CHIMPANZEE RAIDING

SYNONYMS

Lethal raiding, Intergroup aggression, Border patrols, Coalitionary killing, Between-community raiding, Lethal violence, Intergroup conflict, Conspecific killing, Gang attacks

DEFINITION

Lethal raiding is a form of coalitionary, intergroup aggression observed in chimpanzees in which a party leaves its core range to find and attempt to kill strongly outnumbered and isolated members of neighboring communities.

INTRODUCTION

While intergroup conflict is common in social animals, fatal aggression is rare and usually a result of accidental injury during escalated fights (Manson & Wrangham, 1991). However, in some species, such as chimpanzees and humans, intergroup aggression appears to be marked by coalitionary, apparently deliberate attempts to kill conspecifics. In chimpanzees, this behavior is likely facilitated by their fission-fusion dynamics, male philopatry and resource defense polygynandry. We review several proposed hypotheses on the adaptive function of this behavior, which are not mutually exclusive. Critics of this adaptive interpretation suggest that lethal raiding is caused or exacerbated by human disturbances to chimpanzees, though this is not strongly supported by the current evidence. Chimpanzee raiding shares several characteristics with human warfare and is therefore often part of the debate on the origins of human warfare.

CHIMPANZEE INTERGROUP CONFLICT

Across social species, contest competition for access to limited resources can result in conflict between groups (e.g. Kitchen & Beehner, 2007; Radford, 2008). Such intergroup conflict may range from avoidance by one group or exchange of aggressive threats, to sometimes fatal physical aggression between members of rival groups. Certain socio-ecological conditions, such as when resources are highly defensible and the relative power between the opposing groups is great, increase the likelihood of conflict (Enquist & Leimar, 1990; Jaeggi, Boose, White, & Gurven, 2016). Aggressive intergroup conflict has been well documented in primates (Majolo, de Bortoli Vizioli, & Lehmann, 2016), in particular in chimpanzees where it is characterized by coalitionary attacks that involve apparently deliberate attempts to injure and kill the opponent (Glowacki, Wilson, & Wrangham, 2017; Manson & Wrangham, 1991). The term “lethal raiding” refers to such unprovoked gang attacks on strongly outnumbered or isolated members of neighboring chimpanzee communities (Manson & Wrangham, 1991). While the term is often associated with groups of chimpanzees making deep incursions into neighboring territories, often by stealth, this pattern of coalitionary intergroup aggression also occurs in the context of territorial boundary patrols as well as opportunistically, during chance intergroup encounters (Watts, Muller, Amsler, Mbabazi, & Mitani, 2006).

CHIMPANZEE SOCIAL ORGANIZATION

Several features of chimpanzee social organization are thought to be related to the occurrence of lethal raiding and so we first outline some of these aspects before providing descriptions and explanations of raiding behavior. Within chimpanzee groups, competition for access to food resources may be high at certain times of the year, however, fission-fusion dynamics allow individuals to respond adaptively to environmental variability. As a result, members of a chimpanzee community rarely gather together in a single, cohesive group, but rather travel, forage and rest in subgroups, or “parties” that change in size and composition throughout the day in response to fluctuations in local resource availability (Wilson, 2013). Typically, male chimpanzees remain a member of their natal group throughout their lives, a feature known as male philopatry, whereas female chimpanzees disperse from their natal group when they reach sexual maturity (e.g. Boesch et al., 2008; Pusey, 1980). In chimpanzees, as in other primates, male philopatry is associated with remarkable levels of male-male cooperation (Boesch et al., 2008; Manson & Wrangham, 1991) and male mating success may be increased through coalitions with other males (e.g. Watts, 1998). Because, in most mammals, male fitness is primarily determined by access to fertile females, while female fitness is largely determined by access to resources (Davies, Krebs, & West, 2012), chimpanzee males can maximize their fitness by defending a territory containing valuable food resources which increase the reproductive success of the females within the community and may attract additional females (Pandit, Pradhan, Balashov, & Van Schaik, 2016). As chimpanzee males mate with multiple females and females mate with multiple males, this is known as resource defense polygynandry. Fission-fusion dynamics, male philopatry and resource defense polygynandry are inherent to chimpanzee sociality and are crucial to understanding how and why lethal raiding occurs in this species.

