are consistent with this prediction, as males compete aggressively for both dominance status and access to sexually receptive females (Muller, 2002).

1. *Male Status Competition*

Male chimpanzees are famously preoccupied with rank, and chimpanzee society neatly fits Vehrencamp's (1983) criteria for despotism (Boehm, 1999). Accordingly, status rivalry among males is prominent and observable, mitigating the problems associated with conceptualizing dominance systems in some species (e.g., Fedigan, 1983; Drews, 1993). For example, chimpanzees have a distinct vocalization, the pant-grunt, which functions as a formal signal of subordination (Bygott, 1979; Goodall, 1986; Hayaki *et al.*, 1989). Pant-grunt orientation has repeatedly been shown to correlate with a range of aggressive and submissive interactions (Boesch and Boesch-Achermann, 2000; Bygott, 1979; Hayaki *et al.*, 1989; Nishida and Hosaka, 1996). Within communities, alpha males are normally easy to identify, and it is often possible to rank all males in a linear hierarchy (Goodall, 1986; Newton-Fisher, 2004; Nishida, 1979; Wittig and Boesch, 2003a). When insufficient dyadic interactions have been observed to produce a linear hierarchy, males can be assigned to dominance levels (i.e., alpha, high, middle, or low) (Bygott, 1979; Watts, 1998).

Males regularly perform elaborate agonistic displays to intimidate conspecifics, and thereby maintain or challenge the existing dominance hierarchy. These displays involve exaggerated locomotion, piloerection, and a combination of vigorous branch swaying, branch dragging, rock throwing, ground slapping, and stomping; they can persist for a few seconds to several minutes. Dominance reversals are regularly preceded by a period of heightened aggression and increased rates of display by one or both males in the dyad (Goodall, 1986). Reversals are frequently the result of dyadic fights, but coalitions can also play a critical role in challenges to status (see Section IV.A).

High rank is normally associated with increased aggression among male chimpanzees, even within stable dominance hierarchies (Muller, 2002). This relationship has been quantified in several ways. High-ranking males have been found to exhibit higher rates of agonistic display (Boesch and Boesch-Achermann, 2000; Bygott, 1979; Muller and Wrangham, 2004a), to employ escalated forms of aggression more often (Muller and Wrangham, 2004a; Wittig and Boesch, 2003a), and to initiate aggression more frequently (Nishida and Hosaka, 1996; Wittig and Boesch, 2003a) than lower-ranking conspecifics. High-ranking males also tend to win the aggressive interactions that they initiate (Muller and Wrangham, 2004b; Wittig and Boesch, 2003a).

Among primates generally, high rank is most often associated with aggression in unstable hierarchies when the status of high-ranking males is threatened (Sapolsky, 1992). The frequent positive association between rank and aggression in chimpanzee males suggests that their hierarchies are

perpetually unstable in comparison to other primates, with more or less continuous status challenges. Muller (2002) suggested that two characteristics of chimpanzee society might account for this phenomenon: fission-fusion sociality, and the frequent use of coalitionary aggression. Because chimpanzee parties frequently break apart and come together, males may not see each other for hours, days, or weeks. It follows that high-ranking males should find it difficult to closely monitor the social relationships of other community members. Because coalitions are important to males in maintaining and improving their status (see Section IV.A), and because coalitions are fluid, with males showing high degrees of “allegiance fickleness” (Newton-Fisher, 2002; Nishida, 1983), a level of uncertainty is expected in male status relationships that necessitates frequent aggression to reassert dominance (Muller and Wrangham, 2001, 2004a).

Despite the difficulties of maintaining high rank in chimpanzee society, males are regularly able to maintain the alpha position for years at a time, through skillful social manipulation (Boesch and Boesch-Achermann, 2000; Goodall, 1986). Ntologi, for example, was the alpha male at Mahale for more than 15 years (Uehara *et al.*, 1994). Imoso, the current alpha male at Kanyawara, has held his position for more than seven years.

