PART FOUR

The Primatological Context of Human Nature

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Chimpanzees, Warfare, and the Invention of Peace

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Many features of human societies are clearly inventions, such as agriculture (Bocquet-Appel, 2011), the domestication of cattle (Zeder, 2011), and writing (Woods, 2010). Other human traits are genetic adaptations and thus the products of evolution by natural selection, such as malaria resistance (Hedrick, 2011), lactase persistence (Leonardi, Gerbault, Thomas, & Burger, 2012), and, arguably, language (Pinker & Bloom, 1990). Anthropologists have long debated whether warfare is an invention (Gabriel, 1990; Haas, 2001; Kelly, 2000; Mead, 1940; Montagu, 1976) or an adaptation (Alexander, 1979; Gat, 2006; Tooby & Cosmides, 1988; Wrangham & Peterson 1996; van der Dennen, 1995). This debate largely follows the intellectual traditions established by Hobbes and Rousseau (Otterbein, 1999; Gat, 2006). Hobbes (1651/1997) considered "Warre" to be the natural state of humans, with strong institutions (the "Leviathan") being necessary to keep in check natural tendencies toward selfishness, theft, and violence. In contrast, Rousseau (1754/1964) argued that people were basically peaceful and cooperative, until corrupted by institutions such as property ownership. Hobbes and Rousseau illustrated their arguments with imagined states of nature, based mainly on their own intuitions and experiences, combined with travelers' tales of "savages" in the Americas and elsewhere, and, for Rousseau, early descriptions of the behavior of African apes (Rousseau 1754/1964).

While rooted in competing philosophical traditions, the question of whether warfare is an invention or an adaptation is ultimately an empirical one, which can be answered (at least in principle) by evidence from archaeology, ethnography, and other sources, including animal behavior. Field studies of our evolutionary cousins, chimpanzees, have played an important role in this debate (Boehm, 1992; Bowles, 2009; Eibl-Eibesfelt, 1979; Kelly, 2005; Otterbein, 2004; Sussman, 1999; Wrangham & Peterson, 1996). Here I review the evidence for warlike behavior in chimpanzees and discuss what these findings can tell us about human warfare. I begin with a review of the behavioral ecology of aggression, continue with an overview of the behavioral ecology of intergroup aggression in chimpanzees, and conclude with discussion of the implications for understanding the origins of war and prospects for peace in humans.

Behavioral Ecology of Aggression

A widespread impression is that biological explanations lead to models of human behavior that are simplistic and inflexible, and as a result, pessimistic about the possibilities for improving the human condition. For example, Thorpe (2003) rejects the view that warfare could be an adaptation because he infers that "universal theories" such as evolutionary psychology "imply uniformity." However, identifying a process as biological by no means implies that it occurs uniformly. Sweating, for example, is clearly a biological adaptation designed to cool the body by evaporation, but sweating does not occur uniformly: it occurs when people are hot. Moreover, some people sweat more than others, depending on their physiology and degree of experience with a particular environment.

Equating "biological" with "uniform" applies to an outmoded view of biology. For several decades, behavioral ecologists have argued differently: that animals are designed by evolution to respond appropriately to the various contexts in which they are likely to find themselves. Behavioral ecology is a branch of animal behavior studies that focuses on the ecological and evolutionary basis of the behavior of animals, including humans (Krebs & Davies, 1993). It broadly shares conceptual foundations with its intellectual offshoot, evolutionary psychology (White, Dill, & Crawford, 2007), but retains a greater emphasis on how behavior responds to specific contexts.

The central working hypothesis of behavioral ecology is that organisms are designed by natural selection to solve one basic problem: making more copies of their genes, or in more technical terms, maximizing their inclusive fitness (Dawkins, 1976/1989). Natural selection designs organisms to respond to features of their environment adaptively—that is, in ways that increase the probability that they will survive and reproduce. Some features are invariant or predictable, such as gravity or daily light cycles, while other features recur regularly, but are difficult to predict, such as the location of key food sources, the relative quality of different food sources, or the behavior of potential predators, prey, mates, and rivals. Simple rules may provide adaptive outcomes for invariant or predictable features, but organisms whose lives depend on suitable interactions with less predictable features of the environment have evolved complex sensory and nervous systems to evaluate and respond appropriately to the current state of their environment.

For animals, the most important features of their environment and yet most difficult to predict are often members of their own species (conspecifics). Animals that reproduce sexually typically need other conspecifics in order to reproduce, and they therefore may court and/or coerce potential mates. They may care for their offspring, cooperate with allies, and threaten and fight their rivals. Aggressive behavior thus constitutes only one of many dimensions of social behavior. Sussman and colleagues (2005) have argued that researchers have paid excessive attention to aggression, as it constitutes only a small proportion of the activity budget of most primate species. However, the amount of time that animals spend doing something is at best an incomplete measure of the importance of that activity in evolutionary terms. Mating, for example, occupies a tiny proportion of the activity budget for most species. For example, female ringtailed lemurs are sexually active for only 6 to 24 hours per year (Sauther, Sussman, & Gould, 1999). Nonetheless, without mating, lemurs would have no reproductive success. Likewise, being preyed upon, or being killed by a conspecific, takes up very little of an animal's activity budget, but prevents future reproduction entirely.

Natural selection involves competition, and competition is frequently lethal (Darwin 1859/2003). Predators kill their prey, as do seed predators that kill the embryos of unborn plants. Parasites consume the flesh and blood of their living hosts. Parasitoid wasps lay their eggs in living hosts, which will be eaten alive from within by the growing larvae. Animals fight other members of their species over access to key resources, and under some circumstances, fighting may be fatal.

Behavioral ecologists view aggression as a strategy that animals use when assessment indicates that the benefits will outweigh the costs, with costs and benefits measured in terms of inclusive fitness (Parker, 1974; Maynard Smith & Parker, 1976). Individuals may benefit by behaving aggressively by displacing rivals from key resources, such as mates, food, or shelter. Costs of aggression include time and energy that could be spent on other activities, as well as the risk of injury or death. Because aggression generally involves costs, animals usually avoid getting into direct fights if they can (Fry & Szala, chapter 23). Instead, they threaten and display at their rivals. If they do get into a direct fight, animals usually seem content to chase rivals off, rather than pursuing, capturing, and killing them. Fatal fights may occur, however, when the value of the resource is particularly high, or when the fighters do not expect to live long, or when the cost of killing their opponent is low (Enquist & Leimar, 1990). In some species of spider, for example, females are scattered widely across the landscape. Because males can only travel slowly and face high risks of predation, males may expect to mate with at most one female during their life. If two males happen to encounter the same female, they often fight to the death for her. This tendency is explicable given that this may be their only lifetime mating opportunity (Enquist & Leimar, 1990).

Thus, rather than following a simple strategy of always behaving aggressively, animals instead appear designed to employ aggression selectively, escalating to damaging fights only when the stakes are high, and/or assessment indicates they have a reasonable chance of winning (Keil & Watson, 2011). Animals must therefore assess likely benefits, such as the value of a particular mate or food resource, as well as their chances of winning, should a fight occur. In cases of fights, several factors influence the outcome. Most important is the relative competitive ability of opponents. Larger individuals, as well as those better equipped with weapons such as canine teeth, tusks, or horns, are generally more likely to win (Parker, 1974). In fights between groups, the larger group usually has an advantage, which can be expected to increase with increasing disparity in numbers. Motivation also plays a role, in that individuals may fight harder to defend something they already have, or if their life depends on the outcome. For example, in a series of playback experiments conducted in Serengeti National Park, Tanzania, female lions (*Panthera leo*) were more likely to approach simulated intruders the more they outnumbered them (McComb et al., 1994). Male lions, however, whose entire lifetime reproductive success depends on maintaining control of a pride of females, approached simulated intruders even when outnumbered (Grinnell, Packer, & Pusey, 1995).