PATTERNS OF LETHAL RAIDING IN CHIMPANZEES

OBSERVATIONS OF LETHAL RAIDING

Intercommunity killings are mainly observed when large parties, consisting mostly of adult males, encounter isolated and/or greatly outnumbered individuals (Manson & Wrangham, 1991; Wilson et al., 2014; Wrangham, 1999). The most common context in which this occurs is during territorial boundary patrols into areas of range overlap with neighboring communities (Manson & Wrangham, 1991; Watts et al., 2006). During these patrols, the males move cautiously and quietly, often in single file, stopping to listen intently and/or inspect signs of outgroup chimpanzees such as feces, nests and discarded food wadges (Boesch & Boesch-Achermann, 2000; Wilson, 2013; Wrangham, 1999). If the males encounter members of the neighboring community, their response depends on the size and composition of this outgroup party. Lethal intercommunity attacks most often occur when the attackers greatly outnumber their opponent, with a median ratio of eight to one (Wilson et al., 2014). If the encountered party contains two or more males, the raiders will typically retreat (Manson & Wrangham, 1991). However, an isolated male, sexually unreceptive female, consorting male-female pair, or an infant may be stalked and attacked. Sexually receptive females without infants are potential immigrants and therefore less likely to be aggressed by the raiding party (Boesch & Boesch-Achermann, 2000; Pusey, 1980). The targeted individual is often restrained or immobilized by the superior numbers of attackers, enabling the attackers to inflict potentially lethal injuries with little to no risk to themselves (Boesch et al., 2008; Manson & Wrangham, 1991; Wilson et al., 2014). In fact, there are no reports of attacking parties suffering any major injuries (Manson & Wrangham, 1991; Pandit et al., 2016). If members of the neighboring community are not found, the party may either return to their territory or penetrate deeper into the neighboring range (Manson & Wrangham, 1991).

Intergroup killings also occur opportunistically, for example, during chance encounters between hunting or foraging parties, often after auditory contact (Boesch et al., 2008; Watts et al., 2006). The frequency of such chance encounters can be affected by food distribution, as observed in Kanyawara (Uganda) where chimpanzees spent more time near the southern border of their territory when fruits there were ripe (Wilson, Kahlenberg, Wells, & Wrangham, 2012). The majority of observed intergroup interactions occurred during this seasonal fruit availability, likely because chimpanzees from different communities were attracted to the same area and ranges overlapped simultaneously (Wilson et al., 2012). Upon making auditory contact with members from a neighboring community, chimpanzees may silently approach them, after which the encounter follows a similar pattern to those that arose during boundary patrols. Regardless of whether the attack results from a patrol or chance encounter, once the victim is isolated, attackers often persist until the individual is dead, after which they may continue to drag, hit, kick and jump on the body (Wilson, 2013). Should the victim attempt to escape during the attack, the attackers may give chase and attempt to restrain them and/or inflict further harm (Watts et al., 2006). Inspection of the bodies reveals that male victims are frequently emasculated during the attack by removal of the testes and/or penis (Boesch et al., 2008; Watts et al., 2006). Attackers sometimes twist limbs, inflict wounds with their canines, remove extremities and appendages such as fingernails and ears and rip off strips of flesh (Watts et al., 2006; Wilson, 2013). There are also many documented cases of intercommunity infanticide, following attacks on neighboring females with dependent offspring, after which the infant is often cannibalized (Boesch et al., 2008).

If, during an attack, auditory contact is made with nearby members from the attacked individual's community, the attackers may become wary of these potential supporters and retreat before killing the targeted individual (Watts, Mitani, & Sherrow, 2002; Watts et al., 2006). In these cases, the victim may still die in the following days, most likely from internal injuries (Watts et al., 2006).

FREQUENCY OF LETHAL RAIDING

Observations of lethal raiding in chimpanzees all come from long-term study sites (e.g. Gombe and Mahale in Tanzania), as the large ranges and low population densities of chimpanzees make intergroup encounters relatively infrequent (Wilson, 2013). In more densely populated areas, such as Taï Forest (Côte d'Ivoire) and Ngogo (Uganda), encounters between communities occur around once or twice per month (Boesch et al., 2008; Wilson, 2013).

The majority of intergroup interactions are limited to acoustic contact, where members of neighboring communities remain separated by hundreds of meters (Boesch et al., 2008; Wilson, 2013). Chimpanzees use long-distance vocalizations, such as pant-hoots, to communicate with members of their community (Goodall, 1986). When hearing calls from another community, chimpanzees might respond with their own chorus of pant hoots (Watts et al., 2006; Wilson, 2013). In some cases, however, the chimpanzees remain silent and either stay still, looking in the direction of the vocalization, rapidly retreat, or move toward the callers, potentially escalating the interaction to visual contact which, depending on the size and composition of the encountered party, could in turn escalate to physical contact, often leading to injuries or death (Wilson, 2013). Most intergroup interactions are limited to acoustic contact. In the Taï Forest, for instance, only 27% of intergroup encounters included visual contact, of which 1.5% (0.4% of all intergroup encounters) involved lethal aggression (Boesch et al., 2008; Wilson, 2013).