Maintaining rank, however, is a costly exercise. The performance of agonistic displays and maintenance of social alliances both demand significant investments of time, energy, and valuable resources such as meat (Mitani and Watts, 2001; Nishida *et al.*, 1992). They also incur significant physiological costs, which include elevated levels of the steroid hormones testosterone and cortisol (Muller and Wrangham, 2004a,b). Finally, dominance-related agonistic interactions frequently lead to injury, and they can result in potentially lethal wounds (Fawcett and Muhumuza, 2000; Goodall, 1992; Nishida, 1996; Nishida *et al.*, 1995; Watts, 2004).

2. *The Benefits of Status*

The substantial costs associated with status striving in chimpanzees imply the existence of compensatory benefits. High rank could theoretically confer a survival advantage through enhanced access to resources, an indirect reproductive advantage via kin selection, or a direct reproductive benefit through greater access to cycling females (Muller and Wrangham, 2001). Direct reproductive benefits of male dominance have received the most attention in the primate literature (e.g., Cowlishaw and Dunbar, 1991), as they will here. We first consider other possibilities.

a. *Increased survival* Preferential access to resources could theoretically provide a survival advantage to high-ranking males. Goodall (1986) argued that such an advantage would likely be minor because, when food is scarce,

chimpanzees predictably fragment into small parties or travel alone. Long-term data on weights of individuals from Gombe, however, suggest an advantage to male rank; dominant individuals there show less variance in weight across seasons than subordinates (Pusey *et al.*, 2005). This indicates that contest competition over food is potentially important among males (Pusey *et al.*, 1995). The specific mechanism, however, remains unclear.

Dominant males do tend to occupy prime feeding sites (Goodall, 1986), and may also monopolize high-quality foods such as meat. At Gombe and Ngogo, for example, dominants are more likely than subordinates to steal carcasses from other males, though outright theft of meat is still rare among adult males (Goodall, 1986; Mitani and Watts, 1999). Quantifying the effects of contest competition over food, however, has proven difficult.

Recent work by Houle (2004) documenting predictable within-tree variation in fruit quality suggests a possible way forward in this regard. Houle showed that because the availability of light is higher in the upper canopy than the lower canopy, fruits in the former are larger, more abundant, and higher in sugar content than fruits in the latter. Behavioral observations across four frugivorous primate species in Kibale confirm that dominant species and dominant individuals within species tend to monopolize the upper part of the canopy, presumably gaining feeding benefits.

Kahlenberg (unpublished data) has recently studied the relationship between rank and feeding height in chimpanzees at Kanyawara, Kibale National Park. She found that high-ranking males consistently fed higher in the canopy than low-ranking males when co-feeding in trees. There were no rank-related differences in height when males were in trees but not feeding, however. Furthermore, in cases where males were observed fighting over food, losers predictably fed lower in the canopy or left the tree altogether after the aggressive interaction. These data suggest a role for contest competition within fruiting trees, but more work is necessary to quantify rank-related differences in actual caloric intake over time. Work is currently in progress on this topic at the Kanyawara study site.

Even if high-ranking males do gain advantages in intragroup feeding competition, it is not certain that this translates into a direct survival advantage. The physiological costs associated with maintaining high rank might still outweigh any benefits of increased food. Long-term data on mortality rates across high- and low-ranking males could eventually settle this issue.

b. Indirect reproductive advantage Little is known about the potential kin-selected benefits of male rank. Evidence from Gombe suggests that female rank has significant effects on reproduction, through increased infant survivorship and decreased interbirth intervals (Pusey *et al.*, 1997).

The possibility that a male's status can influence the dominance standing of his mother or brothers, however, remains unexplored. Since most females transfer from their natal community during adolescence, males would not normally be expected to influence the rank of their sisters.

c. Direct reproductive advantage Altmann's (1962) "priority of access" model proposes that across primates, dominance rank and reproductive success should be positively correlated because high-ranking males monopolize matings with estrous females. Historically, tests of the model have employed indirect measures of reproductive success, such as copulation frequency, that may or may not reflect actual paternity (Fedigan, 1983). More recently, advances in extracting, amplifying, and sequencing DNA from non invasively collected samples have facilitated direct assessment of male reproductive success in wild chimpanzees (Constable *et al.*, 2001; Vigilant *et al.*, 2001).