In summary, behavioral ecologists view aggression as a strategic option to be used in circumstances under which, over evolutionary time, such aggression has tended to pay off. In the next section, I review what has been learned about the behavioral ecology of intergroup aggression in chimpanzees.

Intergroup Aggression in Chimpanzees

Since 1960, when Jane Goodall began the first long-term field study of chimpanzees at what is now Gombe National Park, Tanzania, field researchers have learned much about the lives of chimpanzees. Chimpanzees have been studied at over 50 sites across Africa (Wrangham, McGrew, de Waal, & Heltne, 1994). The longest-term studies include Gombe (1960–present; Goodall, 1986) and Mahale (1965–present; Nishida, 1990) in Tanzania, Kanyawara (1987–present; Wrangham, Chapman, Clark-Arcadi, & Isabirye-Basuta, 1996), Budongo (1990–present; Reynolds, 2005) and Ngogo (1995–present; Watts, 2012) in Uganda, Bossou (1976–present; Matsuzawa, Humle, & Sugiyama, 2011) in Guinea, and Taï (1979–present; Boesch & Boesch-Achermann, 2000) in Côte d'Ivoire. More recently, other study sites have reached or exceeded 10 years of detailed observation, including Kalinzu (1997–present; Hashimoto & Furuichi, 2006) in Uganda, Goualougo (2000–present; Sanz, Call, & Morgan, 2009) in Republic of Congo, and Fongoli (2001–present; Pruetz & Bertolani, 2007) in Senegal. Together, these studies have documented aspects of chimpanzee social behavior that are common among sites, such as basic patterns of social behavior (Mitani, 2009), as well as aspects that vary considerably, such as patterns of tool use and other local traditions (Whiten et al., 1999).

In the following sections, I review what we have learned from these studies about intergroup aggression in chimpanzees, including (i) patterns of intergroup interaction, (ii) the frequency of intergroup killing, (iii) ultimate causes of intergroup aggression, and (iv) proximate causes, including social and ecological factors, affecting rates of intergroup aggression.

Patterns of Intergroup Interaction

Chimpanzees live in groups called communities that may number more than 150 individuals (Mitani & Watts, 2005) but usually number around 40 individuals (median = 46.3, range 10 –144, $N = 9$; Wrangham, Wilson, & Muller, 2006). Instead of traveling in a cohesive troop like many other primates, chimpanzees have a fission-fusion social organization, in which all members of a community rarely, if ever, come together at once. Instead, they travel, forage and rest in subgroups ("parties") that change in size and composition throughout the day. Parties range in size from one to dozens of individuals. For example, mean party size was 9.2±7.0 independent individuals at Kanyawara ($N = 5527$; Wilson, Kahlenberg, Wells, & Wrangham, 2012) and somewhat larger at Ngogo (mean = 10.3±10.2; $N = 827$; Mitani, Watts, & Lwanga, 2002), where parties of up to 44 independent individuals were observed (Wakefield, 2008). Males usually spend their entire lives in the community of their birth, whereas females usually emigrate to another community at sexual maturity, presumably to avoid inbreeding with male kin (Pusey, 1980). When sexually receptive, female chimpanzees display a large pink swelling of the ano-genital skin (Tutin & McGinnis, 1981), which in addition to other functions, may act as a "social passport" when females transfer to new communities, as males are more likely to affiliate with and protect such females when they have a fully tumescent swelling (Boesch & Boesch-Achermann, 2000).

It may take many years for researchers to learn all the members of a previously unstudied community. For example, at Gombe, it was only by about 1966 that all the individuals of the Kasekela community were habituated to observers and individually recognized (Pusey, Wilson, & Collins, 2008). Chimpanzees, however, appear to know perfectly well who belongs in their community. When chimpanzees hear, see, or encounter evidence of unfamiliar individuals, they typically respond with fear and/or hostility, unless the stranger is a sexually receptive female without dependent offspring (Boesch et al., 2008; Goodall, 1986; Williams, Oehlert, Carlis, & Pusey, 2004).

Chimpanzees occupy large home ranges, with annual ranges covering 10–30 km^2 in forest (e.g., Kanyawara: median = 16.4 km^2, range 10.8–29.5 km^2, $N = 15$ years [Wilson, Kahlenberg et al., 2012]; Ngogo: 28.76 km^2 [Mitani et al., 2010]) and more than 50 km^2 in dry habitats (Hunt & McGrew, 2002). Males are generally more social and range more widely than females (Chapman & Wrangham, 1993; Wrangham, 1979), though males and females have more similar ranging patterns at Taï (Lehmann & Boesch, 2005). At sites in East Africa, females spend more time ranging alone, and when alone, concentrate their ranging in individual core areas, which may in turn be grouped with core areas of other females in "neighborhoods" (Gombe: Williams, Pusey, Carlis, Farm, & Goodall, 2002; Kanyawara: Emery Thompson, Kahlenberg, Gilby, & Wrangham, 2007). Chimpanzees spend most of their time toward the center of their range; for example, at Kanyawara, chimpanzees spent 85 percent of observation time within the core of their range (Wilson, Hauser, & Wrangham, 2007).

Because chimpanzees live in fission-fusion communities with large ranges, early observers only gradually recognized that chimpanzees live in groups with social and territorial boundaries. Van Lawick-Goodall (1968) and Reynolds & Reynolds (1965) initially believed that chimpanzees lived in fluid communities with open membership, separated only by geographical boundaries. In contrast, Nishida realized early on that chimpanzees at Mahale lived in distinct social groups (Nishida, 1968; 1979). Researchers eventually found this to be the case at Gombe (Goodall, 1977; Goodall et al., 1979) and among chimpanzees in general (Mitani, 2009; Wilson & Wrangham, 2003).

Males may visit the periphery of their range for multiple reasons, including searching for food and/or mates, or to conduct boundary patrols, during which they appear to search for neighbors and/or signs of encroachment (Goodall et al., 1979). Boundary patrols involve distinctive patterns of behavior, during which large parties consisting mainly of adult males travel to the periphery of their range and move cautiously and quietly, often in single file (Boesch & Boesch-Acherman, 2000; Goodall et al., 1979; Goodall, 1986; Mitani & Watts, 2005; Watts & Mitani, 2001; Wrangham, 1999). When conducting boundary patrols, chimpanzees spend more time traveling and less time feeding than at other times (Amsler, 2010). They move slowly and cautiously, but travel further, because they spend less time feeding (Amsler, 2010). Patrols thus represent an investment in defense of group territories that imposes time, energy, and opportunity costs, but is likely necessary to prevent encroachment by rival communities (Amsler, 2010). Variation exists among sites in the extent to which males conduct such distinctive patrols, with patrols occurring frequently at some sites, such as Ngogo (Amsler, 2010; Mitani & Watts, 2005) and Taï (Boesch & Boesch-Achermann, 2000), but rarely at others, such as Budongo (Reynolds, 2005). However, even at sites where males rarely exhibit distinctive patrolling behavior, males visit the range periphery more often than lactating females (Chapman & Wrangham, 1993; Bates & Byrne, 2009).