Just over a third of all lethal aggression between chimpanzees occurs during aggression within communities (37%) whilst the remaining two-thirds occur (63%) during intergroup aggression (Wilson et al., 2014). The higher percentage of intergroup fatalities becomes even more prominent when the frequency of contact is considered. In theory, chimpanzees have the opportunity to lethally attack members of their own community every day, yet only rarely encounter members from other communities (Wilson et al., 2014). The two types of lethal aggression are also distinct in that most intragroup killings are infanticides, whereas lethal intergroup aggression often targets adults (Wrangham, Wilson, & Muller, 2006). Though relatively rare, intraspecific killing (including intragroup aggression) is a highly significant cause of death in chimpanzees, second only to dying from disease (Williams et al., 2008). When taking the low population sizes and observation times into account, a study of nine chimpanzee communities estimated that intraspecific aggression caused 271 deaths per 100,000 individuals per year (69 deaths per 100,000 individuals per year from intergroup aggression alone) (Wilson, 2013; Wrangham et al., 2006). To put these numbers into perspective, the rate of intentional homicides in the United States in 2016 was 5.35 deaths per 100,000 individuals per year ("UNODC Statistics Online," n.d.). The relatively high percentage of intergroup fatalities, combined with the brutal and perseverant nature of the attacks, suggests that the killing of adult opponents is characteristic to chimpanzee intergroup conflict, rather than merely a consequence of escalated resource competition. If so, chimpanzee raiding shares one of the most important distinguishing characteristics of human intergroup aggression and warfare: the deliberate killing of conspecifics (Manson & Wrangham, 1991).

ADAPTIVE EXPLANATIONS

In order for a behavioral strategy to be adaptive and evolve, the benefits of performing the behavior must outweigh any potential costs to the animal, leading to an increase in reproductive success, that is, an increase in the number of direct and/or indirect descendants (Davies et al., 2012; Wilson, 2013). It is difficult to test and evaluate the adaptive benefits of lethal intergroup aggression in chimpanzees, due to their relatively slow life histories (Watts et al., 2006). There are several adaptive hypotheses in the literature that offer explanations for lethal raiding in chimpanzees, and whilst they all share the ultimate function of increased fitness through greater access to resources and/or reproductive females, they differ in their emphasis on the proximate mechanisms and socio-ecological conditions that elicit lethal aggression. These explanations are not mutually exclusive and a combination of factors likely selects for lethal raiding (Watts et al., 2006; Wilson, 2013).

RESOURCE DEFENSE HYPOTHESIS

The resource defense hypothesis (Emlen & Oring, 1977) suggests that intergroup aggression benefits the attacking community by allowing them to defend food resources, which, due to resource defense polygynandry in chimpanzees, affect both the males' access to females and the reproductive success of these females, and therefore the fitness of the defending males (Williams, Oehlert, Carlis, & Pusey, 2004). Performing raids in a particular area might induce the targeted community to avoid using that area and/or its resources (Pandit et al., 2016). This hypothesis is consistent with an observed increase in patrol frequencies with the availability of ripe fruit (Watts et al., 2006). Additionally, the resource acquisition hypothesis suggests that chimpanzees attack other groups, not just to defend their resources, but to further expand their territories, gain access to more food, increase the feeding success of their community and therefore potentially increase female reproduction (Mitani, Watts, & Amsler, 2010; Williams et al., 2004; Wrangham, 1999). This is supported by observations of coalitionary attacks on a neighboring group, followed by territorial expansion into areas previously occupied by that group (Mitani et al., 2010). The resource defense hypothesis broadly explains the reproductive benefits of intergroup conflict in chimpanzees, predicting that male philopatry should arise as a consequence of resource defense (Greenwood, 1980; Ostfeld, 1987). It can therefore provide the socio-ecological context in which male-driven lethal intergroup aggression is expected. (Jaeggi et al., 2016; Pandit et al., 2016). It has been suggested that, while resource defense polygynandry explains the reproductive benefits of intergroup conflict in chimpanzees, it is insufficient to explain why chimpanzee raiding appears to be aimed at killing their opponent, rather than merely displacing them from the contested area (Pandit et al., 2016). If so, lethal intergroup aggression in chimpanzees must be promoted by additional factors, as suggested by the fact that this behavior is not commonly reported in other primate species with a resource defense mating system (Pandit et al., 2016).

