

REVIEW ARTICLE

Warfare in an evolutionary perspective

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Abstract

The importance of warfare for human evolution is hotly debated in anthropology. Some authors hypothesize that warfare emerged at least 200,000–100,000 years BP, was frequent, and significantly shaped human social evolution. Other authors claim that warfare is a recent phenomenon, linked to the emergence of agriculture, and mostly explained by cultural rather than evolutionary forces. Here I highlight and critically evaluate six controversial points on the evolutionary bases of warfare. I argue that cultural and evolutionary explanations on the emergence of warfare are not alternative but analyze biological diversity at two distinct levels. An evolved propensity to act aggressively toward outgroup individuals may emerge irrespective of whether warfare appeared early/late during human evolution. Finally, I argue that lethal violence and aggression toward outgroup individuals are two linked but distinct phenomena, and that war and peace are complementary and should not always be treated as two mutually exclusive behavioral responses.

KEYWORDS

aggression, competition, conflict, cooperation, peace, social evolution, violence, war

1 | INTRODUCTION

The question of whether humans are innately peaceful or aggressive has fascinated scientists and philosophers for centuries.^{1,2} Wars, ethnic or religious contests, and intra-group or intra-family violence are scattered across historic periods and cultures, suggesting that aggression and violence are key aspects of human societies. At the same time, peaceful interactions between individuals or groups are ubiquitous and by far more common than aggression, and various warless societies have been described.³

In the last few decades, the evolutionary bases of warfare (see Table 1 for definition of key terms) and its role in human evolution have been hotly debated by scientists. Since a comprehensive review of the literature on warfare is beyond the scope of this manuscript (for in-depth reviews see References 1, 5, 9–24, here I briefly present the debate over the evolutionary bases of warfare and focus on some of the main points of the controversy in the following sections. There is no agreement on how we define warfare; some definitions mention the use of weapons, some focus on the intention/occurrence of killing

and others on the importance of organized/cooperative actions among members of one social group against members of the opposing group.⁵ Clearly, how we define warfare affects how deep we can go back in time in human evolution to investigate its emergence and evolutionary bases. The degree of organization among group members, advance planning, division of labor, and use of tactic observed in state-level warfare is rather unique. Such “complex” wars are probably not comparable to pre-state warfare or to aggressive between-group interactions in early hominins, in extant nonhuman primates and other social species, perhaps with the exception of some eusocial insects.²⁵ However, the propensity to be aggressive toward out-group conspecifics is a necessary trait for the emergence of warfare under specific socio-ecological conditions (see below) and in order to out-perform competing groups and gain fitness-related benefits. This trait is likely to be deeply rooted in human evolutionary history and potentially shared with other species.^{26,27} In the context of warfare, aggression is usually intra-specific and inter-personal,¹² excluding other forms of aggression (e.g., slow violence; for in-depth discussion on this see Reference 5). Wrangham^{2,24} (see also Reference 7) further differentiated

TABLE 1 Description of key terms used, with references to studies that have discussed these terms in-depth

Term	Description
War	Unless otherwise stated, here this term refers to “simple warfare” ⁴ : Aggressive interactions, with no chain of command, between members of socially distinct groups. Aggression may range from ritualized displays to close combat leading to injuries and death. Warfare often involves coalitions or organized actions among members of one group against another group (for a review of definitions of warfare see Reference 5).
Aggression	Here this term refers to intra-specific displays signaling the intention to arm, threats, physical attacks, injuries and killing performed by one individual/group toward another individual/group (for in-depth discussion on human aggression and its role for warfare see References ⁵ and ⁶). Aggression can be reactive or proactive. ^{2,7}
Propensity to act aggressively toward out-group individuals	Intra-specific aggression displayed by one individual/group toward a socially distinct group or single individual of that group, when the benefits of aggression for the aggressive individual/group outweigh the costs, and when those benefits cannot be obtained without aggression.
Raid	A surprise attack where the attacking party enters the territory/home range of another group; the attacking party usually out-numbers the target of the attack.
Ambush	Similar to raids, but in ambushes the attacking party is already in place and has prepared a trap for the target of the attack.
Ingroup/outgroup biases	Differences in the perception or behavior toward conspecifics based on their group membership. A typical example of ingroup/outgroup bias is parochial altruism, where altruism is directed toward ingroup individuals (i.e., group companions) whereas avoidance or aggression is directed toward outgroup individuals. ⁸

between proactive aggression, a trait humans probably share with chimpanzees, and reactive aggression, which is more frequently observed in nonhuman primates and other animals but less frequently in humans.

