

The evolutionary anthropology of war

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ABSTRACT

Evolutionary anthropologists seek to understand the evolution of warfare across multiple timescales, from the roots of warfare in the intergroup aggression of our primate ancestors, to the causes of warfare among contemporary societies today. While warfare remains a contentious subject, considerable evidence supports the view that warfare is a strategy by which coalitions of males cooperate to acquire and defend resources necessary for reproduction. This strategy is not the result of a single “instinct” for war, but is instead an emergent property resulting from evolved psychological mechanisms (such as xenophobia and parochial altruism). These mechanisms are sensitive to ecological and social conditions, such that the prevalence and patterns of warfare vary according to subsistence strategies, military technology, cultural institutions, and political and economic relations. When economic conditions enable intergroup relations to change from zero-sum to positive-sum games, peaceful intergroup relations can emerge.

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1. Introduction

Although rates of death from violence have declined in recent centuries and outright warfare among states has become increasingly rare (Eisner, 2001; Pinker, 2011), intergroup violence persists at all scales of human society, from urban gangs to global terrorism. Great powers have avoided direct mutual confrontation since World War II, but proxy wars, cold wars, deterrence and aggressive posturing continue to dominate international relations. Civil wars have meanwhile become increasingly common (Cederman et al., 2011; Collier and Hoeffler, 2004).

Warfare is a central topic for evolutionary anthropology (Fig. 1), in part because in many respects it is a uniquely human trait, yet one with intriguing similarities to intergroup aggression in other species, particularly our close relatives, chimpanzees.

Warfare thus presents a puzzle: why did warlike behavior arise in humans but few other species? Warfare requires intensive levels of cooperation while risking death, raising questions about how such behaviors could have evolved in a world of self-interested actors. As a major cause of mortality in many societies, warfare has likely been an important source of selection pressure for both biological and cultural evolution. If, as many evolutionary anthropologists suppose, the roots of warfare extend deeper than the origin of our species (ca. 300,000 years ago), warfare is likely to have shaped the evolution of human psychology, including traits such as courage, risk-taking, parochial altruism, patriarchy and xenophobia (Alexander,

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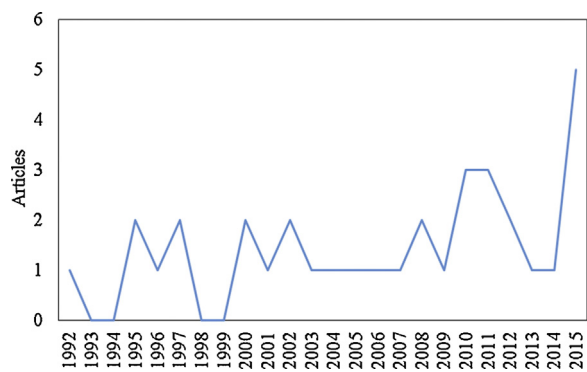


Fig. 1. Conflict-Related Papers in top Evolutionary Anthropology Journals, 1992–2015.
Fig. 1 displays conflict-related papers that were published in top anthropology journals between 1992 and 2015. The figure was generated based on five journals (*Current Anthropology*, *Evolution and Human Behavior*, *Evolutionary Anthropology*, *Animal Behaviour*, *Human Nature*) and the search terms (war(fare), collective violence, coalitionary aggression, intergroup conflict) commonly associated with theories of conflict in anthropology. Web of Science searches for articles within the given journals with these terms in the title were performed on 29 September 2016.

Table 1
 Research on war and conflict in evolutionary anthropology.

	Description
1) A formal definition of war	A critical component of most anthropological definitions of war is that coalitions attempt to injure or kill members of other groups. However definitions vary widely, e.g. by including or excluding feuding and revenge raiding, internal and external war, or war above and below the military horizon.
2) Foundational studies on war in evolutionary anthropology	Bowles (2009); Chagnon (1988); Durham (1976); Ember (1978); Goodall (1986); Keeley (1996); Kelly (2000); Mathew and Boyd (2011); Otterbein (1989); Tooby and Cosmides (1988); Turney-High (1949); van der Dennen (1995); Wrangham (1999)
3) Methods used to study conflict/war	To study conflict, evolutionary anthropologists most commonly use: - Systematic behavioral studies of non-humans and humans - Archaeological studies from prehistory - Ethnographic studies of small-scale societies - Agent-based and game theoretical modeling
4) Main models of conflict/war	Models of war and conflict: 1) Intergroup dominance hypothesis 2) Imbalance of power hypothesis 3) Cultural incentives and sanctions 4) Evolved psychology for war (e.g. Male Warrior hypothesis) 5) Multi-level selection 6) Cultural group selection