IMBALANCE OF POWER HYPOTHESIS

Currently, one of the most widely accepted explanations for the lethal intergroup aggression in chimpanzees builds on this prior explanation of resource defense polygynandry, to suggest that the behavior is promoted by their fission-fusion sociality and male philopatry, which create opportunities for intergroup encounters where one party has a superior number of cooperating males (Glowacki et al., 2017; Manson & Wrangham, 1991; Pandit et al., 2016; Watts et al., 2006). By nature of numerical superiority, attackers can greatly reduce the costs of aggression (risk of injury) and more easily inflict injury on others. An important factor in this risk reduction is the cooperative, coordinated nature of the attacks, facilitated by coalitionary bonds between philopatric males, in which opponents are quickly subdued or immobilized, further minimizing potential costs (Manson & Wrangham, 1991; Watts et al., 2006). The "imbalance of power hypothesis" therefore proposes that lethal attacks are promoted not by high benefits but primarily by low costs (Manson & Wrangham, 1991; Wilson et al., 2014). Despite acknowledging the substantial benefits of lethal raiding, Manson & Wrangham (1991) highlight the fact that there is only one confirmed, and one suspected, case of group extinction due to lethal raiding. They therefore conclude that the benefits, while potentially great, are likely to be much less important than the costs when considering the evolution of lethal raiding behavior. The hypothesis has been well-supported by observations that most lethal intergroup aggression occurs when large parties attack a greatly outnumbered individual and by the fact that there are no reports of major injuries incurred by the attackers (Manson & Wrangham, 1991; Pandit et al., 2016).

It must be stated that, while most intergroup aggression has been observed to occur in low-cost situations, chimpanzees sometimes appear to accept large risks and engage in conflict with numerically superior communities, even when in very small parties (Boesch et al., 2008). In these cases, social factors, such as limited access to fertile females, may increase the potential benefits of attacking (or the cost of inaction) to exceed the potential cost of attacking, even without a favorable imbalance of power (Boesch et al., 2008).

REDUCE RIVALS HYPOTHESIS

The benefits of killing an opponent, rather than chasing them off, could simply be to eliminate a potential competitor or reduce the coalitionary strength of the rival group (Boesch et al., 2008; Mitani et al., 2010; Watts et al., 2006; Wilson, 2013; Wilson et al., 2014; Wrangham, 1999). This “rival coalition reduction hypothesis”, also called the “dominance drive hypothesis”, is strongly linked to the imbalance of power hypothesis. The benefits of killing a rival hold true for any species with group-level conflict (Wilson et al., 2014). However, in species without a mechanism to facilitate a sufficient imbalance of power, this benefit is likely outweighed by the potential cost of killing (Wilson et al., 2014). In these cases, animals would likely not risk injury by pursuing and attempting to kill their opponent but would simply displace them from the contested resource (Wilson, 2013). Enabled by the fission-fusion social system, gang attacks and lethal raids provide low-cost opportunities for chimpanzees to decrease a neighboring community’s competitive ability (Wrangham, 1999). As males do not migrate between groups, killing a male reduces the coalitionary strength of the targeted community until the male is replaced through births within that community (Wrangham, 1999).

FEMALE RECRUITMENT HYPOTHESIS

It has also been suggested that intergroup attacks serve to recruit new females, as young females have been observed to join the attacking community (Goodall, 1986). Though this hypothesis has not yet been systematically tested, there are indications that emigrating females may select communities with large numbers of adult males, so these attacks could serve to advertise their community size (Boesch et al., 2008; Wilson, 2013). The observed intergroup infanticides have also been suggested to be a strategy to increase males’ access to fertile females, as is the case in species such as lions, langurs and gorillas (Boesch et al., 2008). However, there is currently no convincing evidence this behavior increases the likelihood of female chimpanzees joining the infanticidal males’ community (Boesch et al., 2008). As stated before, the proposed adaptive explanations are not mutually exclusive. Males may be able to attract new females by defending and expanding their resources (Manson & Wrangham, 1991; Pandit et al., 2016). This territorial expanse could in turn be facilitated by the reduction of the rival coalitionary strength (Mitani et al., 2010; Watts et al., 2006), which is made strategically viable through the imbalance of power.

FEMALE-TARGETED ATTACKS

If chimpanzee raiding is a strategy by which coalitions of chimpanzee males are able to decrease the coalitionary strength of males from neighboring communities, as per the rival reduction hypothesis, this raises the question of why these attacks have also been observed to target adult females (see Marchant & McGrew commentating in Mason & Wrangham 1991). While female involvement in intergroup conflict has been observed to vary between populations, the killing of adult females also occurs in populations where females do not actively participate and is therefore not sufficiently explained by the rival reduction hypothesis (Boesch et al., 2008; Watts et al., 2006).

Furthermore, the female recruitment hypothesis proposes that lethal raiding benefits participating males via the recruitment of potential reproductive partners. This hypothesis would therefore predict that males would not target adult, sexually receptive females, but would rather predict attempts at affiliative behavior (Boesch et al., 2008; Watts et al., 2006; Wilson & Wrangham, 2003). At Gombe, attacks on sexually receptive females were observed to occur less often than attacks on non-receptive females, but the question remains as to why females are attacked at all (Williams et al., 2004).

