Chapter 8
Intergroup Aggression in Primates and Humans: The Case for a Unified Theory

Margaret C. Crofoot and Richard W. Wrangham

Abstract Human warfare and intergroup aggression among primates have traditionally been considered to be largely unrelated phenomena. Recently, however, chimpanzee intergroup violence has been proposed to show evolutionary continuities with war among small-scale societies because both systems involve interactions among temporary subgroups, deliberate attempts to hunt and maim, and demographically significant death rates. Here, we ask whether the functional similarities between intergroup aggression among humans and chimpanzees can be extended to troop-living primates. In most primates, patterns of intergroup aggression involve brief encounters among stable troops, rare violence, and almost no killing. Although they, therefore, show little behavioral resemblance to warfare, growing evidence indicates that intergroup dominance is adaptively important in primates because it predicts long-term fitness. This suggests that in all primates, including humans, individuals use coalitions to maintain or expand access to resources by dominating their neighbors. Thus, while the style of coalitionary aggression depends on each species' evolutionary ecology, we propose that the essential functional reasons for intergroup competition are consistent across group-living primates and humans: strength in numbers predicts long-term access to resources.

8.1 Introduction

Although societies can sometimes spend decades without practicing war, the capacity for warfare is clearly a human universal. However, the question of why humans readily engage in war is unresolved from an evolutionary perspective. In this chapter, we review evidence suggesting that war between groups of

---

M.C. Crofoot (✉) and R.W. Wrangham
Department of Human Evolutionary Biology, Harvard University, Cambridge, MA, USA
email: mccrofoot@gmail.com, wranghamrichard@gmail.com

P.M. Kappeler and J.B. Silk (eds.), *Mind the Gap*,
DOI 10.1007/978-3-642-02725-3_8,

humans tends to serve the same essential functions as aggression between nonhuman primates. This might seem unsurprising given that there are obvious and extensive behavioral similarities between human and nonhuman primate intergroup aggression (van der Dennen 1995). Until recently, however, two major barriers have inhibited the development of a unified theoretical explanation for these two phenomena.

First, there has been considerable resistance among war scholars towards using evolutionary theory to explain why war occurs. Thus, military organization has been widely viewed as a socially constructed device that challenges rather than conforms to evolutionary principles. For instance, Collins (2008) argues that war systems are designed to overcome an instinctive tendency to avoid conflict. Furthermore, because warfare is not archeologically visible until about 10,000 years ago, it is sometimes claimed to be a recent invention which, therefore, requires explanation in terms of culture rather than biology (Ferguson 2000). A similar argument notes that warfare is rare or unknown in some hunter-gatherers and must therefore be unnatural (Fry 2006). The fact that aggression is oftentimes not the main motivation of soldiers in battle also suggests an important discontinuity from intergroup aggression among animals (Hinde 1993). For these and many other reasons, such as the complexity of human military and political organization and the novelty of weapon technology, as well as the fear that an evolutionary explanation of warfare will encourage more war (Sponsel 1996; Fry 2006), the problem of war has often been considered to be social or cultural rather than biological.

A second obstacle to conceptual unification has been the lack of a coherent theory for intergroup aggression among primates. Aggression between primate social groups is highly variable, whether in terms of the frequency and intensity of encounters, the resources being contested, or the sex of the participants (Cheney 1987). This variation is observed not only between species, but also between populations of the same species (e.g., *Macaca fuscata*: Saito et al. 1998; Sugiura et al. 2000) and between seasons within the same population (e.g., *Cercopithecus sabaeus*: Harrison 1983; *Cercocebus galeritus*: Kinnaird 1992). It has been difficult to discern unifying patterns amid such variation, especially since studies of intergroup interactions (IGIs) tend to be opportunistic and have relatively small sample sizes.

Other factors have also hampered the efforts to understand the broader significance of intergroup aggression in primates. First, a tendency to treat feeding and mating competition between social groups as unrelated and, oftentimes, mutually exclusive phenomena, has created an artificial division between species where males compete over mates and species where females compete over food. Recent studies have demonstrated that males can defend food resources either directly, or as a by-product of their mate defense (Fashing 2001; Harris 2005, 2006a), highlighting the flaws of this dichotomy and indicating that closer attention must be paid to the functional implications of intergroup aggression (Harris 2007). Second, the role that intergroup resource competition plays in determining individual fitness remains disputed. While Wrangham (1980) proposed that success in intergroup competition provides reproductive advantages for individuals living in large social groups, empirical data (Janson 1985), meta-analyses (Majolo et al. 2008), and literature reviews (van Schaik 1983) have suggested. If, as van Schaik claims, "*intergroup feeding competition ... [is not an] important determinant of an individual's fitness*," this calls into question the need for an adaptive theory for intergroup aggression among primates.

Thus, traditionally neither students of war nor primatologists had much reason to develop a common theory uniting human and primate intergroup aggression. However, in recent decades, the discovery of human-like patterns of killing between neighboring communities of chimpanzees (*Pan troglodytes*) has provoked evolutionary explanations of chimpanzee violence (Manson and Wrangham 1991; Wrangham and Peterson 1996; Wrangham 1999; Wilson and Wrangham 2003; Williams et al. 2004; Wilson et al. 2004; Watts et al. 2006; Boesch et al. 2008), and has inspired parallel development of an evolutionary biology of human warfare (van der Dennen 1995; Thayer 2004; Kelly 2005; Gat 2006; Roscoe 2007; Smith 2007). These efforts, which we review below, suggest that important elements of intergroup violence among humans and chimpanzees can be explained by the hypothesis that groups use aggression to achieve dominance over their neighbors. According to this idea, intergroup dominance promotes fitness by a variety of mechanisms, including access to more land and more females. We call this the intergroup dominance hypothesis.

In this chapter, we consider whether the intergroup dominance hypothesis can account for patterns of IGI among troop-living primates, chimpanzees, and humans.

8.2 Nonhuman Primates Living in Troops

Intergroup relationships have long been of interest to primatologists, as dominance relationships are known to mediate competition for resources at the individual level, and could therefore also do so at the group level (Huntingford and Turner 1987; Dunbar 1988). Yet, few studies have quantitatively investigated the relationships among neighboring primate social groups or explored how group-level dominance influences access to resources. For example, of the 60 studies cited in Cheney's 1987 review of primate IGIs that included information about intergroup dominance relationships, approximately half (25) concluded that such relationships existed. However, most of these studies provided only verbal descriptions of the relationships between social groups and only one-third (20/60) reported the number of interactions on which their conclusions were based. In addition, the majority (28/35) of studies that failed to find evidence for intergroup dominance were of species in which groups defended home ranges as territories, and in which dominance relations are therefore hard to detect (Cheney and Seyfarth 1987). Single interactions between territorial groups rarely result in noticeable boundary changes, but large groups have been shown to have higher quality ranges (Cheney and Seyfarth 1987), make more incursions into their neighbors' ranges (Struhsaker 1967), and expand their range at the expense of smaller neighboring groups (Cheney and Seyfarth 1987). Thus, it is not clear if these studies failed to detect intergroup dominance relationships because such relationships did not exist or because the studies were too short or too narrowly focused to adequately address the question.

To test the intergroup dominance hypothesis, three kinds of data are required. First, numerous observations of encounters between neighboring, habituated primate groups are needed to determine if intergroup dominance relationships exist. Investigating the relationships among several habituated social groups, rather than a single habituated group and its unhabituated neighbors, is critical because the presence of human observers may alter the behavior of unhabituated primates and potentially decrease their competitive ability (Zinner et al. 2001). Large sample sizes are essential because many factors can affect the outcome of intergroup encounters; multivariate statistics may be needed to elucidate how these factors interact to shape the relationships between neighboring groups (e.g., Kitchen et al. 2004a; Pride et al. 2006; Crofoot et al. 2008). Relatively few studies meet both these criteria, and several that do have not yet published relevant analyses (e.g., *Presbytis thomasi*: Steenbeek 1999; Steenbeek and van Schaik 2001, *Cercopithecus mitis*: Cords 2002, 2007). Nevertheless, studies meeting these criteria demonstrate the presence of consistent intergroup relationships in a range of phylogenetically, socially, and ecologically disparate species (see Table 8.1), suggesting that the pattern may well be widespread among primates.

