

---

## Conflict and Cooperation in Wild Chimpanzees

---

MARTIN N. MULLER\* and JOHN C. MITANI<sup>†</sup>

\*DEPARTMENT OF ANTHROPOLOGY  
BOSTON UNIVERSITY  
BOSTON, MASSACHUSETTS, 02215, USA

<sup>†</sup>DEPARTMENT OF ANTHROPOLOGY  
UNIVERSITY OF MICHIGAN  
ANN ARBOR, MICHIGAN, 48109, USA

### 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 km<sup>2</sup> 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

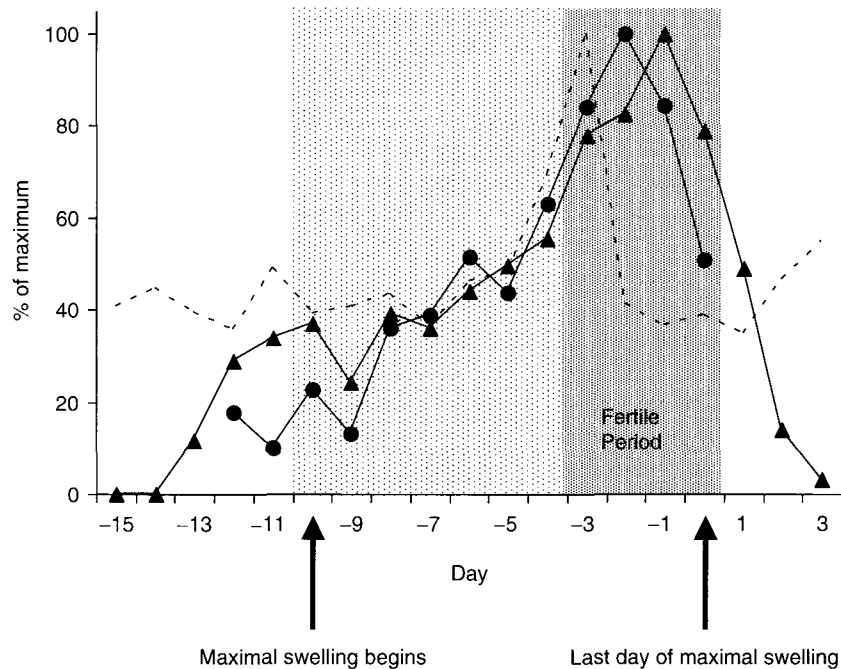


FIG. 1. Relationship between female swelling stage and rates of copulation and mate-guarding. Composite figure shows copulation rates from Mahale (circles), mate-guarding rates from Gombe (triangles), and levels of urinary estrone conjugates (E2) from captive chimpanzees (dashed line), across days of 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

Boesch-Achermann, 2000; Goodall, 1986; Nishida, 1979; Watts and Mitani, 2001). In the course of such defense, they sometimes cooperate to inflict lethal wounds on vulnerable strangers (Goodall *et al.*, 1979; Watts *et al.*, in press; Wilson *et al.*, 2004). We briefly review what is currently known about the patterns, mechanisms, and functional significance of intergroup aggression in chimpanzees. More comprehensive treatments of this topic can be found in recent reviews by Wrangham (1999) and Wilson and Wrangham (2003).

Intergroup encounters occur both by chance, when chimpanzees feed in peripheral parts of their range, and by design, when males patrol those areas. Patrolling males move to the periphery of their territories, where they actively search for signs of members of other communities (Boesch and Boesch-Achermann, 2000; Goodall, 1986; Watts and Mitani, 2001). An unusual suite of behaviors makes patrolling one of the most distinctive aspects of wild chimpanzee behavior (*ibid.*). Chimpanzees are uncharacteristically silent during patrols, moving in single file and maintaining close proximity to each other. In contrast, chimpanzee parties of similar size are usually noisy and scattered as individuals feed, travel, and socialize. Patrolling individuals are extremely wary. They stop frequently to scan the environment and are attentive to motion in the trees and on the ground; patrollers also sniff the ground and vegetation and inspect signs of conspecifics such as nests, food remains, urine, and feces. Chimpanzees only rarely feed during patrols. Instead they alter their normal foraging movements, occasionally making deep incursions (or “commando attacks”: Boesch, 2003; Boesch and Boesch-Achermann, 2000) into the territories of their neighbors, traveling two or more kilometers past the border, with the apparent intention of finding and attacking strangers (Wrangham, 1999). Patrolling is primarily a male activity, with the extent of female participation varying among populations. Females occasionally join males on deep incursions but play a bystander role during attacks (Boesch and Boesch-Achermann, 2000; Muller and Mitani, personal observation).

### 1. *Aggression Against Males*

When a group of males encounters a lone male from another community, or isolates a single male from a larger party, prolonged and vicious attacks can occur. During such gang attacks, males cooperate to immobilize their victim, and subsequently take turns biting, kicking, and pummeling him (Goodall *et al.*, 1979; Watts *et al.*, in press; Wilson *et al.*, 2004). Because they outnumber their target, the risk to aggressors appears low. Attacks can last for more than 20 minutes, during which the antagonists receive no apparent injuries (*ibid.*).

Targets of gang attacks, on the other hand, may be killed. In some situations, death occurs immediately, whereas in other cases victims are left alive, but with obviously fatal injuries. The latter may be more likely when an attack is interrupted by the arrival of additional chimpanzees from the victim's community (Watts *et al.*, in press). A detailed summary of observed, lethal intercommunity attacks on adults and adolescents is presented by Wilson and Wrangham (2003). These include nine killings at Gombe (two of females), two at Kanyawara, and three at Ngogo. Two additional killings of adults were observed at Ngogo in 2004 (Watts *et al.*, in press; S. Amsler and H. Sherrow, personal communication). In Table II, we update information from Wilson and Wrangham's (2003) Table I to include more recent observations.

The relative rarity of lethal intercommunity attacks makes it problematic to estimate a reliable rate (Wrangham, 1999). The actual number of killings

TABLE II  
INTERCOMMUNITY KILLINGS OF ADULTS AND ADOLESCENTS, 1972–2004

Site	Year	Victim (Sex)	Aggressors' Community	Victim's Community	Evidence
Gombe	1972	Unknown (F)	Kahama?	Kalande?	Inf. <sup>a</sup>
Gombe	1974	Godi (M)	Kasekela	Kahama	Obs. <sup>b</sup>
Gombe	1974	Dé (M)	Kasekela	Kahama	Obs. <sup>b</sup>
Gombe	1975	Goliath (M)	Kasekela	Kahama	Obs. <sup>b</sup>
Gombe	1975	Madam Bee (F)	Kasekela	Kahama	Obs. <sup>b</sup>
Gombe	1977	Sniff (M)	Kasekela	Kahama	Obs. <sup>b</sup>
Gombe	1977	Charlie (M)	Kasekela	Kahama	Inf. <sup>b</sup>
Gombe	1998	Unknown (M)	Kasekela	Kalande	Obs. <sup>d</sup>
Gombe	2002	Rusambo (M)	Kasekela	Mitumba	Inf. <sup>d</sup>
Kibale	1992	Ruwenzori (M)	Rurama	Kanyawara	Inf. <sup>c</sup>
Kibale	1998	Unknown (M)	Kanyawara	Sebitole	Inf. <sup>c</sup>
Kibale	2002	Unknown (M)	Ngogo	Unknown	Obs. <sup>e</sup>
Kibale	2002	Unknown (M)	Ngogo	Unknown	Obs. <sup>e</sup>
Kibale	2002	Unknown (M)	Ngogo	Unknown	Obs. <sup>e</sup>
Kibale	2004	Unknown (M)	Ngogo	Unknown	Obs. <sup>e</sup>
Kibale	2004	Unknown (M)	Ngogo	Unknown	Obs. <sup>e</sup>

Table has been updated from Wilson and Wrangham (2003). "Evidence" denotes whether the attack was directly observed (Obs.) or inferred from strong evidence, such as finding a body with wounds consistent with a chimpanzee attack (Inf.).

<sup>a</sup> Wrangham, 1975.

<sup>b</sup> Goodall, 1986.

<sup>c</sup> Wrangham, 1999.

<sup>d</sup> Wilson *et al.*, 2004.

<sup>e</sup> Watts *et al.*, in press.

must be higher than the observed number, as fission-fusion grouping patterns make it difficult to keep track of all community members, even at long-term study sites. At Mahale, six healthy males disappeared under suspicious circumstances. Researchers attributed these disappearances to probable intergroup attacks (Nishida *et al.*, 1985). Healthy young males have also disappeared suddenly from other communities, suggesting, but by no means confirming, intercommunity aggression as the cause (Wrangham, 1999). Given the number of chimpanzee deaths from known causes, however, it is clear that lethal intercommunity aggression is a significant contributor to mortality (*ibid.*). Wrangham (1999) estimated a rate of 0.25 lethal attacks per year for communities of eastern chimpanzees.

Current data suggest a lower rate of intercommunity killing among western chimpanzees (Boesch and Boesch-Achermann, 2000; Wilson and Wrangham, 2003; Wrangham, 1999). Despite strikingly similar patterns of patrolling and territorial aggression between Tai and the eastern study sites, including gang attacks with wounding, adult fatalities have never been witnessed at Tai. One possible reason for this is that food availability at Tai is comparatively high, resulting in consistently large party sizes and a low rate of solitary foraging (Boesch and Boesch-Achermann, 2000). This probably reduces imbalances of power during intergroup encounters, significantly increasing the cost of prolonged attacks. Consistent with this idea, during some gang attacks at Tai, males have been “rescued” by the arrival of other community members (Boesch and Boesch-Achermann, 2000). Additionally, males in one community at Tai stopped patrolling and avoided their neighbors altogether when predation and disease had killed all but four of them (Boesch and Boesch Achermann, 2000).

## 2. *Aggression Against Females and Infants*

When multiple males from one community encounter a strange female, responses vary according to her age and reproductive state (Williams *et al.*, 2004). Males normally interact peacefully with cycling, swollen females, but frequently attack older non-swollen females and females with infants. Although these attacks can lead to serious wounds, it appears that males are less interested in killing strange females than males. Only two documented cases of females being killed in intergroup encounters exist; both of these were at Gombe (Wilson and Wrangham, 2003).

Males do appear to target infants, however, during encounters with strange females. Intergroup infanticides have been recorded at Gombe (Goodall, 1986; Wilson *et al.*, 2004), Mahale (Kutsukake and Matsusaka, 2002), Kibale (Watts and Mitani, 2000; Watts *et al.*, 2002), and Budongo (Newton-Fisher, 1999c). In one case at Tai, females were found consuming

a dead infant, but it was not clear whether inter- or intracommunity infanticide was responsible (Boesch and Boesch-Achermann, 2000).

As with lethal attacks on adults, it is difficult to estimate a rate of intercommunity infanticide, but in the eastern study sites it is clearly a significant source of infant mortality. In Table III we update Wilson and Wrangham's (2003) Table II to present a current tally of observed instances of intergroup infanticide in chimpanzees.

### 3. *Proximate Mechanisms*

The leading proximate explanation for lethal intercommunity aggression in chimpanzees is Manson and Wrangham's (1991) "imbalance of power hypothesis." This hypothesis focuses on the costs rather than the benefits of aggression, suggesting that males are motivated to attack conspecifics when they can do so with little or no risk to themselves (Wrangham, 1999). The proximate benefit of wounding or killing neighbors is suggested to be an increase in relative intercommunity dominance (*ibid.*).

Wrangham (1999) and Wilson and Wrangham (2003) reviewed observational evidence supporting the imbalance of power hypothesis from Gombe, Mahale, Kibale, and Tai. At all of these sites, relative party size appears to be a strong predictor of the intensity of aggression during intergroup encounters. At Tai, for example, large parties are more likely than small ones to make incursions into neighboring territories and to attack strangers (Boesch and Boesch-Achermann, 2000). At Ngogo, small patrols are more likely than large ones to flee upon encountering strangers, and large parties are more likely than small ones to attack strangers (Watts and Mitani, 2001). A recurrent problem with such observational data, though, is that precise numbers of males in neighboring parties are rarely known, so it is difficult to accurately assess relative party size and power imbalances (Mitani *et al.*, 2002b).

Experimental evidence from Kanyawara confirms that males are extremely sensitive to imbalances of power. In a series of playbacks, Wilson *et al.* (2001) showed that male decisions to approach a simulated intruder depended primarily on whether a favorable numerical asymmetry existed. When the pant-hoot call of a single foreign male was played to parties of varying size and composition, Wilson and colleagues found that: (1) all-female parties predictably stayed silent, or moved away from the call; (2) parties with one or two males remained silent, but moved cautiously toward the call about 50% of the time; and (3) parties with three or more males tended to respond immediately with loud calls, moving quickly and excitedly toward the playback site.

Finally, patterns of ranging and association are consistent with the imbalance of power hypothesis, and they highlight the pervasive effects of

TABLE III  
OBSERVED AND INFERRED INTERCOMMUNITY INFANTICIDES, 1967–2005

Site	Year	Infant's sex	Aggressors' Community	Victim's Community	Evidence
Budongo	1995	Unknown	Sonso	N15	Inf. <sup>e</sup>
Budongo	1995	M	Sonso	N15	Obs. <sup>e</sup>
Gombe	1971	Unknown	Kasekela	Unknown	Obs. <sup>a</sup>
Gombe	1975	M	Kasekela	Unknown	Inf. <sup>b</sup>
Gombe	1975	F	Kasekela	Unknown	Obs. <sup>b</sup>
Gombe	1979	Unknown	Kasekela	Unknown	Obs. <sup>d</sup>
Gombe	1993	F	Kasekela	Mitumba	Obs. <sup>i</sup>
Gombe	1998	Unknown	Kasekela	Kalande	Obs. <sup>i</sup>
Kibale	1999	Unknown	Ngogo	Unknown	Obs. <sup>f</sup>
Kibale	1999	Unknown	Ngogo	Unknown	Obs. <sup>f</sup>
Kibale	2001	Unknown	Ngogo	Unknown	Obs. <sup>g</sup>
Kibale	2001	Unknown	Ngogo	Unknown	Inf. <sup>g</sup>
Kibale	2004	M	Ngogo	Unknown	Obs. <sup>j</sup>
Kibale	2004	Unknown	Ngogo	Unknown	Obs. <sup>j</sup>
Kibale	2005	Unknown	Ngogo	Unknown	Inf. <sup>k</sup>
Mahale	1974	M	Mahale	M Group	Inf. <sup>c</sup>
Mahale	1976	M	Mahale	K Group	Sus. <sup>c</sup>
Mahale	2000	M	Mahale	Unknown	Inf. <sup>h</sup>

Table has been updated from Wilson and Wrangham (2003). "Evidence" denotes whether the attack was directly observed (Obs.), inferred from strong evidence, such as finding males eating a freshly killed infant (Inf.), or suspected from the sudden disappearance of a healthy individual (Sus.).