One possibility is that attacks on females may serve to weaken bonds between adolescent females and their mothers to induce the younger females to transfer communities and thus benefit the recruitment of females (Goodall, 1986). A second possibility is that infanticide of the female’s infant is the primary goal (Hiraiwa-Hasegawa & Hasegawa, 1994) and a third, is that aggression elicits mating with the female (Boesch & Boesch-Achermann, 2000). However, there appears to be little evidence for such transfer of females after attacks (females transfer at adolescence due to female dispersal anyway), targeting of infants or post-attack mating (Williams et al., 2004). Of the adaptive explanations for lethal intergroup aggression in chimpanzees covered in this text, only the resource defense hypothesis offers an explanation for attacking adult females as it may be a way for chimpanzees to further induce a neighboring community to limit their use of certain areas or resources (Wilson, 2013). If so, the killing of sexually receptive outgroup females should occur in cases where the potential expansion of territory provides greater reproductive benefits than the recruitment of a potential reproductive partner.

Further insight, into conditions influencing whether males should attack females in neighboring communities, is provided by a model that incorporates the degree of reproductive skew among males (Pradhan et al 2014). When the highest-ranking male has priority of access to females, the addition of neighboring females to his community (whilst increasing birth rate) increases the number of females that have overlapping periods of sexual receptivity. This in turn decreases the level of skew, as the dominant male(s) can no longer monopolize all females. Thus, high ranking males should prefer to expand their territory, attacking females rather than tolerating them, whereas lower-ranking males can gain greater fitness benefits by tolerating new females. As the reproductive skew decreases, mating success is more equally distributed across males and therefore both high and low ranking males benefit from fatal attacks on females. Current observations provide initial support for this model, but further data are required to test predictions in detail.

INFLUENCE OF HUMAN DISTURBANCE

Critics of the adaptive interpretation of chimpanzee intergroup aggression, have suggested that killing is merely incidental to intergroup aggression, exacerbated by human influences such as human encroachment (deforestation, hunting, etc.) and food provisioning by researchers (Power, 1991; Sussman & Marshack, 2010; Watts et al., 2006).

Several aggressive, territorial behaviors, including boundary patrols and intergroup killing, were first observed at Gombe and Mahale, contrasting with earlier reports from short-term studies at other sites that seemed to indicate peaceful chimpanzee communities with open membership (Goodall, 1977; Goodall et al., 1979; Nishida, 1968, 1979; Reynolds & Reynolds, 1965; van Lawick-Goodall, 1968; Wilson, 2013). The Gombe and Mahale sites both used artificial feeding to facilitate observations, raising the possibility that the intergroup aggression was caused by food provisioning, rather than being part of a natural behavior repertoire (Power, 1991). It was shown that provisioning impacted the chimpanzees' behavior, with increased aggression on days that food was provided, though this impact might not have extended to behavior away from the feeding station (Wilson, 2013; Wrangham, 1974).

This "human impact hypothesis" further expanded to include other human influences that could cause or increase aggressive behavior. Human encroachment or disturbance of habitat (e.g. the conversion of forest into cropland) could affect intergroup aggression by increasing competition for the space available (Goodall, 1977; Pusey, Pintea, Wilson, Kamenya, & Goodall, 2007; Wilson, 2013). Poaching and human-transmitted diseases could decrease coalition sizes within a community and leave them vulnerable to attack (Goodall, 1977; Pusey et al., 2007; Wilson, 2013). However, since then, data from sites that were habituated without food provisioning do not support this "human impact hypothesis" and show that observed variations in rates of lethal aggression in chimpanzees were not explained by either provisioning by researchers or any other measured indication of human disturbance (Wilson, 2013; Wilson et al., 2014). In fact, the highest rate of killing was observed at Ngogo, an unprovisioned and relatively undisturbed site (see Richard Wrangham commentating in Sussman & Marshack, 2010). Current studies not only support the adaptive explanation of lethal coalitionary aggression as part of an evolved behavioral strategy, but also indicate that the rate at which this behavior occurs is unrelated to the suggested human influences (Watts et al., 2006; Wilson et al., 2014).

RELEVANCE TO HUMAN WARFARE

Adaptive explanations of chimpanzee raiding as a natural behavioral strategy are central to the debate on the origins of human warfare (Gat, 2006; van der Dennen, 1995; Wilson, 2013). It is often cited as evidence against the argument that war is a relatively recent cultural invention, originating within the past 12,000 years (Ferguson, 2011; Gat, 2015; Otterbein, 1999).

