

Violent Cousins

Chimpanzees, Humans, and the Roots of War

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In 1916, during the Battle of the Somme, millions of soldiers from the German, French, and British Empires spent months using machine guns, artillery, aircraft, and the first battle tanks to injure or kill roughly a million people; during the course of which the French and British forces advanced the line some ten kilometers into German territory (Philpott 2009). The scale of such battles far exceeds anything observed in other vertebrates. Only in some social insects, such as supercolonies of Argentine ants, do battles involve similar numbers of individuals (Moffett 2012). Like other examples of modern warfare, the Battle of the Somme depended on many uniquely human traits: advanced technology, including not only weapons but also ships, trains, and horses transporting millions of soldiers to the battlefield; complex hierarchical societies; division of labor, with agriculture and industry providing food and matériel for full-time soldiers; motivations for fighting rooted in views about morality and honor; and many historical contingencies, including cultural glorification of war and particular tangles of alliances.

Such industrial-scale warfare emerged only recently in history, and following the devastation of the world wars, great powers have fought mainly through proxy wars rather than direct confrontation (Pinker 2011). The empires that fought the Battle of the Somme have long since dissolved, and the German, French, and British nations now peacefully coexist within Europe. Even with Brexit looming, war between France, Britain, and Germany now seems unthinkable. The observation that such patterns of warfare vary greatly over time leads many scholars to view warfare as entirely the result of historical contingency and cultural inventions, such as weapons (Lorenz 1966), agriculture and population growth (Haas 2001), or segmentary societies (Kelly 2000). Nonetheless, despite recognition that particular instances of warfare depend on many specifics of history and technology, the fact that warfare occurs so widely across human societies, and throughout recorded history, suggests that war has deeper evolutionary roots, and can be explained within the same evolutionary framework used to explain intergroup aggression in other species (Ghiglieri 1989; Manson and Wrangham 1991; Gat 2006; Crofoot and Wrangham 2010; LeBlanc 2014).

Observations of intergroup violence in chimpanzees have provided important contributions to the debate about warfare's origins. Male chimpanzees defend group territories and sometimes kill members of other groups (Goodall 1986). While chimpanzee "warfare" occurs at a vastly smaller scale than modern industrial warfare, the resulting rates of mortality from intergroup aggression are similar in scale to those of subsistence-level human societies (Wrangham et al. 2006; Gurven et al. 2013).

Controversy continues over whether the roots of warfare are deep, shallow, or somewhere in between. One possibility is that the roots of warfare extend at least as deep as the last common ancestor (LCA) of humans, chimpanzees, and bonobos (Wrangham and Glowacki 2012; Gat 2015). Alternatively, coalitionary killing may have evolved separately in chimpanzees and humans, but for similar reasons (Manson and Wrangham 1991; Wilson and Wrangham 2003). Some have argued that warfare has deep or moderately deep roots, but has varied in frequency over time. For example, Knauff (1991) proposed that intergroup killing followed a U-shaped trajectory, occurring frequently in the LCA but infrequently for most of the evolutionary history of *Homo sapiens*, then becoming more common in more complex prestate societies. Otterbein (2004) proposed that warfare emerged with *Homo*, occurred frequently among heavily armed Paleolithic big game hunters, became rare following the depletion of big game, and then reemerged with the development of agricultural societies. An extreme version of the shallow roots hypothesis posits that neither humans nor chimpanzees have a biological propensity toward coalitionary killing. Instead, such killing has emerged only recently as a consequence of cultural inventions (in humans) and human disturbance (in chimpanzees; Ferguson 2011; Fry 2011). We consider the most extreme version of the shallow roots hypothesis unlikely, given widespread archaeological evidence for warfare among hunter-gatherers (Allen and Jones 2014), and evidence that rates of lethal aggression in chimpanzees are unrelated to measures of human disturbance (Wilson et al. 2014). In this chapter we will examine similarities and differences in patterns of coalitionary killing in chimpanzees and humans, and attempt to infer whether the roots of war in humans are deep, shallow, or somewhere in between.

In considering the time depth of warfare's roots, it is worth noting that no serious discussion of the evolution of warfare assumes it to be the result of a single psychological mechanism or genetic pathway. Instead, warfare is a complex phenomenon that emerges from a combination of psychological adaptations, under the influence of demographic, ecological, and cultural factors. Many psychological mechanisms involved in warfare surely have roots extending far deeper than the LCA. Aggression occurs almost universally among animals and involves highly conserved neuroendocrine mechanisms (Waltes et al. 2016). The capacity for assessing the relative costs and benefits of fighting is likely also widespread (Parker 1974). A preference for avoiding fights if outnumbered may be nearly universal among animals capable of fighting, because even animals that never fight conspecifics in coalitions may nonetheless face risks posed by group-hunting animals such as lions and wolves. Recent observations of lethal coalitionary aggression by mountain gorillas (Rosenbaum et al. 2016) suggest that psychological mechanisms shared broadly among primates can be sufficient to support coalitionary killing when socioecological circumstances make this an effective strategy.

Intergroup Violence in Chimpanzees and Hunter-Gatherers

Chimpanzees

Since 1960, long-term field studies have logged a total of more than 426 years of observing chimpanzees (Wilson et al. 2014), providing a detailed picture of chimpanzee social structure and intergroup relations. Considerable diversity exists across sites, but many aspects of chimpanzee social behavior are nonetheless similar across a broad range of habitats (Boesch et al. 2002; Mitani 2009; Nishida 2012). Chimpanzees live in fission-fusion communities in which members travel in parties of varying size (Figure 13.1a). Communities change in size slowly, through births, deaths, and migration, whereas parties change in size and composition throughout the day. Parties may consist of lone individuals, small groups of females with young offspring, or mixed-sex groups of various sizes. Males almost always spend their entire lives in their natal community, whereas females generally transfer to a new community at adolescence, presumably to avoid the risk of breeding with closely related males (Pusey 1980). Male chimpanzees show higher levels of affiliation than female chimpanzees (Machanda et al. 2013), and engage in various group activities, including hunting, mutual grooming, coalitions, boundary patrols, and intergroup aggression (Goodall 1986; Mitani 2009).

Each chimpanzee community occupies a territory that males defend from other communities during intergroup encounters (Figure 13.1a; Goodall et al. 1979; Nishida 1979). Substantial overlap may exist between the ranges of neighboring communities (Herbinger et al. 2001). Nonetheless, intercommunity interactions occur infrequently (e.g., 0.67 per month at Kanyawara [Wilson et al. 2012]; 0.94 per month at Kasekela [Gilby et al. 2013]). This is partly because chimpanzees live in large ranges at low population densities (median home range = 12.2 km², range: 4.1– 86; median density = 3.3 individuals / km², range: 0.37– 9.2; Wilson et al. 2014; Figure 13.2a). Even given low densities, intergroup interactions occur less frequently than expected based on Waser's (1976) gas law models (Kanyawara: 2.4 / month predicted, 0.67 / month observed; Kasekela: 3.2 / month predicted, 0.94 / month observed; predicted rates calculated with the following assumptions: velocity $v = 3.4$ km / day (Williams 1999); party spread $s = 100$ m; approach distance $d = 100$ m). The rarity of intergroup encounters thus likely reflects active avoidance of other groups (found also by Wrangham et al. 2007).

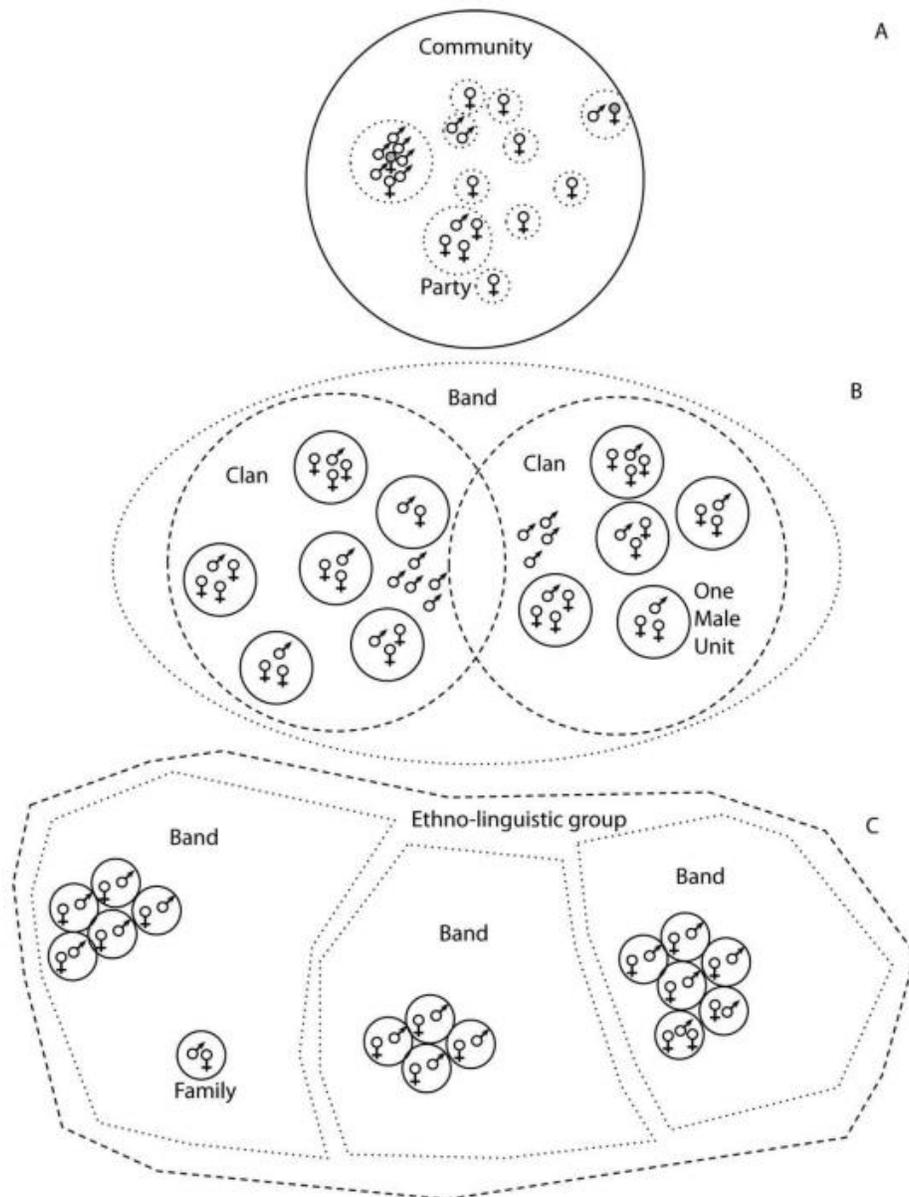


FIGURE 13.1. Schematic depictions of social organization. Panels illustrate societies of (a) chimpanzees, (b) multilevel papionins, and (c) hunter-gatherers. Closed circles enclose individuals with stable, regular associations and social bonds. Dotted and dashed lines enclose temporary or fluid groupings.

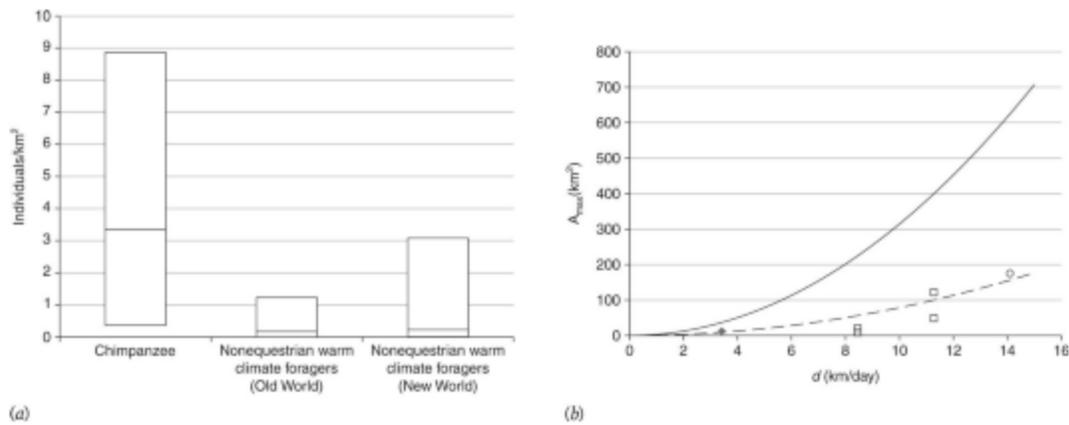


FIGURE 13.2. Population density and territory defendability for chimpanzees and humans. (a) Range of population densities reported for chimpanzees and hunter-gatherers. (b) Predicted economic defendability of territories for chimpanzees and humans. Curves indicate the predicted maximum economically defendable territory size as a function of daily travel distance, with societies with one (dashed line) or two (solid line) parties capable of defending boundaries at any given time. Estimated mean daily travel distances and home range sizes are given for chimpanzees (closed diamond), hunter-gatherer bands (open circle), and a range of four estimates for australopiths (open squares). The average home range sizes for both chimpanzees and hunter-gatherers are close to or just above the limit for predicted economically defendable range if only a single party is involved in defense, but well within the defendable range if more than one party is involved in defense. Estimates for australopith home ranges are highly uncertain but fall within the range of economic defendability.