<sup>a</sup> Bygott, 1972.

<sup>b</sup> Goodall, 1977.

<sup>c</sup> Nishida *et al.*, 1979.

<sup>d</sup> Goodall, 1986.

<sup>e</sup> Newton-Fisher, 1999.

<sup>f</sup> Watts and Mitani, 2000.

<sup>g</sup> Watts *et al.*, 2002.

<sup>h</sup> Kutsukake and Matsusaka, 2002.

<sup>i</sup> Wilson *et al.*, 2004.

<sup>j</sup> S. Amsler and H. Sherrow, personal communication.

<sup>k</sup> Mitani, personal observation.

territoriality and intergroup aggression on chimpanzee life (Wrangham, 1999). Chimpanzees tend to use the central parts of their territories most intensely, visiting peripheral areas infrequently (Boesch and Boesch-Achermann, 2000; Herbinger *et al.*, 2001). When they do pass through peripheral parts of their territories or patrol, they tend to do so in parties that are large or contain many males (Mitani and Watts, in press; Wrangham, 1999).

#### 4. *Functional Explanations*

Wrangham (1999) proposed that male chimpanzees employ lethal inter-group aggression to reduce the coalitionary strength of their neighbors and to expand their territories. Until recently, however, the functional significance of territorial expansion was not clear. Two benefits seemed possible. First, larger territories might include more females. Second, females living in larger territories might have higher reproductive rates, due to enhanced access to resources.

Recent data from Gombe favor the latter explanation. As described previously, at both Gombe and Kibale males can be extremely aggressive toward strange females, attacking them and their infants. Perhaps because of this, territorial expansion does not automatically result in new females being added to a community (Williams *et al.*, 2004). Rather, females living in shrinking territories often shift or contract their ranges to stay within the new border areas (Williams *et al.*, 2002b).

The clearest examples of females being added to a community through territorial expansion occurred with the extinction of community males at Gombe and Mahale. Following these extinctions, neighboring males at both sites appropriated territory and females from the affected communities (Goodall, 1986; Goodall *et al.*, 1979; Nishida *et al.*, 1985). It is not currently clear how common it is for communities to lose all of their adult males in this fashion.

The primary benefit of territorial aggression, then, appears to be the acquisition of a secure feeding area. Two recent studies from Gombe support this idea. First, long-term data on chimpanzee weights show that in years when the community range was larger, the density of chimpanzees was lower, and mean weights were higher (Pusey *et al.*, 2005). Chimpanzees were about 4.4% lighter in the high-density than the low-density years (*ibid.*). Second, interbirth intervals of resident females at Gombe were shorter during periods when the territory was larger (Williams *et al.*, 2004). During these times both males and females became more gregarious, suggesting increased food availability (*ibid.*).

If males defend a territory primarily to secure feeding benefits, then attacks against infants may simply function to remove future competitors and drive strange females away from border areas. Infanticide by males might also be a strategy to coerce females to leave their community, and join that of the aggressors (mountain gorillas: Watts, 1989), but the apparently low rate of secondary female transfer in chimpanzees argues against this hypothesis (Watts *et al.*, 2002; Williams *et al.*, 2004). Given the significant number of observed gang attacks on adult females and their infants, the low number of fatalities in comparison to males is striking. Could males

be less motivated to kill strange females because such females do occasionally transfer between communities, offering potential reproductive opportunities? The answer is not presently known; more long-term data on females from adjacent communities is needed.

### 5. *Controversies*

Although the preceding outline of intergroup aggression would probably satisfy most researchers studying chimpanzees in the wild, this picture has proven controversial among some anthropologists (e.g., Ferguson, 1999; Marks, 2002; Power, 1991; Sussman, 1999). These critics have maintained that escalated aggression in chimpanzees is the result of human influence and that chimpanzees in an “undisturbed” state are generally peaceful and “egalitarian” (Power, 1991). The original argument is based on the observations that early researchers did not witness lethal aggression among chimpanzees and that provisioning at Gombe and Mahale led to increased rates of aggression among chimpanzees (*ibid.*).

However, the failure of early chimpanzee researchers to observe intercommunity aggression is entirely predictable, given that the study communities were not fully habituated, nor were individuals routinely followed to the borders of their territory (Watts *et al.*, in press). Although Goodall began working at Gombe in 1960, early observations were largely restricted to a banana feeding station located in the center of the community range. Observations of chimpanzees away from this area were rare before 1968, and all-day follows of males were not routine until well after that date. The first lethal intercommunity attacks at Gombe were observed in 1971 (Bygott, 1972).

Power (1991) took Ghiglieri’s (1984) failure to observe intergroup aggression during early work at Ngogo as evidence that this unprovisioned community was not territorial and aggressive. However, the Ngogo chimpanzees were not well habituated during this study. Ghiglieri (1984) estimated a community size of 55 chimpanzees and concluded that predation on monkeys was rare or absent. Further habituation and subsequent observations at Ngogo have revealed that the community size is actually greater than 140, and predation on monkeys is more frequent than at any other site (Mitani and Watts, 1999; Watts and Mitani, 2002). Similarly, with the identification of territorial boundaries at Ngogo, territorial aggression and intergroup killings are regularly observed, despite the fact that the Ngogo chimpanzees have never been provisioned (Watts and Mitani, 2000, 2001; Watts *et al.*, 2002; Watts *et al.*, in press).

With the provisioning hypothesis convincingly refuted (Watts *et al.*, in press; Wilson and Wrangham, 2003; Wrangham, 1999), critics have increasingly focused on alternative forms of human interference as hypothetical



causes of chimpanzee aggression. Ferguson (2002), for example, recently suggested that experiments in which calls from strange males were played to chimpanzees at Kanyawara were responsible for the lethal attack observed there in 1998. This scenario is unlikely, for at least three reasons. First, as described previously, similar attacks have been observed at Ngogo, where chimpanzees have never been subjected to playback experiments. Second, long-term data from Kanyawara indicate that the rate of intergroup encounters during 1998, when playbacks were conducted, was indistinguishable from those of previous years (Wrangham, unpublished data). Third, long-term data from Ngogo indicate that the rate of territorial boundary patrolling by chimpanzees is not affected by the rate at which chimpanzees encounter their neighbors, either vocally or visually (Mitani and Watts, in press).

Both Ferguson (1999) and Sussman (2004) have also proposed that escalated aggression in chimpanzees is simply the result of general "stress" from human encroachment. As Wrangham (1999) has noted, however, attributing lethal coalitionary attacks in chimpanzees to human interference, whether in the form of playbacks, provisioning, deforestation, or poaching, fails to explain why other primate species, such as bonobos or baboons, that are regularly provisioned by humans, subjected to playback experiments by researchers, or killed by poachers, do not exhibit lethal coalitionary aggression between groups. This is not to suggest that human disturbance cannot influence rates of intercommunity aggression in chimpanzees. Deforestation of a community's range could potentially lead to more intercommunity encounters, and poaching of a community's males could change the balance of power during these encounters. However, similar demographic and spatial changes occur naturally in chimpanzee habitats, even in the absence of human interference. The underlying motivations driving male chimpanzee behavior are clearly not the result of such interference.

#### IV. COOPERATION

The cooperative interactions that take place in chimpanzee societies stand in stark contrast to the aggression displayed within and between communities. As is the case with aggression, there is a clear sex difference in chimpanzee cooperation. The relatively asocial nature of female chimpanzees limits the number of cooperative interactions in which they participate. In the absence of frequent interactions, it has been difficult to study female chimpanzee social behavior in the wild, and as a result, our current understanding of the form, frequency, and contexts of female cooperation remains incomplete. In contrast, male chimpanzees are much more gregarious than females, and males cooperate in a wide variety of behavioral

situations. Cooperation between male chimpanzees generates considerable theoretical and empirical interest because the resource over which they primarily compete, females, is not easily divided and shared (Trivers, 1972). In the following, we review patterns of cooperation between male chimpanzees in the contexts of coalition and alliance formation, grooming, group territoriality, hunting, and meat sharing.

#### A. COALITIONS AND ALLIANCES

Nowhere is cooperation in chimpanzees on better display than in their coalitionary behavior. Male chimpanzees form short-term coalitions by cooperating to direct aggression toward conspecifics (Mitani, in press; Nishida, 1983; Nishida and Hosaka, 1996; Riss and Goodall, 1977; Uehara *et al.*, 1994; Watts, 2002). Coalitions between male chimpanzees are notable for their frequent occurrence and complexity. The fluid nature of coalitions contributes to part of this complexity. Some males repeatedly engage in coalitionary behavior with each other over several months or years, in which case they are referred to as alliances (de Waal and Harcourt, 1992; Goodall, 1986; Riss and Goodall, 1977). In contrast, chimpanzees are also extremely opportunistic, occasionally switching between coalition partners from one interaction to another (Newton-Fisher, 2002; Nishida, 1983).

Early research suggested that alliances play a critical role in male chimpanzee status competition. Riss and Goodall (1977) described a situation at Gombe where one adult male, Figan, rose to the top of the dominance hierarchy only after receiving consistent support from Faben, an older male presumed to be his brother. Continued support from Faben helped Figan maintain his position as the alpha male for the next 2 years (Goodall, 1986). Because male chimpanzee dominance rank is positively related to mating and reproductive success (see Section III.A.2.c), coalitions likely have significant fitness consequences.

Fieldwork at Mahale illustrates the complex nature of coalitions and the unsuspected fitness benefits that males can derive through their strategic use (Nishida, 1983). In one small community consisting of three adult males, the alpha male (Kasonta) maintained his position for several years with the help of the gamma male (Kamemanfu). The beta male (Sobongo) was able to take over the top position, however, after the gamma began to aid him instead of the former alpha. The two alpha males achieved the highest mating success before and after the rank reversal. Intriguingly, the other two males appeared to cede matings to the gamma male while they competed for his help during the period of rank instability (Fig. 2).

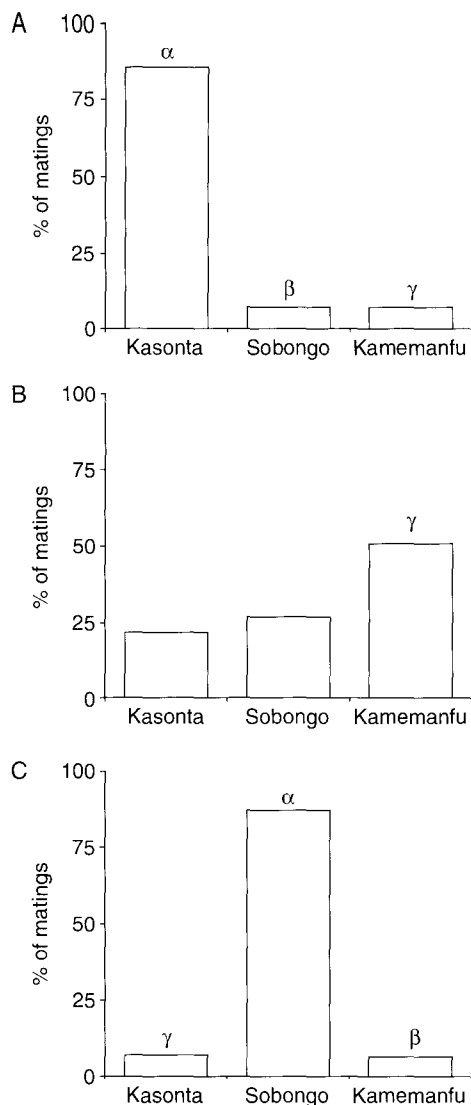


FIG. 2. Temporal changes in male chimpanzee mating success at Mahale. (A) During a stable period preceding a rank reversal, the alpha male (Kasonta) maintained his position at the top of the dominance hierarchy and copulated more frequently than two other males. (B) During a period of instability, the alpha (Kasonta) and beta (Sobongo) males competed for coalitionary support from the gamma male (Kamemanfu). The alpha and beta ceded matings to the gamma who mated most frequently. (C) After a rank reversal involving the former alpha and beta males, the new alpha asserted his dominance to achieve the most matings (adapted from Table IV in Nishida, 1983).

Additional research at Ngogo has documented a novel coalitionary tactic employed by males and confirms the critical role of coalitions in mating competition (Watts, 1998). The Ngogo chimpanzee community is unusually large, and estrous females typically attract several males. Under these circumstances, high-ranking duos and trios of males have been witnessed to mate-guard females (Watts, 1998). These mate-guarding coalitions form, both successfully and unsuccessfully, when the male party size grows so large that it becomes difficult for a single male to mate-guard females (Fig. 3). Males who engage in mate-guarding coalitions share matings with each other and achieve higher mating success in coalitions than they would by mate guarding alone (*ibid.*).

Given the significant fitness effects derived from coalitions, male chimpanzees compete for coalition partners in several, sometimes complex, ways. Observations at Mahale indicate that alpha males frequently associate, groom, and support their alliance partners, who in turn aid alphas secure their position at the top of the hierarchy (Nishida, 1983; Nishida and Hosaka, 1996). Alpha males are responsible for maintaining relationships with their allies, and they perform “separating interventions” (*sensu* de Waal, 1998) to keep their rivals apart. Studies by de Waal (de Waal 1992; de Waal and Luttrell, 1988) indicate that male chimpanzees in captivity may adopt coercive tactics by supporting others against those who have previously formed coalitions against them.