Even when scientists do not disagree on the definition of warfare, there is controversy over when warfare first emerged, how frequent it was and what role it played in human evolution. Some authors argue that human ancestors faced an extensive period of warfare, dating back to at least 200,000 year BP,²⁸ and probably much earlier, which has significantly shaped human social evolution.^{29–33} According to this view, war is an adaptive response that mostly emerges under specific socio-ecological conditions (e.g., scarcity of valuable resources) and that has fitness consequences.^{20,34} Conversely, other authors propose that warfare is a relatively recent phenomenon in human evolution, appearing (or becoming common) around or after 15,000–8,000 years BP.^{3,35} According to this view, the late emergence of warfare and/or its low frequency in prehistoric times suggests that warfare played a minor role in human evolution. One cause of the controversy is that it is difficult to gather reliable data to support or disprove the hypotheses.^{36,37} For example, scarce but reliable archeological data supporting the occurrence of warfare do exist for the Holocene.³⁸ Conversely, archeological data of earlier (>15,000–20,000 year BP) warfare are often unreliable. Indeed, weapons or skeletal traumas could indicate war or be due to other factors, including hunting of game or intra-group violence.^{35,37}

An additional aspect of the controversy is that theories on whether warfare has occurred or not have sometimes been presented as a set of mutually exclusive hypotheses. Stemming from the controversy over the early/late emergence of warfare in human evolution,³⁶ some researchers suggest that war is mainly due to culture, because warfare is a recent phenomenon in evolutionary terms and often occurred at low frequency before state-level societies. Therefore,

warfare has not exerted significant evolutionary pressure on humans.^{3,5,7,16–39} Moreover, differences on whether, how often, why and how pre-state human societies wage war are too extensive to be explained by an innate propensity to be aggressive toward outgroup individuals.¹⁶ The Extended Evolutionary Synthesis^{40–42} shows that cultural and evolutionary forces do not “act” in opposition with one another but should be considered together when explaining behavior, including warfare. For example, an evolved capacity to recognize ingroup and outgroup members, to act aggressively (or peacefully) toward outgroup individuals under specific socio-ecological conditions and/or to follow group norms can drive cultural differences in whether/when/how different societies wage war.^{16,39} If so, the lack of a reliable estimate of the emergence of warfare in human evolution poses significant problems to both cultural and evolutionary models on the causes of war.⁴³ However, some of the leading authors in this field have presented cultural and evolutionary hypotheses on warfare as alternative, or have completely dismissed the role that Darwinian evolution may play in explaining warfare.³ Margaret Mead⁴⁴ was one of the first to discard the importance of evolutionary explanations in her seminal paper eloquently entitled “Warfare is only an invention—not a biological necessity”. More recently, this conclusion has been supported by Sussman⁴⁵ (p. 109) who wrote: “Ultimately, differences in the expression and frequency of violence among humans will be explained mainly by differences in their culture and enculturation, and in their environment, and not in their biology and genetics”. Similarly, Ferguson⁴⁶ entitled “War may not be in our nature after all” as his contribution to a special volume of *Scientific American* on human uniqueness. Related to the controversy over the evolutionary and cultural bases of warfare, is the debate over whether human's ancestral state is violent or peaceful. The so-called “myth of the peaceful or warlike savage” has been the focus of philosophical discussions for

centuries and a controversial topic in anthropology.⁴⁷ Otterbein⁴⁸ described these two opposing views as hawks and doves, depending on whether researchers categorized humans as either warlike or peaceful. Some researchers^{3,45} have pointed out that we may have a bias toward over-emphasizing the impact of warfare in human societies, at the expenses of peaceful interactions, since war and aggression have more immediate and evident consequences on our everyday life: "Violence tends to grab the headline, but violence constitutes only a minute part of social life".³ (p. 1).

In summary, the controversy over the cultural and evolutionary hypotheses and over the peaceful or violent nature of human beings risk bringing this research field back to the nature/nurture debate, potentially constraining theoretical advancements on the role of warfare in human evolution.²⁰ Here, my aim is to critically evaluate some of the key controversial points over the evolutionary bases of warfare. I aim to show that evolutionary and cultural explanations on the occurrence of warfare are not incompatible and both contribute to explain this phenomenon, that hypotheses on the role of warfare for human evolution based on the timing of its emergence and its frequency are not biologically appropriate, and that describing peace and aggression as mutually exclusive limits our understanding of the intertwined nature of these traits. To this end, I identify and discuss six key points on the evolutionary bases of warfare: (a) differences and similarities between cultural and evolutionary explanations; (b) the adaptive value of war; (c) the frequency; and (d) emergence of war in human evolution; (e) the relationship between aggression toward outgroup individuals and lethal violence; (f) the relationship between peaceful and aggressive traits.