Behavioral assessment of chimpanzee paternity is complicated by the fact that mating takes place in three distinct contexts (Tutin, 1979). *Opportunistic mating* occurs in multi-male parties with no male herding or coercion. *Possessive mating* is characterized by male attempts to gain exclusive access to a female by directing aggression at both her and rival males. In a *consortship*, a male restricts access to a female by accompanying her to a peripheral part of the territory for several days to more than a month. Goodall (1986) argued that rank should not be expected to show a strong relationship with reproductive success in male chimpanzees because low-ranking males have ample mating opportunities in the opportunistic and consortship contexts. She further hypothesized that the intense drive for status that characterizes male chimpanzees must have evolved in a different social context from the one that chimpanzees currently find themselves in (Goodall, 1986).

Long-term observations, however, indicate that, despite variation in the frequency of consortships across study sites, this is never the predominant male strategy (Muller and Wrangham, 2001). Gombe falls at one end of the distribution, with an estimated 25% of conceptions resulting from consortships (Wallis, 1997). At the other extreme, only one clear consortship has been recorded in more than 15 years of observation at Kanyawara (Wrangham, 2002). Consortships have been estimated to account for between 8–20% of conceptions at Mahale (Hasegawa and Hiraiwa-Hasegawa, 1990), and around 6% at Tai (Boesch and Boesch-Achermann, 2000).

Why the number of consortships at Gombe appears to be higher than at other sites is not currently known, but it may be related to the low rate of female transfer recorded there (Constable *et al.*, 2001). Constable and

colleagues (2001) noted that Gombe females often consorted with low-ranking males when they had high-ranking male relatives in the community. This, together with the fact that males sometimes attempt to force copulations with their unwilling mothers or sisters, suggests that consortships with low-ranking males may be a female strategy to avoid inbreeding.

Most conceptions result from mating in multi-male parties. At first glance, observations of such parties do not strongly support the priority of access model. For when total copulation rate is plotted against male rank, the results are inconsistent, even within study sites across time. Most studies find no significant relationship between dominance rank and total copulation rate (Gombe: 1972–1975; Tutin, 1979; Mahale: 1980–1982 and 1991; Hasegawa and Hiraiwa-Hasegawa, 1990; Nishida, 1997; Tai: Boesch and Boesch-Achermann, 2000; Kanyawara: Wrangham, 2002; Budongo: Newton-Fisher, 2004), though occasionally a significant relationship exists (Gombe: 1973–1974; Goodall: 1986; Mahale, 1992; Nishida, 1997). It has recently become clear, however, that total copulation rate is not an informative behavioral measure, because all copulations do not have an equal probability of conception. Variation in the likelihood of conception is predictable: (1) between females, (2) between cycles within a female, and (3) at different times within a female's cycle. Male chimpanzees respond to this variation, and it now appears that high-ranking males consistently monopolize the copulations that are most likely to result in conceptions.

Variation between females in the likelihood of conception is pronounced in nulliparous versus parous females. Wrangham (2002) reviewed evidence that nulliparous females consistently exhibit more cycles per conception than parous females. Thus, each copulation with a nulliparous female is less likely to result in conception than one with a parous female. Males respond by showing less interest in nulliparous females. They do not mate-guard nulliparous females, nor do they employ other forms of sexual coercion when nulliparous females are in estrous (reviewed in Wrangham, 2002). Furthermore, males do not show increased testosterone levels in response to fully swollen nulliparous females, as they do with parous females (Muller and Wrangham, 2004a). Presumably, this is due to the lack of male competition for nulliparous females. The net result is that while total copulation rates for high-versus low-ranking males and for parous versus nulliparous females are similar, high-ranking males consistently show higher copulation rates with parous females (Hasegawa and Hiraiwa-Hasegawa, 1990; Wrangham, 2002). Low-ranking males, then, are copulating most frequently with less fecund nulliparous females.

Individual females also show variation in the probability of conception across cycles. Female fecundity has been quantified in a number of field studies by measuring urinary or fecal metabolites of ovarian steroids that

have a significant influence on reproduction (Emery Thompson, in press). Early and late follicular estrogen levels, luteal estrogen levels, and luteal progesterone levels are all measures that have been shown to correlate with conceptive success in humans and other apes (Emery Thompson, in press; Lipson and Ellison, 1996; Nadler and Collins, 1991; Wasser, 1996).