Second, data on how group dominance affects access to resources is required to understand the functional implications of these relationships. Typically, high-ranking groups are predicted to have priority of access to food resources and consume a higher quality diet than their lower-ranking neighbors. However, few studies have collected the detailed behavioral and ecological data required to demonstrate such patterns (but see Table 8.1).

Finally, demographic data are needed to investigate whether the foraging advantages attained through intergroup dominance lead to increased fitness. Members of high-ranking groups are expected to have higher reproductive rates, higher offspring survival rates, and/or lower mortality rates than their counterparts in low-ranking groups.

In short, the combination of detailed behavioral, ecological, and demographic data required to test the intergroup dominance hypothesis is found in only a small number of primates. For this reason, we focus on three species where the data are particularly complete.

8.2.1 Wedge-Capped Capuchins (Cebus olivaceus)

While studies of competition between primate social groups sometimes treat numerical superiority as a sufficient proxy for group dominance (e.g., Koenig 2000; Cooper et al. 2004), the balance of power between opposing primate social groups can be influenced by a range of additional factors, including the behavior,

Table 8.1 Intergroup interactions and dominance relationships in nonhuman primates: a selective review

Species	Groups studied	Interactions observed	Length of study	IG dominance?	Description of IG relationship	Effects of IG dominance on foraging success or behavior	Effects of IG dominance on demographics	Reference
Verreaux's sifaka *(Propithecus verreauxi)*	5	19	3 months	Yes	In 10 of the 11 interactions with a clear winner, the group with more individuals (or, if groups were equal in size, with more males) won	Subordinate groups slept in the core area of their range	No data available	Benadi et al. (2008)
White-faced capuchins *(Cebus capucinus)*	6	58	6 months	Yes	Large group size and proximity to home range center increased the likelihood of winning interactions	Groups traveled further, faster, and stopped less frequently after losing interactions. Small groups spent more time feeding and foraging and less time socializing than large groups	No data available	Crofoot et al. (2008), Crofoot (2008)
Tibetan macaques *(Macaca thibetana)*	5	58	7 months	Seasonal	An IG dominance hierarchy based on group size existed in the birth season, but not in the mating season	Dominant groups were able to monopolize tourist feeding sites	No data available	Zhao (1997, 1999)
Savannah baboons (1) *(Papio cynocephalus ursinus)*	4	10	12 months	No	Most encounters did not involve agonism and mingling of troops was observed. Displacements occurred in two of ten encounters	The two groups with more males had larger, higher quality home ranges, used overlap areas more frequently, and had shorter day ranges than their neighbors	The two groups with more males also had higher birth rates and a higher proportion of juveniles	Anderson (1981)
Savannah baboons (2)	4	110	23 months	Yes	Both location and rival group identity influenced the outcome of intergroup encounters, and group-dominance seemed to depend on the relative number of males	No data available	No data available	Kitchen et al. (2004a)

(*continued*)

Table 8.1 (continued)

Species	Groups studied	Interactions observed	Length of study	IG dominance?	Description of IG relationship	Effects of IG dominance on foraging success or behavior	Effects of IG dominance on demographics	Reference
Black and white colobus (*Colobus guereza*)	6	115	19 months	Yes	Group dominance relationships were strong and linear and depended on characteristics of each group's male	High ranking groups had higher quality home ranges than low ranking groups	No data available	Harris (2006a,b)
Japanese macaques (*Macaca fuscata* (Yakushima))	7	151	14 years intermittently	Yes	Dominance relationships were consistent and stable over time. Larger groups were generally dominant to smaller groups, especially when the difference in group size was large	Large social groups frequently displaced their smaller neighbors from food trees	The ratio of infants to adult females was higher in large groups, suggesting that members of large groups had higher reproductive rates	Suzuki et al. (1998), Takahata et al. (1998), Sugiura et al. (2000)
Japanese macaques (*Macaca fuscata* (Kinkazan))	3	63	14 years intermittently	?	Groups rarely displaced one another during intergroup interactions (IGIs) (7/63 interactions), but in cases with clear outcomes, larger social groups tended to dominate their smaller neighbors (5/7 interactions)	Large social groups rarely excluded their smaller neighbors from food resources	Group size was not related to reproductive rate	see Yakushima
Wedge-capped capuchins (*Cebus olivaceus*)	12	169	9 years	Yes	Strong, stable dominance relationships existed among groups. Large groups were dominant to smaller groups, but dominance may have been more closely tied to the number and identity of adult males than group size per se	High-ranking groups had priority of access to high quality areas and consumed fruits with higher sugar contents. They spent less time traveling and foraging than their lower ranking neighbors	Both male and female members of large social groups had higher reproductive rates than their counterparts in small social groups	Robinson (1988), Srikosamatara (1987)

Ring-tailed lemurs (1) *(Lemur catta)*	6	188	12 months	Territorial	Encounter location, rather than group size determined the outcome of IGIs	Large social groups had higher quality home ranges, and their members maintained higher food intake rates than members of small groups except during a period of atypically low food availability. The costs of range defense were lower for individuals living in large social groups	Long-term data from this study site show that reproductive rate decreases with group size, but that females in large social groups may experience lower mortality	Pride et al. (2006), Jolly et al. (2002), Pride (2005a,b)
Ring-tailed lemurs (2)	10		13 years		No data available	No data available	Females in intermediate sized groups had higher reproductive rates than females in either large or small groups	Takahata et al. (2008)

temperament or size of the alpha male (e.g., Harris 2006b), the strength of relationships between group-mates (e.g., Starin 1991) and the location of the interaction (e.g., Pride et al. 2006; Crofoot et al. 2008). For example, using 9 years of data on interactions among 12 wedge-capped capuchin social groups, Robinson (1988) demonstrated a linear dominance hierarchy among groups. Rather than depending solely on group size, this hierarchy was ordered by the number and identity of the adult and subadult males in each group (Robinson 1988). Groups with many males tended to be high-ranking, but in some group dyads, the identity of the interacting males also influenced intergroup relationships, such that a group with a smaller but more potent male cohort outranked a group with a larger number of males.

Group dominance afforded several foraging benefits in this capuchin population. High-ranking groups had greater access to fruit species that were clumped and relatively uncommon, and were able to concentrate their foraging effort in areas with high fruit tree density (Srikosamatara 1987). The fruit species consumed by members of large groups also tended to have higher sugar content than the fruits that made up the majority of small groups' diets. Perhaps to compensate for the costs of subordinacy, low-ranking groups spent more time moving and foraging than high-ranking groups. They traveled further, particularly on days when they encountered one of their neighbors (Srikosamatara 1987), presumably in an effort to make up for decreased foraging efficiency. Such attempts, however, appeared to be ineffective because females belonging to low-ranking groups had lower reproductive rates than their counterparts in high-ranking groups (Robinson 1988).

The demographic ramifications of the relationship between group size and reproductive success in this capuchin population were striking. Because high-ranking groups grew faster than small groups, over time the percentage of the population living in high-ranking groups is expected to increase. However, past a certain size, resource competition within groups is expected to promote group fissioning. The interaction between these opposing pressures structured population growth in Robinson's study population (1988). Low-ranking groups tended to be small and to go extinct, while high-ranking groups grew and eventually "budded off" new small groups. Resource competition between social groups also shaped the genetic structure of this population, as both the female and male members of high-ranking groups contributed disproportionately to population growth, and thus to future generations (Robinson 1988; Valderrama Aramayo 2002).

8.2.2 Japanese Macaques (*Macaca fuscata*)

Relationships between neighboring social groups, and the effect that these relationships have on individual fitness, are expected to depend not only on the physical and social characteristics of the species in question, but also on the distribution and abundance of food and the density of conspecifics in their habitat (Horiuchi 2008). The Japanese macaque populations on Yakushima and Kinkazan Islands illustrate the strong effects that environmental variables can have on intergroup relationships.