Intergroup interactions have been described in detail for Mahale (Nishida and Kawanaka 1972; Nishida 1979; Nishida et al. 1985; Kutsukake and Matsusaka 2002); Gombe (Goodall et al. 1979; Goodall 1986; Williams et al. 2004; Wilson et al. 2004), Tai (Boesch and Boesch-Achermann 2000; Boesch et al. 2008), Ngogo (Watts and Mitani 2001; Mitani and Watts 2005; Mitani et al. 2010), and Kanyawara (Wilson et al. 2012). The following description draws on these studies, focusing on features that appear to be common across these sites. For chimpanzees, the community boundary marks the frontier of friendly social relations. Males may visit the periphery of their range for various reasons, including searching for food, females, and boundary patrols, which appear to involve intentional searches for signs of strangers. When visiting border areas, chimpanzees frequently stop to look and listen for neighbors, sometimes standing bipedally. Any sign of strangers is treated with apparent fear and hostility. On hearing calls of strangers in the distance, males may erect their hair, embrace, touch each other's genitalia in reassurance, and either give loud calls in response, or silently move toward or away from the calls. Whether they approach or move away from the strangers, and whether they give a vocal response, depends mainly on the number of males present. Parties with many males are more likely to give a loud vocal response and approach distant calls, both in experimentally simulated (Wilson et al. 2001) and naturally occurring encounters (Wilson et al. 2012). The great majority of intercommunity encounters in chimpanzees involve "shouting matches" between parties that are far out of visible range of one another, and may be hundreds of meters apart (Wilson et al. 2012). Chimpanzees give pant-hoots and other loud calls, and also "drum," producing resonant booming sounds by kicking or hitting tree buttresses.

Chimpanzees come within visual range of their neighbors infrequently, but when they do, the outcome almost invariably involves displays of mutual hostility. Upon seeing strangers, chimpanzees frequently raise their hair (presumably to appear larger and more intimidating) and may perform charge displays, rapidly moving toward their opponents, sometimes dragging or throwing vegetation, sticks, and / or stones.

The outcome of intergroup encounters depends mainly on the number of males present on each side. If many males are present on both sides, a “battle” may ensue, with individuals displaying at, charging, and chasing one another. Fatalities rarely occur in such battles, unless a lone male or mother becomes isolated from the rest of the party. Males often behave peacefully toward females with sexual swellings and without dependent infants, as these females are potential immigrants (Williams et al. 2004). Males behave aggressively toward individuals in all other age-sex classes.

Most fatalities occur when many males encounter a lone stranger of either sex (Wilson et al. 2014). In such cases, the isolated individual generally attempts to flee, while those in the more numerous party seek to capture and attack the victim en masse. Sixty-three percent of killings (62/ 99 cases) involved intercommunity violence. Attackers outnumbered victims by a median 8: 1 ratio. Just over half of all victims were infants, which were usually forcibly removed from the mother (32/ 62 = 52 percent of intergroup killings). Adult males were the next most common category of victims (20/ 62 = 32 percent of intercommunity killings) Adult females were often beaten severely but were less commonly killed (6/ 62 = 10 percent of intergroup killings; all figures from Wilson et al. 2014).

In some ways it is surprising that adult females are ever killed, because they are potential future mates for males. Males may gain fitness benefits from such attacks by reducing feeding competition, either by directly eliminating competitors or (if the females survive) inducing them to avoid border regions (Williams et al. 2004; Pradhan et al. 2014). However, given that in many cases of intercommunity infanticide, the many males attacking the infant could presumably have killed the mother as well, males generally appear to show restraint toward adult females.

Infants taken from their mother are often killed quickly by bites to the head and / or abdomen, and are frequently consumed. Adults are typically pinned to the ground by attackers and are bitten, hit, and kicked until immobile. Victims typically suffer numerous canine puncture wounds. Attackers commonly bite fingers and toes and other soft tissue, including the face, throat, and genitalia. In at least nine cases attackers removed or otherwise damaged the genitalia of adult male victims (Wilson et al. 2015), and in at least two cases attackers tore out the victim’s trachea (Figure 13.3; Watts et al. 2006; Wilson et al. 2015).

Rates of intercommunity killing vary greatly among study communities. For example, the percentage of deaths attributed to intercommunity killing was only 5/ 130 = 3.8 percent for M-group at Mahale (Nishida et al. 2003), whereas at Gombe, intercommunity killing accounted for 8/ 86 = 9.3 percent for Kasekela (Williams et al. 2008) and 2/ 15 = 13 percent for Kalande (Rudicell et al. 2010). While comparisons of chimpanzee and human aggression tend to focus on intercommunity killing, intracommunity killing also occurs, and can cause an even greater

proportion of mortality (e.g., $13/130 = 10$ percent of deaths for M-group [Nishida et al. 2003]; $9/86 = 11$ percent of deaths for the Kasekela community [Williams et al. 2008]). As with intercommunity killing, intracommunity killing typically involves coalitions of males, who usually target grown males or infants (Wilson et al. 2014). Females sometimes participate in coalitionary killing, but at a much lower rate than males (Wilson et al. 2014).



FIGURE 13.3. Adult male victim of intergroup killing by M-group males in Kalinzu Forest, Uganda (photo courtesy Kathelijne Koops).

Male chimpanzees have been proposed to gain two major benefits from intercommunity aggression: food and females. Considerable evidence now supports the view that male chimpanzees defend a group feeding territory for themselves, their mates, and their offspring. At Kanyawara, the great majority of intercommunity interactions occurred when chimpanzees were drawn to groves of an abundant food source (fruits of *Uvariopsis congensis* trees) located in a border region. The Ngogo community expanded their range by 22 percent by occupying a region where they killed thirteen strangers in ten years (Mitani et al. 2010). In contrast, the Kanyawara chimpanzees contracted their range away from an area where they frequently encountered powerful neighbors (Wilson et al. 2012). At Gombe, when territory size was larger, chimpanzees traveled in larger parties (Williams et al. 2004), females had shorter interbirth intervals (Williams

et al. 2004), and, controlling for age, sex, and reproductive condition, individuals had heavier body mass (Pusey et al. 2005), indicating that food was more abundant in larger territories (Figure 13.4).

While males sometimes increase the number of females in their communities through intercommunity killing, it remains unclear whether males attack other groups mainly to acquire new females or to gain other benefits, such as acquiring key food resources. Boesch and colleagues (2008) describe males taking stranger females “prisoner,” but it is not clear whether those females subsequently transferred to the attackers’ community. Williams and colleagues (2004) found that even peripheral females appear to affiliate with a single community, contracting their ranges when the community’s range contracted, indicating that males are unlikely to acquire new females merely by expanding their range. Parous females rarely transfer into a new community, doing so only when the number of males in their resident community is dramatically reduced (Nishida et al. 1985; Rudicell et al. 2010). Nulliparous females generally transfer from their natal communities in any case, though perhaps their decision of where to settle is affected by male displays of numerical strength. Presumably, females seek to transfer to a community with a large, well-defended territory and many potential mates. In cases of community extinction, males may be able to acquire females from vanquished rivals. Of eighteen chimpanzee communities in long-term studies (Wilson et al. 2014), at least five (28 percent) have suffered precipitous declines. One or more parous females transferred following the declines of Kahama (Williams et al. 2004), K-group (Nishida et al. 1985), and Kalande (Rudicell et al. 2010), and at least one of two declining groups at Tai (Roman Wittig, personal communication).

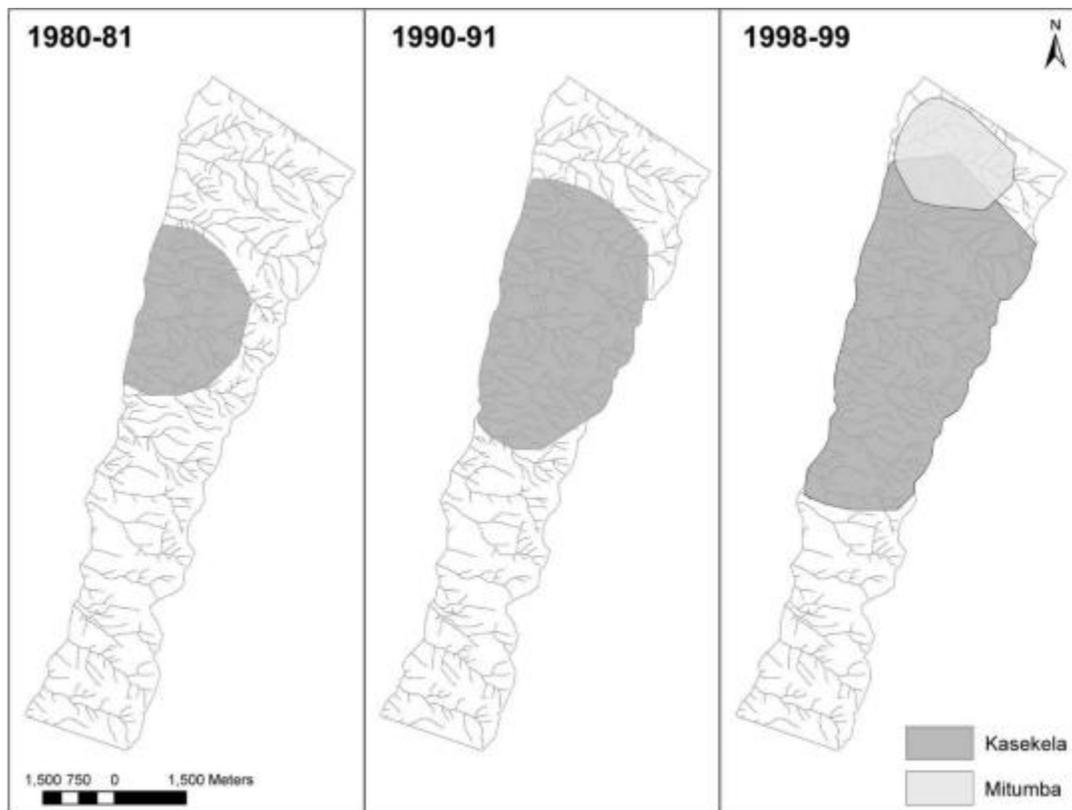


FIGURE 13.4. Home range of the Kasekela community for selected years (1973– 2000), including their minimum (1980– 1981) and maximum (1998– 1999) ranges for this period. Previous studies of this community have found that larger home range was correlated with heavier body mass (Pusey et al. 2005) and shorter interbirth interval (Williams et al. 2004).

While the evidence for acquiring females as a result of intergroup aggression remains ambiguous, multiple lines of evidence support the view that by increasing territory size, victors in intergroup aggression increase their food supply. Controlling for age, sex, and reproductive state, Kasekela chimpanzees weighed more when territory size was larger (Pusey et al. 2005), indicating a general benefit of increased food supply. Females particularly benefit by having shorter interbirth intervals (Williams et al. 2004). Males that are successful at mating will benefit disproportionately from faster reproduction by females. Not surprisingly, then, participation in boundary patrols is correlated with mating success (Watts and Mitani 2001).

Group-living species commonly compete over food and females. Intergroup killing, however, is less common. The best supported reason that chimpanzees kill their opponents, rather than simply chasing them off, is the imbalance of power hypothesis (Manson and Wrangham 1991). This hypothesis begins with the observation that in some species, including chimpanzees, intense scramble competition for food leads to variation in party size. When parties with many males encounter isolated individuals from rival communities, they can kill at low risk of being injured in return. In support of this hypothesis, male chimpanzees avoid the periphery of their territory except when in parties with many males (Wilson et al. 2007); are more likely to conduct boundary patrols when in parties with many males (Mitani and Watts 2005); and are more likely to approach and call in response to simulated (Wilson et al. 2001) and real (Wilson et al. 2012) intruders, the more males they have in their party. Moreover, the great majority of intercommunity killings occur when attackers have an overwhelming numerical advantage (median ratio of attackers to victim = 8: 1; Wilson et al. 2014). By killing adult males, attackers reduce the current coalition size of rival groups, increasing their odds of winning future intergroup interactions (Wrangham 1999), and thereby improving their ability to acquire territory, food, and / or females.