2 | SIX DEBATED POINTS ON THE ROLE OF WARFARE IN HUMAN EVOLUTION

2.1 | Evolution and culture explain biological phenomena at two distinct levels

Contrary to the view that sees cultural and evolutionary explanations of warfare (or of any other trait) as mutually exclusive, culture, and Darwinian evolution affect one another^{40,42} but address different aspects of biological phenomena. Hence, as argued by various authors,^{26,42,49} culture and Darwinian evolution should not be treated as providing contrasting explanations. Questions related to the evolutionary bases of a trait (e.g., the propensity to act aggressively toward outgroup individuals) focus on "why" that trait has emerged and spread in a population, that is, on its fitness consequences: if a trait gives benefits to individuals' fitness, and these benefits exceed possible costs, that trait will spread in a population through natural selection. Conversely, questions related to the role of culture focus on "how" traits are transmitted, looking, for example, at the horizontal/vertical diffusion rate of a trait or at the role of conformity. These two sets of questions are distinct but not mutually exclusive. Support for an evolved propensity to act aggressively toward outgroup individuals would come from a relationship between war and fitness, regardless

of the proximate causes of outgroup aggression. For example, outgroup aggression could give fitness benefits and be caused by resource scarcity, fear of outgroup individuals, aggressive attitude, conformity to group norms or to a combination of these and other factors. Therefore, adherence to group norms^{16,50} does not rule out the role that an evolved propensity to be aggressive toward outgroup individuals may have on the occurrence of war. In conclusion, discarding the adaptive function of war significantly limits our understanding on this phenomenon; evolutionary and cultural approaches are not incompatible in explaining warfare.

2.2 | War is an adaptive response

Since culture and Darwinian evolution explain the occurrence of war at two distinct and not mutually exclusive levels, estimating the fitness consequences of war is essential to analyze whether warfare is an evolutionary-driven phenomenon. To do so, the focus should be on warfare in extant hunter-gatherers because human ancestors have lived in this form of society for the largest portion of the evolution of the genus *Homo*.³¹ Since the majority of extant hunter-gatherers have come in contact with, or are aware of large-scale, state-level warfare, studies on hunter-gatherers should be integrated with archeological data on pre-state societies.³⁷

If humans have an evolved propensity for acting aggressively toward outgroup individuals, war should be an adaptive response, that is, it should be observed under specific ecological conditions where the fitness benefits of aggression out-weight the potential costs.^{34,51} For war, and more broadly for aggression, these ecological conditions are^{20,52–56}: (a) fitness-enhancing resources (e.g., mating partners, water or shelter) are a limiting factor, that is, they cannot be shared among all of the agents (be these cells, individuals, groups or states) in a given area; (b) agents cannot access those resources by moving to another area or by depleting the same resource at different times (scramble competition); (c) there are small differences (or small perceived differences) in the fighting ability of the agents competing for the same resource. These three ecological conditions appear to be important predictors of warfare in humans. In a sample of 19 hunter-gatherer societies, Kelly⁵⁷ found a positive correlation between the occurrence of war and population pressure, as measured by how much food is available per person. Moreover, Allen et al.⁵⁸ found that lethal violence was significantly and better predicted by resource scarcity than by socio-political complexity (a proxy of the extent to which leaders can coerce their subordinates to go to war), using archeological data on hunter-gatherer societies in Central California. Finally, it has been proposed that lethal aggression in humans became more frequent in the last 15,000–8,000 year BP^{33,59} (but see Reference 60), when population density increased, groups settled down near resource-rich locations (e.g., river estuaries) and started monopolizing those locations.⁶¹

Warfare and participation in battle have significant fitness costs (e.g., death or reduced lifespan^{31,62}). Even in technologically advanced wars, children born during War World I, whose fathers were killed in

battle, had a shorter lifespan than children whose fathers survived the war.⁶³ In terms of the fitness benefits of war, monopolization of food and acquisition of women by warriors are two of the principal causes of warfare in hunter-gatherers.^{1,31,64,65} Some evidence suggests that taking part in battles increases reproductive success,^{51,66–68} whereas some other studies report no fitness benefits.^{69–71} Warriors may employ a “high-risk-high-yield” strategy where the costs of warfare are high (death) but so are the potential benefits.^{4,20,51,72} Moreover, raids and ambushes may give warriors benefits at a much lower risk than battles where there is an approximately equal number of warriors in the two opposing parties (see Section 2.5).