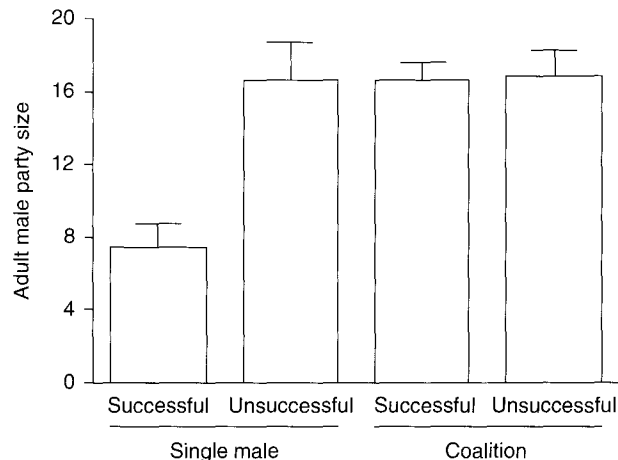


FIG. 3. Mate-guarding form and success vary with male chimpanzee party size. Mean ( $\pm 1$  SE) values are shown for single male and coalitionary mate-guarding episodes at Ngogo (adapted from Watts, 1998 and Mitani *et al.*, 2002b).

Research at Ngogo suggests that males manipulate the frequency of support they receive by engaging in reciprocal exchanges that involve goods and services that are both similar and different in kind. Studies there reveal that male chimpanzees exchange coalitionary support reciprocally at a group level (Mitani, in press; Watts, 2002). These exchanges are evenly balanced within dyads, with males and their partners initiating coalitions a similar number of times (Mitani, in press). Male chimpanzees at Ngogo also trade other commodities, in the form of grooming and meat, for support (Mitani, in press; Mitani and Watts, 2001; Watts, 2002).

Before concluding that giving depends on receiving in these cases, it is important to exclude other factors that might confound the relationship. Because of their fission-fusion society, chimpanzees do not associate with all members of their community equally often. Thus, reciprocal exchanges could result as by-products of association if males directed behaviors toward those with whom they remained in contact frequently (de Waal and Luttrell, 1988; Hemelrijk and Ek, 1991). In some primate species, similarity in age and rank affect association patterns (de Waal and Luttrell, 1986), leading to the expectation that reciprocity in behavior may result from exchanges between closely bonded individuals who share common characteristics. Additional analyses are not consistent with these interpretations. At Ngogo, reciprocity in coalition formation at the group level persists after controlling for several potential confounds, including association frequency, male age, male rank, and maternal kinship (Mitani, in press; Watts, 2002). The trade of different commodities, such as grooming and meat for support, is also unaffected by these confounds (*ibid.*).

Reciprocal exchanges underscore the cooperative nature of chimpanzee coalitions. Between-site variation in coalitionary behavior adds another layer to their complexity. Variability occurs at two levels. First, coalitions at Tai often involve two subordinate individuals directing aggression jointly toward dominants (60%,  $N = 30$ , Boesch and Boesch-Achermann, 2000). In contrast, similar "revolutionary" coalitions (Chapais, 1995) occur very rarely at Mahale (1%,  $N = 23$ , Nishida and Hosaka, 1996) and Ngogo ( $< 5\%$ ,  $N = 885$ , Watts, 2002). Second, substantial variation exists in the frequency of "loser-support" coalitions (de Waal *et al.*, 1976) in which subordinate individuals are helped in disputes with higher-ranking chimpanzees (Boesch and Boesch-Achermann, 2000; Nishida and Hosaka, 1996; Watts, 2002). While most coalitions observed at Tai (90%) and Mahale (68%) are of this type, they occur infrequently at Ngogo ( $< 5\%$ ).

Because coalitions play a critical role in the acquisition and maintenance of male rank, the variability described is likely to reflect important aspects of dominance relationships. For example, revolutionary and loser-support coalitions tend to destabilize dominance hierarchies (de Waal, 1992), and

the reported variability in their occurrence across study sites may reflect differences in male social relationships. During periods of rank instability, the frequency of such coalitions is expected to increase. In contrast, “conservative” and “winner-support” coalitions involve dominant individuals directing aggression toward subordinates and chimpanzees supporting high ranking over low ranking individuals. These types of coalitions tend to reinforce the status quo and are expected to characterize times of stable rank relationships between chimpanzees. Observations at Mahale and Ngogo furnish some support for these predictions. Frequent observations of loser-support coalitions at Mahale were made while three high-ranking males were jockeying for dominance status (Nishida and Hosaka, 1996), while the recurrent conservative and winner-support coalitions at Ngogo were recorded during periods when male rank relationships were relatively stable (Watts, 2002).

#### B. GROOMING

Social grooming is the most frequent affiliative behavior observed among primates (Goosen, 1981). Chimpanzees are no exception, although some individuals do so more than others. A consistent sex bias in chimpanzee grooming behavior exists; males groom each other much more frequently than do females (Arnold and Whiten, 2003; Boesch and Boesch-Achermann, 2000; Goodall, 1986; Takahata, 1990a,b; Watts, 2000a; Wrangham, *et al.*, 1992). The paucity of grooming by female chimpanzees is easily understood given their general asocial nature (Arnold and Whiten, 2003; Goodall, 1986; Wrangham *et al.*, 1992). In contrast, the substantial amount of time male chimpanzees devote to grooming requires explanation.

In three communities at Mahale, Ngogo, and Budongo, males groomed seven to nine other males (Arnold and Whiten, 2003; Nishida and Hosaka, 1996; Watts, 2000a). This consistency occurs despite major differences in the total number of potential male grooming partners at each site (Mahale = 8; Ngogo = 23–24; Budongo = 8–10), and probably reflects the fact that time, energy, and social constraints limit the amount of time available to groom (Dunbar 1984, 1991). Male chimpanzees do not distribute their grooming randomly. They tend to groom others with whom they frequently associate (Boesch and Boesch-Achermann, 2000; Mitani *et al.*, 2000; Newton-Fisher, 2002). In addition, male chimpanzees distribute their grooming disproportionately to only a few individuals, giving and receiving most of their grooming (66–81%) to their top three partners (Arnold and Whiten, 2003; Nishida and Hosaka, 1996; Watts, 2000a).

Grooming undoubtedly serves a hygienic function (Barton, 1985; Hutchins and Barash, 1976), but studies of several primates suggest that

it also plays an important role in the development and maintenance of social relationships (Cords, 1997; Dunbar, 1991; Seyfarth, 1977; Walters and Seyfarth, 1987). In this context, several researchers have hypothesized that male chimpanzees use grooming tactically to invest in partners from whom they receive fitness benefits (Arnold and Whiten, 2003; Mitani, in press; Newton-Fisher, 2002; Nishida, 1983; Nishida and Hosaka, 1996; Watts, 2002). The tactical deployment of grooming can result in several direct benefits for participants. Grooming can be reciprocated either immediately within the same bout or at a later time. Recent fieldwork indicates that male chimpanzees groom each other reciprocally at a group level (Arnold and Whiten, 2003; Mitani, in press; Newton-Fisher, 2002; Watts, 2000a, 2002). Mutual grooming during the same bout may contribute to this pattern (Barrett *et al.*, 1999), but the immediate exchange of grooming does not furnish a complete explanation because reciprocity in grooming holds after excluding bouts of mutual grooming (Arnold and Whiten, 2003).

Grooming can also be exchanged for other goods and services, such as coalitionary support. In an influential model, Seyfarth (1977) proposed that agonistic support is the primary benefit received by grooming. According to this model, individuals are assumed to vary in their quality as grooming partners. Because high-ranking individuals are competitively superior to low-ranking animals, the former should be the most attractive grooming partners. Thus, low-ranking individuals should invest in grooming high-ranking partners, and grooming should be directed up the dominance hierarchy. Competition to groom high-ranking individuals will force some animals to compromise, with the result that adjacently ranked individuals will groom most often.

Observations of male chimpanzees provide only partial support for Seyfarth's model. While some studies show that grooming is directed up the hierarchy (Arnold and Whiten, 2003; Newton-Fisher, 2002; Watts, 2000b), additional research indicates that dominant males sometimes give as much grooming to subordinate individuals as they receive from them (Takahata, 1990b). Grooming is common between adjacently ranked males at Ngogo and Budongo (Arnold and Whiten, 2003; Watts, 2000b), but rank distance between partners does not affect grooming between males at Mahale (Nishida and Hosaka, 1996; Watts, 2000b). Whether chimpanzees exchange grooming for coalitionary support has seldom been investigated. In the only tests of this hypothesis, recent work at Ngogo has shown that adult males there consistently trade grooming for support (Mitani, in press; Watts, 2002).

High-ranking male chimpanzees use grooming to cultivate social bonds with low-ranking individuals. The latter in turn form coalitions with

high-ranking males to help them maintain their dominance status (Nishida, 1983; Nishida and Hosaka, 1996; Takahata, 1990b). Given these circumstances, grooming will not always be directed up the hierarchy as predicted by Seyfarth's grooming competition hypothesis. Other factors may also affect the distribution of grooming between male chimpanzees. For example, de Waal (de Waal, 1991; de Waal and Luttrell, 1986) has hypothesized that instead of being attracted to high-ranking individuals, primates form selective bonds with others whom they resemble in terms of kinship, rank, and age. This "similarity" principle predicts that male kin will groom frequently, independent of rank differences between them, and that grooming between pairs close in rank will be prevalent, irrespective of kinship. It does not assume that grooming will be directed up the hierarchy and thus differs from Seyfarth's grooming competition model. Kin may obtain indirect fitness benefits by grooming each other. In contrast, mutualism or reciprocity may account for frequent grooming by animals who belong to the same age and rank class. Members of the same age cohort and rank class share similar needs, access to resources, and power; and for these reasons they are likely to be in the best position to provide and exchange fitness benefits (de Waal and Luttrell, 1986).

Current evidence does not support the hypothesis that kinship plays a significant role in structuring patterns of grooming among male chimpanzees. Maternal kinship, as assayed by mtDNA haplotype sharing and genetic distance, does not correlate with male grooming at a group level in the Kanyawara and Ngogo communities of chimpanzees (Goldberg and Wrangham, 1997; Mitani *et al.*, 2000). Moreover, male pairs that groom more often than expected by chance are not typically related to each other through the maternal line (Mitani *et al.*, 2002c). In contrast, additional studies reveal strong effects of male age and rank on grooming patterns. At Gombe and Tai, older males groom more often than younger males, and high-ranking chimpanzees groom more frequently than low-ranking individuals (Boesch and Boesch-Achermann, 2000; Simpson, 1973). Similarly, pairs of males at Ngogo who groom significantly more than chance expectation tend to belong to the same age and rank classes (Mitani *et al.*, 2002c).

The preceding observations reinforce the view, held by many, that male chimpanzees use grooming in multiple ways to compete for socially valuable partners from whom they derive fitness benefits (Arnold and Whiten, 2003; Newton-Fisher, 2002; Nishida, 1983; Nishida and Hosaka, 1996; Watts, 2000b). Males trade grooming for the direct benefits that it provides, either during bouts of mutual grooming or reciprocally over time. Male chimpanzees use grooming to cultivate and reinforce social bonds with others upon whom they rely for coalitionary support. The grooming



ties that bind male chimpanzees together within communities are displayed in their group territorial behavior.

### C. GROUP TERRITORIALITY

Coalition formation and grooming relationships among males are two well-known examples of chimpanzee cooperation that take place within communities. Male chimpanzees also cooperate to compete between communities during group territorial behavior. Group territoriality is rare in non-primate mammals, though it does occur in some social carnivores (Caro, 1994; Creel and Creel, 2002; Heinsohn and Packer, 1995; Mech and Boitani, 2003). It is equally uncommon among primates, having been described in a few species such as howler monkeys, red colobus monkeys, and mountain gorillas (Pope, 1990; Struhsaker, 1975; Watts, 1994). Group territoriality in chimpanzees is of particular interest because of boundary patrols and coalitionary attacks on neighbors, two unusual forms of cooperative behavior displayed by males in this context.

Patrolling is an integral part of chimpanzee territoriality (see Section III. D), and males are likely to obtain several benefits by doing so. By engaging in patrols and defending their territory, males could increase their access to food, improve their safety, recruit new females into their community, and improve the foraging efficiency and hence reproduction of resident females. As reviewed previously (Section III.D.3), current evidence is consistent with the hypothesis that male chimpanzees communally defend territories to increase their access to food resources. In this case, the benefits obtained via patrolling and territoriality are shared among all individuals. Further observations are not consistent with the hypothesis that males cooperate with kin during boundary patrols; males who are closely related genetically through the maternal line, as assayed by mtDNA haplotype sharing, do not show any tendency to patrol together (Mitani *et al.*, 2000, 2002c). Additional research, however, indicates that some males accrue direct fitness benefits. Observations at Ngogo reveal that there is considerable inter-individual variation in the tendency to patrol. Some males participate frequently, while others do so less often (Watts and Mitani, 2001). Analyses reveal that patrol participation is positively correlated with male mating success. Males who mate frequently, and potentially have the most offspring in the group to protect, appear to be motivated to patrol more often.

While patrolling yields direct fitness payoffs, it is also costly. Patrols occasionally lead to encounters with neighbors; these are typically hostile and sometimes result in fatalities (see Section III.D). The risk of attack by

members of other communities constitutes a potentially significant cost of patrols. Male chimpanzees appear to reduce this cost by patrolling with as many males as possible. Recent work at Ngogo reveals considerable temporal variation in the frequency of patrols, ranging between 0–9 times per month (Mitani and Watts, in press). Much of this variation depends on a single factor, male party size. When the Ngogo chimpanzees gather in parties with a large number of males, the odds of patrolling increase (*ibid.*). Additional observations indicate that male chimpanzees further minimize the costs of patrols by doing so with partners with whom they have developed strong social bonds and on whom they might be able to rely to take risks (Watts and Mitani, 2001). At Ngogo, males who patrol together also groom and form coalitions with each other frequently. In addition, patrolling effort is positively correlated with the frequency of participation in red colobus hunts. Pursuing prey is a dangerous activity (see Section IV.E) and likely to give others an indication of a male's willingness and ability to take risks in intercommunity aggression (Watts and Mitani, 2001).