Hunter-Gatherers

Hunter-gatherers live in societies ranging from egalitarian, mobile bands such as those of the Ju /'hoansi (Lee 1979), Aché (Hill and Hurtado 1996), and Hadza (Marlowe 2010) to hierarchical, sedentary chiefdoms such as the Nootka (Drucker 1951). Because the development of stratified societies is thought to be relatively recent, dependent upon newer technologies such as fishing weirs and food storage, anthropologists have focused on mobile foragers as the best living models of Paleolithic societies. The possibility exists that this focus on mobile foragers underestimates the importance of more densely settled societies that may have existed in areas such as lakeshores and river valleys that are now densely settled by farmers (LeBlanc 2014). In any case, even within the more limited subset of mobile hunter-gatherers, considerable diversity exists across varied habitats and cultural regions (Kelly 1995; Binford 2001).

While hunter-gatherers are diverse, compared to the range of possible societies exhibited by other primate species, the variation documented in human societies is actually rather limited (Rodseth et al. 1991). In no human society do people regularly live as solitary foragers (as in orangutans), as isolated monogamous families (like gibbons), as isolated polygynous families (like gorillas), or in promiscuously mating communities (like chimpanzees and bonobos). Instead, humans everywhere live in multilevel societies that include diverse and overlapping social networks (Rodseth et al. 1991; Rodseth and Wrangham 2004; Hill et al. 2009; Chapais 2010). Unlike chimpanzees, in which females sever their social ties on transferring to a new community, both men and women maintain lifelong relations with kin of both sexes (Rodseth et al. 1991). Humans differ strikingly from the promiscuous mating of chimpanzees (Tutin 1979), in that men and women commonly form long-lasting and relatively exclusive sexual relationships (Chapais 2010; Walker et al. 2011).

In contrast to chimpanzees, in which friendly relations are limited to members of a single community, forager societies include at least three distinct levels of social organization, known by various names in the literature, which we call here family, band, and ethnolinguistic group. Families, usually consisting of a husband, a wife, their children, and sometimes one or more close kin, such as a parent or son-in-law, constitute the basic unit of hunter-gatherer societies. In some societies, such as Western Shoshoni (Dyson-Hudson and Smith 1978), families forage independently during times when food resources are scarce. Usually, however, several families stay together in a group variously called a band, camp, or the local group, staying at a temporary campsite within a larger home range. Estimates of median band size range from 18.3 (range: 5.80–81.6; $n = 32$) from a detailed study of census records (Hill et al. 2011) to 26 people (range: 13–250; $n = 130$) for a sample containing more societies but less detailed records (Marlowe 2005). Each family usually builds its own simple shelter and maintains its own fire for cooking. Bands move to different campsites periodically (median = 7 times per year; Marlowe 2005) when local food supplies run short. Band members may regard themselves as part of a larger ethnolinguistic group that numbers a median 565 individuals (range: 23–11,800; Marlowe 2005; Figure 13.1c). Some or all bands of an ethnolinguistic group may come together periodically during times of food abundance to socialize and exchange goods and members (Grubb 1911; Meggitt 1962; Clastres 2000; Burch 2005). Kinship relations provide an additional, overlapping set of memberships that cut across band and even ethnolinguistic boundaries (Rodseth and Wrangham 2004; Chapais 2010).

In contrast to chimpanzees, in which males and females spend most of their time searching for the same sorts of foods, a striking sexual division of labor exists in humans. During the day, men and women usually forage separately. Women gather food such as fruit, seeds, and underground storage organs (USOs) of plants, usually in small groups with other women and their children. Men travel separately, hunting alone or in small groups. Some individuals of both sexes may stay in camp throughout the day, looking after small children, making tools or clothing, resting, or socializing. Both sexes bring food back to camp for further preparation and sharing with other camp members. Men share meat widely with other camp members, whereas women share foods they have gathered mainly with their own families (Kelly 1995). Women do the great majority of the cooking of both meat and plant foods (Kelly 1995). Bands and / or individual

members of bands may claim ownership of specific territories (Heinz 1972; Peterson 1975; Dyson-Hudson and Smith 1978; Cashdan 1983).

Anthropologists continue to debate the extent to which hunter-gatherers engage in intergroup violence, and whether it merits the term “warfare.” Some reviews find that warfare is widespread and deadly in hunter-gatherers (Ember 1978; Gat 1999a; LeBlanc and Register 2004; Otterbein 2004; Wrangham and Glowacki 2012; Allen 2014), whereas others argue that intergroup killing is relatively unimportant among most mobile foragers (Kelly 2000; Fry and Söderberg 2013).

Fatal fighting, both within and between groups, has been documented in most hunter-gatherer societies. For example, Fry and Söderberg (2013) reported that in a sample of twenty-one hunter-gatherer societies, a total of 148 killings occurred. A median of four killings occurred per society (range: 0– 69), and killings occurred in all but three societies. It is impossible to compare rates of killings for this dataset, since only the numerator (number of killings) was reported, not the denominator (such as observation time and number of people observed per society, or number of observations of mortality from other causes). Nonetheless, even though Fry and Söderberg argued that these data indicated that intergroup killing was rare in hunter-gatherers, intergroup killings made up 34 percent of the total. Additionally, Fry and Söderberg excluded thirteen cases that would normally be considered examples of aggression between social groups, such as executing outsiders and interfamilial vendettas. Including these cases, intergroup killings made up 43 percent of all killings. Furthermore, the sample chosen for this study included many groups that have been pacified by more powerful neighbors or were living in a state society (Ju /’hoansi, Hadza, Mbuti, Semang, Kaska, Paiute, Vedda, and Yukaghir) or who live in such sparsely populated regions that they rarely encounter neighbors, such as the Copper Inuit (Wrangham and Glowacki 2012). Thus, even in a sample presented as evidence that lethal intergroup is rare in hunter-gatherers, such killings were widespread and represented a substantial proportion of all killings.

Wrangham and colleagues (2006) found that hunter-gatherers and chimpanzees have similar rates of mortality from intergroup aggression. Hunter-gatherers had a median mortality rate from intergroup aggression of 164.5 per 100,000 people per year (range: 0– 1,000; $n = 12$), which was within the upper and lower estimates for chimpanzees (median = 69– 287 individuals killed per 100,000 chimpanzees per year; $n = 5$ populations). An independent estimate based on different datasets also found that violence caused a similar proportion of deaths for chimpanzees and people living as hunter-gatherers and hunter-horticulturalists (Gurven 2013). Similarly, a recent review found that ethnographically documented “bands” (mostly hunter-gatherers) had a median percentage of death from violence that was higher than any other category of society, including tribes, chiefdoms, and states (Gómez et al. 2016). The median percentage of deaths attributed to violence for prehistoric societies was lower, but highly variable (Gómez et al. 2016), and must be treated with caution, given the many uncertainties involved with prehistoric data. For modern hunter-gatherers, where ethnographers can be confident they have obtained data on all causes of death, the likelihood of dying from violence is high even compared to modern state societies, including the horrific world wars of the twentieth century (Pinker 2011).

Despite considerable variation among groups, recent reviews have found that several aspects of warfare were remarkably similar among a broad range of societies in different ecological and subsistence contexts, from the deserts of Australia to the rainforests of South America (Gat 1999a; Wrangham and Glowacki 2012). While relationships between groups can often be peaceful, fatal fighting occurs at every level of social organization, including among individuals, bands, and ethnolinguistic groups. The most common method of attack is the ambush, which results in the majority of deaths from warfare (Gat 1999a). Most ambushes are by a group of male warriors who seek out an enemy settlement. While women rarely participate in offensive attacks, they sometimes provide support by accompanying raiding parties to cook and act as lookouts (Funk 2010). Raiders usually hide outside an enemy village at night or in the early morning with the hope of attacking the first person or two to exit the village. While raiders might have a specific victim in mind, in practice any individual from the enemy group will usually suffice as a victim. Immediately after the attack, raiders generally flee lest they be discovered by the enemy group or overtaken on their retreat. Opportunities for plunder are limited by the concerns about being overtaken by the enemy group, but sometimes include material goods, or more often captives, especially women and children, who are incorporated into the capturing group (Bridges 1948; Meggitt 1962; Clastres 1972; Burch 2005; Mendoza 2007). Deaths and injuries to raiders are rare but do occur, usually due to being detected by the enemy group while en route to the ambush (Wrangham and Glowacki 2012).

While ambushes were the most common type of intergroup violence, many groups were distrustful of strangers and would attack any they encountered (Burch 2005; Mendoza 2007; Wrangham and Glowacki 2012). Clastres (1972: 163) succinctly summarizes the ethos when two strange parties encountered each other: “If two strange bands meet by chance in the forest they either try to massacre each other or flee in opposite directions.”

Some hunter-gatherers occasionally have what are described as “battles,” in which dozens or even hundreds of warriors gather (Bridges 1948; Meggitt 1962; Burch 2007). Conflict in battles usually appears to involve small skirmishes along a fluid front rather than pitched conflict with a concerted effort. Formal leadership and chains of command are rare to nonexistent, and conflicts usually cease after one or two deaths or serious injuries. Battles could occasionally result in mass casualties if one side is routed (Burch 2007), but documented instances of this occurring are rare.

Whereas in chimpanzees the benefits from intergroup aggression are primarily through increased territory, humans may benefit through multiple pathways including access to territory, the acquisition of captives, transportable goods, and within-group cultural rewards. While in some cases, successful groups take over territory from defeated groups (e.g., Meggitt 1977), warfare can also occur without any obvious resource competition or territorial gain on the part of the victors (Glowacki and Wrangham 2013). Women and children are commonly captured in warfare, but there is significant intercultural variation, and in some societies, taking captives is rare. Commonly, warriors in small-scale societies gain status and prestige and may have increased reproductive success (Chagnon 1988; Glowacki and Wrangham 2015). The crucial difference between chimpanzees and humans is that human culture allows for multiple pathways by which warriors can benefit from their participation, some of which involve intangible rewards such as

status or prestige. These pathways may create the opportunity for reproductive benefits for participants in intergroup aggression. These may increase the incentives for warriors as compared to chimpanzees, and account for the increased risk-taking humans encounter in warfare through conflict with armed individuals.

Coalitionary Killing in the Human Lineage

Chimpanzees and humans thus share many similarities in their patterns of intergroup violence. However, whether these patterns have been inherited from a common ancestor, or evolved convergently, or followed some more complicated path (such as being present in the LCA but rare or absent in some subsequent species), remains unclear. Little direct evidence exists for coalitionary killing for any early hominin, but this is not surprising, given the scarcity of fossils and the difficulty of unambiguously determining the cause of skeletal trauma. In the absence of direct evidence of killing, we can make inferences based on theoretical predictions and evidence related to key socioecological traits. According to the imbalance of power hypothesis (Manson and Wrangham 1991; Wrangham 1999), coalitionary killing should be most likely to occur in species with fission-fusion grouping patterns, intergroup hostility, and coalitionary bonds, which together make killing more likely by lowering costs to the attackers. In the following, we consider whether earlier hominins were likely to have these traits. Given the importance of territorial competition in intergroup relations of both chimpanzees and modern humans, we also consider whether earlier hominins were likely to defend territories. Territorial competition appears neither necessary nor sufficient for coalitionary killing to occur, given that many primates are territorial but few kill. Nonetheless, territorial behavior provides a useful marker of the intensity of intergroup competition, as the territory contains the key resources over which males compete: food, water, shelter, and females.

Grouping Patterns

Did australopiths live in large, stable groups like olive baboons? In small, stable groups like gorillas? Were they solitary, like orangutans, or did they live in large fission-fusion communities like chimpanzees? Or in complex multilevel societies like some papionins living in dry habitats: hamadryas baboons, Guinea baboons, and gelada monkeys? Such grouping patterns leave little in the way of fossil evidence, and what evidence exists is difficult to interpret. For example, if we possessed only skeletons of hamadryas and olive baboons, would we ever guess that these two species live in such strikingly different societies? Speculations are prone to wishful thinking, confirmation bias, and the limitations of our imaginations. Adding to the challenge of the task, the feeding adaptations of australopiths differed from any living apes, including humans (Nelson and Hamilton, this volume). Aspects of feeding ecology unique to australopiths surely affected their patterns of grouping and foraging, but in ways we can only dimly infer. Moreover, considerable variation likely existed both among and within species distributed over broad and varied landscapes, just as we observe today.