1987; Bowles, 2009; Rusch, 2014a; Wrangham, 1999). Warfare indisputably has had a profound effect on the evolution of material culture, including technology for weapons and defenses, and social institutions, including the formation of cities, states and empires (Gat, 2006; Morris, 2014). Warfare itself has evolved rapidly in historical times, growing exponentially in its destructive power, so that thermonuclear warfare now threatens the existence of contemporary civilizations, and perhaps our species. At the same time, declining rates of death from warfare raise the tantalizing hope that warfare may one day follow institutions such as feudalism and slavery into extinction (Morris, 2014).

Evolutionary anthropologists approach the study of warfare from a broad set of perspectives, employing a variety of methods to understand the origins and evolution of war at a range of time scales (Table 1). Comparative studies of primates and other species examine intergroup aggression within a phylogenetic context that spans tens of millions of years. Paleo-anthropologists examine fossils, tools and other evidence from humans ancestors in the roughly 6–9 million years since our lineage diverged from that of chimpanzees. Archaeologists examine skeletal trauma, weapons, fortifications, and other evidence of conflict during thousands of years of prehistory, including material contexts for historically documented conflict. Ethnographers studying modern human societies seek insights into what drives conflict today. In particular, studies of mobile hunter-gatherers and other small-scale subsistence societies provide modern analogues of the sorts of societies that humans are thought to have inhabited for most of our evolutionary existence. Evolutionary anthropologists also study the motivations of people participating in state-level and international conflicts, including soldiers and terrorists (Atran et al., 2014; Whitehouse et al., 2014). Contemporary evolutionary anthropological studies of war connect and intersect with perspectives from multiple academic specializations, including biology, psychology, history, political science, economics and international relations to address questions including the evolutionary origins of warfare (Boehm, 1987; Choi and Bowles, 2007; Johnson and Toft, 2013; Lehmann and Feldman, 2008; Pietraszewski, 2016; Rusch, 2014b; Wrangham and Peterson,

1996) variation in patterns of war across societies and through time (Kelly, 2000; Knauff, 1987; LeBlanc and Register, 2003; Otterbein, 2004); as well as factors promoting war and peace today, within and among nations (Glowacki and Gönc, 2013; McDermott, 2013; Wiessner and Pupu, 2012).

Because warfare involves many aspects that are uniquely human, such as the use of manufactured weapons, symbols of group identity, and the use of language for planning and giving orders, it is possible to define war in ways that exclude other species, such as “lethal armed combat,” or by requiring an understanding of intentions or other factors that are unknowable for other species. To better understand human warfare in an evolutionary context, we focus on an aspect of war that can be operationalized across species: coalitionary killing (Table 1). Below we discuss evolutionary approaches to behavior before turning to explanations for intergroup aggression in primates and humans.

2. Evolutionary approaches to warfare

Discussions of the origins and evolution of warfare have long been polarized by arguments about whether warfare is a biological adaptation, with deep roots – perhaps extending as far back as the common ancestor of chimpanzees and humans – or is a cultural invention with shallow roots, perhaps no deeper than the past 10,000 years or so (Ferguson, 2011; Gat, 2015; Otterbein, 1999). This debate runs along channels carved centuries ago by political philosophers arguing whether in the state of nature, human life was “solitary, poor, nasty, brutish and short,” a “warre of all against all” (Hobbes, 1997 [1651]) or whether “savage man” was basically peaceful: “wandering in the forests, without work, without speech, without a home, without war, and without relationships,...equally without any need of his fellow men and without any desire to hurt them” (Rousseau, 1984 [1754]).

Within anthropology, the debate about warfare’s roots is deeply entwined with a larger debate, which has raged for over a century, about the degree to which human behavior can be explained by biological principles, including evolutionary theory (Harris, 1968; Sanderson, 2007).