At Taï and Ngogo about 25–33% of all patrols result in aural or visual contact with chimpanzees from other groups (Boesch and Boesch-Achermann, 2000; Watts and Mitani, 2001). Patrollers at Taï have been described to employ some complex, cooperative tactics to attack conspecifics (Boesch, 2003; Boesch and Boesch-Achermann, 2000). These include “lateral” attacks on the smallest and most vulnerable parties encountered and surprise assaults supported from the rear by fellow patrollers. Attacks described at most sites, however, involve direct, frontal confrontations between members of different communities.

Cooperative attacks on neighbors are one of the most striking aspects of chimpanzee group territorial behavior. During attacks, males assist each other in holding victims down and taking turns beating them (see Section III.D). Because attacks are made only when males enjoy overwhelming numerical superiority, aggressors do not appear to be subject to retaliation by victims. Attackers suffer few, if any wounds, and generally remain unharmed.

#### D. COOPERATIVE HUNTING

Unlike humans, few nonhuman primate species habitually hunt and eat meat. Chimpanzees are a prominent exception. Field studies reveal that some individuals hunt frequently and consume several kilograms of meat per year (Boesch and Boesch-Achermann, 2000; Hosaka *et al.*, 2001; Stanford, 1998; Watts and Mitani, 2002). Meat, a scarce and valuable resource, is shared readily with others. The predatory behavior of

chimpanzees provides an unusual opportunity to examine cooperation in the contexts of hunting and meat sharing.

Chimpanzee hunting behavior has been studied intensively at four sites—Gombe, Mahale, Tai, and Ngogo (Table I)—and, as a result, we possess considerable information about prey choice, the identity of hunters, hunting frequency, and success (Boesch and Boesch-Achermann, 2000; Gilby, 2004; Hosaka *et al.*, 2001; Stanford, 1998; Watts and Mitani, 2002). Chimpanzees prefer to hunt red colobus monkeys (*Procolobus badius*). These monkeys represent 81–88% of all vertebrate prey captured. Chimpanzees prey selectively on members of the youngest age classes. Juvenile and infant red colobus compose over 50% of all prey. Although adult male chimpanzees make the majority of kills, other chimpanzees show a keen interest in hunting. Hunting frequency shows substantial variation across study sites. Part of this variability is due to the fact that chimpanzees do not hunt uniformly over time. At all study sites, seasonal hunting “binges” or “crazes” occur. During these times, chimpanzees hunt almost every day for periods that last up to 10 weeks. Chimpanzees are very successful predators. Hunting success rates, measured by the percentage of hunts that result in kills, average over 50% across sites.

Controversy exists about the degree to which chimpanzees cooperate during hunts. Some fieldworkers describe high levels of behavioral coordination during hunts. In contrast, others examine the outcomes of group hunting to determine whether cooperation yields fitness benefits. Boesch and Boesch (1989) reported that chimpanzees at Tai cooperate behaviorally to capture prey. Most hunts of red colobus involve groups of chimpanzees, and hunters at Tai assume different roles when pursuing red colobus (Boesch and Boesch-Achermann, 2000). While some chimpanzees serve as “drivers” by chasing prey in one direction, “blockers” anticipate the movements of monkeys to obstruct their escape routes. These tactics permit “ambushers” to encircle and capture monkeys or to force them back toward “drivers.” Most hunts (77% = 211/274) at Tai appear to involve chimpanzees collaborating and performing these different complementary roles (Boesch and Boesch-Achermann, 2000).

Researchers studying the hunting behavior of chimpanzees at other sites have not been able to replicate observations made at Tai. Fieldwork at Gombe suggests that chimpanzees there act individually while pursuing prey during group hunts (Stanford, 1998). In contrast, limited coordination has been described in the hunting behavior of chimpanzees at Mahale and Kibale (Hosaka *et al.*, 2001; Watts and Mitani, 2002). Most observers agree that it is extremely difficult to follow individual chimpanzees as they move rapidly in the treetops and on the ground in pursuit of monkeys (Hosaka

*et al.*, 2001; Stanford, 1998; Watts and Mitani, 2002). Hunts typically involve several chimpanzees attempting to capture monkeys spread over large areas, exacerbating the problem of documenting cooperation. Those studying social carnivores who hunt communally in much more open conditions concur that establishing whether animals cooperate behaviorally while hunting is neither straightforward nor easy (e.g., Creel and Creel, 2002).

Given the difficulty of observing the behavior of individual chimpanzees during hunts, several investigators have turned to analyzing the outcomes of hunts to evaluate the fitness effects of cooperation. Cooperative hunting will evolve if individuals who hunt in groups obtain fitness payoffs relative to solitary hunters. Packer and Ruttan (1988) proposed a widely adopted criterion to assess the efficacy of cooperative hunting: that cooperation occurs when hunting success increases with the group size of hunters. Results of some studies satisfy this criterion, while others do not. Busse (1978) was the first to show that hunting success, measured by the number of kills per individual, decreases with group size at Gombe. Additional studies that employ other variables to assay hunting success have failed to demonstrate that communal hunting yields feeding benefits. The per capita amount of meat obtained from hunts shows no relationship with group size at most sites (Gombe: Gilby, 2004; Stanford, 1998; Tai: Stanford, 1998; Ngogo: Watts and Mitani, 2002). In contrast to these studies, other research has produced positive results. Using the percentage of hunts that result in kills to assay hunting success, Packer and Ruttan (1988) and Stanford (1998) showed that hunting success increases with group size at Gombe. Similarly, the percentage of successful hunts and the total amount of meat obtained from hunts increase significantly with group size at Tai and Ngogo (Boesch, 1994b; Watts and Mitani, 2002).

Reconciling these different results is not easy, but, in the end, they may have little bearing on the question of whether chimpanzees hunt cooperatively. To assess the fitness payoffs of cooperative hunting, we require information about the net gains achieved by individuals who hunt in groups and those who hunt alone. The studies we have outlined, however, have focused exclusively on the feeding benefits acquired by chimpanzee hunters. Various measures of hunting success, such as the per capita amount of meat obtained from hunts, do not take account of potentially important costs. For example, chimpanzees are likely to expend more energy to capture prey when hunting alone compared with when they hunt in large groups. Even if per capita meat intake decreases with group size, factoring in these costs may yield a situation in which the net benefit accrued by individuals who hunt in groups is actually higher than that of solitary

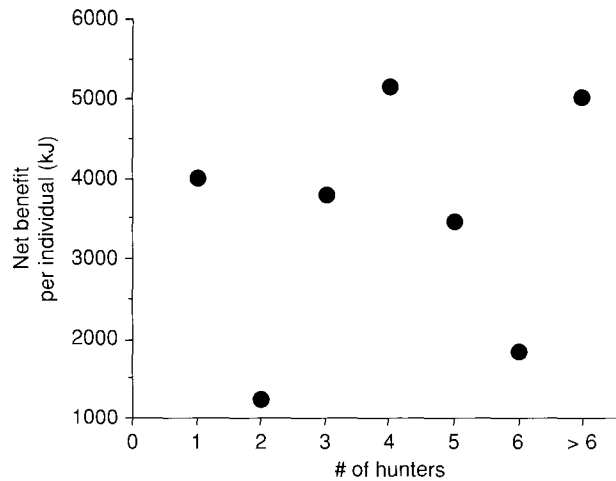


FIG. 4. The relationship between hunting success and hunting party size. Hunting success is estimated as the kiloJoules of meat acquired per individual per hunt. There is no correlation between these two variables (adapted from Table I in Boesch, 1994b).

hunters. These considerations illustrate that conclusions based on measures of hunting success do not constitute strong tests of the efficacy of cooperative hunting. Instead, measures of net energy intake are necessary (Creel, 1997; Packer and Caro, 1997).

Only one study has quantified costs and benefits to estimate the net energy obtained by chimpanzee hunters. Boesch (1994b) suggested that in the Tai National Park the net benefit of hunting was greater for chimpanzees who hunt in groups compared with solitary hunters. A close examination of his data, however, reveals that the net benefit accrued by chimpanzees shows no relationship with hunting group size (Spearman  $r = 0.14$ ,  $N = 7$ ,  $p > 0.70$ ) (Fig. 4). Solitary hunters at Tai acquire large amounts of meat for their efforts ( $X = 4015$  kJ), but their net benefits do not differ from chimpanzees who hunt in groups ( $X = 3427$  kJ, Student's  $t = 0.34$ ,  $df = 5$ ,  $p > 0.50$ ).

In sum, the role of cooperation in chimpanzee hunting is unclear. Most fieldworkers emphasize the apparent lack of behavioral coordination during hunts (Hosaka *et al.*, 2001; Stanford, 1998; Watts and Mitani, 2002). These same observers indicate that cooperation sometimes increases hunting success (Stanford, 1998; Watts and Mitani, 2002), but firm evidence on this matter in the form of the net benefits of hunting remains elusive. More convincing data for cooperation exists in the context of meat sharing.

## E. MEAT SHARING

Chimpanzee hunting involves several costs. At two sites, Taï and Ngogo, chimpanzees actively search for prey during hunting "patrols" (Boesch and Boesch, 1989; Mitani and Watts, 1999). Patrols at Ngogo can last up to 5 to 6 hours during which chimpanzees move several kilometers in search of suitable prey (Mitani and Watts, 1999; Watts and Mitani, 2002). After encountering red colobus prey, chimpanzees can continue to pursue monkeys for more than 2 hours (Boesch, 1994a). In addition to the energetic costs incurred during the search for and pursuit of prey, chimpanzees run the risk of injury during hunts. Male colobus monkeys mob chimpanzee hunters, occasionally inflicting severe wounds on them (Busse, 1977; Goodall, 1986; Mitani and Watts, 1999; Stanford, 1995; Uehara *et al.*, 1992).

Wild chimpanzees share meat readily and widely with conspecifics (Boesch, 1994b; Mitani and Watts, 2001; Stanford *et al.*, 1994; Teleki, 1973). Meat is a scarce and valuable resource, representing less than 5% of a chimpanzee's total annual dietary intake (Goodall, 1986; McGrew 1992). Because of this and the known costs incurred by chimpanzees while hunting, meat sharing is paradoxical. Three hypotheses have been advanced to explain meat sharing in chimpanzees.

One hypothesis invokes an important role for cooperation during hunts. As noted previously, Boesch and Boesch-Achermann (2000) have suggested that chimpanzees display a high degree of behavioral coordination while hunting. Boesch (1994b) has gone on to make a distinction between chimpanzees who cooperate and hunt together and "bystanders," individuals who are present but fail to participate in hunts. Observations at Taï indicate that individuals who cooperate to capture prey derive greater net benefits in terms of net energy obtained than do bystanders (Fig. 2 in Boesch, 1994b). This difference is reported to result from meat sharing. At Taï, chimpanzees share meat selectively with others who have cooperated with them to make kills. This pattern of selective sharing ensures that individuals who fail to hunt cannot exploit the efforts of cooperators.

While the cooperative hunting hypothesis may explain meat sharing among the Taï chimpanzees, methodological problems preclude evaluating its generality. Observers at Gombe, Mahale, and Ngogo report that the distinction between hunters and bystanders is not clear cut, as chimpanzees often switch between pursuing prey and standing by during the same hunt (Hosaka *et al.*, 2001; Stanford, 1998; Watts and Mitani, 2002). Prevailing observation conditions further hamper describing the activities of chimpanzees during hunts. For example, hunting parties are large, averaging over 20 chimpanzees at Ngogo (Mitani and Watts, 1999; Watts and Mitani,

2002), and, because of this, it is not feasible to track the rapid movements of all hunters as they pursue red colobus high in the trees over areas that cover several hundred meters. Taken together, these factors make it difficult to differentiate reliably between cooperators and cheaters.

A second hypothesis, advocated by Stanford (Stanford, 1996, 1998; Stanford *et al.*, 1994), suggests that cooperation between the sexes accounts for chimpanzee meat sharing patterns. His observations of the Gombe chimpanzees revealed that male chimpanzees often hunt in the presence of estrous females. This finding, combined with additional observations that male chimpanzees frequently possess meat (mentioned previously) and occasionally exchange meat for matings with females, led Stanford to propose a provocative “meat-for-sex” hypothesis. According to this hypothesis, male chimpanzees hunt to obtain meat that they can swap for matings.

Despite its simplicity and allure, the meat-for-sex hypothesis has not been validated empirically. For example, Stanford failed to provide evidence for the regular occurrence of predicted behaviors. Observations at Ngogo indicate that estrous females obtain meat less than half the time after begging from males and that matings do not always follow meat exchanges (Mitani and Watts, 2001). Recent work at Gombe confirms both of these findings (Gilby, 2004). Furthermore, the presence of estrous females does not affect whether male chimpanzees hunt at Ngogo (Mitani and Watts, 2001). In a recent reanalysis of 25 years of observations from Gombe, Gilby (2004) has shown that the presence of estrous females actually decreases the probability of hunting by male chimpanzees there. Gombe males apparently suffer opportunity costs in the form of lost matings if they hunt when estrous females are present. The strongest evidence against the meat-for-sex hypothesis, however, is the finding that males who share meat with females do not gain any mating advantage by doing so. The mating success of males who share does not exceed that of males who do not share (Mitani and Watts, 2001).