Two recent studies of ovarian function in wild chimpanzees (Deschner *et al.*, 2004, Emery Thompson, in press) suggest that males assess female fecundity across cycles, and that high-ranking males show greater interest in females when they are more likely to conceive. Emery Thompson (in press), for example, found that at Gombe, Kanyawara, and Budongo, urinary estrone conjugates in female chimpanzees were significantly higher in the swelling and post-swelling phases of conception cycles than in non-conception cycles. Female copulation rates were also higher in conception cycles than non-conception cycles. Because most copulations are initiated by males (Goodall, 1986), this suggests increased male interest during conception cycles. It is not clear from this study whether males competed more intensely for females in conception cycles. Deschner *et al.* (2004), however, found that as the number of cycles to conception decreased at Taï, the alpha male associated with individual females significantly more often and copulated more frequently during the periovulatory period. Urinary estrogen levels in Taï females also increased significantly as the number of cycles to conception decreased (*ibid.*).

The cue that males use to monitor female reproductive condition is not known, but swelling size probably plays a role, as both wild and captive data show a positive relationship between swelling size and hormonal measures of fecundity (Deschner *et al.*, 2004; Emery and Whitten, 2003). At Taï, Deschner *et al.* (2004) showed that swelling size within individual females grew progressively larger with each cycle as females approached the conception cycle. At the same time, urinary estrogen concentrations in the periovulatory period also increased across cycles, peaking during the conception cycle.

Finally, chimpanzee females show variation in the probability of conception within periods of peak sexual swelling. Maximal swelling lasts for 10–12 days on average, and mating is normally restricted to this period (Goodall, 1986; Tutin, 1979; Wallis, 1997). Hormonal studies of wild (Deschner *et al.*, 2003; Emery Thompson, in press) and captive (Emery and Whitten, 2003; Graham, 1981) females indicate that ovulation consistently occurs during the last 6 days of maximal swelling, and most frequently (though not exclusively) in the 2 days prior to detumescence.

Because of limitations on gamete survival, copulations during the first half of a female's maximal swelling are extremely unlikely to lead to conception (Emery Thompson, in press). Male behavior is consistent with

the idea that early copulations are less valuable. High-ranking males are more likely to mate-guard females during the periovulatory period, resulting in increased rates of aggression and increased intensity of aggression at this time (Muller and Wrangham, 2004a; Watts, 1998; Wrangham, 2002) (Fig. 1). As a result, high-ranking males regularly have more copulations with females in the periovulatory period than low-ranking males do (Hasegawa and Hiraiwa-Hasegawa, 1990; Matsumoto-Oda, 1999a; Nishida, 1997; Tutin and McGinnis, 1981).

In sum, behavioral data from across study sites are consistent with the priority of access model. Male interest in females varies with female fecundity, and high-ranking males use aggression to maintain preferential access to females when they are most likely to conceive. However