The imbalance of power hypothesis predicts that lethal coalitionary attacks should occur in species where intergroup conflict is beneficial to reproductive success, party sizes are variable (facilitated by fission-fusion sociality in chimpanzees) and individuals form long-term coalitionary bonds (Glowacki et al., 2017; Wrangham, 1999; Wrangham & Glowacki, 2012). Human hunter-gatherer societies generally display coalitionary bonding between males, a fission-fusion social system and may often have hostile relationships with neighboring communities (Glowacki et al., 2017; Heinz, 1972; Wrangham, 1999; Wrangham & Glowacki, 2012). Hunter-gatherer conflict often involves low-risk, coalitionary attacks on strongly outnumbered members of a rival community (Glowacki et al., 2017). These raids are performed by groups of men, who leave their territory with the intent to ambush, or otherwise surprise, small groups (Gat, 1999), after which, the raiders quickly retreat to their own territory (Glowacki et al., 2017). They are relatively low-risk to the raiding party, though some injuries can occur (Chagnon, 2009; Glowacki et al., 2017). Intergroup conflict appears to allow these male coalitions to defend and increase resources (e.g. territory and food) crucial to their reproductive success, as is thought to be the case for chimpanzees (Wilson, 2013; Wrangham & Glowacki, 2012).

Despite these similarities, several key differences distinguish raiding behavior in humans and chimpanzees. The use of weaponry, such as bows, clubs and spears, introduces an unpredictability to the imbalance of power and therefore affects the potential cost of lethal raiding (Boesch et al., 2008; Kelly, 2005). During surprise attacks on unarmed individuals, weaponry can greatly amplify the difference in instantaneous fighting ability and further reduce the cost of killing (Pandit et al., 2016). However, if an attacked individual also has access to weapons, they may seriously injure or kill members of the attacking coalition (Glowacki et al., 2017; Kelly, 2005), greatly increasing the cost relative to chimpanzee raiding. Humans can also affect the imbalance of power through the strategic use of terrain, deception and other relatively complex tactics (Wadley, 2003).

The origin of human warfare is too complex to determine from chimpanzee data alone, but the similarities between the two species support the view that warfare in humans is a behavioral strategy by which coalitions of males increase their fitness as a result of defending and expanding relevant resources (Glowacki et al., 2017; Wilson, 2013). War is likely not caused by a single instinct, but is facilitated by several evolved psychological traits, such as xenophobia and parochial altruism (Glowacki et al., 2017). As a result, the frequency and methods of warfare are heavily influenced by cultural differences, technological advances, and political and economic relations. Unlike chimpanzees, who can only benefit from intergroup interactions at the expense of the other party (e.g. by taking over parts of their territory), human intergroup interactions are not always a zero-sum game (Wilson, 2013). Humans can trade with neighboring groups as an alternative, peaceful strategy to obtain their resources with a potentially lower cost than warfare.

It is important, therefore, to emphasize that the possibility of a biological basis for warfare in humans does not mean that this behavior is inevitable or even justifiable (Glowacki et al., 2017; Wilson, 2013). There is no reason to believe that warfare cannot be reduced or even eliminated (Glowacki et al., 2017). Whether it is cultural or biological in nature, intergroup aggression is only a viable strategy if the benefits outweigh the costs. Throughout history, political institutions have increased the cost of violence and facilitated peaceful interactions within a certain region (e.g. a nation) and pushed warfare to the borders of that region (Glowacki et al., 2017). These zones of peace have expanded from small regions of allied communities to the borders of a single nation to large regions of friendly nations, such as the European Union. By expanding such regions in which the costs of warfare and/or the benefits of peaceful, mutually beneficial interactions are increased, global peace could be a practically achievable goal.

CONCLUSION

Current evidence indicates that the coalitionary killing of intergroup conspecifics in chimpanzees is an adaptive behavior facilitated by fission-fusion dynamics, resource defense polygynandry and male philopatry. The adaptive explanations presented in this text are not mutually exclusive and a combination of factors are likely to interact. For instance, fission-fusion dynamics and male philopatry create opportunities in which the imbalance of power is such that coalitions of males are able to kill members from other communities with little to no risk of incurring serious injuries. The imbalance of power therefore makes it strategically viable for chimpanzee males to reduce the coalitionary strength of a neighboring group. This could be necessary for territorial expansion (Mitani et al., 2010; Watts et al., 2006), which, in turn, could increase their access to fertile females (Manson & Wrangham, 1991). Contrary to the human disturbance hypotheses, lethal aggression in chimpanzees appears to be part of their naturally evolved behavioral repertoire. While raiding in human hunter-gatherer societies may have had a similar adaptive function, there is no reason to believe that warfare in humans is unavoidable.

CROSS-REFERENCES (related chapters selected from the table of contents)

REFERENCES

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest*. New York, NY: Oxford University Press.