A third hypothesis suggests that male chimpanzees use meat as a political tool (de Waal, 1982) and that meat sharing represents an integral part of male cooperative behavior. Observations of a former alpha male at Mahale led Nishida *et al.* (1992) to hypothesize that male chimpanzees share meat strategically with others to build and strengthen social bonds between them. This particularly cunning alpha male shared meat nonrandomly and selectively with other males, who in turn supported him in long-term alliances. These alliances helped the alpha male to maintain his position at the top of dominance hierarchy for over 16 years (Uehara *et al.*, 1994). Observations at Ngogo are consistent with the male social bonding hypothesis (Mitani and Watts, 2001). Male chimpanzees are the most frequent

participants in meat sharing episodes. Males swap meat nonrandomly with specific individuals, and sharing is evenly balanced within dyads (Mitani, in press). Meat is also shared reciprocally at the group level, with males exchanging meat for coalitionary support (Mitani and Watts, 2001). Additional analyses indicate that males also trade grooming for meat (Mitani, in press). Observations from Gombe, on the other hand, do not support the hypothesis that meat exchange is related to male cooperation. Gilby (2004) found that Gombe males did not share meat preferentially with adult males who were frequent associates or grooming partners.

Stevens and Gilby (2004) have recently pointed out that reciprocal food sharing may occur as a by-product of other processes. For example, sharing between two individuals will likely show a reciprocal pattern if they spend considerable time together and thus have more opportunities to share (see Section IV.A). In addition, similarities in age and rank might affect association patterns (de Waal and Luttrell, 1986), with the result that reciprocal exchanges might occur disproportionately between males who share these characteristics. We can rule out these possibilities in cases involving the Ngogo chimpanzees. At Ngogo, reciprocity in sharing between males at a group level persists after controlling for their joint participation in hunts, and for male age, and male rank (Mitani, in press).

#### F. EVOLUTIONARY MECHANISMS

The preceding review illustrates that male chimpanzees derive important fitness benefits by developing strong social bonds with each other and by cooperating. Males form well-differentiated grooming relationships. Grooming is reciprocated and traded for coalitionary support. Coalitionary support is frequently necessary for males to achieve and maintain high dominance rank, and high rank in turn is correlated with mating and reproductive success. Given the importance of coalitions, male chimpanzees work hard to obtain this valuable social service. Individuals exchange meat, a scarce and valuable resource, for support in agonistic contests. Male chimpanzees not only cooperate in contests with their own community members, but also defend their territories communally against members of other groups.

While the fitness benefits obtained by male chimpanzees who cooperate are reasonably clear, the evolutionary mechanisms that ultimately account for such cooperation require further study. Kin selection, reciprocity, and mutualism are three well-known evolutionary processes that lead to cooperation in animals (Clutton-Brock, 2002; Hamilton, 1964; Trivers, 1971). Kin selection has historically been invoked to explain the evolution of cooperation between male chimpanzees. In a pioneering study conducted



at Gombe, Morin *et al.* (1994) suggested that philopatric male chimpanzees are more closely related to each other than are dispersing females. This finding was used to explain why male chimpanzees typically cooperate more than females and supported the hypothesis that kin selection accounts for the evolution of cooperation between males (*ibid.*). Additional research at Tai and reanalysis of the previously published Gombe data, however, paint a different picture; despite a sex-biased pattern of dispersal, male chimpanzees appear to be no more closely related to each other than females are (Vigilant *et al.*, 2001). Research at Ngogo has combined genetic data with observations of male social behavior to investigate directly the relationship between kinship and cooperation. Using mtDNA haplotype sharing and genetic distances to assay genetic relatedness between individuals, results indicate that kinship is a poor predictor of who cooperates with whom (Mitani *et al.*, 2000, 2002c). Male chimpanzees who are closely related through the maternal line do not selectively form coalitions, groom each other, patrol together, or share meat (*ibid.*).

Interpreting these results is problematic. The failure to show a strong effect of kinship may reflect demographic constraints that limit the number of kin with whom males can cooperate (Mitani *et al.*, 2002c). Given the fission-fusion nature of chimpanzee society, interactions between close kin may not always be possible. Alternatively, males might simply lack the time to cooperate with all of their collateral kin. These and other factors will likely combine to limit the deployment of cooperation between closely related chimpanzees (Chapais, 2004). Additional theoretical and empirical work suggests that, in cases where individuals do not disperse, high levels of local competition act to offset the potential indirect benefits obtained via kin selection (Griffin and West, 2002). This finding provides a possible rationale to explain why male kin fail to cooperate in chimpanzee societies. Male chimpanzees are philopatric; they remain in their natal communities and compete vigorously with other males in their own social groups. In this case, the costs of competing with collateral kin may dampen the indirect fitness benefits accrued by helping them.

Although results to date do not implicate an important role for kin selection in the evolution of male chimpanzee cooperation, additional research will be necessary to resolve this issue completely. Thus far, our ability to assess the genetic relatedness of male chimpanzees has been limited to relatively crude measures utilizing mtDNA. Ongoing research employing nuclear DNA markers will provide a better resolution of who is related to whom. These data will allow us to conduct more precise tests of the effects of kinship on male chimpanzee social behavior. This information will also be required to evaluate the role of reciprocal altruism in the evolution of male chimpanzee cooperation.

Reciprocal altruism has frequently been proposed to account for the evolution of cooperative behavior between unrelated individuals (Dugatkin, 1997). Reciprocity occurs when individuals restrict their help to those who aid them in return (Trivers, 1971). Theoretical analyses of reciprocal altruism emphasize the contingent nature of interactions; in situations where partners defect, reciprocity dissolves (Axelrod and Hamilton, 1981). The studies outlined in this chapter indicate that male chimpanzees reciprocally exchange commodities that are both similar and different in kind. Males show reciprocity in coalition formation, grooming, and meat sharing at a group level. In addition, they trade grooming for support, meat for support, and grooming for meat. These relationships persist after controlling for potential confounds such as maternal kinship, male age, and male rank. While consistent with reciprocal altruism, these correlational results do not provide strong tests of the hypothesis that reciprocal exchanges between male chimpanzees have evolved as a result of this process. Critical tests will require much more information than is presently available regarding the pattern of exchanges within dyads. For any given pair, is there a contingent nature to the exchange with giving depending on receiving? Do males terminate exchanges with those who fail to reciprocate? Obtaining these data in the wild will be difficult, if not impossible. The fission-fusion nature of chimpanzee society makes it hard to track and record the behavior of single individuals reliably over periods sufficiently long enough to determine whether males trade commodities in a reciprocally altruistic fashion. Rigorous tests are more likely to be made in captivity, where the temporal sequence of interactions between individuals can be controlled and monitored in detail (e.g., de Waal, 1997; Hauser *et al.*, 2003).

The lack of compelling evidence regarding reciprocal altruism in wild chimpanzees may not be surprising, given our current understanding of other animals. Despite many years of study, few convincing examples of reciprocal altruism exist (Hammerstein, 2003). Mutualism represents an alternative evolutionary route to cooperation and occurs in situations where both participants benefit through interaction. Mutualism provides an evolutionary explanation for cases in which individuals cooperate in the pursuit of a common goal, such as joint hunting and group territoriality in chimpanzees. Mutualism has also been hypothesized to explain cooperation in the contexts of coalitions, grooming, and meat sharing (Chapais, 1995; Henzi and Barrett, 1999; Stevens and Gilby, 2004).

At first blush, coalitionary behavior involves a tangible cost to the intervener who exposes himself to attack while helping another individual. This cost may be more illusory than real, however, in cases of “conservative” coalitions (*sensu* Chapais, 1995) where interveners outrank both

opponents. In these situations, individuals engage in relatively low-risk cooperative attacks on vulnerable targets. By reinforcing their own dominance ranks, they obtain an immediate benefit through their coalitionary behavior. When grooming is reciprocated between two individuals within the same bout, individuals may cooperate to receive the immediate benefit that grooming itself provides (Barrett *et al.*, 1999; Henzi and Barrett, 1999). Finally, coercion has been invoked to furnish a mutualistic explanation for meat sharing. According to this interpretation, individuals harass others into sharing food with them; sharers cooperate and relinquish food to avoid the costs of further harassment (Gilby, 2004; Stevens and Gilby, 2004).

While mutualism may provide a simple and parsimonious explanation for several examples of chimpanzee cooperation, some patterns continue to defy easy explanation. For instance, reciprocity in grooming between pairs of individuals persists after excluding bouts of mutual grooming (Arnold and Whiten, 2003). In these situations, the immediate exchange of grooming for itself does not provide an adequate explanation for cooperation. By virtue of their high status, dominant males are not easily coerced by others. These males nevertheless share meat quite readily and often (Mitani and Watts, 2001). Why does meat sharing occur in the absence of any harassment? Male chimpanzees reciprocally exchange goods and services that differ in kind (Watts, 2002). For instance, males trade meat for coalitionary support (Mitani, *in press*; Mitani and Watts, 2001; Nishida *et al.*, 1992). Such complex exchanges take place over time and are not easily interpreted in terms of trading immediate, mutual benefits. As these examples attest, answers to many questions about the evolution of chimpanzee cooperation remain elusive. Additional research is clearly needed.

## V. COOPERATING TO COMPETE

The preceding review illustrates that cooperation and competition are fundamentally interrelated. The most prevalent forms of cooperation among chimpanzees, however, are rooted in male contest competition. Chimpanzee males maintain short-term coalitions and long-term alliances to improve their dominance status within communities and defend their territories cooperatively against foreign males. Other prominent cooperative activities, such as grooming and meat sharing, relate strategically to these goals. Females are far less social than males, and they do not cooperate as extensively. Nevertheless, the most conspicuous examples of female cooperation also involve contest competition, as females sometimes cooperate to kill the infants of rivals.

The competitive context of most male cooperation prompted Sugiyama (1999, 2004) to ask whether male chimpanzees form long-term social bonds primarily to communally defend a range against their neighbors. His observations at Bossou shed some light on this question. Because the Bossou community is isolated from its neighbors by agricultural land, it is the only group in which males do not show cooperative territorial behavior. It is also the only community in which male emigration has been documented (Sugiyama, 1999, 2004). Sugiyama (1999, 2004) has argued that the lack of intergroup aggression at Bossou eliminates the principal incentive for male cooperation. Because young males cannot serve as allies in territorial defense, their relationship with the alpha male is solely a competitive one. Consequently, alphas are intolerant of young males, who emigrate from the community. Additional studies of chimpanzees across a range of habitats are needed to test the hypothesis that male sociality is critically affected by the costs and benefits of territoriality. Male emigration represents a behavioral extreme in this regard. Other cooperative behaviors could provide an alternate means to examine this issue. For instance, one might expect patterns of male grooming and meat sharing to be affected by levels of intercommunity aggression.

By the same logic, the rate of peaceful post-conflict interactions might also be expected to vary with the intensity of intergroup aggression. Current theory suggests that such interactions function to repair valuable relationships that have been damaged by conflict (Aureli and de Waal, 2000; de Waal and van Roosmalen, 1979; but see Silk, 2002). Reconciliation should thus be more common where territorial aggression is more intense and male relationships more valuable. This has not yet been tested, although Wittig and Boesch (2003c) reported that patterns of reconciliation at Tai fit well with the expectations of the valuable relationship hypothesis. Specifically, male dyads exhibited higher rates of reconciliation than female dyads, and individuals reconciled most frequently with cooperative partners and frequent associates.

Further research is also necessary to clarify the ultimate effects of cooperation on chimpanzee competition. Variation in alpha tenure, and presumably reproductive success, exists both within and between sites, but our understanding of what makes a successful alpha is incomplete. Data from Pusey *et al.* (2005) suggest that body size is not a primary factor as, in contrast to females, high-ranking males at Gombe do not weigh more than low-ranking males. Although it is clear that coalitions can play an important role in male dominance striving, their significance varies. In some cases, males rely on coalitions to achieve alpha status, yet in other situations males attain high rank with little help from others (Boesch and

Boesch-Achermann, 2000; Goodall, 1986; Nishida, 1983). Why some males are able to maintain high status without aid requires more study.

Despite its variable importance, chimpanzee coalitionary behavior appears to have a long evolutionary history. Across primates, species with relatively high rates and high intensities of aggression exhibit relatively large canines (Plavcan *et al.*, 1995). Species in which coalitions frequently affect the outcome of agonistic behavior represent an exception to this pattern, presumably because the benefits of enhanced canine size in these species are insufficient to offset their costs. Male chimpanzees possess smaller than expected canines, a fact possibly attributable to their frequent coalitionary behavior in aggressive contexts (Plavcan *et al.*, 1995).

We do not suggest that all chimpanzee cooperation is driven by contest competition. Although direct observations are few, chimpanzees do sometimes cooperate to mob predators such as pythons or leopards (Goodall, 1986; Hiraiwa-Hasegawa *et al.*, 1986). And, as discussed previously, male hunting provides a potential, yet ambiguous, example of cooperation in the context of resource acquisition. In comparison with humans, however, the general lack of cooperative behavior by chimpanzees in noncompetitive contexts, such as foraging, is conspicuous. Cooperative food gathering occurs routinely among all human foragers (e.g., Hill, 2002). Even the simplest forms of such behavior, such as Hadza men climbing baobab trees to shake down fruits for the women below (Muller, personal observation), lack an apparent equivalent in chimpanzee behavior. Thus, although chimpanzees may provide striking examples of cooperation, we see nothing in their behavior to challenge the idea that the extent of human cooperation is unique in the animal world (Fehr and Fischbacher, 2003).

Unfortunately, humans are so successful in their own cooperative behavior that chimpanzees are now critically endangered. It is becoming increasingly doubtful whether the next generation of fieldworkers will have an opportunity to conduct studies of chimpanzee behavior in the wild. If we are to pursue answers to the questions posed here, it will take considerable political skill and some bold, new initiatives to save chimpanzees.