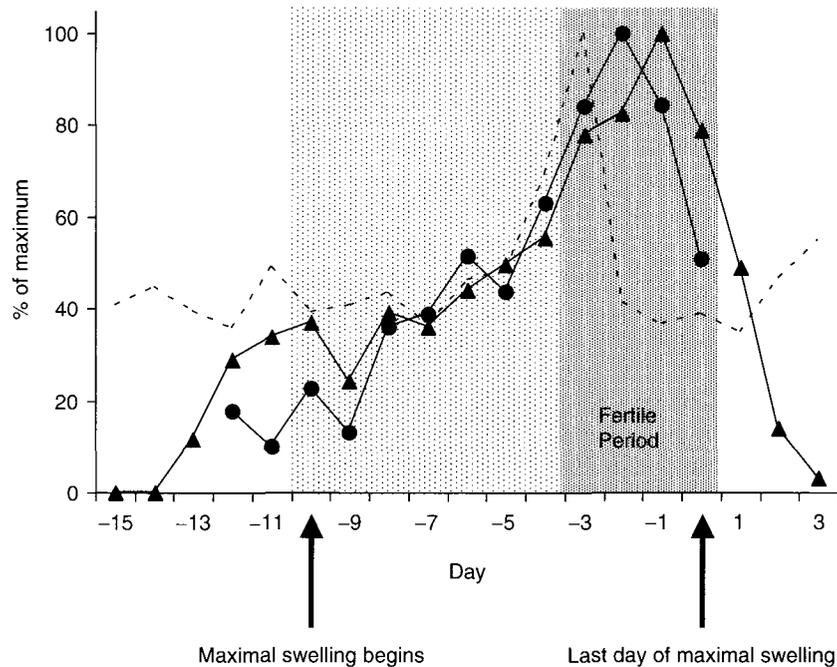


FIG. 1. Relationship between female swelling stage and rates of copulation and mate-guarding. Composite figure shows copulation rates from Mahale (circles), mate-guarding rates from Gombe (triangles), and levels of urinary estrone conjugates (E2) from captive chimpanzees (dashed line), across days of maximal tumescence (shaded areas). Within the period of maximal swelling, rates of copulation and mate-guarding increase in the days surrounding ovulation. Ovulation is assumed to occur approximately 2 days after the peak in E2. Captive estrogen data adapted from Emery and Whitten (2003). Mahale data adapted from Hasegawa and Hiraiwa-Hasegawa (1990). Gombe data adapted from Tutin and McGinnis (1981).

persuasive the behavioral data, they are still an indirect measure of reproductive success, and genetic data on actual paternity would provide convincing corroboration. Preliminary genetic data from Tai, however, seemed to undermine these behavioral data because they indicated that a large number of conceptions were from extra-community males (Boesch and Boesch-Achermann, 2000; Gagneux *et al.*, 1997). This claim was even more surprising because in some cases the behavioral data allowed for an extremely narrow window during which females might have mated with extra-community males. This suggested a deliberate attempt to cuckold the community males, but no clear benefit to the females was evident (e.g., Wrangham, 1997).

Ultimately, it was discovered that the genetic data from Tai were flawed, due to mislabeling of samples and other technical problems (Vigilant *et al.*, 2001). Because of these errors, Gagneux *et al.* (2001) later retracted the original publication. More recent genetic studies from Gombe (Constable *et al.*, 2001) and Tai (Boesch *et al.*, in press; Vigilant *et al.*, 2001) have confirmed that high-ranking males, and particularly alphas, have significantly higher reproductive rates than lower-ranking males.

B. MALE AGGRESSION AGAINST FEMALES

Despite the intense competition among chimpanzee males for dominance status, female chimpanzees are as likely as males to be victims of male aggression (Goodall, 1986; Muller, 2002). Much of this aggression probably functions as sexual coercion, as it appears to make females more likely to mate with some males and less likely to mate with others (Smuts and Smuts, 1993). Systematic tests of this idea have yet to be performed, however, and few published data exist.

Forced copulations represent an apparently straightforward example of sexual coercion, but these are uncommon (Goodall, 1986). Tutin (1979) recorded only two instances in 1137 observed copulations at Gombe. Males at Gombe, Mahale, and Ngogo occasionally direct aggression at both anestrus and estrus females until they accompany them on consortships (Goodall, 1986; Smuts and Smuts, 1993; Mitani, personal observation), but forced consortships are apparently rare or absent at Tai (Boesch and Boesch-Achermann, 2000).

Establishing that other forms of male aggression function as sexual coercion is difficult, as this requires knowledge not only of the aggression itself, but the subsequent behavior of the aggressor, the victim, and other individuals (Smuts and Smuts, 1993). Much male aggression against females takes place in contexts suggestive of sexual coercion, however. For example, estrus females are subject to significantly higher rates of

aggression from males than anestrus females (Mahale: Matsumoto-Oda and Oda, 1998; Kanyawara: Muller, 2002). This includes aggressive interference in copulations and herding by mate-guarding males (Goodall, 1986; Watts, 1998; Wrangham, 2002).

Preliminary evidence from Kanyawara suggests that male sexual aggression imposes serious physiological costs on females (Muller, unpublished data). Parous females there show dramatic increases in urinary cortisol excretion during periods of maximal swelling, when they receive increased aggression from males. Nulliparous females, on the other hand, are not mate-guarded by males, and they do not exhibit such cortisol increases during periods of maximal swelling.