Boesch, C., Crockford, C., Herbinger, I., Wittig, R., Moebius, Y., & Normand, E. (2008). Intergroup conflicts among chimpanzees in Taï National Park: lethal violence and the female perspective. *American Journal of Primatology*, *70*(6), 519–532. https://doi.org/10.1002/ajp.20524

Chagnon, N. (2009). Interview: Newsletter of the Human Behaviour and Evolution Society.

Davies, N. B., Krebs, J. R., & West, S. A. (2012). *An introduction to behavioural ecology* (4th ed.). Wiley-Blackwell.

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, *197*(4300), 215–223.

Enquist, M., & Leimar, O. (1990). The evolution of fatal fighting. *Animal Behaviour*, *39*(1), 1–9.

Ferguson, R. B. (2011). Born to live: challenging killer myths. In R. W. Sussman & C. R. Cloninger (Eds.), *Origins of Altruism and Cooperation* (pp. 249–270). New York, NY: Springer.

Gat, A. (1999). The pattern of fighting in simple, small-scale, prestate societies. *Journal of Anthropological Research*, *55*(4), 563–583.

Gat, A. (2006). *War in human civilization*. Oxford: Oxford University Press.

Gat, A. (2015). Proving communal warfare among hunter-gatherers: The quasi-Rousseauan error. *Evolutionary Anthropology*, *24*, 111–126. https://doi.org/10.1002/evan.21446

Glowacki, L., Wilson, M., & Wrangham, R. (2017). The evolutionary anthropology of war. *Journal of Economic Behavior and Organization*. https://doi.org/10.1016/j.jebo.2017.09.014

Goodall, J. (1977). Infant killing and cannibalism in free-living chimpanzees. *Folia Primatologica*, *22*, 259–282.

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

Goodall, J., Bandora, A., Bergmann, E., Busse, C., Matama, H., Mpongo, E., & Riss, D. (1979). Intercommunity interactions in the chimpanzee population of the Gombe National Park. In D. A. Hamburg & E. R. McCown (Eds.), *The great apes* (pp. 13–53). Benjamin/Cummings.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, *28*(4), 1140–1162. https://doi.org/10.1016/S0003-3472(80)80103-5

Heinz, H. J. (1972). Territoriality among the bushmen in general and the ! ko in particular. *Anthropos*, *67*(3/4), 405–416.

Hiraiwa-Hasegawa, M., & Hasegawa, T. (1994). Infanticide in nonhuman primates: sexual selection and local resource competition. In S. Parmigiani & F. S. Vom Saal (Eds.), *Infanticide and Parental Care* (pp. 137–154). Harwood

Academic Publishers.

Jaeggi, A. V, Boose, K. J., White, F. J., & Gurven, M. (2016). Obstacles and catalysts of cooperation in humans , bonobos , and chimpanzees : behavioural reaction norms can help explain variation in sex roles , inequality , war and peace. *Behaviour*. https://doi.org/10.1163/1568539X-00003347

Kelly, R. C. (2005). The evolution of lethal intergroup violence. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(43), 15294–15298. https://doi.org/10.1073/pnas.0505955102

Kitchen, D. M., & Beehner, J. C. (2007). Factors affecting individual participation in group-level aggression among non-human primates. In *Behaviour* (Vol. 144, pp. 1551–1581). https://doi.org/10.1163/156853907782512074

Majolo, B., de Bortoli Vizioli, A., & Lehmann, J. (2016). The effect of intergroup competition on intragroup affiliation in primates. *Animal Behaviour*, *114*, 13–19.

Manson, J. H., & Wrangham, R. W. (1991). Intergroup aggression in chimpanzees and humans. *Current Anthropology*, *32*(4), 369–390.

Mitani, J. C., Watts, D. P., & Amsler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology*, *20*(12), R507–R508. https://doi.org/10.1016/j.cub.2010.04.021

Nishida, T. (1968). The social group of wild chimpanzees in the Mahale Mountains. *Primates*, *9*(3), 167–224. https://doi.org/10.1007/BF01730971

Nishida, T. (1979). The social structure of chimpanzees of the Mahale Mountains. In D. A. Hamburg & E. R. McCown (Eds.), *The great apes* (pp. 73–121). Benjamin/Cummings.

Ostfeld, R. S. (1987). On the distinction between female defense and resource defense polygyny. *Oikos*, *48*(2), 238–240.

Otterbein, K. F. (1999). A history of research on warfare in anthropology. *American Anthropologist*, *101*(4), 794–805.