## VI. SUMMARY

Competition and cooperation are fundamentally interrelated in chimpanzee society. Chimpanzee males are more gregarious than females, and they exhibit both higher rates of aggression and more complicated forms of cooperation. Within groups, males compete over status and access to fecundable females. High-ranking males gain clear reproductive benefits,

as they monopolize matings with females when they are most likely to conceive. Rank striving also incurs significant physiological costs, and the extent to which these are mitigated by survival benefits, such as increased access to resources, is not clear. Males direct frequent aggression against females, much of which appears to function as sexual coercion, decreasing the chance that a female will mate with other males. Females are aggressive primarily in the context of feeding competition. Despite evidence that female rank has important effects on reproduction, aggression by parous females against other parous females is rare, and female dominance ranks are stable over long periods of time. Intergroup relations among chimpanzees are predictably hostile. Male chimpanzees are territorial, and they cooperatively defend their feeding range against neighboring groups. When costs are low, males employ lethal intergroup aggression, primarily against infants and adult males, to reduce the coalitionary strength of their neighbors and to expand their territories. The primary benefit of territorial expansion appears to be enhanced access to resources, which increases female reproductive rates. Although chimpanzees cooperate in a variety of contexts, most of these relate strategically to male contest competition. Chimpanzee males form short-term coalitions and long-term alliances to improve their dominance standing within communities, and they use grooming and meat sharing to cultivate and reinforce social bonds. At Ngogo, males show reciprocity in coalition formation, grooming, and meat sharing at a group level, and they trade grooming for support, meat for support, and grooming for meat. Reciprocity persists, even after controlling for potential confounds such as association patterns, male age, male rank, and maternal kinship. Males who frequently groom and form coalitions with each other also tend to patrol the territory together. Despite long-term data from multiple sites, the role of cooperation in chimpanzee hunting is ambiguous. Cooperation sometimes increases hunting success, but clear evidence of net energetic gains is elusive. The evolutionary mechanisms that account for chimpanzee cooperation require further study. Current data suggest little role for kin selection. Some patterns of exchange are suggestive of reciprocal altruism, but better data are required to rule out the alternative hypothesis of mutualism.

#### **Acknowledgments**

We thank Professors Charles Snowdon and Peter Slater for inviting us to prepare this review. Our fieldwork in Uganda has been sponsored by the Makerere University, the Uganda National Council for Science and Technology, and the Ugandan National Parks. We are grateful to: G. I. Basuta, J. Kasenene, and the staff of the Makerere University Biological Field Station for providing logistical assistance in the field; our Ugandan field assistants,

without whom our research would not have been possible; D. Watts and R. Wrangham for their help and collaboration at home and abroad; and S. Amsler, M. Emery Thompson, I. Gilby, and S. Kahlenberg for comments on the manuscript. We also thank M. Emery Thompson, I. Gilby, A. Houle, S. Kahlenberg, A. Pusey, R. Stumpf, and R. Wrangham for providing access to unpublished data, and R. Wrangham for compiling the Gombe and Mahale data in Fig. 1. Our research on chimpanzees has been funded by grants from the Detroit Zoological Institute, the L. S. B. Leakey Foundation, the National Geographic Society, the National Science Foundation, the National Institutes of Health, the University of Michigan, and the Wenner-Gren Foundation for Anthropological Research.

### References

- Alcock, J. (2001). "Animal Behavior: An Evolutionary Approach," 7th ed. Sinauer, Sunderland, MA.
- Altmann, S. (1962). A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. *Ann. NY. Acad. Sci.* **102**, 338–435.
- Arnold, K., and Whiten, A. (2003). Grooming interactions among the chimpanzees of the Budongo Forest, Uganda: Tests of five explanatory models. *Behaviour* **140**, 519–552.
- Aureli, P., and de Waal, F. (2000). "Natural Conflict Resolution." University of California Press, Berkeley, CA.
- Axelrod, R., and Hamilton, W. D. (1981). The evolution of cooperation. *Science* **211**, 1390–1396.
- Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J., and Hill, R. (1999). Market forces predict grooming reciprocity in female baboons. *Proc. Roy. Soc. Lond. B* **266**, 665–670.
- Barton, R. (1985). Grooming site preferences in primates and their functional implications. *Int. J. Primatol.* **6**, 519–531.
- Boehm, C. (1999). "Hierarchy in the Forest: The Evolution of Egalitarian Behavior." Harvard Univ. Press, Cambridge, MA.
- Boesch, C. (1994a). Chimpanzees-red colobus monkeys: A predator-prey system. *Anim. Behav.* **47**, 1135–1148.
- Boesch, C. (1994b). Cooperative hunting in wild chimpanzees. *Anim. Behav.* **48**, 653–667.
- Boesch, C. (1996). Social grouping in Tai chimpanzees. In "Great Ape Societies" (W. McGrew, L. Marchant, and T. Nishida, Eds.), pp. 101–113. Cambridge University Press, Cambridge.
- Boesch, C. (2003). Complex cooperation among Tai chimpanzees. In "Animal Social Complexity" (F. de Waal and P. Tyack, Eds.), pp. 93–110. Harvard University Press, Cambridge, MA.
- Boesch, C., and Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai National Park. *Am. J. Phys. Anthropol.* **78**, 547–573.
- Boesch, C., and Boesch-Achermann, H. (2000). "The Chimpanzees of the Tai Forest." Oxford Univ. Press, Oxford.
- Boesch, C., Kohou, G., Néné, H., and Vigilant, L. (in press). Male competition and paternity in wild chimpanzees of the Tai forest. *Am. J. Phys. Anth.*
- Bradbury, J., and Vehrencamp, S. (1977). Social organization and foraging in emballonurid bats. III. Mating systems. *Behav. Ecol. Sociobiol.* **2**, 1–17.
- Busse, C. (1977). Chimpanzee predation as a possible factor in the evolution of red colobus monkey social organization. *Evolution* **31**, 907–911.
- Busse, C. (1978). Do chimpanzees hunt cooperatively? *Am. Nat.* **112**, 767–770.

- Bygott, J. D. (1972). Cannibalism among wild chimpanzees. *Nature* **238**, 410–411.
- Bygott, J. D. (1974). "Agonistic Behaviour and Dominance Among Wild Chimpanzees." Ph.D. thesis, Cambridge University.
- Bygott, J. D. (1979). Agonistic behavior, dominance, and social structure in wild chimpanzees of the Gombe National Park. In "The Great Apes" (D. Hamburg and E. McCown, Eds.), pp. 405–427. Benjamin Cummings, Menlo Park, CA.
- Caro, T. (1994). "Cheetahs of the Serengeti Plains." University of Chicago Press, Chicago.
- Chapais, B. (1995). Alliances as a means of competition in primates: Evolutionary, developmental, and cognitive aspects. *Ybk. Phys. Anthropol.* **38**, 115–136.
- Chapais, B. (2004). Constraints on kin selection in primate groups. In "Kinship and Behavior in Primates" (B. Chapais and C. Berman, Eds.), pp. 365–386. Oxford University Press, Oxford.
- Chapman, C., and Wrangham, R. (1993). Range use of the forest chimpanzees of Kibale: Implications for the understanding of chimpanzee social organization. *Am. J. Primatol.* **31**, 263–273.
- Chapman, C., Wrangham, R., and Chapman, L. (1995). Ecological constraints on group size: An analysis of spider monkey and chimpanzee subgroups. *Behav. Ecol. Sociobiol.* **36**, 59–70.
- Clark Arcadi, A., and Wrangham, R. (1999). Infanticide in chimpanzees: Review of cases and a new within-group observation from the Kanyawara study group in Kibale National Park. *Primates* **40**, 337–351.
- Clutton-Brock, T., and Parker, G. (1992). Potential reproductive rates and the operation of sexual selection. *Q. Rev. Biol.* **67**, 437–456.
- Clutton-Brock, T. (2002). Breeding together: Kin selection and mutualism in cooperative vertebrates. *Science* **296**, 69–72.
- Constable, J., Ashley, M., Goodall, J., and Pusey, A. (2001). Noninvasive paternity assignment in Gombe chimpanzees. *Mol. Ecol.* **10**, 1279–1300.
- Cords, M. (1997). Friendships, alliances, reciprocity, and repair. In "Machiavellian Intelligence II: Extensions and Evaluations" (A. Whiten and R. Byrne, Eds.), pp. 24–49. Cambridge Univ. Press, Cambridge.
- Cowlishaw, G., and Dunbar, R. (1991). Dominance rank and mating success in male primates. *Anim. Behav.* **41**, 1045–1056.
- Creel, S. (1997). Cooperative hunting and group size: Assumptions and currencies. *Anim. Behav.* **54**, 1319–1324.
- Creel, S., and Creel, N. (2002). "The African Wild Dog." Princeton Univ. Press, Princeton, NJ.
- Darwin, C. (1859). "On the Origin of Species by Means of Natural Selection." John Murray, London.
- Deschner, T., Heistermann, M., Hodges, K., and Boesch, C. (2003). Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees, *Pan troglodytes verus*. *Anim. Behav.* **66**, 551–560.
- Deschner, T., Heistermann, M., Hodges, K., and Boesch, C. (2004). Female sexual swelling size, timing of ovulation, and male behavior in wild West African chimpanzees. *Horm. Behav.* **46**, 204–215.
- de Waal, F. (1991). Rank distance as a central feature of rhesus monkey social organization; a sociometric analysis. *Anim. Behav.* **41**, 383–395.
- de Waal, F. (1992). Coalitions as part of reciprocal relations in the Arnhem chimpanzee colony. In "Coalitions and Alliances in Humans and Other Animals" (A. Harcourt and F. de Waal, Eds.), pp. 233–257. Oxford Univ. Press, Oxford.
- de Waal, F. (1997). The chimpanzee's service economy: Food for grooming. *Evol. Hum. Behav.* **18**, 375–386.



- de Waal, F. (1998). "Chimpanzee Politics: Power and Sex Among Apes. Revised Edition." Johns Hopkins University Press, Baltimore.
- de Waal, F., and Harcourt, A. (1992). Coalitions and alliances: A history of ethological research. In "Coalitions and Alliances in Humans and Other Animals" (A. Harcourt and F. de Waal, Eds.), pp. 1–27. Oxford University Press, Oxford.
- de Waal, F., and Luttrell, L. (1986). The similarity principle underlying social bonding among female rhesus monkeys. *Folia Primatol.* **46**, 215–234.
- de Waal, F., and Luttrell, L. (1988). Mechanisms of social reciprocity in three primate species: Symmetrical relationship characteristics or cognition? *Ethol. Sociobiol.* **9**, 101–118.
- de Waal, F., and van Roosmalen, A. (1979). Reconciliation and consolation among chimpanzees. *Behav. Ecol. Sociobiol.* **5**, 55–66.
- Drews, C. (1993). The concept and definition of dominance in animal behavior. *Behaviour* **125**, 283–313.
- Dugatkin, L. (1997). "Cooperation Among Animals." Oxford University Press, New York.
- Dugatkin, L. (2004). "Principles of Animal Behavior." W. W. Norton, New York.
- Dunbar, R. (1984). "Reproductive Decisions. An Economic Analysis of Gelada Baboon Social Strategies." Princeton University Press, Princeton, NJ.
- Dunbar, R. (1991). Functional significance of social grooming in primates. *Folia Primatol.* **57**, 121–131.
- Emery, M., and Whitten, P. (2003). Size of sexual swellings reflects ovarian function in chimpanzees (*Pan troglodytes*). *Behav. Ecol. Sociobiol.* **54**, 340–351.
- Emery Thompson, M. (in press). Ovarian function in wild chimpanzees: The role of hormones in sex and conception. *Am. J. Primatol.*
- Emery Thompson, M., Wrangham, R., and Reynolds, V. (in press). Urinary estrone conjugates and reproductive parameters in Kibale (Kanyawara) and Budongo (Sonso) chimpanzees. In "Primates of Western Uganda" (J. Paterson, Ed.). Kluwer Academic Press, New York.
- Emlen, S., and Oring, L. (1977). Ecology, sexual selection and the evolution of mating systems. *Science* **197**, 215–223.
- Fawcett, K., and Muhumuza, G. (2000). Death of a wild chimpanzee community member: Possible outcome of intense sexual competition. *Am. J. Primatol.* **51**, 243–247.
- Fedigan, L. (1983). Dominance and reproductive success in primates. *Ybk. Phys. Anthropol.* **26**, 91–129.
- Fehr, E., and Fischbacher, U. (2003). The nature of human altruism. *Nature* **425**, 785–791.
- Ferguson, R. B. (1999). Perilous positions. *Foreign Affairs* **78**, 125–127.
- Ferguson, R. B. (2002). Hit and myth: Facts and projections regarding the antiquity and ubiquity of war. Paper presented at the Annual Meetings of the American Anthropological Association, New Orleans, LA.
- Gagneux, P., Woodruff, D., and Boesch, C. (1997). Furtive mating in female chimpanzees. *Nature* **387**, 358–359.
- Gagneux, P., Woodruff, D., and Boesch, C. (2001). Retraction: Furtive mating in female chimpanzees. *Nature* **414**, 508.
- Ghiglieri, M. (1984). "The Chimpanzees of the Kibale Forest." Columbia University Press, New York.
- Gilby, I. (2004). "Hunting and Meat Sharing Among the Chimpanzees of Gombe National Park, Tanzania. Ph.D. thesis, University of Minnesota.
- Goldberg, T., and Wrangham, R. (1997). Genetic correlates of social behaviour in wild chimpanzees: Evidence from mitochondrial DNA. *Anim. Behav.* **54**, 559–570.
- Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream area. *Anim. Behav. Monogr.* **1**, 161–311.