It is important to point out that these studies do not imply that war is an unavoidable consequence of the conditions described above, or that those conditions are the only factors eliciting warfare.³⁴ Indeed, a positive relationship between taking part in battle and reproductive success may not be observed, for example, due to mate choice of individuals who did not fight or to cultural norms (e.g., social exclusion of individuals who committed violent acts at war). Social groups at every level of socio-political complexity, from family units to large states, can still peacefully resolve competitive interactions over limited resources. For example, between-group marriage is frequently used to reduce tension between groups and form alliances.³ However, these findings suggest that war is an adaptive response: humans have an evolved propensity to act aggressively (or peacefully) under specific socio-ecological conditions, but such propensity does not rule out the importance of culture. In fact, the cultural diversification of human societies, which accelerated in the last 15,000 year BP together with population growth, the emergence of agriculture and technological advancements, has “acted” on our evolved propensity to be aggressive or peaceful and significantly shaped our social behavior.

2.3 | The frequency of occurrence of a trait says very little about the role of evolution

As mentioned above, there is controversy over how frequently human ancestors waged war.⁷³ Bowles³¹ claims that groups of early humans frequently encountered one another and aggressively competed over valuable resources such as food or shelter. If so, he argues, the high fitness consequences of war, for example, in terms of injuries or monopolization of/exclusion from resources, significantly shaped human social evolution. These ecological conditions led to an evolved propensity to be aggressive toward outgroup individuals and to ingroup-outgroup biases (e.g., parochial altruism; Table 1). Some researchers oppose this scenario. They argue that population density of human groups has been estimated to be very low until around 15,000–8,000 years BP. Therefore, groups had few chances to meet with one another, were not competing over limited resources and were rarely waging war.^{3,35} According to this view, the prevalence and diversity of warfare in humans cannot be explained by a genetically driven process: humans do not have an evolved tendency to wage war, otherwise war would be ubiquitous across human societies and historic times.¹⁶ Finally, between-group peaceful interactions are

much more frequent than aggressive interactions. Therefore, the role of aggression and war in human evolution has been over-emphasized.^{3,45,74,75} To support this claim, Sussman⁴⁵ (p. 107) wrote (italics from the original text): “The overwhelming majority of our six billion conspecifics are having days, weeks, even entire lives devoid of violent interpersonal conflicts. This is not to naively underplay crimes, wars, and state-level aggression found in modern times, but it puts them in the domain of *anomalous*. Why do murder rates vary so greatly from country to country, from culture to culture? Are war, crimes, and violence the genetic, unalterable norm, or are they specific to stresses that occur when too many people want too few resources, or to social inequality, or environmental perturbations, or a plethora of other causes, including atypical psychopathic personalities?”

There are several problems with arguments related to the frequency of warfare. First, warfare is observed even when population density is low, as shown by studies on Australian Aboriginal people (Figure 1).³⁶ Second, selection should favor aggression only under specific ecological conditions (including some highlighted by Sussman’s quote); a ubiquitous display of aggression irrespective of its associated benefits and costs would be maladaptive.^{20,52,76} Even in species with specialized weaponry, such as claws, tusks and horns, intra-specific aggression only occurs under appropriate ecological conditions, rather than inevitably at a constant rate.⁷⁷ Third, there is not always a straightforward positive relationship between how often an event occurs and its role in shaping evolutionary trajectories, regardless of the importance of culture. For example, an arboreal species may be unable to exploit resources on the ground due to the presence of terrestrial predators, and thus be constrained to the canopy of dense forests, even if actual cases of predation on that species are virtually absent. No occurrence of predation does not mean that predation does not shape the ecology of that arboreal species. Fourth, the perceived risk of an event’s happening, and the actual occurrence of that event, may be unrelated to one another and they can differently shape evolution. For example, risk perception of terrorism, cancer or amniocentesis is not strongly and positively related to the “real” risk of these events in humans, and perceived risk may affect individual choices more than “real” risk.^{78–80} Even warriors in societies/historic times characterized by intense warfare are likely to have had more opportunities, in their life, for peaceful social interactions than instances when aggression was needed, as Sussman correctly claims in the quote above. However, one single battle can kill an individual with significant consequences on individual fitness even if that individual has sired some offspring before the battle.⁶³ Conversely, it may take a large number of friendly interactions, for example, to build a network of social relationships that have a positive effect on individual fitness.⁸¹ Claiming that humans have an evolved propensity to wage war means that we are likely to act aggressively toward outgroup individuals under given ecological conditions (see Section 2 above); it does not mean that we should always act aggressively toward outgroup individuals regardless of factors like resource at stake or the fighting ability of the opposing group. The same can be said for our propensity to be peaceful (see Section 2.6 below). The argument that war is not an evolved response, because its occurrence is not ubiquitous across human societies and historic

FIGURE 1 Australian Aboriginal people in an ambush during a mystic Bora ceremony from around 1900–1927 (picture taken by Kerry & Co.; State Library of New South Wales, Australia)



times, is not biologically meaningful. Such an argument “makes no more sense than to argue that the fact that humans have the genetically determined biological propensity to run means that everyone has to run everywhere” (Dunbar 1991; p. 379 in Reference 26. Therefore, hypotheses based on how many and how often societies wage war are biologically ineffective in opposing (or supporting) the view that warfare is an evolutionary driven phenomenon. Investigating the frequency of warfare during human evolution and across societies has high scientific value, but it should not be considered to support or oppose hypotheses on the evolutionary bases of warfare.