Pandit, S. A., Pradhan, G. R., Balashov, H., & Van Schaik, C. P. (2016). The conditions favoring between-community raiding in chimpanzees, bonobos, and human foragers. *Human Nature*, *27*(2), 141–159. https://doi.org/10.1007/s12110-015-9252-5

Power, M. (1991). *The egalitarians-human and chimpanzee:An anthropological view of social organization*. Cambridge University Press.

Pusey, A. E. (1980). Inbreeding avoidance in chimpanzees. *Animal Behaviour*, *28*, 543–582.

Pusey, A. E., Pintea, L., Wilson, M. L., Kamenya, S., & Goodall, J. (2007). The contribution of long-term research at Gombe National Park to chimpanzee conservation. *Conservation Biology*, *21*(3), 623–634. https://doi.org/10.1111/j.1523-1739.2007.00704.x

Radford, A. N. (2008). Duration and outcome of intergroup conflict influences intragroup affiliative behaviour. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1653), 2787–2791. https://doi.org/10.1098/rspb.2008.0787

Reynolds, V., & Reynolds, F. (1965). Chimpanzees of the Budongo Forest. In I. DeVore (Ed.), *Primate behaviour: Field studies of monkeys and apes* (pp. 368–424). New York, NY: Holt, Rinehart & Winston.

Sussman, Robert W., & Marshack, J. L. (2010). Are humans inherently killers? *Global Nonkilling Working Papers*, *1*, 7–50.

UNODC Statistics Online. (n.d.). Retrieved July 27, 2019, from https://dataunodc.un.org

van der Dennen, J. M. G. (1995). *The origin of war: The evolution of a male-coalitional reproductive strategy*. Groningen: Origin Press.

van Lawick-Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe stream reserve. *Animal Behaviour*

Monographs, *1*, 163–311.

Wadley, R. L. (2003). Lethal treachery and the imbalance of power in warfare and feuding. *Journal of Anthropological Research*, *59*(4), 531–554.

Watts, D. P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behav. Ecol. Sociobiol.*, *44*, 43–55.

Watts, D. P., Mitani, J. C., & Sherrow, H. M. (2002). New cases of inter-community infanticide by male Chimpanzees at Ngogo, Kibale National Park, Uganda. *Primates*, *43*(4), 263–270. https://doi.org/10.1007/BF02629601

Watts, D. P., Muller, M. N., Amsler, S. J., Mbabazi, G., & Mitani, J. C. (2006). Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. *American Journal of Primatology*, *68*, 161–180. https://doi.org/10.1002/ajp

Williams, J. M., Lonsdorf, E. V., Wilson, M. L., Schumacher-Stankey, J., Goodall, J., & Pusey, A. E. (2008). Causes of death in the Kasekela chimpanzees of Gombe National Park, Tanzania. *American Journal of Primatology*, *70*(8), 766–777. https://doi.org/10.1002/ajp.20573

Williams, J. M., Oehlert, G. W., Carlis, J. V., & Pusey, A. E. (2004). Why do male chimpanzees defend a group range? *Animal Behaviour*, *68*(3), 523–532. https://doi.org/10.1016/j.anbehav.2003.09.015

Wilson, M. L. (2013). Chimpanzees, warfare and the invention of peace. In D. P. Fry (Ed.), *War, peace, and human nature: The convergence of evolutionary and cultural views* (pp. 361–388). Oxford University Press. https://doi.org/10.1093/acprof

Wilson, M. L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I. C., Hashimoto, C., … Wrangham, R. W. (2014). Lethal aggression in Pan is better explained by adaptive strategies than human impacts. *Nature*, *513*(7518), 414–417. https://doi.org/10.1038/nature13727

Wilson, M. L., Kahlenberg, S. M., Wells, M., & Wrangham, R. W. (2012). Ecological and social factors affect the occurrence and outcomes of intergroup encounters in chimpanzees. *Animal Behaviour*, *83*(1), 277–291. https://doi.org/10.1016/j.anbehav.2011.11.004

Wilson, M. L., & Wrangham, R. W. (2003). Intergroup relations in chimpanzees. *Annual Review of Anthropology*, *32*, 363–392. https://doi.org/10.1146/annurev.anthro.32.061002.120046

Wrangham, R. W. (1974). Artificial feeding of chimpanzees and baboons in their natural habitat. *Animal Behaviour*, *22*, 83–93.

Wrangham, R. W. (1999). Evolution of coalitionary killing. *American Journal of Physical Anthropology*, *Suppl 29*, 1–30. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10601982

Wrangham, R. W., & Glowacki, L. (2012). Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers. *Human Nature*, *23*(1), 5–29. https://doi.org/10.1007/s12110-012-9132-1

Wrangham, R. W., Wilson, M. L., & Muller, M. N. (2006). Comparative rates of violence in chimpanzees and humans. *Primates*, *47*(1), 14–26. https://doi.org/10.1007/s10329-005-0140-1