- Goodall, J. (1977). Infant-killing and cannibalism in free-living chimpanzees. *Folia Primatol.* **28**, 259–282.
- Goodall, J. (1986). “The Chimpanzees of Gombe.” Belknap Press, Cambridge, MA.
- Goodall, J. (1992). Unusual violence in the overthrow of an alpha male chimpanzee at Gombe. In “Topics in Primatology. Volume 1. Human Origins” (T. Nishida, W. McGrew, P. Marler, M. Pickford, and F. de Waal, Eds.), pp. 131–142. Univ. of Tokyo Press, Tokyo.
- Goodall, J., Bandora, A., Bergmann, E., Busse, C., Matama, H., Mpongo, E., Pierce, A., and Riss, D. (1979). Intercommunity interactions in the chimpanzee population of the Gombe National Park. In “The Great Apes” (D. Hamburg and E. McCown, Eds.), pp. 13–54. Benjamin Cummings, Menlo Park, CA.
- Goosen, C. (1981). On the function of allogrooming in Old-World monkeys. In “Primate Behaviour and Sociobiology” (A. Chiarelli and R. Corruccini, Eds.), pp. 491–499. Springer-Verlag, Berlin.
- Graham, C. (1981). Menstrual cycle of the great apes. In “Reproductive Biology of the Great Apes” (C. Graham, Ed.), pp. 1–43. Academic Press, New York.
- Griffin, A., and West, S. (2002). Kin selection: Fact and fiction. *Trends Ecol. Evol.* **17**, 15–21.
- Halperin, S. (1979). Temporary association patterns in free ranging chimpanzees: An assessment of individual grouping preferences. In “The Great Apes” (D. Hamburg and E. McCown, Eds.), pp. 491–499. Benjamin Cummings, Menlo Park, CA.
- Hamai, M., Nishida, T., Takasaki, H., and Turner, L. A. (1992). New records of within-group infanticide and cannibalism in wild chimpanzees. *Primates* **33**, 151–162.
- Hammerstein, P. (2003). Understanding cooperation. An interdisciplinary challenge. In “Genetic and Cultural Evolution of Cooperation” (P. Hammerstein, Ed.), pp. 1–6. MIT Press, Cambridge, MA.
- Hamilton, W. D. (1964). The genetical evolution of social behavior. I, II. *J. Theoret. Biol.* **7**, 1–52.
- Hasegawa, T. (1990). Sex differences in ranging patterns. In “The Chimpanzees of the Mahale Mountains” (T. Nishida, Ed.), pp. 99–114. Univ. of Tokyo Press, Tokyo.
- Hasegawa, T., and Hiraiwa-Hasegawa, M. (1990). Sperm competition and mating behavior. In “The Chimpanzees of the Mahale Mountains” (T. Nishida, Ed.), pp. 115–132. University of Tokyo Press, Tokyo.
- Hauser, M., Chen, M., Chen, F., and Chuang, E. (2003). Give unto others: Genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proc. Roy. Soc. Lond. B* **270**, 2363–2370.
- Hayaki, H., Huffman, M., and Nishida, T. (1989). Dominance among male chimpanzees in the Mahale Mountains National Park, Tanzania. *Primates* **30**, 187–197.
- Heinsohn, R., and Packer, C. (1995). Complex cooperative strategies in group-territorial African lions. *Science* **269**, 1260–1262.
- Hemelrijk, C., and Ek, A. (1991). Reciprocity and interchange of grooming and “support” in captive chimpanzees. *Anim. Behav.* **41**, 923–935.
- Henzi, S. P., and Barrett, L. (1999). The value of grooming to female primates. *Primates* **40**, 47–59.
- Herbinger, I., Boesch, C., and Rothe, H. (2001). Territory characteristics among three neighboring chimpanzee communities in the Tai National Park, Cote d’Ivoire. *Int. J. Primatol.* **22**, 143–167.
- Hill, K. (2002). Altruistic cooperation during foraging by the Ache, and the evolved human predisposition to cooperate. *Human Nature* **13**, 105–128.
- Hiraiwa-Hasegawa, M., Byrne, R., Takasaki, H., and Byrne, J. (1986). Aggression toward large carnivores by wild chimpanzees of Mahale Mountains National Park, Tanzania. *Folia Primatol.* **47**, 8–13.

- Hosaka, K., Nishida, T., Hamai, M., Matsumoto-Oda, A., and Uehara, S. (2001). Predation of mammals by the chimpanzees of the Mahale Mountains, Tanzania. In "All Apes Great and Small. Volume 1. African Apes" (B. Galdikas, N. Briggs, L. Sheeran, G. Shapiro, and J. Goodall, Eds.), pp. 107–130. Kluwer Academic Publishers, New York.
- Houle, A. (2004). "Mécanismes de coexistence chez les primates frugivores du Parc National de Kibale en Ouganda." PhD Thesis, University of Montreal Quebec.
- Hutchins, D., and Barash, D. (1976). Grooming in primates: Implications for its utilitarian function. *Primates* **17**, 145–150.
- Kawanaka, K., and Nishida, T. (1975). Recent advances in the study of inter-unit-group relationships and social structure of wild chimpanzees of the Mahali Mountains. In "Symposium of the Fifth Congress of the International Primatological Society" (S. Kondo, M. Kawai, E. Ehara, and S. Kawamura, Eds.), pp. 173–186. Japan Science Press, Tokyo.
- Koenig, W., and Dickinson, J. (2004). "Ecology and Evolution of Cooperative Breeding in Birds." Cambridge University Press, Cambridge.
- Krebs, J., and Davies, N. (1997). "Behavioral Ecology: An Evolutionary Approach," 4th ed. Sinauer, Sunderland, MA.
- Kutsukake, N., and Matsusaka, T. (2002). Incident of intense aggression by chimpanzees against an infant from another group in Mahale Mountains National Park, Tanzania. *Am. J. Primatol.* **58**, 175–180.
- Lehmann, J., and Boesch, C. (2003). Social influences on ranging patterns among chimpanzees (*Pan troglodytes verus*) in the Taï National Park, Cote d'Ivoire. *Behav. Ecol.* **14**, 642–649.
- Lipson, S., and Ellison, P. (1996). Comparison of salivary steroid profiles in naturally occurring conception and non-conception cycles. *Hum. Reprod.* **11**, 2090–2096.
- Manson, J., and Wrangham, R. (1991). Intergroup aggression in chimpanzees and humans. *Curr. Anthro.* **32**, 369–390.
- Marks, J. (2002). "What It Means To Be 98% Chimpanzee." University of California Press, Berkeley, CA.
- Matsumoto-Oda, A. (1999a). Mahale chimpanzees: Grouping patterns and cycling females. *Am. J. Primatol.* **47**, 197–207.
- Matsumoto-Oda, A. (1999b). Female choice in the opportunistic mating of wild chimpanzees (*Pan troglodytes schweinfurthii*) at Mahale. *Behav. Ecol. Sociobiol.* **46**, 258–266.
- Matsumoto-Oda, A., and Oda, R. (1998). Changes in the activity budget of cycling female chimpanzees. *Am. J. Primatol.* **46**, 157–166.
- Matsumoto-Oda, A., Hosaka, K., Huffman, M., and Kawanaka, K. (1998). Factors affecting party size in chimpanzees of the Mahale Mountains. *Int. J. Primatol.* **19**, 999–1011.
- McGrew, W. (1992). "Chimpanzee Material Culture." Cambridge Univ. Press, Cambridge.
- Mech, D., and Boitani, L. (2003). Wolf social ecology. In "Wolves: Behavior, Ecology, Conservation" (D. Mech and L. Boitani, Eds.), pp. 1–34. Univ. of Chicago Press, Chicago.
- Mitani, J. (in press). Reciprocal exchange in chimpanzees and other primates. In "Cooperation in Primates: Mechanisms and Evolution" (P. Kappeler and C. van Schaik, Eds.), Springer-Verlag, Berlin.
- Mitani, J., and Watts, D. (1999). Demographic influences on the hunting behavior of chimpanzees. *Am. J. Phys. Anthropol.* **109**, 439–454.
- Mitani, J., and Watts, D. (2001). Why do chimpanzees hunt and share meat? *Anim. Behav.* **61**, 915–924.
- Mitani, J., and Watts, D. (in press). Correlates of territorial boundary patrol behavior in wild chimpanzees. *Anim. Behav.*
- Mitani, J., Merriwether, D. A., and Zhang, C. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Anim. Behav.* **59**, 885–893.

- Mitani, J., Watts, D., and Lwanga, J. (2002a). Ecological and social correlates of chimpanzee party size and composition. In "Behavioural Diversity in Chimpanzees and Bonobos" (C. Boesch, G. Hohmann, and L. Marchant, Eds.), pp. 102–111. Cambridge University Press, Cambridge.
- Mitani, J., Watts, D., and Muller, M. N. (2002b). Recent developments in the study of wild chimpanzee behavior. *Evol. Anthro.* **11**, 9–25.
- Mitani, J., Watts, D., Pepper, J., and Merriwether, D. A. (2002c). Demographic and social constraints on male chimpanzee behaviour. *Anim. Behav.* **64**, 727–737.
- Moore, J. (1996). Savanna chimpanzees, referential models and the last common ancestor. In "Great Ape Societies" (W. McGrew, L. Marchant, and T. Nishida, Eds.), pp. 275–292. Cambridge Univ. Press, Cambridge.
- Morin, P., Moore, J., Chakraborty, R., Jin, L., Goodall, J., and Woodruff, D. (1994). Kin selection, social structure, gene flow, and the evolution of chimpanzees. *Science* **265**, 1193–1201.
- Muller, M. N. (2002). Agonistic relations among Kanyawara chimpanzees. In "Behavioural Diversity in Chimpanzees and Bonobos" (C. Boesch, G. Hohmann, and L. Marchant, Eds.), pp. 112–124. Cambridge University Press, Cambridge.
- Muller, M. N., and Wrangham, R. (2001). The reproductive ecology of male hominoids. In "Reproductive Ecology and Human Evolution" (P. Ellison, Ed.), pp. 397–427. Aldine de Gruyter, New York.
- Muller, M. N., and Wrangham, R. (2004a). Dominance, aggression and testosterone in wild chimpanzees: A test of the "challenge hypothesis." *Anim. Behav.* **67**, 113–123.
- Muller, M. N., and Wrangham, R. (2004b). Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behav. Ecol. Sociobiol.* **55**, 332–340.
- Nadler, R., and Collins, D. (1991). Copulatory frequency, urinary pregnanediol, and fertility in great apes. *Am. J. Primatol.* **24**, 167–179.
- Newton-Fisher, N. (1999a). The diet of chimpanzees in the Budongo Forest Reserve, Uganda. *Afr. J. Ecol.* **37**, 344–355.
- Newton-Fisher, N. (1999b). Association by male chimpanzees: A social tactic? *Behaviour* **136**, 705–730.
- Newton-Fisher, N. (1999c). Infant killers of Budongo. *Folia Primatol.* **70**, 167–169.
- Newton-Fisher, N. (2002). Relationships of male chimpanzees in the Budongo Forest, Uganda. In "Behavioural Diversity in Chimpanzees and Bonobos" (C. Boesch, G. Hohmann, and L. Marchant, Eds.), pp. 125–137. Cambridge University Press, Cambridge.
- Newton-Fisher, N. (2003). The home range of the Sonso community of chimpanzees from the Budongo Forest, Uganda. *Afr. J. Ecol.* **41**, 150–156.
- Newton-Fisher, N. (2004). Hierarchy and social status in Budongo chimpanzees. *Primates* **45**, 81–87.
- Newton-Fisher, N., Reynolds, V., and Plumpton, A. (2000). Food supply and chimpanzee (*Pan troglodytes schweinfurthii*) party size in the Budongo Forest Reserve, Uganda. *Int. J. Primatol.* **21**, 613–628.
- Nishida, T. (1968). The social group of wild chimpanzees in the Mahale Mountains. *Primates* **9**, 167–224.
- Nishida, T. (1979). The social structure of chimpanzees of the Mahale Mountains. In "The Great Apes" (D. Hamburg and E. McCown, Eds.), pp. 72–121. Benjamin Cummings, Menlo Park, CA.
- Nishida, T. (1983). Alpha status and agonistic alliance in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Primates* **24**, 318–336.

- Nishida, T. (1989). Social interactions between resident and immigrant female chimpanzees. In "Understanding Chimpanzees" (P. Heltne and L. Marquardt, Eds.), pp. 68–89. Harvard University Press, Cambridge, MA.
- Nishida, T. (1990). "The Chimpanzees of the Mahale Mountains." University of Tokyo Press, Tokyo.
- Nishida, T. (1996). The death of Ntologi, the unparalleled leader of M group. *Pan Africa News* **3**, 4.
- Nishida, T. (1997). Sexual behavior of adult male chimpanzees of the Mahale Mountains National Park, Tanzania. *Primates* **38**, 379–398.
- Nishida, T., and Hosaka, K. (1996). Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In "Great Ape Societies" (W. McGrew, L. Marchant, and T. Nishida, Eds.), pp. 114–134. Cambridge Univ. Press, Cambridge.
- Nishida, T., and Kawanaka, K. (1972). Inter-unit-group relationships among wild chimpanzees of the Mahale mountains. *Kyoto Univ. Afr. Studies* **7**, 131–169.
- Nishida, T., and Kawanaka, K. (1985). Within-group cannibalism by adult male chimpanzees. *Primates* **26**, 274–284.
- Nishida, T., and Uehara, S. (1983). Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): Long-term record from the Mahale Mountains, Tanzania. *Afr. Study Monogr.* **3**, 109–130.
- Nishida, T., Uehara, S., and Nyundo, R. (1979). Predatory behavior among wild chimpanzees of the Mahale Mountains. *Primates* **20**, 1–20.
- Nishida, T., Hiraiwa-Hasegawa, M., Hasegawa, T., and Takahata, Y. (1985). Group extinction and female transfer in wild chimpanzees in the Mahale Mountains National Park, Tanzania. *Z. Tierpsychol.* **67**, 281–301.
- Nishida, T., Hosaka, K., Nakamura, M., and Hamai, M. (1995). A within-group gang attack on a young adult male chimpanzee: Ostracism of an ill-mannered member? *Primates* **36**, 207–211.
- Nishida, T., Hasegawa, T., Hayaki, H., Takahata, Y., and Uehara, S. (1992). Meat-sharing as a coalition strategy by an alpha male chimpanzee? In "Topics in Primatology. Volume 1. Human Origins" (T. Nishida, W. McGrew, P. Marler, M. Pickford, and F. de Waal, Eds.), pp. 159–174. Univ. of Tokyo Press, Tokyo.
- Nishida, T., Corp, N., Hamai, M., Hasegawa, T., Hiraiwa-Hasegawa, M., Hosaka, K., Hunt, K., Itoh, N., Kawanaka, K., Matsumoto-Oda, A., Mitani, J., Nakamura, M., Norikoshi, K., Sakamaki, T., Turner, L., Uehara, S., and Zamma, K. (2003). Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. *Am. J. Primatol.* **59**, 99–121.
- Packer, C., and Caro, T. (1997). Foraging costs in social carnivores. *Anim. Behav.* **54**, 1317–1318.
- Packer, C., and Ruttan, L. (1988). The evolution of cooperative hunting. *Am. Nat.* **132**, 159–198.
- Pepper, J., Mitani, J., and Watts, D. (1999). General gregariousness and specific social preferences among wild chimpanzees. *Int. J. Primatol.* **20**, 613–632.
- Plavcan, J., van Schaik, C., and Kappeler, P. (1995). Competition, coalitions and canine size in primates. *J. Hum. Evol.* **28**, 245–276.
- Pope, T. (1990). The reproductive consequences of male cooperation in the red howler monkey: Paternity exclusion in multi-male and single-male troops using genetic markers. *Behav. Ecol. Sociobiol.* **27**, 439–446.
- Power, M. (1991). "The Egalitarians: Human and Chimpanzee." Cambridge University Press, Cambridge.