Because chimpanzees live at low densities in large ranges and concentrate their range use toward the center of their ranges, encounters between members of neighboring groups occur infrequently. For example, at Kanyawara, intergroup encounters occurred on only 1.9 percent of days on which researchers followed chimpanzees (Wilson, Kahlenberg et al., 2012). Chimpanzees living in more densely populated areas might encounter neighbors more frequently. Chimpanzees at Taï and Ngogo encountered their neighbors 1–2 times per month (Boesch et al., 2008). When encounters do occur, they are usually limited to acoustic contact. At Taï, 73 percent of 485 intergroup encounters observed among three communities involved only acoustic contact (Boesch et al., 2008), as did 85 percent of 120 encounters observed at Kanyawara (Wilson, Kahleberg et al., 2012). During acoustic encounters, chimpanzees produce loud vocalizations, including pant-hoots, which are most frequently produced by high-ranking adult males, and are often given in choruses, with many individuals calling at once (Goodall, 1986). Chimpanzees use pant-hoots to communicate with other group members over long distances (Mitani & Nishida, 1993). When chimpanzees hear pant-hoots or other calls from neighboring communities, they often show signs of fear and/or excitement, such as looking intently in the direction of the calls, standing bipedally for a better view, embracing, mounting one another, and touching each other's genitalia, and may respond with chorused calls of their own (Goodall, 1986). Chimpanzees sometimes remain silent after hearing strangers calling, and may either stay still, looking toward the source of the calls, or rapidly approach or retreat from the direction of the calls (Boesch et al., 2008; Goodall, 1986; Watts et al., 2006; Wilson et al., 2004; Wilson, Kahlenberg et al., 2012).

Most intergroup interactions remain limited to shouting matches, with members of rival groups separated by hundreds or even thousands of meters. Less frequently, chimpanzees come within visual range of each other (27 percent of encounters at Taï (Boesch et al., 2008); 15 percent of encounters at Kanyawara (Wilson, Kahlenberg et al., 2012)). Whether these close-range encounters result in hostility depends on the sex and reproductive state of the individuals involved, with aggression being most likely toward males and least likely toward potential immigrants: sexually receptive females without infants (Pusey, 1980; Boesch & Boesch-Achermann, 2000). For example, during 18 years of observation of Gombe (1975–1992), observers reported a total of 97 close-range interactions between males from the Kasekela community and unfamiliar individuals of either sex (Williams et al., 2004). Interactions with unfamiliar males always involved aggression (*N* = 22), as did one case where the sex of the stranger was not determined. The percentage of interactions with unfamiliar females that involved aggression depended on the reproductive status of the unfamiliar females, being highest when they were nonswollen females with infants (71%, *N* = 31), and considerably less when they were nonswollen females without infants (40%, *N* = 20). Swollen females, in contrast, elicited aggression less frequently, with (20%, *N* = 10) or without (8%, *N* = 13) infants (Williams et al., 2004). Resident females, however, may attack and severely injure unfamiliar females, presumably because these females are potential rivals for food resources (Boesch et al., 2008; Pusey, Murray, et al., 2008; Townsend et al., 2007).

While interactions with direct physical contact represent only a small proportion of intergroup interactions, when they do occur, the outcome is often injury, and sometimes death. At Kanyawara, 17 percent of encounters within visual range resulted in serious injuries; the two intergroup killings that were inferred to have taken place at Kanyawara were not directly observed (Wilson, Kahlenberg et al., 2012). Killings occurred during two of the 485 intergroup encounters observed at Taï (0.4 percent of all encounters, or 1.5 percent of encounters with visual contact; Boesch et al., 2008). (More killings have been observed at other sites, but the proportion of encounters leading to injury or death has not yet been published.)

Detailed observations of intergroup killings have now been reported from multiple sites (Budongo: Newton-Fisher, 1999; Townsend et al., 2007; Gombe: Bygott, 1972; Goodall, 1977; Goodall et al., 1979; Goodall, 1986; Wilson, Wallauer, & Pusey, 2004; Mahale: Kutsukake & Matsusaka, 2002; Ngogo: Watts & Mitani, 2000; Watts, Mitani, & Sherrow, 2002; Watts, Muller, Amsler, Mbabazi, & Mitani, 2006; Sherrow & Amsler, 2007; Taï: Boesch et al., 2008). Additional killings have been inferred from the discovery of recently killed bodies with wounds typical of chimpanzee attack, and/or other circumstantial evidence (Kalinzu: Hashimoto & Furuichi, 2005; Loango: Boesch et al., 2007;

other cases reviewed in Wrangham et al., 2006). Killings usually occur when the attackers encounter a lone victim, or manage to isolate a victim from a larger party, such as when the others flee (Manson & Wrangham, 1991). Attackers are usually adult and adolescent males, and demonstrate a high level of excitement, with hair erected. They may produce roar-like pant-hoots, waa-barks, screams, and other loud vocalizations, and often give charge displays before and during the attack, and generally appear eager to attack and inflict damage on the victim. Males have been observed to attack males of all ages as well as adult females and infants (Boesch et al., 2008; Goodall, 1986; Watts et al., 2006; Williams et al., 2004). Adult females may participate indirectly, by giving screams and other loud vocalizations during encounters (e.g., Newton-Fisher, 1999), and in some cases adult females also participate directly in attacks, threatening (Goodall, 1977), grabbing, and/or hitting victims (Boesch et al., 2008).

If the stranger is a mother with an infant, both mother and infant may be attacked, though sometimes attackers focus on just one or the other. At Gombe, males attacked nonswollen females more often then swollen females, and such attacks were sometimes severe (Williams et al., 2004). Nine of these females had small infants, of which three were killed (Williams et al., 2004.). The attackers may take the infant from the mother, biting the infant's head, throat, or abdomen, killing it much the way they kill monkey prey (Newton-Fisher, 1999; Sherrow & Amsler, 2007; Watts & Mitani, 2000; Watts et al., 2002; Wilson et al., 2004;), and/or flailing it against the ground or branches (Boesch et al., 2008; Goodall, 1977). Sometimes the attackers begin eating the infant while it is still alive (Goodall, 1977). Attackers often partially or completely consume infant victims, treating them much like monkey prey, begging for and sharing meat (Goodall, 1977; Newton-Fisher, 1999; Sherrow & Amsler, 2007; Watts et al., 2002; Wilson et al., 2004). However, attackers sometimes discard the carcass without eating it (Boesch et al., 2008). Figures 18.1 and 18.2 show images of Andromeda, a female infant killed during an intergroup encounter between chimpanzees of the Mitumba and Kasekela communities at Gombe. Andromeda suffered canine puncture wounds to the head in addition to other injuries (Kirchhoff et al., in press).

During attacks on weaned individuals, attackers may gang up on the victim, pinning it to the ground. Severe attacks may be directed toward individuals of either sex (Goodall, 1986; Boesch & Boesch-Achermann, 2000), though documented cases of killings involve far more male than female victims (Wrangham et al., 2006; Wilson, Boesch et al., 2012). At Ngogo, up to 16 adult and 3 adolescent males have been observed surrounding a single victim (Watts et al., 2006). During the rapid course of events, especially with numerous attackers piled onto the victim, detailed observations of individual behavior may become difficult or impossible, though when attacks are videotaped some details may be determined later (Watts et al., 2006; Wilson et al., 2004). Attackers often hit the victim with their hands, kick with their feet, and bite, inflicting canine puncture wounds (Boesch et al., 2008; Goodall, 1986; Watts et al, 2006; Wilson et al., 2004). Extremities such as tips of fingers, fingernails, and genitalia may be chewed, bitten, or pulled off. In at least

FIGURE 18.1 Andromeda, an 8-month-old female infant chimpanzee from the Mitumba community, with her mother on August 10, 2005. (Photo credit: Michael L. Wilson)

FIGURE 18.2 Andromeda's skull, showing canine puncture wounds. Andromeda was killed during an intergroup encounter between chimpanzees from the Mitumba and Kasekela communities on August 13, 2005. (Photo credit: Claire A. Kirchhoff, PhD)

one case, attackers ripped the trachea out of the victim's throat (Muller, 2002). Attackers may twist the victim's limbs around or rip strips of flesh from the victim (Goodall, 1986). Attackers sometimes continue hitting, kicking, jumping on, displaying at, and/or dragging the victim until after it is dead, but in other cases attackers leave while the victim remains alive. In some cases, the victims appear to have died from internal injuries (Watts et al., 2006). Attacks may inflict skeletal damage, including fractures and canine punctures (Terio et al., 2011).