Recognizing the limitations of what we can know, we can nonetheless make some inferences based on what we know about living species. Modern humans and chimpanzees both live in communities with fission-fusion dynamics, because they rely on high-quality food resources that occur in patches of variable size and abundance (Wrangham 1987; Aureli et al. 2008). At some times of the year, abundant food supplies support many individuals foraging together, while at other times, individuals must spend much of their time alone or in small parties. As Wrangham (2001) argues, it seems unlikely that any hominins could have lived in large, stable groups in dry open country as several species of baboons do, because they presumably lacked the feeding and digestive adaptations peculiar to baboons.

Chapais (this volume) has argued that a multilevel society consisting of multiple polygynous family groups is a likely intermediate between chimpanzee-like promiscuity and the human pattern of pair-bonds with extensive paternal provisioning. Chapais does not attempt to infer the social systems exhibited by particular hominin species, but available evidence suggests that australopiths are reasonable candidates for having multilevel societies. They appear to have had higher sexual dimorphism in body size and facial structure than chimpanzees (Muller and Pilbeam, this volume), consistent with a more polygynous social structure. Living in drier, more open, and seasonal habitat likely would prevent individuals from foraging in large, stable troops throughout the year, forcing them to adopt fission-fusion dynamics. Nonetheless, suitable sleeping sites, such as cliffs and groves of trees, may have been sufficiently scarce to promote nighttime aggregations even when food scarcity prevented large foraging parties.

In contrast to australopiths, the body size, shape, and dentition of earlier *Homo* were broadly similar to those of modern humans. It therefore seems likely that diet and social organization were also similar to modern humans, and included fission-fusion dynamics. An increasing reliance on meat eating likely increased the extent to which males and females foraged separately, if males obtained most of the meat (as they do in chimpanzees and modern humans).

Intergroup Hostility

Primate groups commonly have hostile and competitive intergroup relations (Crofoot and Wrangham 2010). Even bonobos, well known for having less violent intergroup relations than chimpanzees, nonetheless commonly exhibit hostility toward other groups: 87 percent of encounters observed at Lomako involved aggressive displays, 35 percent involved physical aggression, and females unaccompanied by males fled from strangers (Hohmann and Fruth 2002).

One of the primary drivers proposed for the evolution of social behavior is improved effectiveness in competing for resources, since larger groups tend to defeat smaller groups (Wrangham 1980). Intergroup hostility is expected to be absent only if groups rely on resources that are too dispersed to be defensible. For example, gelada monkeys, like many grass-eating mammals, form herds of variable size (Dunbar 1992). Male geladas defend their females against other males, and individuals may defend valuable food patches, but no effort appears to be made to prevent new subgroups from joining the herd, presumably because the costs of doing so outweigh the benefits. Thus, australopiths, like the majority of other group-living primates, would

be expected to have generally hostile intergroup relations, unless they relied on an undefendable resource such as grass. Additionally, whatever australopiths ate, they likely required some resources that were scarce and defensible, including water and sleeping sites. Baboon groups living in environments similar to those reconstructed for australopiths compete over access to food, water, and sleeping sites (Markham et al. 2012). Moreover, as with other primates, it is likely that males would have been hostile to extragroup males as potential competitors for mates. We therefore consider intergroup hostility a likely aspect of australopith social life.

As with australopiths, groups of earlier Homo probably competed for key resources, including plant foods, water, shelter, and mates. Additionally, the increasing proportion of meat in the diet likely increased intergroup hostility (Schaller and Lowther 1969; Smith et al. 2012), because of the importance of territory for hunting. Social carnivores such as lions, spotted hyenas, and wolves defend group territories and are intolerant of other groups, presumably to prevent depletion of the prey population in their hunting territories (Smith et al. 2012).

Male Coalitions

In both chimpanzees and hunter-gatherers, intergroup fighting is generally undertaken by coalitions of males. Whether various hominins also had male coalitions likely depended on two factors: dispersal patterns and reproductive skew.

Dispersal patterns affect coalition patterns by determining whether members of either sex are likely to have access same-sex coalition partners. In many species, members of one or both sexes disperse at sexual maturity, presumably to avoid inbreeding (Pusey and Packer 1987). Due to kin selection, close kin are generally preferred as coalition partners (Hamilton 1964). Accordingly, sex-biased dispersal appears to favor the evolution of cooperation among members of the nondispersing sex. In many cercopithecine monkeys, males disperse and females participate in matrilineal coalitions (Wrangham 1980). In chimpanzees, females disperse and rarely form coalitions, whereas males stay in their natal group and engage in many group-level behaviors, including hunting and territory defense (Pusey 2001). Determining dispersal patterns of extinct species is challenging, but recent studies using stable isotope signatures and ancient DNA have begun to provide intriguing hints of female-biased dispersal in australopiths (Copeland et al. 2011) and Neanderthals (Lalueza-Fox et al. 2011). If these species did in fact have female-biased dispersal, that would favor the evolution of male coalitions. Nonetheless, dispersal patterns appear to be only part of the story, given that modern human foragers have strong coalitions among males despite only moderate female bias in dispersal patterns (Hill et al. 2011).

High levels of reproductive skew may be associated with low levels of cooperation among males. For example, in gorillas, a single male usually monopolizes reproduction, and male coalitions are rare (Robbins and Sawyer 2007). Conversely, in chimpanzees, reproductive skew is lower and male coalitions are common (Mitani 2009). Sexual dimorphism in body size and canine length is generally higher when reproductive skew is high (Plavcan 2012). Given the consistent correlation between high sexual dimorphism and high reproductive skew, high sexual dimorphism may also indicate a low level of cooperation among males. This relationship is not precise,

however. For example, if reproductive competition is mainly between male coalitions, rather than within male coalitions, significant body size dimorphism might be favored. This appears to be the case in lions, where males are both much larger than females and form strong coalitions with other males in order to control access to female prides and associated territories (Packer et al. 1988). Likewise, in hamadryas baboons, males are substantially larger than females, but within clans, males appear to respect the mating bonds of other males. Instead, most male-male competition appears to take place during encounters between bands, when males seek to abduct females from other bands (Kummer 1968; Swedell and Plummer 2012).

If australopith males were substantially larger than females (Muller and Pilbeam, this volume), australopiths likely had a relatively high level of reproductive skew. In this case, males would likely have had highly competitive relationships, which would reduce incentives for males to cooperate closely with one another. Coalitions among males therefore may have been weaker among australopiths than in chimpanzees, unless (as in lions and hamadryas baboons) males competed mainly against coalitions of other males. Starting with earlier *Homo*, however, sexual dimorphism appears to decrease compared to australopiths (Muller and Pilbeam, this volume), which may indicate reduced reproductive skew, and thus stronger coalitions among males.

Territorial Behavior

In both chimpanzees and human foragers, competition over territory plays a central role in intergroup relations. As in many other species, chimpanzees and humans depend for their existence on limited resources associated with specific locations: food, water, and shelter. By defending territories, territory owners prevent outsiders from depleting the resources they need to survive and reproduce (Maher and Lott 2000). Whether animals defend territories depends on whether it is economical for them to do so: the costs of territory defense must be outweighed by the benefits (Brown 1964). Whether earlier members of the human lineage defended territories likewise would depend upon whether it was economically feasible to do so.

Among primates, territorial behavior varies considerably among species, and among populations within species. Mitani and Rodman (1979) proposed a simple index to assess the economic defensibility of territories. They found that in primates, species that defended territories generally had average daily travel distances that were at least as long as the diameter of their home range. More recently, Lowen and Dunbar (1994), argued that in species with fission-fusion dynamics, the maximum defendable area should take into account the number of independent foraging parties, or at least those parties that contain members of the territorial sex: Lowen and Dunbar (1994) estimated that chimpanzees have on average 5.5 parties containing males. This estimate seems high, however, given that parties with few males are unlikely to visit boundaries (Wilson et al. 2007) or approach strangers (Wilson et al. 2001, 2012), and only parties containing a substantial portion of the community's males are likely to have sufficient males to repel parties from other communities. It seems reasonable to assume, though, that chimpanzee communities commonly contain more than one party large enough to visit boundaries.

Similarly, in human foragers, men travel a median 14.1 km each day (Marlowe 2005), yielding a maximum defensible home range of 156 km², which is smaller than the median home range size for bands of nonequestrian, warm-climate foragers (median = 175 km², range: 22–4,500 km², n = 125; Marlowe 2005). However, if bands on average contain at least two independently foraging parties with multiple men, the maximum defensible home range increases to 625 km². Thus, for both chimpanzees and human foragers, home ranges of typical size should be economically defensible, though extremely large home ranges should be too large to defend. This is consistent with reports that many foragers defend territories, but that in areas of extremely low density, foragers are nonterritorial (Dyson-Hudson and Smith 1978).

Australopiths appear to have lived in drier, more seasonal habitats than those favored by chimpanzees (Cerling et al. 2011; Nelson and Hamilton, this volume). They therefore would likely have required larger home ranges, and would have defended territories only if their daily travel distances also increased (Mitani and Rodman 1979). Evidence reviewed by Pontzer (this volume) indicates that australopiths had a humanlike efficiency of locomotion, and thus longer daily travel distances than chimpanzees. Even if, as Kramer and Eck (2000) argue, *Australopithecus afarensis* traveled 20–40 percent less each day than modern humans, reducing the median 14.1 km / day traveled by male hunter-gatherers (Marlowe 2005) by this amount yields a daily travel distance of 8.5–11.3 km / day for male *A. afarensis*, which is still much further than the average of 3.4 km / day traveled by male chimpanzees at Gombe (Williams 1999). Anton and colleagues (2002) estimated per capita home range requirements for australopiths based on whether they had ape-like or human-like ranging requirements. We don't know the likely group size of australopiths, nor whether their home range requirements scaled linearly with group size. Using two estimates of group size (twenty or fifty individuals) to bracket the median local group size for humans (n = 26; Marlowe 2005) and community size for chimpanzees (n = 42.3; Wilson et al. 2014), we estimate that australopith home ranges commonly would have been economically defensible as territories (Figure 13.2b).

Given that earlier *Homo* had body size and shape similar to modern humans, it seems probable that they would have had economically defensible ranges in typical habitats. Additionally, in earlier *Homo*, the intensity of territorial competition was likely increased by a combination of four factors. First, as the proportion of meat in the diet increased, *Homo* entered a higher trophic level, and thus required larger territories (Anton et al. 2002). Second, earlier *Homo* shows evidence of adaptations for improved endurance running and / or distance walking (Bramble and Lieberman 2004). Whether these adaptations evolved mainly for running or walking, they indicate an increased daily travel distance for earlier *Homo*, which would permit economical defense of larger territories. Third, at some point during the evolution of *Homo*, our ancestors stopped sleeping in cliffs and trees and began sleeping on the ground instead. This is presumably due to more effective defense against predators (either through improved weapons, use of fire, or both; Wrangham 2010). This independence from sleeping cliffs and trees would permit more efficient range use, enabling *Homo* to set up camp wherever they liked, rather than being limited to sites with safe sleeping locations. Prior to this, scarcity of sleeping sites may have limited populations and provided natural spacing between them. Fourth, compared to *Pan*, modern humans have shorter interbirth intervals (Schwartz 2012). The ability to produce infants more quickly

likely depends on increases in available energy due to practices already present in earlier Homo: increased meat in the diet, more efficient extraction of energy from plant and animal foods, and the availability of softer, more easily chewed weaning foods, due to food processing and possibly cooking (Wrangham 2010). All else being equal, shorter interbirth intervals would lead to faster population growth, which in turn would increase competition for available resources.

Coalitionary Killing

Australopiths thus seem likely to have had fission-fusion grouping patterns, hostile intergroup relations, and economically defensible ranges, but at the same time seem likely to have had weaker coalitions among males than exist in chimpanzees and humans. Additionally, even if australopiths had fission-fusion grouping patterns, individuals may have rarely foraged alone. If females regularly foraged in small parties, as modern humans do when utilizing similar resources, and if males regularly foraged with those females, as in the one-male units (OMUs) of hamadryas baboons and geladas, then australopiths may have rarely foraged alone, and thus had few opportunities for coalitionary killing. In this case, australopiths would have had lower rates of coalitionary killing than either chimpanzees or modern humans.