These macaque populations have been studied intensively for almost three decades, and numerous comparative studies of their social structure, behavior, ecology, and demography have been undertaken (Yamagiwa 2008). These studies show that intergroup relationships have much larger consequences in the high density Yakushima population than in the low density Kinkazan population.

In Yakushima, relationships among social groups were determined by relative group size (the difference in the number of adults belonging to each group), and interactions between neighbors were found to influence both immediate foraging opportunities and long-term resource access. Dominance relationships among groups were consistent and stable over time (Saito et al. 1998). Larger groups generally displaced smaller groups (74% of interactions: Sugiura et al. 2000) especially when they had a large numeric advantage: when the larger group had at least ten more members than their opponent, they won 94% of interactions (Sugiura et al. 2000). This competitive advantage likely increased the short-term foraging efficiency of females living in large social groups because the majority of IGIs (100/151, i.e., 66.2%) ended with one group displacing the other (Sugiura et al. 2000), and 17% of interactions occurred when two groups simultaneously approached a fruit or nut tree. Thus, members of small groups lost feeding opportunities as a direct consequence of encountering their neighbors. Intergroup dominance also appeared to have long-term consequences because, on average, larger groups had higher reproductive rates, with the number of infants per female increasing linearly with group size (Takahata et al. 1998). This effect emerged, however, only during periods of resource scarcity; birth rates of large (high-ranking) groups were higher than those of their smaller (lower-ranking) neighbors only during years with poor fruit production (Suzuki et al. 1998).

On the island of Kinkazan, approximately 1,300 km northeast of Yakushima, a very different picture of Japanese macaque ecology and behavior emerges. In the Kinkazan population, large group size did not confer competitive or reproductive advantages. Groups encountered one another about one-third as often (0.012 encounters/hour on Kinkazan compared to 0.039 encounters/hour on Yakushima), and fewer interactions were agonistic (11% vs. 49% in Kinkazan and Yakushima, respectively) or involved one group displacing the other (11% on Kinkazan compared to 66% in Yakushima: Sugiura et al. 2000). Although bigger social groups were dominant in five of the seven interactions with a clear winner (Sugiura et al. 2000), these rare displacements did not appear to affect the resource access of smaller groups. As expected, therefore, larger groups did not have higher reproductive rates than their smaller neighbors. Group size was unrelated to reproductive rate both in years with good fruit crops and in years with poor fruit crops (Suzuki et al. 1998).

Why were intergroup relationships different in the Yakushima and Kinkazan populations? In theory, Kinkazan population density could have been low relative to food resources, thanks to hunting, predation, or disease. However, in groups of all sizes on Kinkazan, birth rates were higher during years with large fruit crops than in years with small fruit crops (Suzuki et al. 1998), indicating that the population was food limited. Furthermore, the Kinkazan macaques had no

Table 8.2 Comparison of the Kinkazan and Yakushima population of Japanese macaques

	Yakushima	Kinkazan
Intergroup interaction (IGI) rate[a]	0.039/h	0.012/h
Aggressive IGIs[a]	70/151 encounters	7/63 encounters
Displacements[a]	100/151 encounters	7/63 encounters
Troop density[b]	4.7/km^2	0.2/km^2
Average distance between home range centers[b]	361 m	1,232 m
Home range size[b]	90 ha	221 ha
Average home range overlap[b]	58.70%	55.10%
Food tree density[b]	1,802/ha	94/ha
Average distance between feeding bouts[b]	70 m	151 m
Average travel speed[b]	2.19 m/min	3.08 m/min

[a] Sugiura et al. (2000)
[b] Maruhashi et al. (1998)

predators (Takahata et al. 1998). The Kinkazan population, therefore, did not appear to be living below carrying capacity.

Alternatively, the distribution and/or abundance of food resources in Kinkazan might have made resource defense less economical than in Yakushima. If so, feeding competition between groups is expected to be less intense (Wrangham 1980). Certainly, differences in resource distribution were clear (see Table 8.2). Yakushima had a higher density of food patches than Kinkazan, i.e., 19 times more food trees per hectare (Maruhashi et al. 1998), and a higher overall food abundance (the basal area of food trees per hectare was 2.2 times greater than in Kinkazan). On the other hand, the average size of food trees in Kinkazan (those providing fruits and nuts) was larger (Maruhashi et al. 1998). These differences were correlated with differences in foraging behavior. In Kinkazan, macaques had larger, more evenly used home ranges, and traveled faster and further between feeding bouts, indicating that they worked harder to meet their metabolic requirements (Maruhashi et al. 1998). The more dispersed food sources and lower food abundance in Kinkazan were thus associated with greater foraging effort, suggesting groups competed primarily via scramble rather than contest competition. By contrast, the higher resource density in Yakushima could have increased the profitability of active resource defense, leading to a fitness advantage for individuals living in larger and higher-ranking groups. Further research is thus needed to assess the importance of differences in food distribution between Yakushima and Kinkazan, and to distinguish effects of resource distribution and abundance from those due to differences in population density and encounter rates (Horiuchi 2008).

8.2.3 Ring-Tailed Lemurs (*Lemur catta*)

Most, if not all, primate groups share some portion of their home range with their neighbors. In the overlap zone, intergroup aggression can either occur over specific food patches or over space. Dominance in these interactions can be mediated by the characteristics of the groups, as in wedge-capped capuchins where home ranges overlapped completely and dominant social groups defeated their subordinate neighbors throughout the entire area (Robinson 1988) (i.e., absolute dominance *sensu* Kaufmann 1983). In other species, dominance can be context-dependent because it depends on the location of the interaction (e.g., *Lemur catta*: Pride et al. 2006, *C. mitis*: Cords 2002) (i.e., relative dominance *sensu* Kaufmann 1983). Ring-tailed lemurs in Berenty provide the best-studied example of the latter system. In this species a group's fitness appears to depend on its ability to maintain the ownership of a high-quality area (Pride et al. 2006).

In Berenty, groups of ring-tailed lemurs win interactions in their "typical" ranges (their 85% minimum convex polygon home range), and tend to lose outside these areas, regardless of the strength of the opposing group (Pride et al. 2006). Why large social groups are not able to overpower their smaller neighbors is not understood. This problem presents a challenge for the intergroup dominance hypothesis by calling into question whether, in territorial species, groups are able to translate competitive superiority into increased resource access or higher fitness. Although large social groups do not seem to have a competitive advantage in any single IGI, they might achieve high foraging success (and therefore high fitness) by using their power advantage to defend territories of superior quality. The simplest way to test this is by assessing the long-term effect of group size on reproductive rate.

Two studies have yielded conflicting data on this point. Jolly et al. (2002) found that reproductive rate of lemurs at Berenty decreased with group size, thus indicating no benefits for larger groups. In contrast, Takahata et al. (2006) reported that groups with an intermediate number of adult females had higher reproductive rates than those with either few or many females. Since elevated within-group competition is expected in large groups and was demonstrated in their study, Takahata et al. (2008) concluded that their data, based on ten groups over 13 years, supported the hypothesis that large groups use social dominance over smaller groups to achieve higher fitness.

The discrepancy between the results of Jolly et al. (2002) and Takahata et al. (2006, 2008) has not been fully explained. Takahata et al. (2006) suggest that differences in population density may be responsible, as their study groups were in a high-density area of Berenty (542.3 individuals per km^2), whereas Jolly's study included groups from a range of habitats with a broad range of densities (100–580 individuals per km^2 in the scrub forest and near the tourist station, respectively). However, this explanation is not fully supported because Jolly et al. (2002) found a negative relationship between group size and reproductive rate even in the groups near the tourist station where population density was highest.