2.4 | Traits can evolve within a short time

Partially related to the frequency of warfare is the debate over the emergence of warfare during human evolution. Some researchers^{28,31} suggest that skeletal remains with signs of violence from archeological records point toward a prolonged period of warfare faced by human ancestors, dating back to at least 100,000–200,000 year BP.^{82–85} According to this view, these estimates on the emergence of warfare (and on the frequency of its occurrence; see Section 3 above) indicate that human ancestors have been exposed to a sufficiently long period of time for a propensity to act aggressively toward outgroup individuals to evolve and for warfare to shape social evolution. Contrary to this view, other authors^{35,57} argue that war is far more recent. They claim that frequently used archeological indicators of lethal violence are ambiguous, particularly those dating much earlier than around 15,000 years BP: signs of spears and of other weapons on skeletal remains may be related to any kind of violence, such as family disputes and mortuary cannibalism, or to post-mortem burial procedures that have nothing to do with warfare. Similarly, archeological remains of weapons may equally indicate warfare or hunting of large prey. The only relatively unequivocal signs of warfare appear in the last 15,000–8,000 years, approximately around or immediately after the agricultural revolution.^{35,38} If so, proponents of the late emergence of

warfare claim that the time window “available” for the evolution of traits favoring warfare is significantly shorter than what proposed,³¹ suggesting that war is not deeply rooted in human evolution.¹⁶

Even if war is, evolutionarily speaking, a recent phenomenon in *Homo*, it does not necessarily follow that humans do not have an evolved propensity to act aggressively toward outgroup individuals. Traits can rapidly evolve,⁸⁶ including in humans,^{87,88} when there is significant evolutionary pressure and high associated costs and/or benefits for a trait. Thus, a “late” emergence of war might have still posed strong evolutionary pressure on humans. Moreover, regardless of when war became common in human evolution, an evolved propensity to act aggressively under specific ecological conditions may not have been solely driven by outgroup threat.⁸⁹ If aggressive access or monopolization of resources give benefits to individual fitness such propensity to act aggressively may be maintained over evolutionary time regardless of what the target of aggression is. Three traits play a key role in the evolution of aggression: (a) releasing of proactive aggression² when ecological conditions favor aggression over peace; (b) assessing the fighting ability of the opponent(s) and of themselves; (c) categorization of individuals/groups as “friends” or competitors/enemies. These three traits are relevant for aggressive interactions both between members of the same group and between different groups. Within-group aggression, such as coalitions and revenge systems, are observed in virtually every human society, including those societies that do not wage war.^{3,90,91} There is no reason to believe that within-group aggression did not occur during human social evolution. Therefore, selection for aggressive traits was in place even if our ancestors did not wage war.

There are two non-mutually exclusive ways in which aggressive traits, evolved in response to within-group competition, may have been “applied” to war. First, selection may have acted on aggression as a means to obtain resources and on the propensity to differentiate aggressive vs. peaceful social stimuli. Such selection processes would not be related to specific targets (e.g., ingroup or outgroup individuals) and it could thus be maintained over evolutionary time if the outcome

of aggressive interactions affected fitness but regardless of whether aggression was mostly/only within- or between-groups. Ingroup-outgroup biases emerge as soon as groups are artificially formed in children,⁹² suggesting that humans can flexibly apply and modify rules related to group discrimination.²² Such propensity for group discrimination is necessary for aggression toward outgroup. Second, there may be phylogenetic continuity between traits related to warfare and to cooperative hunting or within-group aggression.^{2,13} Traits evolved under different evolutionary pressures could acquire new functions, as exaptations,⁹³ in response to new selective forces (e.g., war) when these emerge. For example, coordinated collective actions and cooperation between group members increase the chances to win a war. However, coordination and cooperation during collective actions may have evolved for other functions (e.g., cooperative hunting of large prey or collective punishment of violent group members²⁴) and then be “applied” to warfare. Cooperative hunting likely appeared 200,000–400,000 years BP,⁹⁴ and potentially much earlier,^{95–98} well before the first conclusive evidence of warfare in *Homo* (see above). Moreover, tools used for hunting, such as spears and projectile weapons (Figure 2), might have appeared around 400,000 years BP.¹⁰⁰ Finally, there seem to be similar physiological responses (i.e., increased stress level¹⁰¹) associated to both within- and between-group contests. Therefore, traits linked to warfare, such as aggression toward outgroup individuals and coordinated collective actions, may have evolved as exaptations from other functions.²⁷ Indeed, cooperative hunting and warfare are related, probably due to the cooperative component of these actions.⁸⁹ In various human communities there is a positive correlation between hunting of big prey and warfare.^{73,102} Moreover, hunting of big game in human ancestors was at least partially due to status acquisition in relation to male–male competition, not just to subsistence,⁹⁶ similarly to what happens with warfare.⁶⁴ In chimpanzees, individuals who often have an active role in hunting are also those who most frequently join raiding parties to attack outnumbered chimpanzees from neighbor communities.^{26,103} In summary, an estimated “late” emergence of war does not represent clear evidence against an evolved propensity to wage war. Testing the adaptive value of war, that is, whether war is more likely to occur under specific ecological conditions (e.g., resource scarcity) and has fitness consequences, is key to prove or disprove the role of evolution.