The extent to which male coercion constrains female choice among chimpanzees is not known. Because females are expected to be choosier when they are more likely to conceive (Stumpf and Boesch, 2005), efforts to quantify female choice have focused on the periovulatory period (POP). At Mahale, Matsumoto-Oda (1999b) found that copulations with high-ranking males increased significantly during the POP, suggesting to her that females preferred high-ranking males at this time. It is nonetheless difficult to discriminate between this hypothesis and the alternative that high-ranking males constrain female behavior during the POP. In the same study, for example, male solicitations were significantly more likely to succeed when higher-ranking males were absent (Matsumoto-Oda, 1999b). Similarly, almost all female solicitations of adult males failed when higher-ranked males were nearby.

Stumpf and Boesch (2005) recently examined female proceptivity and resistance at Tai, and found that females were more selective during periods when they were more likely to conceive. Rates of female proceptivity were lower, and female resistance rates higher, during the POP compared to the non-POP. No significant difference in male aggression toward females was detected from the non-POP to the POP, suggesting that male coercion was not responsible for the pattern.

Similar to Mahale, females at Tai showed a general preference during the POP for males that were high-ranking or soon became high ranking (Stumpf and Boesch, 2005). Thus, it is possible that female interests are generally aligned with those of high-ranking males during the POP. These studies are based on a small sample of males, though, and further observations are needed to establish female preferences.

Infanticide is a final, indirect form of male aggression against females that has been recorded within groups at Mahale, Kanyawara, and Ngogo (Clark Arcadi and Wrangham, 1999; Mitani and Watts, unpublished data; Nishida and Kawanaka, 1985; Takahata, 1985). At Mahale, victims' mothers have sometimes resided in peripheral areas between communities

(Nishida, 1990). This suggested to researchers there (Hamai *et al.*, 1992; Nishida, 1990) that infanticide functions as sexual coercion, forcing females to shift away from peripheral areas and to mate more restrictively. This idea remains speculative, however.

C. WITHIN-GROUP COMPETITION AMONG FEMALES

Whereas dominance rank is easy and reproductive success difficult to assess in male chimpanzees, precisely the opposite is true for females. Female chimpanzees do not exhibit overt concern with status as males do, and their dominance relationships are correspondingly subtle. Observers often find it difficult to rank female chimpanzees, because submissive signals and aggressive interactions between them are rare (Bygott, 1974; Goodall, 1986, Muller, 2002; Nishida, 1989; Pusey *et al.*, 1997). Given the association between low levels of agonistic behavior and stable dominance hierarchies in other primate species (Sapolsky, 1983, 1993), it seems likely that female chimpanzee status relationships are generally more stable than those of males.

Evidence for rank stability comes from Gombe, where Pusey *et al.* (1997) were able to assign females to dominance levels (high, medium, or low) by combining data in 2-year blocks. They found that a female's rank at age 21 strongly predicted her rank a decade later. The importance of early rank acquisition is supported by the fact that parous female residents direct a significant proportion of aggression toward nulliparous immigrants, who represent future resource competitors (Goodall, 1986; Muller, 2002; Nishida, 1989). Nishida (1989) argued that once females have settled into their core areas, they "have no pressing reason to strive for higher rank," and thus show little aggression toward other resident females. By this reasoning, the costs of escalated aggression, which include potential danger to offspring, outweigh any benefits of increased dominance standing.

The idea that females do not incur significant benefits as a result of dominance rank is consistent with the view that scramble competition is more important than contest competition for female chimpanzees (e.g., Sterck *et al.*, 1997). However, two recent studies from Gombe suggest that there, at least, contest competition may be significant. First, as with male chimpanzees, dominant females at Gombe show less variation in weight across seasons, suggesting better access to resources (Pusey *et al.*, 2005). Dominant females are also heavier, though it is not clear whether this is a consequence or a cause of dominance. Second, high-ranking females at Gombe live longer than low-ranking females, and they enjoy shorter inter-birth intervals and higher offspring survival (Pusey *et al.*, 1997). They also produce daughters that reach sexual maturity earlier than those of

low-ranking mothers. Presumably, these benefits are related to improved nutrition (Pusey *et al.*, 1997).