Darwin’s *Origin of Species* (1859) and *Descent of Man* (1871) fundamentally transformed the explanatory framework for anyone interested in understanding human origins and behavior. By providing compelling arguments that evolution occurred through the simple yet elegant mechanism of natural selection, Darwin helped shift discussions of the human “state of nature” from the realm of philosophical speculation to a set of questions resolvable (at least in principle) by empirical research. Darwin considered warfare to be an important force in the evolution of human nature, arguing that the “never-ceasing wars of savages” would result in ongoing selection pressure for greater innovation in weapons, sagacity, and cooperation: “When two tribes of primeval man, living in the same country, came into competition, if the one tribe included (other circumstances being equal) a greater number of courageous, sympathetic, and faithful members, who were always ready to warn each other of danger, to aid and defend each other, this tribe would without doubt succeed best and conquer the other. . . Thus the social and moral qualities would tend slowly to advance and be diffused throughout the world.” (Darwin, 1871: 162–163).

Paleoanthropology, the study of physical evidence of human evolutionary history, emerged within a few years of *The Origin*, when William King (King, 1864) interpreted skeletal remains found in Neanderthal, Germany as belonging to an earlier species of human.

Cultural anthropology likewise emerged as a discipline in the wake of Darwinism; much of the interest in “primitive” societies was motivated by an effort to understand the origins and evolution of human social behavior. Edward Burnett Tylor (1871) and Lewis Henry Morgan (1877) viewed human societies as the product of evolutionary change, driven by material factors. In this view, different societies provided insights into different stages of social evolution, from hunting (“savagery”), through herding (“barbarism”) and farming (“civilization”). Rather than adopting a specifically Darwinian approach, however, these early anthropologists typically viewed evolution as a framework for understanding progress and “the rise of higher forms” (Service, 1962). Societies passed through a series of stages. “Primitive” tribes retained traits from early stages of social evolution. Franz Boas, a leader in the effort to establish anthropology as a formal academic discipline, argued throughout his career against such views. Boas argued that rather than passing uniformly through a necessary series of stages; “human culture does not always develop from the simple to the complex, but that in many aspects two tendencies intercross, one from the complex to the simple, the other from the simple to the complex” (Boas, 1911: 193). Boas thus laid the foundations for what became a generally dismissive attitude towards evolutionary theory among American anthropologists, many of whom remain largely focused on the particulars of the societies they study, and skeptical towards evolutionary explanations (Harris 1968; Sanderson 2007). Skepticism towards evolution was coupled with a focus on human behavior being driven mainly by learned cultural rules rather than innate biological urges.

Keeley (1996) argued that the “myth of the peaceful savage” emerged in the wake of the anti-evolutionist views of Boas. For example, Margaret Mead, a student of Boas, argued that warfare was an invention, rather than an adaptation (Mead, 1940). This view conformed well with increasing skepticism about the glory of war, informed by the horrific destructiveness of the First World War and the descent of Europe and East Asia into the Second World War. In contrast, Otterbein (1999) attributed this myth to lingering evolutionist views: “If war was a monstrous scourge in the twentieth century, it must have been less common and less lethal in the past.” Either way, by the 1940s, the “myth of the peaceful savage” was firmly embedded within anthropology. Starting in the 1960s, though, this myth began to unravel, as a new generation of anthropologists began acquiring detailed field data on war among numerous small-scale societies. This new generation of anthropologists

sought to explain warfare with explicit links to emerging theory in biology, including ecology (Vayda, 1974) and evolution (Chagnon, 1979, 1988; Durham, 1976).

The rise of the evolutionary social sciences in the 1970s deepened the rift within anthropology, such that the field is now sharply divided between those who view evolutionary theory as a powerful explanatory tool, and those who view evolutionary theory at best with indifference, and at worst with deep suspicion of evolution as a smokescreen for justifying a host of social ills (Sanderson, 2007).