2.5 | Aggression toward outgroup and lethal violence are two distinct phenomena

Humans show instinctive inhibition mechanisms toward killing and, in modern warfare, soldiers must go through extensive training to be able to kill in battle.¹⁰⁴ The dehumanization of enemies is considered a psychological mechanism favoring lethal violence.¹⁰⁵ Such mechanisms have been used to support the claim that warfare and lethal violence are learned rather than evolved processes (i.e., we are “naturally” inclined to be peaceful³). However, this scenario may not apply to hunter-gatherer societies where group members have to be

ready to fight and kill enemies for access to contested resources. Killing competitors gives fitness advantages to the winning group when gene flow and degree of relatedness between groups is low.¹⁰⁶ For example, lethal violence toward outgroup individuals eliminates the risk of counter-aggression from the victim (though revenge can still be displayed by relatives of the victim). However, lethal violence also has significant potential costs for the winner of a fight. Before the emergence of projectile weapons, and in the absence of significant numerical advantage for one of the opposing parties (see below), killing required close combat and thus the risk of fatal injuries was high for all combatants.^{67,107} In this type of contest, it is advantageous for both the winner and loser to terminate an aggressive interaction when the outcome is clear and before the interaction escalates any further (i.e., before it leads to lethal violence^{51,77}). The use of projectile weapons in war significantly increased the likelihood of killing from a safe distance²⁴ and reduced the effect of inhibition mechanisms on aggression.¹⁰⁷ Therefore, the emergence of projectile weapons may have significantly changed the costs/benefits of warfare and how it was waged.

The risk of death helps explain the differences in when or how lethal violence is observed in hunter-gatherers. Wars involving several individuals from each opposing group, and with no clear numerical advantage for one of the groups, are often characterized by aggressive displays from a distance and rarely result in lethal violence^{26,67} (but see Reference 108). Conversely, the main purpose of raids and ambushes is to kill enemies and indeed lethal violence is much more common during those events.^{109,110} Raids and ambushes often take place when the attacked individuals are largely out-numbered and taken by surprise, that is, when the risk of injury for the attackers is low due to an imbalance of power and dilution effects.^{9,26} The same pattern is observed in chimpanzees. Encounters between chimpanzee communities, where several members of each community are present, usually involve the exchange of aggressive calls from a distance or threats with rare physical aggression.¹¹¹ However, raids composed of male chimpanzees, silently entering the territory of another community, often result in lethal violence when the raiding party encounters isolated and largely out-numbered individuals, and kills them (Figure 3).^{111,112} According to the imbalance of power hypothesis, asymmetric raids and ambushes were the primary mode of combat in human evolution,⁹ and these can lead to lethal violence because the risk of injury and death for each attacking individual is much lower than in other types of war. Three conclusions can be drawn from these observations. First, wars (involving several individuals from each opposing group and with low numerical disparity between groups) and raids/ambushes are two distinct and probably functionally different types of aggressive interactions between groups. Second, the occurrence of lethal violence appears to be related to the likelihood that there is a significant imbalance of power between opposing groups (i.e., during raids and ambushes). Third, the propensity to act aggressively toward outgroup affects whether and how often groups exchange aggression with one another during between-group encounters but it might not be strictly linked to the likelihood of lethal violence. In other words, humans are likely to be aggressive toward