Frequency of Intergroup Killing

As the number of chimpanzee study sites has increased across Africa, and with accumulating observations from long-term study sites, it has become clear that intraspecific aggression constitutes a pervasive risk for chimpanzees (Mitani, 2009; Wilson & Wrangham, 2003), with intraspecific killings documented for 71 percent of study communities (*N* = 17 communities at 10 sites; Wilson, Boesch et al., 2012). Killings occurred both within and between communities, but the majority of killings (67 percent) involved intergroup attacks (Wilson, Boesch et al., 2012). Intergroup killing thus appears to be a widespread trait of chimpanzees, rather than the result of circumstances peculiar to one or a few study sites.

Sussman (1999) and others (Hart & Sussman, 2005; Marks, 2002) have argued that intraspecific killings in chimpanzees occur infrequently, implying that they must therefore not be important. However, a proper comparison of rates must compare not just the numerator (e.g., the number of killings observed), but also the appropriate denominator, taking into account population sizes and observation time. To calculate rates of mortality from intraspecific violence for direct comparison with data from human societies, Wrangham et al. (2006) analyzed data from six chimpanzee populations with neighboring communities. The most conservative estimate yielded a median of 271 violent deaths per 100,000 individuals per year (range: 78 – 678). Of these, study communities incurred a median 69 deaths per 100,000 individuals per year from intergroup aggression (range: 0 – 417). (Some study communities, such as Ngogo, inflicted many more intergroup deaths than they incurred, but because the population sizes of the communities are not known in these cases, death rates cannot be calculated). Comparing chimpanzee data with those available for subsistence-level human societies, Wrangham et al. (2006) found that hunter-gatherers incurred a median 164 deaths per 100,000 per year from intergroup violence (range 0 – 1000, *N* = 12), and horticulturalists incurred a median 595 deaths per 100,000 per year (range 140 – 1450, *N* = 20). For comparison, the homicide rate for the entire United States during the 1970s and 1980s was 10 deaths per 100,000 individuals per year, with 45 deaths per 100,000 individuals per year in Detroit (Daly & Wilson, 1988). Thus, when population size and observation time are taken into account, chimpanzees experience a rate of intraspecific killing that is similar in magnitude to that experienced by subsistence level human societies, and much higher than that typical of industrialized democracies; indeed, six times higher than that of one of the most violent cities in the United States.

While only a small proportion of intergroup encounters result in killings, because chimpanzees are long-lived and face few other sources of mortality, intraspecific aggression can cause a significant proportion of mortality. Analysis of 47 years of demographic data from the Kasekela and Kahama communities in Gombe found that out of 86 deaths with known causes, intraspecific aggression caused 17 deaths (20 percent of all deaths; 24 percent of male deaths), second only to disease as a cause of death (Williams et al., 2008). Killings were split about evenly between intragroup killings (*N* = 9; 11 percent of deaths) and intergroup killings (*N* = 8; 9.3 percent of deaths; Williams et al., 2008).

A study focusing on a more recent sample that combined behavioral observations with post-mortem investigation of bodies recovered from the Kasekela and Mitumba communities found that intraspecific aggression caused 36 percent of deaths ($N = 4$ of 11 cases), which were evenly split between intragroup ($N = 2$) and intergroup ($N = 2$) attacks (Terio et al., 2011; one of the four killings reported here was also reported in Williams et al., 2008). Kasekela males killed at least two members of the unhabituated Kalande community (Wilson et al., 2004), constituting 13 percent of the 15 deaths with known or inferred causes for that community (Rudicell et al., 2010). Similarly, analysis of 19 years of demographic data from K-group in Mahale found that 18 of 130 deaths with known causes were caused by attack from adult male chimpanzees (16 percent of all deaths), with 5 of these cases (3.8 percent of all deaths) attributed to intergroup aggression (Nishida et al., 2003). For both Gombe and Mahale, the cause of death was uncertain for many chimpanzees (34 percent and 44 percent, respectively), and at both sites, at least some of the individuals that disappeared were thought to have been victims of intergroup aggression (Williams et al., 2008; Nishida, Hiraiwa-Hasegawa, Hasegawa, & Takahata, 1985), suggesting that these figures may underestimate the actual proportion of deaths due to intergroup violence.

Comparable data for human hunter-gatherers are sparse. Data reviewed by Gat (1999) indicate that violence among hunter-gatherers in Australia caused from 10 percent (Tiwi) to 30 percent (Murngin) of adult male deaths, and that violence caused an estimated 5 percent and 6.5 percent of all deaths in arid and well-watered areas, respectively, of Central Australia (Gat, 1999). In comparison, warfare is estimated to have caused less than 1 percent of deaths worldwide in the twentieth century (Pinker, 2011). Thus, intergroup aggression caused a similar proportion of deaths for Gombe chimpanzees and human hunter-gatherers, and a substantially higher proportion of deaths than among the global human population during a century with two world wars.

Causes of Intergroup Aggression

Following Tinbergen (1963), behavioral ecologists recognize that a full explanation of biological phenomena requires answering questions relating to multiple levels of explanation, including ultimate and proximate causes. Ultimate causes address the question: why do animals behave in such a way? Because behaviors must benefit inclusive fitness if they are to evolve by natural selection, ultimate questions can be translated into a general form: does a particular behavioral strategy increase the actor's number of direct and/or indirect descendants, and if so, how? Proximate causes address the question: how do animals behave in such a way? In particular, how do factors such as physiology and the environment influence an animal's responses?

Ultimate causes. At least two questions can be asked about intergroup aggression in chimpanzees at the level of ultimate causation. First, why do male chimpanzees aggressively defend group territories? Second, why do males sometimes kill members of rival communities, rather than merely chase them away?

The first question is in many ways the less difficult one. Intergroup aggression is widespread in group-living species, including many primates (Crofoot & Wrangham, 2010). Indeed, intergroup competition has been proposed to be a central factor in the evolution of social behavior; living in larger groups may provide individuals with a competitive advantage in obtaining scarce resources (Wrangham, 1980). Male chimpanzees may gain several different benefits from defending group territories. Possible benefits include (i) excluding outside males from mating with resident females, (ii) recruiting new females to join their community, (iii) competing for a feeding territory for self, mates, and offspring, and (iv) protecting self, mates and offspring from aggressive attack. These hypotheses are not mutually exclusive, and several or even all of them may play an important role. In support of the first hypothesis, genetic testing has found extragroup paternities to be rare (Constable, Ashley, Goodall & Pusey, 2001; Rudicell et al., 2010; Vigilant et al., 2001; Wroblewski et al. 2009). Thus, males appear to be generally successful in excluding outside males. The second hypothesis, that males participate in intergroup aggression in order to acquire new females, has not been systematically tested. In general, however, females usually emigrate only at adolescence, at which time they appear highly motivated to leave their natal group, presumably to avoid mating with male kin (Pusey, 1980). Once females have started reproducing, they usually stay in the community where they have settled. Females do appear to prefer living in communities with multiple males, as seen by mass migration of females when K-group at Mahale and Kalande at Gombe were reduced to a single male (Nishida et al., 1985; Rudicell et al., 2010). If females have a preference to live in communities with more males, males may be able to recruit new females by advertising their community size during intergroup encounters.