Like australopiths, early members of Homo likely had fission-fusion dynamics, hostile intergroup relations, and defensible territories. In contrast to australopiths, reduced sexual dimorphism in body size suggests reduced reproductive skew, and thus higher levels of within-group cooperation among males, which in turn would promote coalitionary killing. If, as in chimpanzees and modern humans, males in earlier Homo were more engaged than females in obtaining meat, it is possible that males and females foraged separately. This would increase the vulnerability of both sexes to intergroup aggression. Thus, several lines of evidence suggest that circumstances favoring coalitionary killing occurred in earlier Homo. Consistent with this, by the time of later Homo, evidence consistent with coalitionary killing exists, including cut-marks on human bones (suggesting processing of carcasses for cannibalism) and injuries to bones (Churchill et al. 2009; Trinkaus 2012).

Key Differences in Intergroup Aggression between Pan and Hominins

While chimpanzees and humans exhibit some striking similarities in their patterns of intergroup aggression, they also differ in important ways. Here we review some of the key differences, including weapons, benefits gained by aggressors, multilevel societies, and language.

Weapons

One of the striking differences between chimpanzees and humans is that in humans, combat is usually armed. Chimpanzees mainly fight with their hands and teeth, though they sometimes throw stones (Goodall 1986) and use sticks to hit other chimpanzees with sticks while fighting, and probe for and sometimes kill prey items (Pruetz and Bertolani 2007). In contrast, in hunter-gatherer societies, men routinely spend much of their time foraging far from camp, armed with weapons for hunting big game. While many hunter-gatherers made weapons specifically for fighting people, such as the Aleuts (who used the atlatl when hunting sea mammals but the bow and arrow against human enemies; Maschner and Mason 2013), weapons that are effective at killing prey generally can be used to kill people as well. Hunter-gatherer men are thus nearly always armed and dangerous when away from camp, capable of killing at a distance if provoked or threatened, and disposed to strike preemptively.

As Darwin (1871) noted, the evolution of bipedality freed the hands from locomotion to making and using tools, carrying items, and communicating. Australopith hands show clear evidence of evolution toward greater manual dexterity, including more powerful and more precise grips (Young 2003), suggesting the use of tools such as digging sticks. If australopiths regularly used sticks and / or bones for obtaining USOs, insects, and other foods, these same tools also may have been useful as weapons. Marlowe (2005) notes that among the Hadza, “even women armed with only their digging sticks occasionally scare off a leopard and take its kill.” Hadza digging sticks are substantially larger and sturdier than those used by savanna-woodland chimpanzees (Herndandez-Aguilar et al. 2007), but if australopiths regularly dug for USOs they would presumably have used sturdier sticks than those used by chimpanzees. In addition to sticks, australopiths would have been able to throw stones more effectively than chimpanzees, and probably would have done so more often (Young 2003).

Tools for fighting would have complicated and potentially contrasting effects on coalitionary killing: reducing the costs of attacking unarmed or outnumbered opponents, while raising the costs against armed opponents.

By the time of early Homo, tool use had expanded to include various shaped stone implements. If stones were used as weapons, they would have had effects similar to those described above for australopiths, but to a greater extent, given that the sharp cutting edges of stones would have made for more dangerous weapons than the simple sticks and stones of earlier hominins.

It seems likely that regular use of even simple weapons such as sticks and stones would have affected the frequency of coalitionary killing, though scholars have drawn different conclusions about the likely effects of weapons. For example, it is commonly argued that effective hunting weapons during the evolution of Homo made the killing of people more feasible and common (Otterbein 2004). In contrast, Kelly (2005) argues that thrown spears made fighting so dangerous that a long period of Paleolithic warlessness ensued. This argument seems implausible to us, given the widespread prevalence of intergroup killing among documented peoples with projectile weapons. But whatever the overall effects on rates of killing, it seems clear that weapons increase the advantage of armed attackers against unarmed victims. Individuals who used weapons would thus obtain strong advantages against those who didn't, promoting the cultural and biological evolution of more effective weapon use (Young 2003). Two further contrasting effects

of weapons can be predicted. First, weapons, especially projectile weapons, can increase the advantage of numerical superiority, because weapons enable attackers to concentrate force at a single target (e.g., Bingham 2000). Chimpanzees manage to concentrate force in gang attacks by piling up on isolated victims, with some attackers pinning the victim's hands and feet to the ground while others bite and beat the victim to death. Projectile weapons presumably make such concentration of force even more effective, as many attackers can simultaneously throw rocks, spears, or other projectiles at a victim from a distance. Second, while weapons can amplify numerical advantages in gang attacks, in dyadic conflict weapons can have an opposite effect, serving to equalize competitive ability among individuals of different sizes, and thus reducing the advantage of large body size. In contrast with hand fighting sports such as boxing and wrestling, in weapon fighting sports such as fencing, no weight classes are used, because success depends more on skill than body size (Faurie and Raymond 2003). Fights between individuals armed with weapons (even simple weapons such as stones for throwing and sticks for clubbing) can thus become costly for both participants, with outcomes less easily predicted by variables such as body size. One of several possible explanations for the apparent reduction of body mass dimorphism in *Homo* is that weapons increased the costs of within-group fighting, reducing the selection pressure for large body mass in males (Chapais 2013). However, it is worth noting that men have much greater upper body musculature than women (Puts 2010; Muller and Pilbeam, this volume), suggesting that upper body strength has continued to provide men with important competitive advantages in hunting and / or fighting.

With the advent of modern humans, rapid advances in weapons technology appear to have occurred, particularly a proliferation of weapons made from multiple parts (composite weapons). Many of these involve improvements in projectile weapons, promoting the ability to kill at a distance: boomerangs, hafted weapons, spear throwers, bow and arrow. Improved weapons technology may have been important in the replacement of Neanderthals by modern humans (Shea and Sisk 2010).

We suggest that rather than causing qualitative changes in patterns of coalitionary killing, changes in weapons technology would have provided continued pressure for trends that likely began with the use of simple weapons by australopiths. Within-group fighting would become increasingly dangerous. In a world where an angered group member could kill with a single poisoned arrow, maintaining good intragroup relations would be of paramount importance. Between-group fighting would also become increasingly dangerous, perhaps requiring greater rewards to make fighting worthwhile for participants (Glowacki and Wrangham 2013). Additionally, as Gat (1999a) argues, the use of manufactured weapons created a "first strike capability" in humans. In contrast to animals armed with horns, claws, or teeth, humans can be disarmed, for example, when sleeping. This unusual feature of human weapons may destabilize intergroup relations by favoring preemptive surprise attacks (Gat 1999a).

Weapons, whether used for hunting, fighting, or both, enabled humans to attain an unprecedented level of ecological dominance (Alexander 1990). Circumstantial evidence suggests that as early humans expanded into the carnivore niche, they profoundly impacted the populations of competitors and prey species alike, with species of large carnivores (Werdelin and Lewis 2013)

and terrestrial primates (Klein 1988) becoming extinct. Anthropologists have long speculated that violent competition with modern humans contributed to the extinction of Neanderthals, supposing that modern humans were more effective because of either larger social groups (Gat 1999b) or more sophisticated weapons (Shea 2003). Hortolà and Martínez-Navarro (2013) argue that “Neanderthal extinction should be seen as a mere branch of the Quaternary Megafaunal extinction,” in which killing and predation by modern humans caused the extinction of more than 178 large mammal species worldwide. Due to sparse evidence, such explanations remain speculative (Villa and Roebroeks 2014). Nonetheless, such scenarios are consistent with observations from history that asymmetries in weapons technology have led repeatedly to wars of conquest and sometimes extermination (Diamond 1997; Morris 2014).

Benefits Gained by Aggressors

To the extent that australopiths engaged in intergroup aggression, aggressors likely gained benefits similar to those gained by chimpanzees: increased territory size, improved access to key resources, and repelling competitors for mates. Similarly, intergroup conflict in *Homo* likely involved direct benefits similar to patterns found in chimpanzees and foragers. Successful groups would have gained increased access to territory that included resources such as water sources and hunting areas.

Among small-scale societies with warfare, including band-level societies, warriors are almost universally accorded cultural benefits such as status (Glowacki and Wrangham 2013). It is impossible to directly infer when uniquely human cultural benefits such as status and prestige developed. However, status and prestige likely originated with the development of group living with advanced social learning capacities (Henrich and Gil-White 2001). Several lines of evidence indicate that such capacities were probably present at least from *Homo erectus*. Evidence for increased meat consumption around two million years ago has been attributed to the emergence of cooperative foraging behaviors (Anton et al. 2014), including taking meat back to camp to share with others rather than consuming it directly (Potts 2012). The development of the Acheulean stone tool tradition around 1.76 million year ago (Lepre et al. 2011; Beyene et al. 2013) may have required teaching and significant social learning for these sophisticated flint-knapping techniques to spread. Some faunal assemblages from large game dating to approximately 1.7 million years ago have been interpreted as evidence of male displays and status-seeking behaviors (O’Connell et al. 2002). By the emergence of *Homo*, the sophistication of cultural behavior certainly far exceeded that exhibited by chimpanzees. It seems likely that by the time modern *Homo sapiens* emerged, within-group status mechanisms would have been present. However, these were unlikely to have been particularly well developed until the emergence of complex cultural systems found in more recent groups.

Multilevel Societies and Prospects for Peaceful Intergroup Relations

One of the striking differences between chimpanzees and humans is that intergroup relations in chimpanzees are always hostile, whereas in multilevel human societies, relationships among various kinds of groups are sometimes peaceful. The origin of multilevel societies, either in australopiths or in later hominins, would have affected the prospects for peaceful intergroup relations in two major ways: (1) by increasing the range of group identities and (2) by increasing potential for affiliative interactions between kin of both sexes (Chapais 2010, this volume; Swedell and Plummer 2012).

First, in a closed or single-level society, group identity is essentially binary: ingroup (friends) or outgroup (foes). Immigrants must negotiate the transition from foe to friend when they join a new group, and they do not always manage this successfully (Pusey et al. 2008). In contrast, in a multilevel society, individuals have a hierarchy of group identities, such as one-male unit, band, and troop (Swedell and Plummer 2012). This raises the possibility that members of other social groups are evaluated on a sliding scale, from friendly to hostile. For example, within a band, males in one-male units may compete with other band males for access to females or feeding sites, but may join together with those same males to exclude other troops from occupying their sleeping cliffs or abducting females. Thus, if australopiths lived in multilevel groups, they may have had a similar range of group identities, with intergroup relationships ranging from more friendly to more hostile depending on the level.



FIGURE 13.5. Members of a multilevel primate society: gelada baboons (*Theropithecus gelada*). Here a former leader male (Tony) carries an infant (presumably his) on his back while facing off against the current leader male (Ptolomey, to the left, not pictured), while a male coalition partner (Cthulu, behind Tony, to the left) provides support. (Photographed at Guassa, Ethiopia, by M. L. Wilson.)

Second, multilevel societies can make it possible for both sexes to maintain affiliative relationships with kin (Chapais 2010, this volume). In chimpanzees, males stay with male kin, but when females transfer to a new community, they are cut off from female kin for the rest of their lives (unless multiple females immigrate to the same community). In contrast, in multilevel societies, both males and females may have opportunities to interact with kin across some social boundaries. For example, in hamadryas baboons, both males and females commonly stay within their natal band (Swedell et al. 2011; Städele et al. 2016). Females are usually separated from close kin when forcibly transferred from their natal unit by males; nonetheless, because females generally stay close to other female kin, the possibility exists for affiliative relations among female kin, though this may rarely be expressed (Swedell et al. 2011; Städele et al. 2016). Such a scenario might eventually favor the evolution of both sexes maintaining kinship ties, as seen in modern humans (Rodseth et al. 1991; Chapais, this volume).

Language Evolution in Earlier *Homo*

Language would have caused many changes that are relevant for intergroup relations. Different languages divide the social world into two distinct groups: Us and Them. Those who speak a language or dialect that we can understand are real people: we can communicate with them, reason with them, and negotiate peace. When language boundaries are sharp, relations may be more hostile (Marlowe 2005). For example, in the Andaman Islands, speakers of mutually intelligible dialects also shared cultural practices for negotiating peace, whereas across the linguistic divide relations were implacably hostile (Kelly 2000). However, fighting does occur among speakers of the same language; because people who share a language commonly share borders, they may also be more likely to have conflicts.