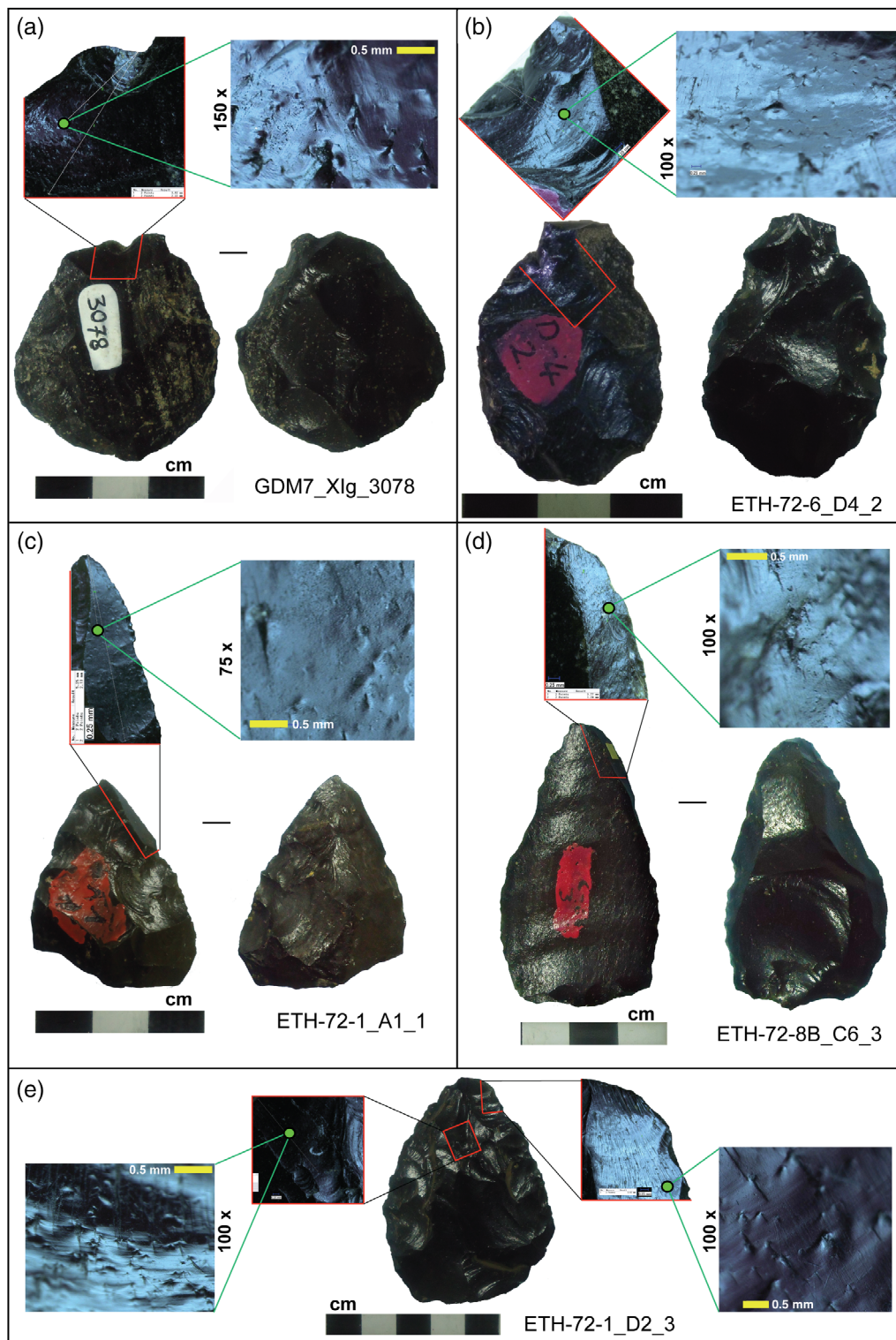


FIGURE 2 Pointed artifacts exhibiting micro- and macro-fracture features indicative of projectile weaponry, dated to >279,000 years BP, from Gademotta, Ethiopia.⁹⁹ (a, b) fracture wings on transverse fractures; (c, d) fracture wings on burin-like fractures; (e) impact fractures on two fracture fronts on the distal portion (pictures taken by Yonatan Sahle; reproduced with permission from the author) [Color figure can be viewed at wileyonlinelibrary.com]

outgroup individuals under some specific ecological conditions but display lethal violence only when the risk of such violence is low (i.e., when one party has significant numerical advantage over the

other). If so, aggression toward outgroup individuals is a necessary but not sufficient requirement for lethal violence, as imbalance of power between combatants plays a crucial role for killing. Indeed, a few



FIGURE 3 Lethal coalitionary aggression in chimpanzees. A group of male chimpanzees have attacked and killed an adult male from another community at Ngogo, Kibale National Park, Uganda. A young adult male jumps on the carcass after (picture taken by John C. Mitani; reproduced with permission from the author) [Color figure can be viewed at wileyonlinelibrary.com]

societies have been described¹¹³ where lethal violence between groups does occur but wars involving several individuals from each opposing group rarely or never take place. Therefore, a distinct set of hypotheses may be needed to explain the propensity to act aggressively and lethal violence toward outgroup individuals.