Ring-tailed lemurs in Jolly et al.'s (2002) study thus show that large group size does not necessarily confer a reproductive advantage. Nevertheless, two additional lines of evidence from this population provide support for the intergroup dominance hypothesis. First, Pride et al. (2006) demonstrated that large groups defend higher quality home ranges than small groups, and are able to do so at a lower cost to individual members. Females in large social groups are able to share the burden of territorial defense with more group mates, and thus can maintain home ranges in the most productive and stable areas at lower *per capita* cost of defense (Pride et al. 2006). Second, members of large social groups may have reduced mortality compared to members of smaller groups. Pride (2005b) demonstrated that glucocorticoid levels in females at Berenty predicted individual survival, and that females in large social groups had lower cortisol levels than females in small groups (Pride 2005a). This pattern may be explained by the fact that individual participation in intergroup contests declined with increasing group size (Pride et al. 2006). The costs of territorial defense and intergroup resource competition thus seem to be lower for females in large groups because they are shared among more individuals, and this appears to have long term consequences for both survival and individual fitness. In addition, competition for space is intense among ring-tailed lemurs, and members of groups that lose control over their "typical" areas experience high mortality (Koyama 1991; Hood and Jolly 1995; Jolly and Pride 1999; Koyama et al. 2002; Gould et al. 2003). For example, Jolly and Pride (1999) recorded a group of ring-tailed lemurs expanding and fissioning over a 6-year period. In this case, the group expanded as a result of increased resources coming from human food (a tourist project). It reached 19 individuals, compared with group sizes of 3–12 in 11 other groups in the same area, and then fissioned. The two daughter groups were both successful, one using aggression to extend its range at the expense of a neighboring group and the other entirely taking over a neighboring range (Jolly and Pride 1999). Thus, it is possible that even if smaller (and less dominant) groups have higher reproductive rates, their long-term fitness is reduced by the mortality risks associated with range loss and group extinction.

8.2.4 Troop-Living Primates: Discussion

Wedge-capped capuchins, Japanese macaques, and ring-tailed lemurs provide rare examples of relatively complete studies of the long-term consequences of intergroup dominance in troop-living primates. In wedge-capped capuchins, the intergroup dominance hypothesis was clearly supported, because groups had predictable dominance relationships that depended on fighting power, and members of higher-ranking groups had access to better resources and achieved higher reproductive rates. In Japanese macaques, a high-density population experienced a similar dynamic, whereas a low-density population did not. The effects of intergroup dominance were more complicated in ring-tailed lemurs. Although it is not clear whether members of large social groups have higher reproductive rates than members of small groups, the data suggest that they experienced reduced mortality.

Similar evidence of the importance of long-term survival comes from toque macaques (*Macaca sinica*, Dittus 1986). For 7 years, a group of 8–15 females consistently dominated a neighboring group of 7–11 females in conflicts over feeding sites, yet during this period, the reproductive rates of the two groups were not significantly different. However, the dominant group then took over the range of its neighbor, and females in the subordinate group became members of the dominant group. Over the next 8 years, differences in reproduction and survival led to the lineages of the dominant group having 20 females, compared to one descendant from those in the subordinate group. This case suggests that over the long term, the ability to control and defend a home range may be more important for fitness maximization than short-term measures of reproductive rates. Where dominant groups do not achieve high reproductive rates, they may alternatively have higher rates of individual survival and/or superior physical condition.

Although data on the intergroup relations of troop-living primates remain too sparse to provide a definitive test of the intergroup dominance hypothesis, intergroup dominance relationships have been shown to be important in an ecologically and socially diverse set of species. These include both frugivores (*Cebus olivaceus*: Robinson 1988) and folivores (*Colobus guereza*: Harris 2006a,b); territorial species (*L. catta*: Jolly et al. 2002) and species with completely overlapping home ranges (*Cebus olivaceus*: Robinson 1988); and in primates with one-male social systems (*C. guereza*: Harris 2006a, b) and multi-male social systems (*M. fuscata*: Sugiura et al. 2000). In each case, the results challenge van Schaik's (1983) contention that intergroup feeding competition is not important in determining an individual's fitness, and they indicate that when long-term data are available, the intergroup dominance hypothesis is at least partly supported, i.e., that troop-living primates can achieve long-term benefits from success in coalitionary aggression against neighbors. Since hostile IGIs often have no obvious immediate effect in determining access to a particular food patch, these case studies suggest that the long-term implications merit further research.

The behavioral implication of the intergroup dominance hypothesis is that conflicts between groups are not necessarily over immediate access to resources, but instead can represent fights over dominance status. Despite indications from wedge-capped capuchins, Japanese macaques, and ring-tailed lemurs that the benefits of winning such contests are high, escalated aggression rarely occurs during intergroup conflicts in troop-living primates. One possible explanation is that the costs of aggression are high. When the outcome of a conflict can be predicted based either on previous interactions or on physical characteristics of the participants, and when the cost of interacting is high, weaker opponents are expected to withdraw rather than engage in a risky fight they are likely to lose (Maynard Smith and Parker 1976). Neighboring primate social groups interact with one another regularly and thus levels of intergroup aggression may be relatively low because the outcome is a foregone conclusion. In addition, the social groups of troop-living primates are, by definition, cohesive and thus intergroup aggression in these species rarely involves the imbalances of power that are implicated in lethal aggression of chimpanzees and human foragers (below). Observations of intergroup killings in capuchin monkeys lend support to this hypothesis because they suggest that troop-living primates will participate in escalated aggression if the costs are sufficiently low (Gros-Louis et al. 2003). In this instance, the coalitionary nature of the attacks meant that the aggressors could inflict serious wounds on their victim without risking substantial injury themselves (Gros-Louis et al. 2003).

An alternative explanation for the low intensity of intergroup aggression observed in troop-living primates is that the collective action problem inherent in group-level resource competition presents an obstacle to high individual investment (Nunn and Lewis 2001; Nunn and Deaner 2004; Kitchen and Beehner 2007). Why should any individual risk injury by participating in intergroup fights when the benefits gained through such confrontations will be enjoyed by all group members, including individuals that did not take part in securing them? Participation in aggressive intergroup encounters is highly variable (Wilson et al. 2001; Wich et al. 2002a, b; Kitchen 2004, 2006; Kitchen et al. 2004b), and why some individuals rush boldly towards an opposing group, risking injury, while others hang back and watch the excitement from a safe distance remains poorly understood (Kitchen and Beehner 2007). The fact that intergroup dominance relationships exist in a number of troop-living species clearly suggests that primates are able to overcome this collective action problem, but further study is required to demonstrate how this is accomplished.

8.3 Chimpanzees

Chimpanzees form social communities that occupy a stable home range. Within communities, individuals forage in parties (sub-groups) of variable size and composition, including sometimes being alone. Intercommunity interactions often occur only at long distance, mostly through auditory contact. In three populations (Taï, Mahale, Ngogo), they occurred at similar rates, 1–1.5 times per month. Aggression is the principal form of interaction between communities. It occurs mostly when parties meet by chance, but also when one party deliberately approaches another, sometimes by stealth.

The principal actors are adult males and there are two main types of interaction. Battles involve mostly bluff, including numerous calls and aggressive charges made alone or jointly towards opponents. Physical contact is occasional and generally mild, though it can lead to one individual being separated and attacked, and in Taï, it includes herding and temporary forced consortships of females (Boesch et al. 2008). Battles may continue in the same location for up to 45 min (Wrangham pers. observ.), and normally end with one or both sides retreating. Attacks, by contrast, involve a coalition of at least two and generally four or more males violently attacking a member of the neighboring community. Attacks occur both when parties meet by chance and when one party searches for potential victims during boundary patrols or after detecting them at long distance. Attacks are much less common than battles (Wilson and Wrangham 2003; Watts et al. 2006; Boesch et al. 2008).

While chimpanzee intercommunity relations have not been studied in depth, they appear to conform to the three components of the intergroup dominance hypothesis. First, relationships between communities are generally predictable. For example, in Gombe parties from the larger Kasekela community consistently defeated those from the smaller Kahama community (Goodall 1986). Nishida et al. (1985) found a similar relationship at Mahale for M-group and K-group. However, the outcome of specific interactions depends on the local context, such as the relative numbers of males in each party, so parties from small communities can sometimes win intergroup encounters (Wrangham 1999; Boesch et al. 2008).