Language can facilitate relationships across group boundaries, even at the tribal level. It helps men and women maintain lifelong ties with both kin and nonkin members of other groups. For example, because female chimpanzees sometimes disperse to neighboring communities, males sometimes encounter their female relatives during intergroup encounters. In the few such encounters that have been observed between known relatives, there is little evidence of kin recognition. However, even if individuals do recognize each other as kin, lacking language, they cannot easily communicate this to one another. Language enables people to say to apparent strangers, “I am the friend of your uncle,” or “I am your half-sister, born after your father left your group and joined our group,” or “I am the cousin you have never met, but I knew your mother.”

With language, group membership does not depend on physical proximity. Even people who have never previously met can use language or other symbolic communication (such as tattoos or other ornaments) to communicate that they are members of the same social group. Language thus enables social groups to expand beyond the number of people who can afford to forage together at a given time. Language also facilitates conflict resolution by enabling peaceful communication, such as negotiation of peaceful relations after periods of strife. Language can produce mutually beneficial relationships such as the promotion of trade networks.

Language facilitates planning and coordination, enabling advanced tactics and strategies found only in humans. Chimpanzees going on border patrol communicate with one another through body posture, facial expression, and vocalizations (in the case of border patrols, by staying unusually quiet). But they cannot plan their course of action in detail. In contrast, people can make elaborate plans for raids, setting up ambushes, inviting rivals to treacherous feasts, and so forth.

Kinship, Marriage, and Trade in *Homo*

In hunter-gatherers, three factors are particularly important for promoting peaceful intergroup interactions: (1) long-term recognition of bilateral kinship, (2) marital exchange, and (3) exchange of goods through gifts and trade. Language permeates all of these interactions, and perhaps none of them were possible before the evolution of language.

Humans are unique among primates in that both males and females maintain lifelong relationships with kin of both sexes (Rodseth et al. 1991). Bilateral recognition of kinship, combined with dispersal from the natal group by one or both sexes, results in a complex network of kinship patterns among social groups (Chapais, this volume). Recognizing kin across group boundaries may promote peaceful interactions. Even during battles, men may position themselves to avoid injuring or killing kinsmen among the opposition (Meggitt 1977). Because language enables people to maintain relations with kin despite long separations, and to discover kinship relations that would be impossible to ascertain without language, such extensive recognition of bilateral kinship may not have existed prior to the evolution of language. Nonetheless, a multilevel social structure may have enabled both sexes to maintain kin relations prior to the evolution of language.

Second, people commonly use marriage as a way to build kinship ties across groups (Chapais 2010, this volume). Exchanging spouses connects groups through kinship, and thus promotes kin-based affiliation. Spousal exchange also creates reciprocal obligations, closely related to those involved in the exchange of goods through gifts and trade.

Third, the exchange of goods has an enormous impact on intergroup relations. In chimpanzees, intergroup encounters are always zero-sum events: any territory gained by group A represents a loss for group B. With trade, however, intergroup interactions can result in mutual benefits. Trade can provide access to otherwise unobtainable materials, such as obsidian, needed to make weapons. Evidence of trade begins in the late Stone Age in Africa, with the long-distance exchange of stone for tools (McBrearty and Brooks 2000), and likely depended both on language (to negotiate trade) and on the development of a sufficiently sophisticated material culture to make trade worthwhile.

Conclusions

In summary, chimpanzees and modern humans share many intriguing similarities in their patterns of intergroup aggression, but also striking differences (Table 13.1). In both species, attacks are

conducted mainly by coalitions of males, who defend territories and attack rivals when favorable numerical advantages reduce the risks to attackers. If the LCA was very much like a chimpanzee, then the roots of intergroup violence in humans may be deep indeed. However, our understanding of the LCA remains sketchy, and several unusual features of australopiths suggest a more complicated history.

One great challenge for answering these questions is determining the likely social behavior of australopiths. Recent advances, particularly in stable isotope studies, have provided new windows into the past (Nelson and Hamilton, this volume), and we can hope that future research will continue to provide both new fossils and new means of gaining information from them. Because australopiths likely experienced seasonal food scarcity, and lived where nighttime refuges from predators were scarce, one possibility is that australopiths lived in multilevel societies, much like those of dry country papionins. Given that coalitionary killing has not been observed among multilevel papionins, coalitionary killing may have occurred rarely, if at all, among australopiths living in similar societies. Whatever form australopith societies took, coalitionary killing seems likely to have varied among populations and species, being more frequent at some times and places than at others.

TABLE 13.1. Summary of hypothesized traits for LCA (if chimpanzee-like) and hominins.

	<i>LCA</i>	<i>Australopiths</i>	<i>Earlier Homo</i>	<i>Later Homo</i>
Fission-fusion dynamics	Yes	Yes	Yes	Yes
Intergroup hostility	Yes	Yes	Yes	Yes
Male coalitions	Yes	Maybe	Yes	Yes
Territorial (when economical)	Yes	Yes	Yes	Yes
Coalitionary killing	Yes	Rare	Yes	Yes
Weapons	Simple (sticks, stones; rarely used)	Simple (sticks, stones; commonly used)	More complex (stone, shaped; routinely used)	Complex (stone, composite; routinely used)
Rewards to aggressors	Direct (territory, mating)	Direct (territory, acquiring females)	Direct and indirect (cultural?)	Direct and indirect (cultural)
Multilevel societies	No	Maybe	Yes	Yes
Language	No	No	Proto-language?	Yes

By the origin of Homo, however, several factors appear likely to have increased rates of coalitionary killing: more efficient walking and running, leading to longer daily travel distances; more reliance on meat, leading to increased trophic level and thus a requirement for larger territories; increased energy from meat and food-processing technology, providing more energy, leading to more rapidly growing populations, further increasing territorial competition; increasingly effective weapons, providing greater advantages to numerically superior attackers; and stronger alliances among males due to reduced reproductive skew.

By the origin of Homo sapiens, if not earlier, the evolution of language multiplied the complexity of intergroup relations, creating ethnolinguistic groups, lifelong relationships among kin and nonkin, leading to larger alliances; prospects for peaceful interactions and mutual benefits of trade; and the ability to communicate long memories of past wrongs, leading to blood revenge and feuds. Intergroup competition fueled ongoing arms races, leading to improvements in projectile technology, body armor, and other tools of war. Archaeology, ethnology, and history document more recent elaborations of warfare within particular human groups: age-graded warrior sets in pastoralist tribes, hierarchically organized armies with professional soldiers in states; industrialized world wars; and, more recently, cyber warfare and “chair-forces” of remote-controlled drones (Morris 2014). At the same time, and despite the seemingly endless parade of dreadful news on our televisions and social media feeds, our species has demonstrated a remarkable ability to forge peaceful intergroup relations across increasingly large geographic and political scales (Pinker 2011). We may have inherited demonic tendencies from our ancestors, but we can learn to listen to our angels.

Summary

Controversy continues over whether the roots of warfare are deep, shallow, or somewhere in between. One possibility is that the roots of warfare extend at least as deep as the last common ancestor (LCA) of humans, chimpanzees, and bonobos. Alternatively, coalitionary killing may have evolved separately in chimpanzees and humans, but for similar reasons. We reviewed patterns of intergroup violence in chimpanzees and hunter-gatherers, and evidence for whether earlier members of our lineage likely had similar patterns of intergroup aggression. In doing so, we focused on key similarities and differences between chimpanzees and humans and their potential effects on the evolution of intergroup aggression. Humans and chimpanzees resemble one another in having (1) fission-fusion societies, (2) intergroup hostility, (3) male coalitions, (4) territorial behavior, and (5) coalitionary killings. At the same time, humans differ strikingly from chimpanzees in having (1) weapons, (2) different benefits gained by aggressors, (3) multilevel societies, and (4) language. If the LCA closely resembled chimpanzees, then the roots of intergroup violence in humans may be deep indeed. However, our understanding of the LCA remains sketchy, and several unusual features of australopiths suggest a more complicated history.

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References

- Alexander, R. D. 1990. How did humans evolve? Reflections on the uniquely unique species. Ann Arbor: Museum of Zoology, University of Michigan.
- Allen, M. W. 2014. Hunter-gatherer conflict: The last bastion of the pacified past? In M. W. Allen and T. L. Jones, eds., *Violence and Warfare among Hunter-Gatherers*. Walnut Creek, CA: Left Coast Press.
- Allen, M. W., and T. L. Jones. 2014. *Violence and Warfare among Hunter-Gatherers*. Walnut Creek, CA: Left Coast Press.
- Anton, S. C., W. R. Leonard, and M. L. Robertson. 2002. An ecomorphological model of the initial hominid dispersal from Africa. *Journal of Human Evolution* 43: 773–785.
- Anton, S. C., R. Potts, and L. C. Aiello. 2014. Evolution of early Homo: An integrated biological perspective. *Science* 345: 1236828.
- Aureli, F., C. M. Schaffner, C. Boesch, S. K. Bearder, J. Call, C. A. Chapman, R. Connor, A. Di Fiore, R. I. M. Dunbar, S. P. Henzi, K. Holekamp, A. H. Korstjens, R. Layton, P. Lee, J. Lehmann, J. H. Manson, G. Ramos-Fernandez, K. B. Strier, and C. P. van Schaik. 2008. Fission-fusion dynamics: New research frameworks. *Current Anthropology* 49: 627–654.
- Beyene, Y., S. Katoh, G. WoldeGabriel, W. K. Hart, K. Uto, M. Sudo, M. Kondo, M. Hyodo, P. R. Renne, G. Suwa, and B. Asfaw. 2013. The characteristics and chronology of the earliest Acheulean at Konso, Ethiopia. *Proceedings of the National Academy of Sciences* 110: 1584–1591.
- Binford, L. R. 2001. *Constructing Frames of Reference*. Berkeley: University of California Press.
- Bingham, P. M. 2000. Human evolution and human history: A complete theory. *Evolutionary Anthropology* 9: 248–257.
- Boesch, C., and H. Boesch-Achermann. 2000. *The Chimpanzees of the Tai Forest: Behavioral Ecology and Evolution*. Oxford: Oxford University Press.
- Boesch, C., C. Crockford, I. Herbinger, R. M. Wittig, Y. Moebius, and E. Normand. 2008. Intergroup conflicts among chimpanzees in Tai National Park: Lethal violence and the female perspective. *American Journal of Primatology* 70: 519–532.
- Boesch, C., G. Hohmann, and L. F. Marchant, eds. 2002. *Behavioural Diversity in Chimpanzees and Bonobos*. Cambridge: Cambridge University Press.
- Bramble, D. M., and D. E. Lieberman. 2004. Endurance running and the evolution of Homo. *Nature* 432: 345–352.
- Bridges, E. 1948. *Uttermost Part of the Earth*. London: Hodder & Stoughton.

- Brown, J. L. 1964. The evolution of diversity in avian social systems. *Wilson Bulletin* 76: 160– 169.
- Burch, E. S., Jr. 2005. *Alliance and Conflict: The World System of the Inupiaq Eskimos*. Lincoln: University of Nebraska Press.
- Burch, E. S., Jr. 2007. Traditional native warfare in western Alaska. In R. J. Chacon and R. G. Mendoza, eds., *North American Indigenous Warfare and Ritual Violence*, 11– 29. Tucson: University of Arizona Press.
- Cashdan, E. 1983. Territoriality among human foragers: Ecological models and an application to four Bushman groups. *Current Anthropology* 24: 47– 66.
- Cerling, T. E., J. G. Wynn, S. A. Andanje, M. I. Bird, D. K. Korir, N. E. Levin, W. Mace, A. N. Macharia, J. Quade, and C. H. Remien. 2011. Woody cover and hominin environments in the past 6 million years. *Nature* 476: 51– 56.
- Chagnon, N. A. 1988. Life histories, blood revenge, and warfare in a tribal population. *Science* 239: 985– 992.
- Chapais, B. 2010. *Primeval Kinship: How Pair-Bonding Gave Birth to Human Society*. Cambridge, MA: Harvard University Press.
- Chapais, B. 2013. Monogamy, strongly bonded groups, and the evolution of human social structure. *Evolutionary Anthropology* 22: 52– 65.
- Churchill, S. E., R. G. Franciscus, H. A. McKean-Peraza, J. A. Daniel, and B. R. Warren. 2009. Shanidar 3 Neandertal rib puncture wound and paleolithic weaponry. *Journal of Human Evolution* 57: 163– 178.
- Clastres, P. 1972. The Guayaki. In M. G. Bicchieri, ed., *Hunters and Gatherers Today: A Socioeconomic Study of Eleven Such Cultures in the Twentieth Century*. New York: Holt, Reinhart and Winston.
- Clastres, P. 2000. *Chronicle of the Guayaki Indians*. New York: Zone. Copeland, S. R., M. Sponheimer, D. J. de Ruiter, J. A. Lee-Thorp, D.
- Codron, P. J. le Roux, V. Grimes, and M. P. Richards. 2011. Strontium isotope evidence for landscape use by early hominins. *Nature* 474: 76– U100.
- Crofoot, M., and R. W. Wrangham. 2010. Intergroup aggression in primates and humans: The case for a unified theory. In P. M. Kappeler and J. B. Silk, eds., *Mind the Gap*. Berlin: Springer.
- Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. New York: Modern Library.
- Diamond, J. 1997. *Guns, Germs, and Steel: The Fates of Human Societies*. New York: W. W. Norton.
- Drucker, P. 1951. *The Northern and Central Nootkan Tribes*. Washington, DC: Smithsonian Institution.
- Dunbar, R. I. M. 1992. A model of the gelada socio-ecological system. *Primates* 33: 69– 83.
- Dyson-Hudson, R., and E. A. Smith. 1978. Human territoriality: An ecological assessment. *American Anthropologist* 80: 21– 42.
- Ember, C. R. 1978. Myths about hunter-gatherers. *Ethnology* 17: 439– 448.
- Faurie, C., and M. Raymond. 2003. Handedness: Neutral or adaptive? *Behavioral and Brain Sciences* 26: 220.