Evidence is growing in support of the third hypothesis: male chimpanzees seek to defend and expand a feeding territory for themselves, their mates and offspring. Interactions occur most frequently when abundant foods are located in border areas (Wilson, Kahlenberg, et al., 2012). Chimpanzees can expand their territory by killing members of other communities (Mitani et al., 2010) or lose territory by losing intergroup contests (Wilson, Kahlenberg, et al., 2012). As territory size increases, chimpanzees have heavier body mass (Pusey, Oehlert, Williams, & Goodall, 2005), forage in larger parties (Williams et al., 2004), and have shorter interbirth intervals (Williams et al., 2004).

The fourth hypothesis, that males participate in intergroup aggression to protect themselves and their mates and offspring, is difficult to rule out, and is compatible with other hypotheses; given that intergroup aggression occurs, the best defense may well be a strong offense.

The question of why chimpanzees kill, rather than simply chase their rivals away, is a challenging one. Fatal fighting does occur in other animal species, but usually when the value of the resource being fought over is unusually high, or when a large fraction of the opponents' reproductive success is at stake (Enquist & Leimar 1990). Among chimpanzees, the value of the resources being contested does not appear unusually large compared to other primate species, nor does a male chimpanzee's lifetime reproductive success usually depend on the outcome of a particular border squabble. The imbalance of power hypothesis, developed by Wrangham and colleagues (Manson & Wrangham, 1991; Wrangham, 1999), focuses on the costs of fighting, rather than the potential benefits. Killing a rival involves both costs and benefits. The main cost of killing is the risk of injury to the attacker, along with the time and effort expended. Benefits of killing the victim include the elimination of a genetic competitor, and a reduction in the strength of a neighboring coalition. In any species with group-level conflict, attackers could potentially benefit from killing the victim, but the costs of doing so are usually too high. But in chimpanzees, and species with similar social structures (such as humans, lions, wolves, and spotted hyenas), variation in party size creates opportunities for gang attacks, thereby reducing the costs (Wrangham, 1999).

Manson and Wrangham based their hypothesis on the observation that most of the attacks observed at Gombe in the 1970s involved gangs of males attacking individuals that were alone or became isolated after their other party members fled (Manson & Wrangham, 1991). The key factor facilitating lethal aggression thus appeared to be numerical asymmetries. When one side has such an overwhelming numerical superiority, attackers may kill an isolated victim at relatively low cost to themselves. The costs need not be zero; indeed, traveling into enemy territory is in itself a potentially costly behavior (Amsler, 2010). But once an encounter begins, participants in a gang attack can quickly subdue a rival at little risk of injury to themselves.

Observational and experimental evidence have supported multiple predictions from the imbalance of power hypothesis. Chimpanzees are more likely to conduct boundary patrols (Mitani & Watts, 2005) and visit the periphery in general (Wilson et al., 2007; Wilson, Kahlenberg et al., 2012) when they are with many males, and thus more likely to win should an intergroup encounter occur. At Kanyawara, parties visiting the periphery had on average twice as many males as parties that stayed in the core of the range (Wilson et al., 2007). Willingness to participate in intergroup encounters likewise appears to depend on numerical assessment. Intergroup encounters often begin with an exchange of vocalizations, which provides a mechanism both for advertising the size of one's own group and assessing the size of a rival group. Experimental (Herbinger, Papworth, Boesch, & Zuberbühler, 2009; Wilson, Hauser, & Wrangham, 2001) and observational (Wilson, Kahlenberg, et al., 2012) studies have found that the response to extragroup calls depends on the number of males in the listening party (Wilson et al., 2001), as well as whether the callers are neighbors or strangers (Herbinger et al., 2009). When males are alone or with only one or two other males, they usually stay silent (Wilson et al., 2001). They are less likely to move toward the calls of strangers when with few males, and if they do approach, they do so more slowly. In contrast, when males are in parties with many males, they often respond with loud choruses of counter-calls and move rapidly toward the strangers (Wilson et al., 2001). Finally, observations in recent decades have provided additional evidence that intergroup fights between large parties are rarely lethal, and that instead, killings usually involve gang attacks on greatly outnumbered individuals, in which the attackers rarely receive injuries (Boesch et al., 2008; Watts et al., 2006; Wilson et al., 2004).

The imbalance of power hypothesis has been further supported by the discovery of boundary patrols (Aureli, Schaffner, Verpooten, Slater, & Ramos-Fernandez., 2006) and lethal aggression (Campbell, 2006) in spider monkeys, which like chimpanzees have fission-fusion social societies. A challenge for this hypothesis is that capuchin monkeys, which live in stable troops, have a high rate of coalitionary killing (Gros-Louis, Perry, & Manson, 2003), suggesting that additional factors are needed to fully explain the observed distribution of coalitionary killing among species.

Proximate causes. Given the ultimate goal of optimizing inclusive fitness, evolutionary game theory predicts that animals should assess current conditions and adopt strategies likely to yield the greatest net benefits (Barash, chapter 2; Kokko, chapter 3). A male chimpanzee that always charged aggressively toward any neighbors that he detected, for example, would eventually find himself picking an unwinnable fight. Instead, animals should assess factors including their own fighting ability, the fighting ability of their opponents, and the value of resources being contested (Fry & Szala, chapter 23). In species such as chimpanzees that fight in coordinated groups, fighting ability may depend largely on the number of opponents on each side, with bigger groups beating smaller groups. The most important proximate factors affecting intergroup aggression in chimpanzees should therefore include numerical asymmetries and ecological factors, particularly the abundance and distribution of food resources. Additional proximate factors include human impacts, such as provisioning and habitat change.

Social factors. Given that intergroup killings occur most often in the context of numerical asymmetries, such asymmetries represent a critical social factor affecting the rates and severity of intergroup aggression. Numerical asymmetries affect intergroup aggression on at least two temporal scales. In the short term, party size varies frequently throughout the day. A given individual may spend part of the day alone, and part of the same day traveling in a large party. These short-term changes in party size depend intimately on ecological factors, and will therefore be discussed further in the next section. In the longer term, individuals live in communities of different size, and community size generally changes slowly as a result of birth, death and migration. While individuals in communities of all sizes spend some time traveling alone, and are thus vulnerable to intercommunity attack, communities with many males are, on average, likely to have an advantage in intergroup competition with smaller communities.

Our understanding of the effects of relative community size is limited, though, in that most studies have focused on a single study community. However, existing evidence supports the prediction that larger communities have a competitive advantage over smaller communities. At Gombe, the larger Kasekela community exterminated the smaller Kahama community (Goodall, 1986). The Kasekela community is now the largest community in Gombe, and has expanded its range greatly at the expense of the smaller neighboring communities (Rudicell et al., 2010; Wilson, 2012). At Mahale, M-group dominated the much smaller K-group during seasonal incursions into the K-group's range (Nishida, 1979). K-group's adult males gradually disappeared from unknown causes, following which M-group took over much of K-group's range (Nishida et al., 1985).