2.6 | Peace and war are not always alternatives

Theories on the aggressive and peaceful nature of humans have often been treated as alternatives during philosophical digressions and, more recently, in some of the literature on the evolution of warfare.^{3,45} However, categorizing a species (including humans) as peaceful or aggressive has little biological value: an individual can be aggressive or peaceful toward the same social partner at different times, toward different group members or other groups. Hypotheses on aggression and peace do not represent opposing views on human nature but are complementary. Indeed, aggressive and peaceful interactions can co-occur and be directed to the same or different targets.^{112,114} For example, humans can display both fierce competition and cooperation between groups.^{91,115} Moreover, the evolution of within-group peace-making and conflict-resolution mechanisms (e.g., reconciliation or third-party affiliation) has been driven by the potential costs that aggression has on individual fitness.¹¹⁶ Conflict-resolution mechanisms should have evolved in species where the risk of aggression is high and where aggression has negative fitness consequences for opponents (e.g., social exclusion, reduced tolerance or cooperation, increased stress). Conversely, no conflict-resolution mechanisms is expected in species where the risk of aggression is low and/or aggression bears no fitness costs. The same explanation could apply to peace-making between groups^{91,115} which may have

emerged with the function of reducing the fitness costs of warfare. Moreover, altruistic punishment and parochial altruism may simultaneously involve elements of pro-sociality and aggression.¹¹⁷ Indeed, mechanisms involved in the display of pro-sociality and aggression are target-specific and thus can co-occur in the same social interaction. Cognitive skills and behaviors that have been proposed as important for pro-sociality (e.g., recognition of different individuals or groups, memory of past interactions, and numerical assessment¹¹⁸) also play a crucial role for warfare. Therefore, the observation of peaceful interactions between conspecifics does not rule out or overshadow the importance of aggression in explaining social dynamics, and vice-versa. Labeling species as either aggressive or peaceful is biologically inaccurate. The occurrence of altruism, compassion toward conspecifics or empathy does not disprove that an individual, group or species could be aggressive, wage war, or display lethal violence.

3 | CONCLUSIONS

Studies on the causes and consequences of war are key for understanding human social evolution. Attempts to describe human nature as either warlike or peaceful are biologically inappropriate because such a dichotomous approach does not consider that aggressive and peaceful behaviors can co-occur. Darwinian evolution and culture are not mutually exclusive explanations for the occurrence of war. Indeed, the fast-growing field of gene-culture co-evolution shows that Darwinian and cultural evolution interplay in shaping biological diversity.^{40,42} For example, genetically based within-group coalition and between-group aggression may evolve in groups of large size ($N > 50$ of each sex), but cultural transmission of these traits may allow for their evolution in groups of any size.⁵¹ There are fitness costs/benefits associated with warfare and the acquisition of limited resources is a predictor of war. Arguments based on the emergence and frequency of warfare in human evolution are not effective to “solve” the controversy over whether we have an evolved propensity to act aggressively toward outgroup individuals. Finally, aggression toward outgroup individuals and lethal violence are two closely linked but distinct phenomena.

The recent theoretical advancements and empirical work on war and conflicts have given several new hypotheses, challenges and questions that need to be tested, addressed and answered. Reviewing these advancements and hypotheses is beyond the scope of this manuscript (for in-depth reviews see References 1, 10–22, 24). From a comparative perspective, one key question to address is whether or to what extent group members cooperate during aggressive interactions with other groups. Anthropologists often highlight the importance that within-group cooperation plays in wars in hunter-gatherers.^{37,74} However, in nonhuman animals individual participation to between-group interactions can be explained by selfish interests rather than by shared intents,¹¹⁹ even when animals apparently cooperate (e.g., when two animals are aggressive toward the same target). Understanding whether

between-group aggressive interactions in nonhuman animals are comparable to pre-state wars in humans, and analyzing inter-specific differences in collective action problems and in punishment of free-riders are some of the key challenges for research on the evolutionary bases of warfare.

In conclusion, current work suggests that humans have an evolved propensity to act aggressively toward outgroup individuals, under specific ecological conditions, irrespective to when warfare first emerged and how frequently occurred during the course of human evolution. The same set of conditions can determine when we act pro-socially: war and peace are two intertwined aspects of human nature. The socio-ecological and technological changes that occurred in the last 15,000 years of our history (e.g., agriculture and population growth), with the associated cultural diversification of human societies, likely resulted in a greater frequency of war and lethal violence, and led to increased variance on whether, how often and why human societies waged war. Culture shaped our evolved propensity to be aggressive toward outgroup individuals. Thus, evolutionary and cultural approaches are not incompatible, and both contribute to explaining human warfare.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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