- Ferguson, R. B. 2011. Born to live: Challenging killer myths, In R. W. Sussman and C. R. Cloninger, eds., *Origins of Altruism and Cooperation*, 249– 270. New York: Springer.
- Fiske, A. P., and T. S. Rai. 2015. *Virtuous Violence: Hurting and Killing to Create, Sustain, End, and Honor Social Relationships*. Cambridge: Cambridge University Press.
- Fitch, W. T. 2010. *The Evolution of Language*. Cambridge: Cambridge University Press.
- Fry, D. P. 2011. Human nature: The nomadic forager model. In R. W. Sussman and C. R. Cloninger, eds., *Origins of Altruism and Cooperation*, 227– 247. New York: Springer.
- Fry, D. P., and P. Söderberg. 2013. Lethal aggression in mobile forager bands and implications for the origins of war. *Science* 341: 270– 273.
- Funk, C. 2010. The Bow and Arrow War days on the Yukon-Kuskokwim Delta of Alaska. *Ethnohistory* 57: 523– 569.
- Gat, A. 1999a. The pattern of fighting in simple, small-scale, prestate societies. *Journal of Anthropological Research*. 55: 563– 583.
- Gat, A. 1999b. Social organization, group conflict and the demise of Neanderthals. *Mankind Quarterly* 39: 437– 454.
- Gat, A. 2006. *War in Human Civilization*. Oxford: Oxford University Press.
- Gat, A. 2015. Proving communal warfare among hunter-gatherers: The quasi-Rousseauian error. *Evolutionary Anthropology* 24: 111– 126.
- Ghiglieri, M. P. 1989. Hominid sociobiology and hominid social evolution. In P. G. Heltne and L. A. Marquardt, eds., *Understanding Chimpanzees*, 370– 379. Cambridge, MA: Harvard University Press.
- Gilby, I. C., M. L. Wilson, and A. E. Pusey. 2013. Ecology rather than psychology explains co-occurrence of predation and border patrols in male chimpanzees. *Animal Behaviour* 86: 61– 74.
- Glowacki, L., and R. W. Wrangham. 2013. The role of rewards in motivating participation in simple warfare. *Human Nature* 24: 444– 460.
- Glowacki, L., and R. W. Wrangham. 2015. Warfare and reproductive success in a tribal population. *Proceedings of the National Academy of Sciences* 112: 348– 353.
- Gómez, J. M., M. Verdú, A. González-Megías, and M. Méndez. 2016. The phylogenetic roots of human lethal violence. *Nature* 538: 233– 237.
- Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, MA: Harvard University Press.
- Goodall, J., A. Bandora, E. Bergmann, C. Busse, H. Matama, E. Mpongo, A. Pierce, and D. Riss. 1979. Intercommunity interactions in the chimpanzee population of the Gombe National Park. In D. A. Hamburg and E. R. McCown, eds., *The Great Apes*, 13– 53. Menlo Park, CA: Benjamin / Cummings.
- Grove, M., E. Pearce, and R. I. M. Dunbar. 2012. Fission-fusion and the evolution of hominin social systems. *Journal of Human Evolution* 62: 191– 200.
- Grubb, W. B. 1911. *An Unknown People in an Unknown Land*. London: Seeley, Service.

- Gurven, M. 2013. Human survival and life history in evolutionary perspective. In J. C. Mitani, J., Call, P. M. Kappeler, R. A. Palombit, and J. B. Silk, eds., *The Evolution of Primate Societies*. Chicago: University of Chicago Press.
- Haas, J. 2001. Warfare and the evolution of culture. In T. D. Price and G. Feinman, eds., *Archaeology at the Millennium: A Sourcebook*. New York: Kluwer Academic / Plenum.
- Hamilton, W. D. 1964. The genetical evolution of social behavior, I, II. *Journal of Theoretical Biology* 7: 1– 52.
- Heinz, H. J. 1972. Territoriality among Bushmen in general and Ko in particular. *Anthropos* 67: 405– 416.
- Henrich, J., and F. J. Gil-White. 2001. The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior* 22: 165– 196.
- Herbinger, I., C. Boesch, and H. Rothe. 2001. Territory characteristics among three neighboring chimpanzee communities in the Tai National Park, Ivory Coast. *International Journal of Primatology* 22: 143– 167.
- Hernandez-Aguilar, R. A., J. Moore, and R. P. Travis. 2007. Savanna chimpanzees use tools to harvest the underground storage organs of plants. *Proceedings of the National Academy of Sciences* 104: 19210– 19213.
- Hill, K., M. Barton, and A. M. Hurtado. 2009. The emergence of human uniqueness: Characters underlying behavioral modernity. *Evolutionary Anthropology* 18: 187– 200.
- Hill, K., and M. A. Hurtado. 1996. *Ache Life History: The Ecology and Demography of a Foraging People*. New York: Aldine de Gruyter.
- Hill, K. R., R. S. Walker, M. Bozicevic, J. Eder, T. Headland, B. Hewlett, A. M. Hurtado, F. W. Marlowe, P. Wiessner, and B. Wood. 2011. Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science* 331: 1286– 1289.
- Hohmann, G., and B. Fruth. 2002. Dynamics in social organization of bonobos (*Pan paniscus*). In C. Boesch, G. Hohmann, and L. F. Marchant, eds., *Behavioural Diversity in Chimpanzees and Bonobos*. Cambridge: Cambridge University Press.
- Hortolà, P., and B. Martínez-Navarro. 2013. The Quaternary megafaunal extinction and the fate of Neanderthals: An integrative working hypothesis. *Quaternary International* 295: 69– 72.
- Kelly, R. C. 2000. *Warless Societies and the Origin of War*. Ann Arbor: University of Michigan Press.
- Kelly, R. C. 2005. The evolution of lethal intergroup violence. *Proceedings of the National Academy of Sciences* 102: 15294– 15298.
- Kelly, R. L. 1995. *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways*. Washington, DC: Smithsonian Institution.
- Klein, R. 1988. The causes of “robust” australopithecine extinction. In F. F. Grine, ed., *The Evolutionary History of the Robust Australopithecines*, 499– 505. New York: Aldine de Gruyter.
- Knauff, B. 1991. Violence and sociality in human evolution. *Current Anthropology* 32: 391– 428.

- Kramer, P. A., and G. G. Eck. 2000. Locomotor energetics and leg length in hominid bipedality. *Journal of Human Evolution* 38: 651– 666.
- Kummer, H. 1968. *Social Organization of Hamadryas Baboons*. Chicago: University of Chicago Press.
- Kutsukake, N., and T. Matsusaka. 2002. Incident of intense aggression by chimpanzees against an infant from another group in Mahale Mountains National Park, Tanzania. *American Journal of Primatology* 58: 175– 180.
- Lalueza-Fox, C., A. Rosas, A. Estalrich, E. Gigli, P. F. Campos, A. Garcia-Taberner, S. Garcia-Vargas, F. Sanchez-Quinto, O. Ramirez, S. Civit, M. Bastir, R. Huguet, D. Santamaria, M. T. P. Gilbert, E. Willerslev, and M. de la Rasilla. 2011. Genetic evidence for patrilineal mating behavior among Neandertal groups. *Proceedings of the National Academy of Sciences* 108: 250– 253.
- LeBlanc, S. A. 2014. Forager warfare and our evolutionary past. In M. W. Allen and T. L. Jones, eds., *Violence and Warfare among Hunter-Gatherers*. Walnut Creek, CA: Left Coast Press.
- LeBlanc, S. A., Register, K. E. 2004. *Constant Battles: Why We Fight*. New York: St. Martin's Griffin.
- Lee, R. B. 1979. *The !Kung San: Men, Women and Work in a Foraging Society*. New York: Cambridge University Press.
- Lepre, C. J., H. Roche, D. V. Kent, S. Harmand, R. L. Quinn, J. P. Brugal, P. J. Texier, A. Lenoble, and C. S. Feibel. 2011. An earlier origin for the Acheulian. *Nature* 477: 82– 85.
- Lorenz, K. 1966. *On Aggression*. New York: Harcourt Brace.
- Lowen, C., and R. I. M. Dunbar. 1994. Territory size and defendability in primates. *Behavioral Ecology and Sociobiology* 35: 347– 354.
- Machanda, Z. P., I. C. Gilby, and R. W. Wrangham. 2013. Male-female association patterns among free-ranging chimpanzees (*Pan troglodytes schweinfurthii*). *International Journal of Primatology* 34: 917– 938.
- Maher, C. R., and D. F. Lott. 2000. A review of ecological determinants of territoriality within vertebrate species. *American Midland Naturalist* 143: 1– 29.
- Manson, J. H., and R. W. Wrangham. 1991. Intergroup aggression in chimpanzees and humans. *Current Anthropology* 32: 369– 390.
- Markham, A. C., S. C. Alberts, and J. Altmann. 2012. Intergroup conflict: Ecological predictors of winning and consequences of defeat in a wild primate population. *Animal Behaviour* 84: 399– 403.
- Marlowe, F. W. 2005. Hunter-gatherers and human evolution. *Evolutionary Anthropology* 14: 54– 67.
- Marlowe, F. W. 2010. *The Hadza: Hunter-Gatherers of Tanzania*. Berkeley: University of California Press.
- Maschner, H., and O. K. Mason. 2013. The bow and arrow in northern North America. *Evolutionary Anthropology* 22: 133– 138.
- McBrearty, S., and A. S. Brooks. 2000. The revolution that wasn't: A new interpretation of the origin of modern human behavior. *Journal of Human Evolution* 39: 453– 563.

- McDonald, M. M., C. D. Navarrete, and M. van Vugt. 2012. Evolution and the psychology of intergroup conflict: The male warrior hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367: 670–679.
- Meggitt, M. 1962. *Desert People: A study of the Walbiri Aborigines of Central Australia*. Sydney: Angus and Robertson.
- Meggitt, M. 1977. *Blood Is Their Argument: Warfare among the Mae Enga Tribesmen of the New Guinea Highlands*. Palo Alto, CA: Mayfield.
- Mendoza, M. 2007. Hunter-gatherers' aboriginal warfare in Western Chaco. In R. J. Chacon and R. G. Mendoza, eds., *Latin American Indigenous Warfare and Ritual Violence*, 198–211. Phoenix: University of Arizona Press.
- Mitani, J. C. 2009. Cooperation and competition in chimpanzees: Current understanding and future challenges. *Evolutionary Anthropology* 18: 215–227.
- Mitani, J. C., and P. S. Rodman. 1979. Territoriality: The relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behavioral Ecology and Sociobiology* 5: 241–251.
- Mitani, J. C., and D. P. Watts. 2005. Correlates of territorial boundary patrol behaviour in wild chimpanzees. *Animal Behaviour* 70: 1079–1086.
- Mitani, J. C., D. P. Watts, and S. J. Amsler. 2010. Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology* 20: R507–R508.
- Moffett, M. W. 2012. Supercolonies of billions in an invasive ant: What is a society? *Behavioral Ecology* 23: 925–933.
- Morris, I. 2014. *War! What Is It Good For? Conflict and the Progress of Civilization from Primates to Robots*. New York: Farrar, Straus and Giroux.
- Nishida, T. 1979. The social structure of chimpanzees of the Mahale Mountains. In D. A. Hamburg and E. R. McCown, eds., *The Great Apes*, 73–121. Menlo Park, CA: Benjamin / Cummings.
- Nishida, T. 2012. *Chimpanzees of the Lakeshore: Natural History and Culture at Mahale*. New York: Cambridge University Press.
- Nishida, T., N. Corp, M. Hamai, T. Hasegawa, M. Hiraiwa-Hasegawa, K. Hosaka, K. D. Hunt, N. Itoh, K. Kawanaka, A. Matsumoto-Oda, J. C. Mitani, M. Nakamura, K. Norikoshi, T. Sakamaki, L. Turner, S. Uehara, and K. Zamma. 2003. Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. *American Journal of Primatology* 59: 99–121.
- Nishida, T., M. Hiraiwa-Hasegawa, T. Hasegawa, and Y. Takahata. 1985. Group extinction and female transfer in wild chimpanzees in the Mahale National Park, Tanzania. *Zeitschrift für Tierpsychologie* 67: 284–301.
- Nishida, T., and K. Kawanaka. 1972. Inter-unit-group relationships among wild chimpanzees of the Mahale Mountains. *Kyoto University African Studies* 7: 131–169.
- O'Connell, J. F., K. Hawkes, K. D. Lupo, and N. G. B. Jones. 2002. Male strategies and Plio-Pleistocene archaeology. *Journal of Human Evolution* 43: 831–872.