Second, communities that win interactions improve their access to resources. Thus, two dominant communities in Gombe and Mahale permanently extended their territories at the expense of their neighbors (Nishida et al. 1985; Goodall 1986; Williams et al. 2004). The M-group community in Mahale also exploited its dominance seasonally by taking control of an area normally occupied by the neighboring K-group, whenever the principal food-plant species in the shared area came into fruit.

Third, success in intercommunity aggression had fitness pay-offs. In particular, the dominant Gombe community experienced variation in territory size, which was suspected to result from varying success in competition with neighboring communities. Larger territory size was associated with several indications of greater access to resources, including higher individual body weights and larger parties, and fitness gains are indicated by shorter interbirth intervals and higher infant survival (Williams et al. 2004). Additionally, subordinate communities have twice been observed to go extinct, apparently as a result of aggression from dominant neighbors (Kahama at Gombe, K-group at Mahale). While some individuals from these subordinate communities survived the dissolution of their groups, almost all males died and the females who were known to survive experienced high rates of infanticide (Nishida et al. 1985).

Intercommunity dominance accordingly appears to be beneficial for chimpanzees because it gives both sexes increased access to resources, while males can also gain increased access to females. The question that links intergroup dominance in chimpanzees to human warfare is why intergroup contests are so much more aggressive among chimpanzees than among troop-living primates. In particular, why do chimpanzees sometimes violently attack and kill members of neighboring communities?

According to the imbalance-of-power hypothesis, the fission–fusion social organization of chimpanzees facilitates lethal aggression against members of neighboring groups. Chimpanzees form temporary subgroups that vary in size, so parties with several males sometimes encounter lone males or isolated mothers from neighboring groups. When loners meet large parties, aggressive power is distributed so asymmetrically that the dominant party can afford to express intense violence while experiencing a very low risk of being hurt themselves. The proposed advantage of damaging or killing an opponent is that by reducing the number of coalitionary aggressors in the neighboring community, the attackers increase the relative power of their community. As a result, they become more likely to win future interactions, and therefore to achieve the fitness gains accruing from elevated intercommunity dominance (Manson and Wrangham 1991; Wrangham 1999; Williams et al. 2004; Wilson et al. 2004; Watts et al. 2006; Sherrow and Amsler 2007). The imbalance-of-power hypothesis predicts that the aggressors will be members of the philopatric sex, whether females (as in spotted hyenas, *Crocuta crocuta*) or males (as in chimpanzees) (Wrangham 1999).

The proposal that an asymmetry of power tends to induce attack is supported by data from Gombe, Mahale, Kibale and Taï on the contexts of aggression. For example, in 20 cases recorded by Watts et al. (2006) involving the Ngogo community in Kibale, attacks were conducted by at least three individuals on a victim that was either alone when encountered, or was rapidly isolated from the rest of his/her party. A victim who has members of his/her own community nearby has sometimes been supported and rescued (Boesch et al. 2008). Thus, where power is more evenly balanced, attacks are less likely or can be stopped. The importance of power asymmetry is also indicated experimentally by playbacks showing that the probability of males approaching the location of a male stranger's call, or the speed at which they do so, is predictably increased by the number of males in the listening party (Wilson et al. 2001). As expected, border zones tend to be avoided in general, and males in small parties are particularly unlikely to visit them (Wilson et al. 2001; Wrangham et al. 2007). In sum, the power asymmetries made possible by fission–fusion grouping make lethal violence cheap, provided that aggressors can assess the relative fighting ability of parties correctly.

If escalated aggression is cheap and serves to increase the future dominance of the aggressors' community, it should be directed towards the most effective fighters among the neighbors. Females are not active aggressors in intercommunity interactions in most sites. However, in Taï, females can take part, perhaps because parties there are more stable than elsewhere, power asymmetries are reduced, and intercommunity attacks are rare (Boesch et al. 2008). In other sites attacks are more common and are indeed directed mostly at males. For instance, the probability of attacks on strangers at Gombe was 100% for males ($n = 6$ single males, 16 in parties), <60% for females without sexual swellings ($n = 51$) and <20% for females with sexual swellings ($n = 23$) (Williams et al. 2004). The sex difference is particularly pronounced for lethal aggression. In a review of data from five populations including 16 known and 16 suspected cases of adult deaths from intercommunity aggression, Wrangham et al. (2006) found that 94% of the victims were adult males ($n = 30$ deaths). Intercommunity aggression also involves attacks on infants. Unfortunately, observers can rarely detect the sex of infant victims, but of eight cases where the sex of the victim was known, six were male (75%) (Wrangham et al. 2006).

The imbalance-of-power hypothesis is thus supported by evidence that chimpanzees are sensitive to power imbalances, tend to reduce the number of males in neighboring communities, and gain fitness advantages by doing so. Competing hypotheses, to explain why chimpanzees make deliberate attacks on victims who are outnumbered and over-powered, have mostly focused on the proximate stimuli eliciting violence, and receive little support (Williams et al. 2004; Wilson et al. 2004). First, chimpanzees could, in theory, have a generalized tendency to attack unfamiliar individuals. However, as we have seen, the likelihood of an attack depends on context. Second, specific individuals might be particularly prone to violence. However, although individual variation has been shown for predatory aggression by chimpanzees (Gilby et al. 2008) and for rank-related frequencies of intracommunity aggression (Muller and Wrangham 2004), Wilson et al. (2001) found equally strong responses to playbacks of strangers among all seven adult males in their study. Third, attacks could be provoked by immediate competition over resources. Relevant stimuli could include the presence of sexually active females, the presence of preferred food patches, a season of ecological stress, or a long-term shortage of land or females. None of these has yet been demonstrated to be important, however (Wilson et al. 2004).

The imbalance-of-power hypothesis predicts that chimpanzees will rarely take risks as aggressors in intercommunity interactions. Against this, Boesch et al. (2008: 531) suggest that "*chimpanzees can take large risks when potential benefits are large or when failure to do so could inflict larger costs*." Aggressors have rarely been wounded to date, but further data will enable these alternatives to be more finely discriminated. In particular, evidence that aggressors expose themselves to risk will suggest that competition over detectable resources is more important than current data indicate. At present, the propensity for chimpanzees to violently attack neighbors appears to be best explained by the intergroup dominance hypothesis, including a tendency to use attacks to weaken the neighbors whenever possible.

Chimpanzees are the best-studied primate living in fission–fusion communities, but spider monkeys (*Ateles* spp.) have similar patterns of grouping and territoriality. According to the imbalance-of-power hypothesis, therefore, spider monkeys should show parallel forms of intergroup violence. No intergroup killing has yet been seen in spider monkeys, but recent observations suggest that important elements of their patterns of aggression are similar to those in chimpanzees. In particular, spider monkeys show active defense of territories, larger parties tend to win interactions, and small parties avoid the border zone (Aureli et al. 2006; Wallace 2008). Males have been seen on intergroup raids making incursion into neighboring ranges and attacking lone individuals (Aureli et al. 2006). Cooperative killing has been seen within groups (Campbell 2006; Valero et al. 2006). On the basis of these observations, the imbalance-of-power hypothesis predicts that lethal attacks will eventually be found also in spider monkeys.

The implication of the imbalance-of-power hypothesis for chimpanzees is that selection has favored the propensity to attack male neighbors whenever the costs are perceived to be sufficiently low. Roscoe (2007) presents an alternative idea. He proposes that the reason why unprovoked attacks on strangers occur in chimpanzees more than other nonhuman primates is that chimpanzees are exceptionally intelligent. As a result, he argues, the attackers are so skilled at assessing the long-term benefits that they can evaluate the merits of a risky attack. The cognitive demands implied by Roscoe's proposal are high. According to Roscoe's idea, a chimpanzee is expected to perceive that a violent attack will lead to a reduction in the fighting power of the neighboring group, and hence to an increased likelihood of the aggressors' community winning intercommunity interactions. The chimpanzees should then be able to realize from this that they will obtain increased access to resources. The cognitive challenges seem to us too great for this scenario to be realistic, and we believe that a more parsimonious explanation is that, faced with an uncertain long-term pay-off, chimpanzees are motivated by a psychological reward system that has been favored evolutionarily by the benefits that tend to accrue to judicious killers.