Patterns of patrolling behavior likely vary according to the level of risk posed by neighboring communities. Observers at several sites note that chimpanzees are unusually quiet when patrolling (Gombe: Goodall, 1986; Ngogo: Amsler, 2010; Mitani & Watts, 2005; Taï: Boesch & Boesch-Achermann, 2000). At both Budongo and Kanyawara, however, such silent boundary patrols appear to occur less frequently, perhaps due to lower risk of encountering neighbors at these sites (Bates & Byrne, 2009; Wilson et al., 2007). The population density at Kanyawara is about a third that of Ngogo (Wilson et al., 2007), and in most seasons, Kanyawara chimpanzees rarely encounter neighbors (Wilson, Kahlenberg et al., 2012). When visiting the periphery of their range, Kanyawara males do not consistently reduce their frequency of pant-hoot production (Wilson et al., 2007). Instead, while they call less frequently when crop-raiding, and when in some parts of their periphery, they actually increase their rate of pant-hoot production along their eastern periphery. Chimpanzees thus appear to modulate vocal production based on the costs and benefits of calling, staying quiet when the risks of detection are high (especially when crop-raiding), but advertising their presence when in parties with many males, perhaps to advertise their coalition strength and territory possession (Wilson et al., 2007).

Chimpanzees may be most likely to conduct distinct boundary patrols when they are members of a community that is sufficiently powerful to encroach on neighboring territory, and yet faced with sufficiently powerful neighbors that traveling to neighboring territory remains risky. At Gombe, the Kasekela community is now so much more powerful than neighboring communities that they face relatively little risk from border visits, and travel deep into neighboring ranges with females and infants (Gombe Stream Research Centre, unpublished data). Males in the smaller Mitumba community, however, show more signs of caution when traveling south into Kasekela territory (Mjungu, 2010).

Ecological factors. Ecology relates to intergroup aggression in chimpanzees in at least two major ways. First, food resources may attract chimpanzees from neighboring groups to the same area, causing intergroup interactions to occur (Wilson, Kahlenberg et al., 2012). Second, local differences in food availability between neighboring communities can lead to differences in foraging party size. Abundant food in one area may enable large parties to form. If scarce food in one territory forces males to forage alone or in small parties, they may become vulnerable to attack by their neighbors (Manson & Wrangham, 1991).

Intergroup encounters are most likely to occur in border areas, which chimpanzees may visit for multiple reasons. Males may conduct boundary patrols, or even raids deep into neighboring ranges, during which they may search for members of neighboring communities to attack (Goodall, 1986; Watts et al., 2006; Wilson et al., 2004). Males may search for mating opportunities, either with peripheral females of their own community, or with females from other communities. Males or females may travel to the periphery searching for food.

At Kanyawara, the abundance and distribution of food are strongly correlated with travel patterns (Wilson, Kahlenberg et al., 2012). Chimpanzees eat a variety of foods, but appear to prefer ripe fruit (Wrangham, Conklin-Brittain & Hunt, 1998). The distribution of fruit trees varies by species; some species occur more frequently in the south, others in the center, and others in the north of the range. Many of these species fruit synchronously over intervals of one, two, or even five years. When fruits located mainly in the south such as *Uvariopsis congensis* and *Psuedospondias microcarpa* are in season, Kanyawara chimpanzees spend more time in the south of their range (Wilson, Kahlenberg et al., 2012). The majority of intergroup encounters at Kanyawara occur when these southern fruits are in season, especially *Uvariopsis* (Wilson, Kahlenberg et al., 2012). These fruits thus appear to attract chimpanzees from neighboring groups to a common area, where they are more likely to meet, exchange vocalizations, display at, chase, and attack each other.

Discussions of aggression and ecology in humans often conclude that intergroup aggression is a response to resource scarcity (e.g., Read & LeBlanc, 2003). In contrast, in chimpanzees, aggression seems to be a consequence of resource abundance. For example, the Ngogo community is the largest chimpanzee community known (Mitani, 2006). The Ngogo community's range is just 12 km from Kanyawara's range, but in a more productive part of the forest (Potts, Watts, & Wrangham, 2011). The abundant food resources at Ngogo support an unusually large community, which is able to forage regularly in parties with many males. The Ngogo community is also unusually aggressive, having killed at least 18 of its neighbors in a 10-year period (Mitani et al., 2010). Having many males that are able to forage in large parties clearly gives Ngogo a competitive advantage against neighboring communities.

Aggression and Human Disturbance. When researchers at Gombe and Mahale observed intergroup aggression and killings in the 1970s, very little was known about chimpanzee behavior at other sites. Shorter-term studies at other sites reported that chimpanzees lived peacefully and did not seem to even have bounded social groups (Reynolds & Reynolds, 1965). This raised the possibility that perhaps the aggression at Gombe and Mahale was due to something unusual about those sites. Both sites are located in Tanzania, near the southeastern limits of the range for chimpanzees. Starting in the 1960s, researchers at both sites practiced provisioning, supplying chimpanzees with bananas (Gombe: 1962–2000) and sugar cane (Mahale: 1966–1987) in order to facilitate observations, photography, and filming. Feeding chimpanzees undoubtedly had multiple unintended consequences. Among them, Wrangham (1974) found that more attacks occurred on days when chimpanzees were provisioned, due both to the larger aggregations resulting from the artificial feeding, and to an increase in rate of attacks per individual.

Following up on the Wrangham's (1974) finding, Power (1991) argued that provisioning had a profound general effect on chimpanzee behavior. Power argued that provisioning caused not only intergroup killings, but also many other features of chimpanzee social behavior observed at Gombe and Mahale. Despite the wealth of new field data that have been reported since 1991, critics regularly cite Power (1991) in support of their arguments that intergroup violence in chimpanzees results from human influence, rather than being an expression of natural behavior (e.g., Ferguson, 1999, 2001a; Marks, 2002; Hart & Sussman, 2009).

Power (1991) argued that the restricted feeding of chimpanzees at Gombe and Mahale created frustration, which in turn resulted in a whole suite of behaviors: male dominance hierarchies, despotic alpha males, possessive sexual behavior, closed membership of social groups, territorial behavior, female dispersal, hunting of monkeys, and intergroup killings. Power divides research at Gombe into two periods: a "wild" period, during which only Goodall observed chimpanzees (1960–1964), and the "provisioning studies of disturbed chimpanzees" period, from 1965 on. (At Gombe and Mahale provisioning ended in 2000 and 1987, respectively.) This division is peculiar, since Goodall began feeding chimpanzees in 1962, several years before Power considered that chimpanzees were "disturbed" by provisioning, and discounts the numerous detailed studies that occurred at Gombe from the 1970s on, and likewise discounts all studies from Mahale as being from "disturbed" chimpanzees. Instead, she bases her view of "wild" chimpanzee behavior on Goodall's earliest observations at Gombe, along with reports from short-term studies of unhabituated chimpanzees (e.g., Budongo: Reynolds & Reynolds, 1965; Ngogo: Ghiglieri, 1984).

In terms of studying "wild" versus "disturbed" chimpanzee behavior, however, Power seems not to appreciate the difficulty of studying unhabituated chimpanzees, and overestimates the impact of artificial feeding on behavior away from the feeding station. Detailed studies of natural chimpanzee behavior at Gombe became possible only after the chimpanzees were habituated and when observers began following chimpanzees away from the feeding station (Goodall, 1986). During the first years of Goodall's study (1960–1962), most of the chimpanzees were unhabituated and fearful of humans, and could be observed only at a distance (Goodall, 1971). Once Goodall discovered that chimpanzees could be brought into view more easily with food, she focused her efforts on observations in and around an increasingly elaborate feeding station (Goodall, 1986). Starting around 1968, though, Goodall's team began shifting their attention back to the forest and began documenting systematically what chimpanzees did on days without banana subsidies (Goodall, 1986; Wilson, 2012). They found that chimpanzees search long and hard for food (Wrangham, 1977), they patrol the boundaries of their range (Goodall et al., 1979), and have hostile interactions with their neighbors (Bygott, 1972, Goodall, 1977; Goodall et al., 1979).