- Otterbein, K. F. 2004. *How War Began*. College Station: Texas A& M University Press.
- Packer, C., L. Herbst, A. E. Pusey, J. D. Bygott, J. P. Hanby, S. J. Cairns, and M. Borgerhoff Mulder. 1988. Reproductive success of lions. In T. H. Clutton-Brock, ed., *Reproductive Success*, 363– 383. Chicago: University of Chicago Press.
- Parker, G. A. 1974. Assessment strategy and the evolution of fighting behavior. *Journal of Theoretical Biology* 47: 223– 243.
- Peterson, N. 1975. Hunter-Gatherer Territoriality: The Perspective from Australia. *American Anthropologist* 77: 53– 68.
- Philpott, W. 2009. *Bloody Victory: The Sacrifice on the Somme and the Making of the Twentieth Century*. New York: Little, Brown.
- Pinker, S. 2011. *The Better Angels of Our Nature: Why Violence Has Declined*. New York: Viking.
- Plavcan, J. M. 2012. Sexual size dimorphism, canine dimorphism, and male-male competition in primates: Where do humans fit in? *Human Nature* 23: 45– 67.
- Potts, R. 2012. Evolution and environmental change in early human prehistory. In D. Brenneis and P. T. Ellison, eds., *Annual Review of Anthropology*, vol. 41, 151– 167. Palo Alto, CA: Annual Reviews.
- Pradhan, G. R., R. K. Pandit, and C. P. van Schaik. 2014. Why do chimpanzee males attack the females of neighboring communities? *American Journal of Physical Anthropology* 155: 430– 435.
- Pruetz, J. D., and P. Bertolani. 2007. Savanna chimpanzees, Pan troglodytes verus, hunt with tools. *Current Biology* 17: 412– 417.
- Pusey, A. E. 1980. Inbreeding avoidance in chimpanzees. *Animal Behaviour* 28: 543– 582.
- Pusey, A. E. 2001. Of genes and apes: Chimpanzee social organization and reproduction. In F. B. M. de Waal, ed., *Tree of Origin*, 9– 38. Cambridge, MA: Harvard University Press.
- Pusey, A. E., C. Murray, W. R. Wallauer, M. L. Wilson, E. Wroblewski, and J. Goodall. 2008. Severe aggression among female chimpanzees at Gombe National Park, Tanzania. *International Journal of Primatology* 29: 949– 973.
- Pusey, A. E., G. W. Oehlert, J. M. Williams, and J. Goodall. 2005. The influence of ecological and social factors on body mass of wild chimpanzees. *International Journal of Primatology* 26: 3– 31.
- Pusey, A. E., and C. Packer. 1987. Dispersal and philopatry. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, T. T. Struhsaker, and R. W. Wrangham, eds., *Primate Societies*, 250– 266. Chicago: University of Chicago Press.
- Puts, D. A. 2010. Beauty and the beast: Mechanisms of sexual selection in humans. *Evolution and Human Behavior* 31: 157– 175.
- Robbins, M. M., and S. C. Sawyer. 2007. Intergroup encounters in mountain gorillas of Bwindi Impenetrable National Park, Uganda. *Behaviour* 144: 1497– 1519.
- Rodseth, L., and R. W. Wrangham. 2004. Human kinship: A continuation of politics by other means? In B. Chapais and C. M. Berman, eds., *Kinship and Behavior in Primates*, 389– 419. New York: Oxford University Press.

- Rodseth, L., R. W. Wrangham, A. M. Harrigan, and B. B. Smuts. 1991. The human community as a primate society. *Current Anthropology* 32: 221–254.
- Rosenbaum, S., V. Vecellio, and T. Stoinski. 2016. Observations of severe and lethal coalitionary attacks in wild mountain gorillas. *Scientific Reports* 6: 8.
- Rudicell, R. S., J. H. Jones, E. E. Wroblewski, G. H. Learn, Y. Li, J. Robertson, E. Greengrass, F. Grossmann, S. Kamenya, L. Pintea, D. C. Mjungu, E. V. Lonsdorf, A. Mosser, C. Lehman, D. A. Collins, B. F. Keele, J. Goodall, B. H. Hahn, A. E. Pusey, and M. L. Wilson. 2010. Impact of simian immunodeficiency virus infection on chimpanzee population dynamics. *PLoS Pathogens* 6: e1001116.
- Schaller, G. B., and G. R. Lowther. 1969. The relevance of carnivore behavior to the study of early hominids. *Southwestern Journal of Anthropology* 25: 307–341.
- Schwartz, G. T. 2012. Growth, development, and life history throughout the evolution of Homo. *Current Anthropology* 53: S395–S408.
- Shea, J. J. 2003. Neandertals, competition, and the origin of modern human behavior in the Levant. *Evolutionary Anthropology* 12: 173–187.
- Shea, J. J., and M. L. Sisk. 2010. Complex projectile technology and Homo sapiens dispersal into western Eurasia. *PaleoAnthropology* 100–122.
- Smith, J. E., E. M. Swanson, D. Reed, and K. E. Holekamp. 2012. Evolution of cooperation among mammalian carnivores and its relevance to hominin evolution. *Current Anthropology* 53: S436–S452.
- Städle, V., M. Pines, L. Swedell, and L. Vigilant. 2016. The ties that bind: Maternal kin bias in a multilevel primate society despite natal dispersal by both sexes. *American Journal of Primatology* 78: 731–744.
- Swedell, L., and T. Plummer. 2012. A papionin multilevel society as a model for hominin social evolution. *International Journal of Primatology* 33: 1165–1193.
- Swedell, L., J. Saunders, A. Schreier, B. Davis, T. Tesfaye, and M. Pines. 2011. Female “dispersal” in hamadryas baboons: Transfer among social units in a multilevel society. *American Journal of Physical Anthropology* 145: 360–370.
- Trinkaus, E. 2012. Neandertals, early modern humans, and rodeo riders. *Journal of Archaeological Science* 39: 3691–3693.
- Tutin, C. E. G. 1979. Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology* 6: 29–38.
- Villa, P., and W. Roebroeks. 2014. Neandertal demise: An archaeological analysis of the modern human superiority complex. *PLoS ONE* 9: e96424.
- Walker, R. S., K. R. Hill, M. V. Flinn, and R. M. Ellsworth. 2011. Evolutionary history of hunter-gatherer marriage practices. *PLoS ONE* 6: e19066.
- Waltes, R., A. G. Chiochetti, and C. M. Freitag. 2016. The neurobiological basis of human aggression: A review on genetic and epigenetic mechanisms. *American Journal of Medical Genetics Part B: Neuropsychiatric Genetics* 171: 650–675.
- Waser, P. M. 1976. *Cercocebus albigena*: Site attachment, avoidance, and intergroup spacing. *American Naturalist* 110: 911–935.

- Watts, D. P., and J. C. Mitani. 2001. Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour* 138: 299–327.
- Watts, D. P., M. N. Muller, S. J. Amsler, G. Mbabazi, and J. C. Mitani. 2006. Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. *American Journal of Primatology* 68: 161–180.
- Werdelin, L., and M. E. Lewis. 2013. Temporal change in functional richness and evenness in the eastern African Plio-Pleistocene carnivoran guild. *PLoS ONE* 8: e57944.
- Williams, J. M. 1999. Female strategies and the reasons for territoriality in chimpanzees: Lessons from three decades of research at Gombe. Ph.D. dissertation, University of Minnesota. Williams, J. M., E. V. Lonsdorf, M. L.
- Wilson, J. Schumacher-Stankey, J. Goodall, and A. E. Pusey. 2008. Causes of death in the Kasekela chimpanzees of Gombe National Park, Tanzania. *American Journal of Primatology* 70: 766–777.
- Williams, J. M., G. Oehlert, J. Carlis, and A. E. Pusey. 2004. Why do male chimpanzees defend a group range? Reassessing male territoriality. *Animal Behaviour* 68: 523–532.
- Wilson, M. L., C. Boesch, B. Fruth, T. Furuichi, I. C. Gilby, C. Hashimoto, C. Hobaiter, G. Hohmann, N. Itoh, K. Koops, J. Lloyd, T. Matsuzawa, J. C. Mitani, D. C. Mjungu, D. Morgan, R. Mundry, M. N. Muller, M. Nakamura, J. D. Pruett, A. E. Pusey, J. Riedel, C. Sanz, A. M. Schel, N. Simmons, M. Waller, D. P. Watts, F. J. White, R. M. Wittig, K. Zuberbühler, and W. R. Wrangham. 2014. Lethal aggression in Pan is better explained by adaptive strategies than human impacts. *Nature* 513: 414–417.
- Wilson, M. L., J. Cossette, K. Koops, I. Lipende, E. V. Lonsdorf, J. C. Mitani, J. D. Pruett, N. Simmons, D. Travis, and D. P. Watts. 2015. The most unkindest cut: Genital wounding by chimpanzees. *American Journal of Physical Anthropology* 156(S60): 326.
- Wilson, M. L., M. D. Hauser, and R. W. Wrangham. 2001. Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Animal Behaviour* 61: 1203–1216.
- Wilson, M. L., M. D. Hauser, and R. W. Wrangham. 2007. Chimpanzees (*Pan troglodytes*) modify grouping and vocal behaviour in response to location-specific risk. *Behaviour* 144: 1621–1653.
- Wilson, M. L., S. M. Kahlenberg, M. T. Wells, and R. W. Wrangham. 2012. Ecological and social factors affect the occurrence and outcomes of intergroup encounters in chimpanzees. *Animal Behaviour* 83: 277–291.
- Wilson, M. L., W. Wallauer, and A. E. Pusey. 2004. New cases of intergroup violence among chimpanzees in Gombe National Park, Tanzania. *International Journal of Primatology* 25: 523–549.
- Wilson, M. L., and R. W. Wrangham. 2003. Intergroup relations in chimpanzees. *Annual Review of Anthropology* 32: 363–392.
- Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75: 262–300.
- Wrangham, R. W. 1987. The significance of African apes for reconstructing human social evolution. In W. G. Kinzey, ed., *The Evolution of Human Behavior: Primate Models*, 51–71. Albany: State University of New York Press.
- Wrangham, R. W. 1999. The evolution of coalitionary killing. *Yearbook of Physical Anthropology* 42: 1–30.

Wrangham, R. W. 2001. Out of the Pan, into the fire: From ape to human. In F. B. M. de Waal, ed., *Tree of Origin*, 119– 143. Cambridge: Harvard University Press.

Wrangham, R. 2010. *Catching Fire: How Cooking Made Us Human*. New York: Basic Books.

Wrangham, R. W., M. Crofoot, R. Lundy, and I. C. Gilby. 2007. Use of overlap zones among group-living primates: A test of the risk hypothesis. *Behaviour* 144: 1599– 1619.

Wrangham, R. W., and L. Glowacki. 2012. Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers: Evaluating the chimpanzee model. *Human Nature* 23: 5– 29.

Wrangham, R. W., M. L. Wilson, and M. N. Muller. 2006. Comparative rates of violence in chimpanzees and humans. *Primates* 47: 14– 26.

Young, R. W. 2003. Evolution of the human hand: The role of throwing and clubbing. *Journal of Anatomy* 202: 165– 174.