8.4 Humans

War is sometimes defined as being a more exclusive activity than intergroup aggression. For instance, Kelly (2000) and Fry (2006) defined warfare to exclude feuding. Such a definition means that warfare is not considered to have occurred among the Andamanese, for example, even though members of neighboring tribes killed each other whenever they met vulnerable opponents (Fry 2006). Similarly, Fry (2006) considered that among the Murngin, an Australian aborigine group, there was no war even though they practiced six types of warfare according to Warner (1958), their principal ethnographer. For example, "maringo" was defined by Warner (1958: 166) as "*Surprise attack by group, in revenge. Always woundings or death.*"

To avoid confusion and allow easy comparisons with primates, here we define warfare inclusively to mean IGIs among humans, in which coalitions attempt to aggressively dominate or kill members of other groups. Using this definition, warfare is characteristic of most human societies. The few in which it has been recently absent tend to be societies that were politically dominated by their neighbors (Fry 2006).

While cultural and socio-political diversity makes generalization difficult, two broad styles of warfare can be recognized, below and above the military horizon (Turney-High 1949). Below the military horizon, warfare is conducted anarchically in the sense that individuals cannot be ordered to participate. Most interactions involve asymmetric attacks, made either opportunistically or as a result of a deliberate plan. In the cases of planned attacks, the typical motivation is revenge for prior killings. Attacks can continue into a massacre if power is sufficiently imbalanced. Males are the chief targets, but children and women can also be killed. Battles involving deliberate confrontation of opposing sides are rare, though not unknown. When battles occur, they tend to stop after a few deaths. This style of warfare is characteristic of hunter-gatherers and small-scale farming societies (Gat this volume). Hostility is often unrelenting between tribes with different language-groups ("external war"). Within tribes, groups tend to oscillate between conditions of war ("internal war") and peace, often brought about by explicit peace-making ceremonies (Wright 1942; Turney-High 1949; Keegan 1993).

Above the military horizon, warfare is practiced by armies, i.e., institutions in which leaders devise plans and have the power to order soldiers into battle. While asymmetric attacks remain common, battles are especially prominent in warfare above the military horizon. Battles are rarely opportunistic and often require the leaders of opposing forces to agree where and when to fight. The leaders' motivation for fighting includes complex political considerations, and tends to be aimed at destroying or subjugating the opposing army (Keegan 1993; Collins 2008). The soldiers' motivation for fighting varies widely. Individuals may fight from a sense of duty; they may wish to fight out of patriotism or opportunities for loot; or they may fear the consequences of not fighting, such as being killed by the enemy, being killed by their leaders, or letting down their immediate comrades (Keegan 1993).

Human warfare clearly conforms to the intergroup dominance hypothesis, because intergroup dominance relationships are routinely stable for years at a time, and they predict access to resources such as valuable locations or trade routes. Dominant groups also commonly flourish by expanding their territorial ranges or by restricting the access to resources of individuals belonging to subordinate groups. Gat (2006) gives numerous examples.

Warfare also appears broadly to fit the imbalance-of-power hypothesis. The fit is particularly clear below the military horizon, though in humans, there are more sources of power asymmetry than in chimpanzees. As in chimpanzees, power asymmetry between opposing sides comes both from differences in party size and from one side having the element of surprise. In addition, humans routinely use night-time attacks (often initiating attacks just before dawn), and devise special tactics and weapons to give themselves a military advantage. Practitioners of internal war also use deceit (ensnaring familiars by guile) and treachery (betrayal of a trust) to establish a power advantage (Turney-High 1949; Zegwaard 1959; Wadley 2003; Gat 2006). The use of such tactics and the tendency to avoid battles suggest that most killing below the military horizon occurs during asymmetric interactions in which the killers experience low risk of being injured (e.g., Chagnon 1997). These generalizations suggest that the pattern of warfare among foragers and small-scale farming tribes largely conforms to the imbalance-of-power hypothesis.

Above the military horizon, the calculus is more complex because of the distinction between leaders (who are motivated to fight or direct others to fight) and soldiers (who may be reluctant to fight). The existence of hierarchical relationships between leaders and soldiers means that leaders can take substantial risks, deliberately allowing their armies to sustain large casualties. The lack of leaders in chimpanzees or hunter-gatherers, therefore, contributes to explaining why they rarely have lethal battles. Nevertheless, although a steep military hierarchy means that warfare above the military horizon does not necessarily conform to the imbalance-of-power hypothesis, we conjecture that within battles, and in numerous engagements during prolonged wars, aggressive interactions tend to be conducted according to the imbalance-of-power hypothesis. For example, military analyses tend to find that most deaths occur not from direct confrontation, but as a result of killing by the winning side, typically of soldiers who are helpless because they are in retreat or have been captured (Collins 2008).

As for chimpanzees, coalitions of humans with a large power imbalance in their favor could kill opponents either as a result of rational calculation or from emotional satisfaction (Roscoe 2007). Both factors seem likely to apply.

8.5 Discussion

Our central question is whether intergroup aggression can be explained by the same principles among troop-living primates, chimpanzees, and humans. Our review suggests that in each case, the intergroup dominance hypothesis has substantial explanatory power. Our findings differ from a number of recent reviews, which have supported van Schaik's claim that large group size does not provide functionally significant benefits in terms of resource competition in primates (Silk 2007; Majolo et al. 2008). A critical component of our analysis, which may explain this discrepancy, is that we focus on long-term rather than short-term reproductive consequences of intergroup competition.

We note two ramifications. First, the intergroup dominance hypothesis suggests that due to the social structuring of primate populations, individuals from dominant social groups are expected to contribute disproportionately to future generations. This indicates that source-sink dynamics will influence primate and human evolution with respect to intergroup aggression. Thus, in preferred habitats, groups are expected to occur at high density and to act as genetic sources, exporting genes to subpopulations in more marginal habitats. Groups within these successful subpopulations should compete aggressively, and success in competition will, therefore, lead to high fitness for individuals that have evolved to fight well against neighboring groups. Dominant groups are thus expected to export genes which promote success in intergroup aggression. This may contribute to explaining why aggressive intergroup relations sometimes prevail in populations where intergroup aggression provides no obvious benefits to dominant social groups, as discussed for Japanese macaques.

Second, the evidence that dominant groups tend to have a fitness advantage in nonhuman primates implies that many of the psychological mechanisms underlying success in intergroup competition may be similar in humans and other primates. Such mechanisms have hardly been studied. Wrangham (1999) suggested that for chimpanzees, they might include the experience of a victory thrill, an enjoyment of the chase, a tendency for easy dehumanization (or its equivalent for nonhuman primates) and deindividuation, ready coalition formation, and sophisticated assessment of power differentials in the context of intergroup conflict. Depending on the species (e.g., how important coalitions are within groups, or how often each sex participates in aggression between groups), such mechanisms may be differentiated by sex. The evidence that intergroup dominance is often critical in group-living primates thus provokes a series of questions about the degree of similarity and difference in the psychological mechanisms underlying coalitionary aggression between humans and other species. (see Gat, this volume).

In sum, there are notable behavioral and functional similarities between human warfare and intergroup aggression among nonhuman primates. They suggest that coalitionary aggression in both systems is explicable by promoting intergroup dominance and therefore tending to promote the aggressors' fitness. There are also important differences between human warfare and primate intergroup aggression, particularly above the military horizon where the interests of leaders and followers are often in conflict and where lethal battles are a prominent feature. The conceptual framework provided by the relatively simple case of nonhuman primates is, therefore, merely a starting-point for understanding the behavioral ecology and evolutionary psychology of warfare. Some basic outstanding evolutionary problems in the study of warfare include a fuller accounting of individual costs and benefits (such as the extent to which warriors are altruistic), understanding the nature and importance of the emotional rewards experienced by fighters, and understanding the role of social rewards conferred on warriors as a way to increase aggressive motivations. Studies of the evolution of war are promising, but they are at a very early stage.