In recent decades, long-term studies of chimpanzees at sites without artificial feeding have confirmed that essentially all of the traits Power argued were the result of artificial feeding are in fact typical of wild, unprovisioned chimpanzees. Males compete with other males for rank and can be ordered in a linear dominance hierarchy (Budongo: Newton-Fisher, 1994; Kanyawara: Muller & Wrangham, 2004; Ngogo: Watts, 2000; Taï: Boesch & Boesch-Achermann, 2000). Males compete actively for matings, with higher-ranking males obtaining more paternities than lower-ranking males (Budongo: Newton-Fisher, Thompson, Reynolds, Boesch & Vigilant, 2010; Taï: Boesch, Kohou, Nene, & Vigilant, 2006). Females disperse from their natal communities (Budongo: Reynolds, 2005; Kanyawara: Stumpf, Emery Thompson, Muller, & Wrangham, 2009; Taï: Boesch & Boesch-Achermann, 2000). Chimpanzees hunt monkeys and other mammalian prey (Budongo: Newton-Fisher, 2007; Kanyawara: Gilby, Eberly, & Wrangham, 2008; Ngogo: Mitani & Watts, 2001; Taï: Boesch, 1994). And intergroup killings have now been reported from the majority of study sites (Wrangham et al., 2006; Boesch et al., 2008). Based on Ghiglieri's short-term study at Ngogo (but contrary to what Ghiglieri [1984] thought to be the case), Power argued that Ngogo chimpanzees exemplified her view of wild chimpanzees as peaceful egalitarians. Long-term study at Ngogo, however, has revealed that, while these chimpanzees were never provisioned, they nonetheless killed 5.7 intergroup victims per 100 adult-male years of observation, more than any other chimpanzee community that has been studied (Wrangham et al., 2006).

In seeking to understand aggression in humans and other animals, one must be careful to avoid preconceptions of what a normal society ought to be like. Such preconceptions can arise easily, and the following passage provides one of many examples, by showing that Power expected alpha males to fulfill a particular social role:

> It is the excessive, apparently unprovoked attacks on the females and young that raise the first suspicions that this aggression-based dominance hierarchy is not the normal form of organization for chimpanzees, and that the alpha Gombe animal is a despot, using his power oppressively, rather than serving the group as protective leader. (Power, p. 76)

As it turns out, chimpanzees frequently behave in ways that differ from what we might prefer them to do. Males commonly display at, chase, and hit other group members for no obvious reason (Bygott, 1979; Muller, 2002), sometimes even killing in apparently unprovoked attacks (Murray, Wroblewski & Pusey, 2007). Males coerce females into mating with them (Muller et al., 2011). They attack, kill, and eat infant chimpanzees (Newton-Fisher, 1999; Watts & Mitani, 2000). Instead of welcoming new immigrants into their community, resident females sometimes attack and severely injure them (Pusey, Murray et al., 2008). This is not to say that chimpanzees are wicked; only that the reality of chimpanzee behavior frequently departs from common preconceptions of what benevolent forest creatures ought to do.

Apart from artificial feeding, human activities could impact rates of intergroup aggression in other ways. Widespread conversion of chimpanzee habitat to cropland may increase competition for available space (Goodall, 1977; Pusey et al., 2007). Deaths from poaching and diseases transmitted from humans can decrease the coalition size of some communities, increasing their vulnerability to intergroup attack (Goodall, 1977; Pusey et al., 2007.). However, comparing chimpanzee sites across Africa, estimates of human disturbance explain little of the variation in rates of lethal violence (Wilson, Boesch et al., 2012.).

Chimpanzees, Humans, and the Invention of Peace

Long-term data from multiple sites across Africa make clear that chimpanzees regularly live under circumstances that Hobbes would describe as Warre: "For Warre, consisteth not in Battel only, or in the act of fighting, but in a tract of time, wherein the will to contend by Battel is sufficiently known" (Hobbes 1651/1997: p. 70). Male chimpanzees compete over access to feeding territories for themselves, their mates, and their offspring. Warlike behavior in chimpanzees thus appears to be adaptive, in that participation leads to inclusive fitness benefits: males who successfully defend and expand their group territory appear likely to sire more offspring, and likely to have more successfully reproducing kin, than males that fail to do so (Williams et al., 2004; Mitani et al., 2010).

The occurrence of warlike behavior in our evolutionary cousins is frequently cited as evidence against arguments such as Mead's (1940) that warfare is an invention (Gat, 2006; Keeley 1996; LeBlanc & Register, 2004; Van der Dennen, 1995). The antiquity of human warfare remains contentious, and cannot, of course, be settled with chimpanzee data alone. Some argue that war originated recently, within the past 12,000 years or so (Kelly, 2000; Ferguson, chapters 7 & 11; Fry & Szala, chapter 23; Haas & Piscitelli, chapter 10; Thorpe, 2003), while others argue that warlike behavior has ancient roots, perhaps dating to the common ancestor of humans and chimpanzees (Wrangham & Peterson, 1996) or perhaps evolving separately in the two lineages for similar reasons (Wilson & Wrangham 2003). A thorough review of this debate is beyond the scope of this chapter. However, warlike behavior in chimpanzees poses some provocative questions. The special features thought to be needed for humans to become warlike—weapons, agriculture, sedentary populations, ideology, states—are not present in chimpanzees, and yet chimpanzees suffer rates of intergroup killing comparable to human societies with endemic warfare (Wrangham et al., 2006). Warlike behavior in chimpanzees appears to depend on features also present in human hunter-gatherer societies: male coalitions, fission-fusion social organization, and competition with hostile neighbors (Wrangham 1999; Wrangham & Glowacki, 2012). Moreover, many striking parallels exist between patterns of warlike behavior in chimpanzees and warfare in small-scale, non-state societies (Gat, 1999; Wilson & Wrangham, 2003). In both chimpanzees and humans, males defend group resources that are essential to their reproductive success. Conflict over land appears to be an important cause of war in hunter-gatherer societies (Wrangham & Glowacki, 2012), and similar ecological factors may affect the occurrence of intergroup conflict in humans and chimpanzees. Like in chimpanzees, where intergroup conflicts result from members of neighboring groups being attracted to seasonally available food resources (Wilson, Kahlenberg et al., 2012), on the Andaman Islands, intergroup conflict occurred most frequently during parts of the year when Jarawa and Bea hunters searched for pigs in the same areas (Kelly, 2000). If humans have lived with chronic warfare for long stretches of evolutionary time, various psychological mechanisms underlying warfare in humans are plausible candidates for adaptations (McDonald, Navarette, & Van Vugt, 2012; Tooby & Cosmides, 1988). If this view is correct, then peace, not war, is the invention—a profoundly important and good invention, but an invention all the same.

A useful analogy, perhaps, is with language and writing. Pinker & Bloom (1990) persuasively argued that the capacity for language is an adaptation. People everywhere spontaneously learn to speak, and language likely has a long history of coevolution with the human brain (Deacon, 1997). Writing, on the other hand, is undoubtedly an invention. Every society was illiterate until the invention of writing some five thousand years ago (Woods, 2010), and even now, literacy rates remain low in some parts of the world. Writing is useful and important, and nearly everyone can learn to do it, but it is not an adaptation.