Wittig and Boesch (2003b) have also stressed the importance of contest competition for female chimpanzees at Tai. They argue that contest competition is more intense there than in other communities because females have frequent access to monopolizable resources such as meat and stone tools for nut cracking, and they are more social than females at other sites. Consistent with this idea, they detected a higher rate of pant-grunting (a formal signal of subordination) among adult females at Tai than at other sites. In addition, they were able to rank females in a linear hierarchy, and they found that dominant females outcompeted subordinates for monopolizable resources. Despite these tantalizing hints, the absence of data on body weights and reproductive outcomes makes it difficult to assess the ultimate importance of dominance rank for Tai females.

The precise mechanism of contest competition among female chimpanzees is not clear, but both long- and short-term processes may be involved. In the short term, high-ranking females probably occupy the best feeding sites. As discussed previously (Section III.A.2.a), the upper canopy represents a particularly high-quality site, because increased light renders fruits there larger, more abundant, and more nutrient dense than those in the lower canopy (Houle, 2004). Kahlenberg (unpublished data) recently discovered consistent differences in feeding height related to female dominance rank among chimpanzees at Kanyawara. When females were classified in broad rank categories based on pant-grunt vocalizations and agonistic interactions, high-ranking females were found to feed higher than low-ranking females when co-feeding in trees. No height difference was found when females were in trees but not feeding. Furthermore, in cases where females were observed fighting over food, losers predictably fed lower in the canopy or left the tree altogether after the aggressive interaction. Detailed observations of feeding rates and nutritional analyses of fruits from different parts of the canopy are currently underway at Kanyawara. These data will permit a more precise evaluation of female feeding competition.

In the long term, high-ranking females may also occupy better core areas within a community's territory. A rigorous test of this hypothesis has not been conducted and would require detailed ecological data from specific habitats within a community range. Currently available observations from Kanyawara and Gombe are suggestive, but ambiguous. Emery Thompson *et al.* (in press) reported that peripheral females at Kanyawara exhibited longer inter-birth intervals and lower levels of ovarian steroids than more central females. At Gombe, Williams *et al.* (2002b) found that peripheral females did either very well or very poorly reproductively and suggested

that being peripheral is a high-risk strategy. It is not clear, however, whether differences between central and peripheral females are related to decreased food availability in peripheral areas, or to an increased threat of aggression and infanticide to peripheral females from males in neighboring territories.

Additional aspects of female ranging at Gombe are consistent with the idea that high-ranking females impose costs on low-ranking females. Williams (2000) found that young females at Gombe tend to settle in areas away from the highest-ranking female. Furthermore, low-ranking females at Gombe are significantly less social than high-ranking females, and they avoid high-ranking females when they do associate with others (Williams *et al.*, 2002a). Again, the specific costs are unclear. Feeding costs, as described previously, represent one possibility. Infanticide by high-ranking females may also be a significant risk for low-ranking mothers. Infanticides and attempted infanticides by high-ranking females are well documented at Gombe (Goodall, 1986; Pusey *et al.*, 1997).

Even as the mechanisms of competition among female chimpanzees become clearer, the significant effect of female status on reproduction at Gombe remains puzzling. For if dominance regularly has important effects on female reproduction, one would expect females to show more overt competition over rank than they do. Ultimately, it will be possible to examine long-term patterns of female reproduction from various study sites to determine whether female dominance rank is consistently associated with a significant reproductive advantage. Until that is done, the possibility remains that female competition at Gombe is extreme compared to most sites. Muller (2002) reviewed three lines of evidence that female competition at Gombe is particularly intense. First, young females at Gombe exhibit a low rate of transfer (Williams, 2000). A female that stays in her natal community presumably bears increased costs associated with inbreeding, but may benefit from associating with a high-ranking mother, for example, by settling in her core area. Second, both infanticide and attempted infanticide by high-ranking females against low-ranking mothers appear to be more common at Gombe than at other sites (Clark Arcadi and Wrangham, 1999; Pusey *et al.*, 1997). Finally, aggressive interactions between parous females appear to be more common at Gombe than at Kanyawara (Muller, 2002).

D. INTERGROUP CONFLICT

Intergroup relations among wild chimpanzees are predictably hostile. Male chimpanzees are philopatric, and they aggressively defend their community range from incursions by neighboring males (Boesch and