- Pusey, A., Williams, J., and Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science* **277**, 828–831.
- Pusey, A., Oehlert, G., Williams, J., and Goodall, J. (2005). The influence of ecological and social factors on body mass of wild chimpanzees. *Int. J. Primatol.* **26**, 3–31.
- Reynolds, V. (1992). Chimpanzees in the Budongo Forest. *J. Zool.* **228**, 695–699.
- Riss, D., and Goodall, J. (1977). The recent rise to the alpha rank in a population of free-living chimpanzees. *Folia Primatol.* **27**, 134–151.
- Sakura, O. (1994). Factors affecting party size and composition of chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea. *Int. J. Primatol.* **15**, 167–183.
- Sapolsky, R. (1983). Endocrine aspects of social instability in the olive baboon (*Papio anubis*). *Am. J. Primatol.* **5**, 365–379.
- Sapolsky, R. (1992). Cortisol concentrations and the social significance of rank instability among wild baboons. *Psychoneuroendocrinol.* **17**, 701–709.
- Sapolsky, R. (1993). The physiology of dominance in stable versus unstable social hierarchies. In “Primate Social Conflict” (W. Mason and S. Mendoza, Eds.), pp. 171–204. SUNY Press, Albany, NY.
- Seyfarth, R. (1977). A model of social grooming among adult female monkeys. *J. Theoret. Biol.* **65**, 671–698.
- Silk, J. (2002). The form and function of reconciliation in primates. *Ann. Rev. Anthro.* **31**, 21–44.
- Simpson, M. (1973). Social grooming of male chimpanzees. In “Comparative Ecology and Behaviour of Primates” (J. Crook and R. Michael, Eds.), pp. 411–505. Academic Press, London.
- Smuts, B., and Smuts, R. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: Evidence and theoretical implications. *Adv. Stud. Behav.* **22**, 1–63.
- Solomon, N., and French, J. (1997). “Cooperative Breeding in Mammals.” Cambridge University Press, Cambridge.
- Stanford, C. (1995). The influence of chimpanzee predation on group size and anti-predator behaviour in red colobus monkeys. *Anim. Behav.* **49**, 577–587.
- Stanford, C. (1996). The hunting ecology of wild chimpanzees: Implications for the evolutionary ecology of Pliocene hominids. *Am. Anthro.* **98**, 96–113.
- Stanford, C. (1998). “Chimpanzee and Red Colobus: The Ecology of Predator and Prey.” Harvard Univ. Press, Cambridge, MA.
- Stanford, C., Wallis, J., Mpongo, E., and Goodall, J. (1994). Hunting decisions in wild chimpanzees. *Behaviour* **131**, 1–18.
- Sterck, E., Watts, D., and van Schaik, C. (1997). The evolution of female social relationships in nonhuman primates. *Behav. Ecol. Sociobiol.* **41**, 291–309.
- Stevens, J., and Gilby, I. (2004). A conceptual framework for nonkin food sharing: Timing and currency of benefits. *Anim. Behav.* **67**, 603–614.
- Stumpf, R., and Boesch, C. (2005). Does promiscuous mating preclude female choice? Female sexual strategies in chimpanzees (*Pan troglodytes verus*) of the Taï National Park, Côte d’Ivoire. *Behav. Ecol. Sociobiol.* **57**, 511–524.
- Struhsaker, T. (1975). “The Red Colobus Monkey.” Univ. of Chicago Press, Chicago.
- Sugiyama, Y. (1999). Socioecological factors of male chimpanzee migration at Bossou, Guinea. *Primates* **40**, 61–68.
- Sugiyama, Y. (2004). Demographic parameters and life history of chimpanzees at Bossou, Guinea. *Am. J. Phys. Anthrop.* **124**, 154–165.
- Sussman, R. (1999). The myth of man the hunter, man the killer and the evolution of human morality. *Zygon* **34**, 453–471.

- Sussman, R. (2004). Interview. In "The Demonic Ape." BBC Horizon documentary.
- Takahata, Y. (1985). Adult male chimpanzees kill and eat a male newborn infant: Newly observed intra-group infanticide and cannibalism in Mahale Mountain National Park, Tanzania. *Folia Primatol.* **44**, 161–170.
- Takahata, H. (1990a). Adult males' social relations with adult females. In "The Chimpanzees of the Mahale Mountains" (T. Nishida, Ed.), pp. 133–148. Univ. of Tokyo Press, Tokyo.
- Takahata, H. (1990b). Social relationships among adult males. In "The Chimpanzees of the Mahale Mountains" (T. Nishida, Ed.), pp. 149–170. University of Tokyo Press, Tokyo.
- Teleki, G. (1973). "The Predatory Behavior of Wild Chimpanzees." Bucknell University Press, Lewisburg, PA.
- Trivers, R. (1971). The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**, 189–226.
- Trivers, R. (1972). Parental investment and sexual selection. In "Sexual Selection and the Descent of Man" (B. Campbell, Ed.), pp. 136–179. Aldine, Chicago.
- Tutin, C. (1979). Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behav. Ecol. Sociobiol.* **6**, 29–38.
- Tutin, C., and McGinnis, P. (1981). Chimpanzee reproduction in the wild. In "Reproductive Biology of the Great Apes" (C. Graham, Ed.), pp. 239–264. Academic Press, New York.
- Uehara, S., Hiraiwa-Hasegawa, M., Hosaka, K., and Hamai, M. (1994). The fate of defeated alpha male chimpanzees in relation to their social networks. *Primates* **35**, 49–55.
- Uehara, S., Nishida, T., Hamai, M., Hasegawa, T., Hayaki, H., Huffman, M., Kawanaka, K., Kobayashi, S., Mitani, J., Takahata, Y., Takasaki, H., and Tsukahara, T. (1992). Characteristics of predation by chimpanzees in the Mahale Mountains National Park, Tanzania. In "Topics in Primatology. Volume 1. Human Origins" (T. Nishida, W. McGrew, P. Marler, M. Pickford, and F. De Waal, Eds.), pp. 143–158. University of Tokyo Press, Tokyo.
- Vehrencamp, S. (1983). A model for the evolution of despotic versus egalitarian societies. *Anim. Behav.* **31**, 667–682.
- Vigilant, L., Hofreiter, M., Siedel, H., and Boesch, C. (2001). Paternity and relatedness in wild chimpanzee communities. *Proc. Nat. Acad. Sci.* **98**, 12890–12895.
- Wallis, J. (1997). A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. *J. Rep. Fert.* **109**, 297–307.
- Walters, J., and Seyfarth, R. (1987). Conflict and cooperation. In "Primate Societies" (B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker, Eds.), pp. 306–317. University of Chicago Press, Chicago.
- Wasser, S. (1996). Reproductive control in wild baboons measured by fecal steroids. *Biol. Reprod.* **55**, 393–399.
- Watts, D. (1989). Infanticide in mountain gorillas: New cases and a reconsideration of the evidence. *Ethology* **81**, 1–18.
- Watts, D. (1994). Comparative socioecology of gorillas. In "Great Ape Societies" (W. McGrew, L. Marchant, and T. Nishida, Eds.), pp. 16–28. Cambridge University Press, Cambridge.
- Watts, D. (1998). Coalitionary mate-guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behav. Ecol. Sociobiol.* **44**, 43–55.
- Watts, D. (2000a). Grooming between male chimpanzees at Ngogo, Kibale National Park. I. Partner number and diversity and grooming reciprocity. *Int. J. Primatol.* **21**, 189–210.
- Watts, D. (2000b). Grooming between male chimpanzees at Ngogo, Kibale National Park. II. Influence of male rank and possible competition for partners. *Int. J. Primatol.* **21**, 211–238.
- Watts, D. (2002). Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour* **139**, 343–370.

- Watts, D. (2004). Intracommunity coalitionary killing of an adult male chimpanzee at Ngogo, Kibale National Park, Uganda. *Int. J. Primatol.* **25**, 507–521.
- Watts, D., and Mitani, J. (2000). Infanticide and cannibalism by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Primates* **41**, 357–365.
- Watts, D., and Mitani, J. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour* **138**, 299–327.
- Watts, D., and Mitani, J. (2002). Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. *Int. J. Primatol.* **23**, 1–28.
- Watts, D., Mitani, J., and Sherrow, H. (2002). New cases of inter-community infanticide by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Primates* **43**, 263–270.
- Watts, D., Muller, M., Amsler, S., Mbabazi, G., and Mitani, J. (in press) Lethal intergroup aggression by chimpanzees in the Kibale National Park, Uganda. *Am. J. Primatol.*
- Williams, J. (2000). “Female Strategies and the Reasons for Territoriality in Chimpanzees: Lessons from Three Decades of Research at Gombe.” PhD Thesis, University of Minnesota.
- Williams, J., Liu, H., and Pusey, A. (2002a). Costs and benefits of grouping for female chimpanzees at Gombe. In “Behavioural Diversity in Chimpanzees and Bonobos” (C. Boesch, G. Hohmann, and L. Marchant, Eds.), pp. 192–203. Cambridge University Press, Cambridge.
- Williams, J., Pusey, A., Carlis, J., Farm, B., and Goodall, J. (2002b). Female competition and male territorial behaviour influence female chimpanzee’s ranging patterns. *Anim. Behav.* **63**, 347–360.
- Williams, J., Oehlert, G., Carlis, J., and Pusey, A. (2004). Why do male chimpanzees defend a group range? *Anim. Behav.* **68**, 523–532.
- Wilson, E. O. (1971). “The Insect Societies.” Belknap Press, Cambridge, MA.
- Wilson, M., Hauser, M., and Wrangham, R. (2001). Does participation in cooperative intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Anim. Behav.* **61**, 1203–1216.
- Wilson, M., and Wrangham, R. (2003). Intergroup relations in chimpanzees. *Ann. Rev. Anthro.* **32**, 363–392.
- Wilson, M., Wallauer, W., and Pusey, A. (2004). New cases of intergroup violence among chimpanzees in Gombe National Park, Tanzania. *Int. J. Primatol.* **25**, 523–549.
- Wittig, R., and Boesch, C. (2003a). “Decision-making” in conflicts of wild chimpanzees (*Pan troglodytes*): An extension of the Relational Model. *Behav. Ecol. Sociobiol.* **54**, 491–504.
- Wittig, R., and Boesch, C. (2003b). Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. *Int. J. Primatol.* **24**, 847–867.
- Wittig, R., and Boesch, C. (2003c). The choice of post-conflict interactions in wild chimpanzees (*Pan troglodytes*). *Behaviour* **140**, 1527–1559.
- Wrangham, R. (1975). “Behavioural Ecology of Chimpanzees in Gombe National Park.” Ph.D. thesis, Cambridge University.
- Wrangham, R. (1977). Feeding Behaviour of chimpanzees in Gombe National Park, Tanzania. In “Primate Ecology” (T. Clutton-Brock, Ed.), pp. 503–538. Academic Press, London.
- Wrangham, R. (1997). Subtle, secret female chimpanzees. *Science* **277**, 774–775.
- Wrangham, R. (1999). The evolution of coalitionary killing. *Ybk. Phys. Anthro.* **42**, 1–30.
- Wrangham, R. (2000). Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In “Primate Males. Causes and Consequences of Variation in Group Composition” (P. Kappeler, Ed.), pp. 248–258. Cambridge University Press, Cambridge.



- Wrangham, R. (2002). The cost of sexual attraction: Is there a tradeoff in female *Pan* between sex appeal and received coercion? In "Behavioural Diversity in Chimpanzees and Bonobos" (C. Boesch, G. Hohmann, and L. Marchant, Eds.), pp. 204–215. Cambridge University Press, Cambridge.
- Wrangham, R., and Pilbeam, D. (2001). African apes as time machines. In "All Apes Great and Small. Volume 1. African Apes" (B. Galdikas, N. Briggs, L. Sheeran, G. Shapiro, and J. Goodall, Eds.), pp. 5–17. Kluwer Academic Publishers, New York.
- Wrangham, R., Clark, A., and Isabiryre-Basuta, G. (1992). Female social relationships and social organization of Kibale Forest chimpanzees. In "Topics in Primatology. Volume 1. Human Origins" (T. Nishida, W. McGrew, P. Marler, M. Pickford, and F. de Waal, Eds.), pp. 81–98. Univ. of Tokyo Press, Tokyo.
- Wrangham, R., Conklin-Brittain, N., and Hunt, K. (1998). Dietary response to chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *Int. J. Primatol.* **19**, 949–970.
- Wrangham, R., Chapman, C., Clark-Arcadi, A., and Isabiryre-Basuta, G. (1996). Social ecology of Kanyawara chimpanzees: Implications for understanding the costs of great ape groups. In "Great Ape Societies" (W. McGrew, L. Marchant, and T. Nishida, Eds.), pp. 45–57. Cambridge Univ. Press, Cambridge.
- Yamakoshi, G. (1998). Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. *Am. J. Phys. Anthropol.* **106**, 283–295.