Like language, war appears to be a human universal—or at least nearly so. Accounts of war from all parts of the world are depressingly similar. Whether the descriptions are from the *Iliad*, the Old Testament, history, ethnography, or the daily newspaper, during times of war people everywhere and every-when seem highly motivated to fight and kill, and often maim and torture, their enemies. Warfare appears to be endemic in tribal societies, with only a few exceptions, and these exceptions demonstrate the special circumstances required to prevent war (Gat 2006; Pinker, 2011). For example, in the 25 hunter-gatherer societies coded by Kelly (2000), "in all but a few cases one or another form of warfare occurs once every five years, or more often" (p. 51), and only in 7 of these societies (28 percent) is warfare infrequent or nonexistent. Some of the more peaceful hunter-gatherers, including the Mbuti, !Kung and Semang, have been profoundly affected by powerful neighbors with evolutionarily novel subsistence practices, including horticulture and pastoralism (Wrangham & Glowacki, 2012). Focusing on the few cases for which data are available on hunter-gatherers living with hunter-gatherer neighbors, Wrangham & Glowacki (2012) conclude that "there was a strong tendency for hostility toward members of different societies, and for killing to occur principally in asymmetric interactions."

In contrast, peace appears to be an achievement, one that may indeed have been essential for the invention of writing. Writing appeared in the early centers of civilization, including Egypt, Mesopotamia, China, and Mesoamerica, where early states and city-states provided a framework for stability, urban life, scholarship, and trade (Woods, 2010). Although many early writings document the chronic warfare that characterized the ancient world, they also include codes of law, such as the Code of Hammurabi. Indeed, writing systems, legal codes, and state formation evolved together in ancient Mesopotamia (Charpin, 2010), where following the invention of writing, disputes over, for example, ownership of land could be resolved by reference to the written deed of purchase rather than by force. Early states carried on wars with each other, but within their boundaries claimed a monopoly on violence, enabling ordinary people to carry out their business without having to assume the full responsibility for deterring theft or personal violence (Boehm, 2011; Pinker, 2011).

For most of human history, the world of peaceful relations has had strict boundaries: peace within the state, anarchy without. Only with the establishment of international organizations such as the United Nations have widespread steps been taken to achieve something like the perpetual peace that Kant (1795/1983) envisioned, and of course that goal remains elusive (Howard, 2000). Some parts of the world that formerly suffered chronic and devastating war, such as much of Europe, have achieved a remarkable degree of international peace in recent decades, but this achievement requires training, education, and the development of institutions and mores that take time and effort to acquire (Pinker, 2011). These institutions have not yet taken root in many parts of the world, with tragic consequences for those living there. But just as the ability to attain widespread literacy is within reach for all human societies, so is the ability to achieve peace.

And yet, despite this hope that global peace is a practical objective, and not just a philosopher's dream, chronic wars drag on in many parts of the world. From the perspective of behavioral ecology, we should expect rates of human warfare to vary according to social and ecological circumstances, just as rates of intergroup violence vary among chimpanzee populations. So what are some factors that should make people more or less peaceful?

As strategic inclusive fitness optimizers, people should assess the costs and benefits of participating in war. When the net costs are too high, or the net benefits too low, people should avoid fighting and choose peaceful means of resolving conflicts instead. In this view, the achievement of peace depends on arranging the costs and benefits correctly so that people adopt peaceful rather than warlike strategies to achieve their goals.

Relatively few scholars of war and peace have adopted a behavioral ecology framework (for an exception, see Mesquida & Weiner, 1996). However, researchers in international studies have independently identified many factors associated with whether nations fight wars (Doyle, 1983; Gelpi & Grieco, 2008; Mousseau, 2009; Rauchhaus 2009). Behavioral ecology provides a useful framework for interpreting these findings.

Factors that raise the costs of war include overwhelmingly powerful opponents and overwhelmingly powerful weapons. Nuclear weapons in particular appear to raise the stakes sufficiently high that nuclear powers avoid fighting one another (Rauchhaus, 2009).

The relative benefits of fighting war may also decline, particularly with the advent of trade. One of the starkest differences between humans and chimpanzees is that intergroup interactions are always a zero-sum gain for chimpanzees. Unlike humans, chimpanzees have nothing to trade with their neighbors. They stand to benefit only by excluding their neighbors from a given plot of land. In contrast, among humans, the neighbors may have key resources that would otherwise be unavailable, and may be willing to trade them: stone for tools, shells and pigments for bodily adornment, or permission to use waterholes or hunting grounds during times of scarcity. The occurrence of stone tools and other items hundreds of kilometers from their sources indicates that humans have engaged in long-distance trade at least since the Middle Stone Age in Africa (McBrearty & Brooks, 2000). Among modern nations, the more countries trade with one another, the less likely they are to fight wars (Gelpi & Grieco, 2008; Rauchhaus, 2009). If one function of war is to obtain resources, trade provides a means to obtain the benefits of war (i.e., the resources in question) at a much lower cost (i.e., the price of the goods being traded, rather than the risk of ruin and death in war). A similar process appears to apply within nations. Countries with functioning market economies have a lower incidence of civil war, presumably because people in such countries can obtain by peaceful means resources that may be unobtainable except by force in other countries (de Soysa & Fjelde, 2010).

Another prediction from behavioral ecology is that people within a society can be expected to differ in their expected payoffs from war. As Ferguson (2001b) notes, elites in general likely stand to benefit from war much more than the soldiers who are recruited or coerced into doing the actual fighting. One of the best-supported findings in international relations is the so-called liberal or democratic peace: democracies are less likely to go to war with one another than are more authoritarian governments (Doyle 1983; Gelpi & Grieco, 2008; Hobson, 2011; Mousseau, 2009). One possible mechanism for this is that democracies better align national policy with the interests of the bulk of the citizens, rather than the elites. Alternatively, citizens of societies with contract-intensive economies may be predisposed toward applying similar rules to international affairs (Mousseau, 2009).

Additional factors promoting peace may include favorable demography and reproductive leveling. Mesquida & Wiener (1996) found that countries with a relatively high proportion of young men experienced a higher rate of conflict-related deaths. The authors argue that under such demographic conditions, young men must compete more intensively for reproductive and material opportunities. Along similar lines, civil war appears to be more common in countries with widespread polygyny (Kanazawa, 2009), perhaps because when many women marry polygynously, unmarried men find their reproductive options severely constrained.

The specific factors that best promote peace continue to be debated, and are difficult to disentangle, given that the world's most peaceful countries today share multiple traits in common (Pinker, 2011). In societies with democratic elections, contract intensive market economies, and transparent laws enforced by a fair government, people can achieve their goals without resorting to violence. Stable, fair governments and the rule of law provide opportunities to benefit from one another, rather than benefit only at the expense of one another. Effective law enforcement both raises the costs of committing violence and reduces the necessity of violence. Additionally, in societies where population growth does not outstrip economic growth, and where reproductive leveling is enforced through legal restrictions on polygyny, young men are generally better off pursuing peaceful strategies.

Many critics of the hypothesis that warfare is an adaptation frame their argument in moralistic terms, as if arguing for a biological basis was equivalent to arguing that warfare is unstoppable, or perhaps even desirable (Marks, 2002; Sussman, 1999). On the contrary, though, those interested in the biology of warfare have often passionately sought ways to prevent war (Goodall & Berman, 1999; Hamburg, 2004; Wrangham, 2010). Moreover, identifying biological roots of warfare by no means implies that warfare is inevitable in humans, any more than other features that were prevalent in our evolutionary history—such as exposure to harsh weather, food scarcity, and death from infectious disease—are unavoidable in modern life. Instead, an understanding of warfare rooted in behavioral ecology seems likely to help point the way toward a better understanding of the contexts that support peaceful intergroup relations.

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