Acknowledgments We are grateful to Robert Hinde, Joan Silk, and two anonymous reviewers for comments.

References

Anderson CM (1981) Intertroop relations of chacma baboon (*Papio ursinus*). Int J Primatol 2:285–310

Aureli F, Schaffner CM, Verpooten J, Slater K, Ramos-Fernandez G (2006) Raiding parties of male spider monkeys: insights into human warfare? Am J Phys Anthropol 131:486–497

Benadi G, Fichtel C, Kappeler PM (2008) Intergroup relations and home range use in Verreaux's sifaka (*Propithecus verreauxi*). Am J Primatol 70:956–965

Boesch C, Crockford C, Herbinger I, Wittig R, Moebius Y, Normand E (2008) Intergroup conflicts among chimpanzees in Tai National Park: lethal violence and the female perspective. Am J Primatol 70:519–532

Campbell CJ (2006) Lethal intragroup aggression by adult male spider monkeys (*Ateles geoffroyi*). Am J Primatol 68:1197–1201

Chagnon NA (1997) Yanomamö. Harcourt College, Fort Worth, TX

Cheney DL (1987) Interactions and relationships between groups. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 267–281

Cheney DL, Seyfarth RM (1987) The influence of intergroup competition on the survival and reproduction of female vervet monkeys. Behav Ecol Sociobiol 21:375–386

Collins R (2008) Violence: a micro-sociological theory. Princeton University Press, Princeton

Cooper MA, Aureli F, Singh M (2004) Between-group encounters among bonnet macaques (*Macaca radiata*). Behav Ecol Sociobiol 56:217–227

Cords M (2002) Friendship among adult female blue monkeys (*Cercopithecus mitis*). Behaviour 139:291–314

Cords M (2007) Variable participation in the defense of communal feeding territories by blue monkeys in the Kakamega Forest, Kenya. Behaviour 144:1537–1550

Crofoot MC (2008) Intergroup competition in white-faced capuchin monkeys (*Cebus capucinus*). PhD thesis, Harvard University, Cambridge, MA

Crofoot MC, Gilby IC, Wikelski MC, Kays RW (2008) Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. Proc Natl Acad Sci USA 105:577–581

Dittus WPJ (1986) Sex differences in fitness following a group take-over among toque macaques: testing models of social evolution. Behav Ecol Sociobiol 19:257–266

Dunbar RIM (1988) Primate social systems. Croom Helm, London

Fashing PJ (2001) Male and female strategies during intergroup encounters in guerezas (*Colobus guereza*): evidence for resource defense mediated through males and a comparison with other primates. Behav Ecol Sociobiol 50:219–230

Ferguson RB (2000) The causes and origins of 'primitive warfare': on evolved motivations for war. Anthropol Q 73:159–170

Fry DP (2006) The human potential for peace: an anthropological challenge to assumptions about war and violence. Oxford University Press, New York

Gat A (2006) War in human civilization. Oxford University Press, New York

Gilby IC, Eberly LE, Wrangham RW (2008) Economic profitability of social predation among wild chimpanzees: individual variation promotes cooperation. Anim Behav 75:351–360

Goodall J (1986) The chimpanzees of Gombe: patterns of behavior. Harvard University Press, Cambridge, MA

Gould L, Sussman RW, Sauther ML (2003) Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: a 15-year perspective. Am J Phys Anthropol 120:182–194

Gros-Louis J, Perry S, Manson JH (2003) Violent coalitionary attacks and intraspecific killing in wild white-faced capuchin monkeys (*Cebus capucinus*). Primates 44:341–346

Harris TR (2005) Roaring, intergroup aggression, and feeding competition in black and white colobus monkeys (*Colobus guereza*) at Kanyawara, Kibale National Park, Uganda. PhD thesis, Yale University, New Haven, NJ

Harris TR (2006a) Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). Behav Ecol Sociobiol 61: 317–329

Harris TR (2006b) Within- and among-male variation in roaring by black and white colobus monkeys (*Colobus guereza*): what does it reveal about function? Behaviour 143:197–218

Harris TR (2007) Testing mate, resource and infant defence functions of intergroup aggression in non-human primates: issues and methodology. Behaviour 144:1521–1535

Harrison MJS (1983) Territorial behaviour in the green monkey, *Cercopithecus sabaeus*: seasonal defense of local food supplies. Behav Ecol Sociobiol 12:85–94

Hinde RA (1993) Aggression and war: individuals, groups, and states. In: Tetlock PE, Husbands JL, Jervis R, Stern PC, Tilly C (eds) Behavior, society, and international conflict. Oxford University Press, Oxford, pp 8–70

Hood LC, Jolly A (1995) Troop fission in female *Lemur catta* at Berenty Reserve, Madagascar. Int J Primatol 16:997–1015

Horiuchi S (2008) High population density promotes the evolution of ownership. Ecol Res 23:551–556

Huntingford FA, Turner AK (1987) Animal conflict. Chapman & Hall, London

Janson CH (1985) Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). Behav Ecol Sociobiol 18:125–138

Jolly A, Pride E (1999) Troop histories and range inertia of *Lemur catta* at Berenty, Madagascar: a 33-year perspective. Int J Primatol 20:359–373

Jolly A, Dobson A, Rasamimanana HM, Walker J, O'Connor S, Solberg M, Perel V (2002) Demography of *Lemur catta* at Berenty Reserve, Madagascar: effects of troop size, habitat and rainfall. Int J Primatol 23:327–353

Kaufmann JH (1983) On the definitions and functions of dominance and territoriality. Biol Rev 58:1–20

Keegan J (1993) A history of war. Alfred A Knopf, New York

Kelly RC (2000) Warless societies and the origin of war. University of Michigan Press, Ann Arbor

Kelly RC (2005) The evolution of lethal intergroup violence. Proc Natl Acad Sci USA 102:15294–15298

Kinnaird MF (1992) Variable resource defense by the Tana River crested mangabey. Behav Ecol Sociobiol 31:115–122

Kitchen DM (2004) Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. Anim Behav 67:125–139

Kitchen DM (2006) Experimental test of female black howler monkey (*Alouatta pigra*) responses to loud calls from potentially infanticidal males: effects of numeric odds, vulnerable offspring, and companion behavior. Am J Phys Anthropol 131:73–83

Kitchen DM, Beehner JC (2007) Factors affecting individual participation in group-level aggression among non-human primates. Behaviour 144:1551–1581

Kitchen DM, Cheney DL, Seyfarth RM (2004a) Factors mediating inter-group encounters in savannah baboons (*Papio cynocephalus ursinus*). Behaviour 141:197–218

Kitchen DM, Horwich RH, James RA (2004b) Subordinate male black howler monkey (*Alouatta pigra*) responses to loud calls: experimental evidence for the effects of intra-group male relationships and age. Behaviour 141:703–723

Koenig A (2000) Competitive regimes in forest-dwelling Hanuman langur females (*Semnopithecus entellus*). Behav Ecol Sociobiol 48:93–109

Koyama N (1991) Troop division and inter-troop relations of ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. In: Ehara A, Kimura K, Takenaka O, Iwamonto M (eds) Primatology today. Elsevier Science, Amsterdam, pp 173–176

Koyama N, Nakamichi M, Ichino S, Takahata Y (2002) Population and social dynamics changes in ring-tailed lemur troops at Berenty, Madagascar between 1989–1999. Primates 43:291–314

Majolo B, de Bortoli Vizioli A, Schino G (2008) Costs and benefits of group living in primates: group size effects on behaviour and demography. Anim Behav 76:1235–1247

Manson JH, Wrangham RW (1991) Intergroup aggression in chimpanzees and humans. Curr Anthropol 32:369–390

Maruhashi T, Saito C, Agetsuma N (1998) Home range structure and inter-group competition for land of Japanese macaques in evergreen and deciduous forests. Primates 39:291–301

Maynard Smith J, Parker GA (1976) The logic of asymmetric contests. Anim Behav 24:159–175

Muller MN, Wrangham RW (2004) Dominance, aggression and testosterone in wild chimpanzees: a test of the ‘challenge hypothesis’. Anim Behav 67:113–123

Nishida T, Haraiwa-Hasegawa M, Hasegawa T, Takahata Y (1985) Group extinction and female transfer in wild chimpanzees in the Mahale National Park, Tanzania. Z Tierpsychol 67:284–301

Nunn CL, Deaner RO (2004) Patterns of participation and free riding in territorial conflicts among ringtailed lemurs (*Lemur catta*). Behav Ecol Sociobiol 57:50–61

Nunn CL, Lewis RJ (2001) Cooperation and collective action in animal behaviour. In: Noë R, van Hooff JARAM, Hammerstein P (eds) Economics in nature. Cambridge University Press, Cambridge, pp 42–66

Pride RE (2005a) Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). Behav Ecol 16:550–560

Pride RE (2005b) High faecal glucocorticoid levels predict mortality in ring-tailed lemurs (*Lemur catta*). Biol Lett 1:60–63

Pride RE, Felantsoa D, Randriamboavonjy R, Randriambelona R (2006) Resource defense in *Lemur catta*: the importance of group size. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 208–232

Robinson JG (1988) Group-size in wedge-capped capuchin monkeys, *Cebus olivaceus,* and the reproductive success of males and females. Behav Ecol Sociobiol 23:187–197

Roscoe P (2007) Intelligence, coalitional killing, and the antecedents of war. Am Anthropol 109:485–495

Saito C, Sato S, Suzuki S, Sugiura H, Agetsuma N, Takahata Y, Sasaki C, Takahashi H, Tanaka T, Yamagiwa J (1998) Aggressive intergroup encounters in two populations of Japanese macaques (*Macaca fuscata*). Primates 39:303–312

Sherrow HM, Amsler SJ (2007) New intercommunity infanticides by the chimpanzees of Ngogo, Kibale National Park, Uganda. Int J Primatol 28:9–22

Silk JB (2007) The adaptive value of sociality in mammalian groups. Phil Trans Roy Soc B 362:539–559

Smith ML (2007) Territories, corridors, and networks: a biological model for the premodern state. Complexity 12:28–35

Sponsel LE (1996) The natural history of peace: a positive view of human nature and its potential. In: Gregor T (ed) A natural history of peace. Vanderbilt University Press, Nashville, TN, pp 95–125

Srikosamatara S (1987) Group size in wedge-capped capuchin monkeys (*Cebus olivaceus*): vulnerability to predators, intragroup and intergroup feeding competition. PhD thesis, University of Florida, Gainesville

Starin ED (1991) Socioecology of the red colobus monkey in the Gambia with particular reference to female-male differences and transfer patterns. PhD thesis, City University of New York, New York

Steenbeek R (1999) Tenure related changes in wild Thomas's langurs. I. Between-group interactions. Behaviour 136:595–625

Steenbeek R, van Schaik CP (2001) Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. Behav Ecol Sociobiol 49:100–110

Struhsaker TT (1967) Social structure among vervet monkeys (*Cercopithecus aethiops*). Behaviour 29:83–121

Sugiura H, Saito C, Sato S, Agetsuma N, Takahashi H, Tanaka T, Furuichi T, Takahata Y (2000) Variation in intergroup encounters in two populations of Japanese macaques. Int J Primatol 21:519–535

Suzuki S, Noma N, Izawa K (1998) Inter-annual variation of reproductive parameters and fruit availability in two populations of Japanese macaques. Primates 39:313–324

Takahata Y, Suzuki S, Okayasu N, Sugiura H, Takahashi H, Yamagiwa J, Izawa K, Agetsuma N, Hill D, Saito C, Sato S, Tanaka T, Sprague D (1998) Does troop size of wild Japanese macaques influence birth rate and infant mortality in the absence of predators? Primates 39:245–251

Takahata Y, Koyama N, Ichino S, Miyamoto N, Nakamichi M (2006) Influence of group size on reproductive success of female ring-tailed lemurs: distinguishing between IGFC and PFC hypotheses. Primates 47:383–387

Takahata Y, Koyama N, Ichino S, Miyamoto N, Nakamichi M, Soma T (2008) The relationship between female rank and reproductive parameters of the ringtailed lemur: a preliminary analysis. Primates 49:135–138

Thayer BA (2004) Darwin and international relations: on the evolutionary origins of war and ethnic conflict. University Press of Kentucky, Kentucky

Turney-High HH (1949) Primitive war: its practice and concepts. University of South Carolina Press, Columbia, SC

Valderrama Aramayo MX (2002) Reproductive success and genetic population structure in wedge-capped capuchin monkeys. PhD thesis, Columbia University, New York

Valero A, Schaffner CM, Vick LG, Aureli F, Ramos-Fernandez G (2006) Intragroup lethal aggression in wild spider monkeys. Am J Primatol 68:732–737

van der Dennen JMG (1995) The origin of war: the evolution of a male-coalitional reproductive strategy. Origin Press, Groningen, NL

van Schaik CP (1983) Why are diurnal primates living in groups? Behaviour 87:120–144

Wadley RL (2003) Treachery and deceit: parallels in tribal and terrorist warfare. Stud Conflict Terrorism 26:331–345

Wallace RB (2008) Towing the party line: territoriality, risky boundaries and male group size in spider monkey fission-fusion societies. Am J Primatol 70:271–281

Warner WL (1958) A black civilization: a social study of an Australian tribe. Harper, New York

Watts DP, Muller MN, Amsler SJ, Mbabazi G, Mitani JC (2006) Lethal inter-group aggression by chimpanzees in Kibale National Park, Uganda. Am J Primatol 68:161–180

Wich SA, Assink PR, Becher F, Sterck EHM (2002a) Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): the effect of location. Behaviour 139:65–78

Wich SA, Assink PR, Becher F, Sterck EHM (2002b) Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): the effect of familiarity. Behaviour 139:79–87

Williams JM, Oehlert GW, Carlis JV, Pusey AE (2004) Why do male chimpanzees defend a group range? Anim Behav 68:523–532

Wilson ML, Wrangham RW (2003) Intergroup relations in chimpanzees. Annu Rev Anthropol 32:363–392

Wilson ML, Hauser MD, Wrangham RW (2001) Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? Anim Behav 61:1203–1216

Wilson ML, Wallauer WR, Pusey AE (2004) New cases of intergroup violence among chimpanzees in Gombe National Park, Tanzania. Int J Primatol 25:523–549

Wrangham RW (1980) An ecological model of female-bonded primate groups. Behaviour 75:262–300

Wrangham RW (1999) Evolution of coalitionary killing. Yearb Phys Anthropol 42:1–30

Wrangham RW, Peterson D (1996) Demonic males: apes and the origins of human violence. Houghton Mifflin, Boston

Wrangham RW, Wilson ML, Muller MN (2006) Comparative rates of violence in chimpanzees and humans. Primates 47:14–26

Wrangham RW, Crofoot MC, Lundy R, Gilby I (2007) Use of overlap zones among group-living primates: a test of the risk hypothesis. Behaviour 144:1599–1619

Wright Q (1942) A study of war. University of Chicago Press, Chicago

Yamagiwa J (2008) History and present scope of field studies on *Macaca fuscata yakui* at Yakushima Island, Japan. Int J Primatol 29:49–64

Zegwaard G (1959) Headhunting practices of Netherlands New Guinea. Am Anthropol 61:1020–1041

Zhao Q-K (1997) Intergroup interactions in Tibetan macaques at Mt. Emei, China. Am J Phys Anthropol 104:459–470

Zhao Q-K (1999) Responses to seasonal changes in nutrient quality and patchiness of food in a multigroup community of Tibetan macaques at Mt. Emei. Int J Primatol 20:511–524

Zinner D, Hindahl J, Kaumanns W (2001) Experimental intergroup encounters in lion-tailed macaques (*Macaca silenus*). Primate Rep 59:77–92