Contemporary evolutionary anthropology (EA) traces its roots, not to the early evolutionists such as Edward B. Tylor and Louis Henry Morgan, but to the revolution in biological thinking that emerged from work by George C. Williams, William D. Hamilton, John Maynard Smith and others, who argued that natural selection is best understood to be acting at the level of the gene, rather than the group or even the individual organism (Boomsma, 2016). This gene's eye view of evolution led to fundamental insights, including answers to why organisms senesce and die (Williams, 1957), why cooperation occurs mainly among kin (Hamilton, 1964), why so many organisms reproduce sexually despite the many disadvantages of doing so (Hamilton, 1975), and why males and females tend to differ in their allocation of mating versus parenting effort (Trivers, 1972). A key theoretical tool in this new biology was evolutionary game theory (Maynard Smith, 1974), which provided numerous insights into aggression, such as why animal contests frequently involve display rather than physical violence. These new approaches gained widespread attention with the publication of Edward O. Wilson's *Sociobiology* (Wilson, 1975) and Richard Dawkins' *The Selfish Gene* (Dawkins, 1976). Around this time, several distinct research approaches emerged, seeking to use these theoretical insights to understand the evolution of human behavior: human sociobiology, human behavioral ecology, dual inheritance theory, and by the 1980s, evolutionary psychology. The term "sociobiology" attracted considerable controversy and is now rarely used by evolutionary social scientists, but the main theoretical approaches underlying what used to be called sociobiology continue to inform the other approaches (Borgerhoff Mulder, 2006). Evolutionary anthropologists contributed to the founding of all these approaches (e.g., human sociobiology: DeVore (1988); Hrdy (1981); human behavioral ecology: Dyson-Hudson and Smith (1978); Caro and Borgerhoff Mulder (1987); dual inheritance theory: Durham (1976, 1991); Richerson and Boyd (2005); evolutionary psychology: Tooby and DeVore (1987), and all contribute to the understanding of coalitionary aggression and other topics in evolutionary anthropology today (Smith et al., 2001; Winterhalder and Smith, 2000).

While these approaches (behavioral ecology, dual inheritance theory, and evolutionary psychology) share the underlying assumption that evolution shaped modern human psychology, they differ in their methods and research programs. Evolutionary anthropologists working within the paradigm of behavioral ecology include those who focus on humans, and those who study other primates, as well as more distantly related species. Generally speaking, behavioral ecologists focus on ultimate, or functional questions about why organisms behave in a particular way (Krebs and Davies, 1993). Behavioral ecologists assume that organisms are designed by natural selection to maximize their inclusive fitness in their current environment, given the costs and benefits posed by a particular socioecology (Nettle et al., 2013). They implicitly assume that humans regularly achieve adaptive solutions to ecological problems. They use mathematical tools, especially evolutionary game theory, to examine which particular strategies are likely to maximize fitness in a given ecological setting. They rely on field studies measuring indices of fitness, such as rates of energy acquisition (as in optimal foraging theory) or number of offspring, to assess the adaptive value of behavior.

Behavioral ecologists seek to understand how social behavior relates to ecological factors, both within species, and among different species. Since Darwin, biologists have employed the comparative method, a cross-species approach to understanding the relationship between behavior, ecology, and evolutionary history. Similarities across closely related species suggest that the trait under consideration has a common origin and likely would have existed in the common ancestor. Differences in traits between closely related species suggest new selection pressures following the divergence of the two species from their common ancestor. For example, discovering that chimpanzees, bonobos, and humans all share a common trait suggests that the common ancestor of these three species also had this trait (Ghiglieri, 1987; Wrangham, 1987). Evolutionary anthropologists have tended to focus on chimpanzees and other primates closely related to humans, but in many cases a broader comparative perspective is needed. Phylogenetically distant species have in many cases evolved similar solutions to ecological problems. Depending on the trait, examples of evolutionary convergence may be found among social carnivores (e.g., cooperative hunting, territory defense, provisioning of young, and central place foraging (Smith et al., 2012)) or even more distant taxa, such as ants (war, farming, herding, and division of labor (Hölldobler and Wilson, 1990)).

Evolutionary psychology (EP) focuses on the cognitive mechanisms underlying behavior and assumes that human psychology evolved to solve recurrent adaptive problems, resulting in psychological mechanisms to solve such problems (Barkow et al., 1992). For example, people generally perform poorly when tested on problems in abstract logic. When problems with the same logical structure are framed as problems of detecting cheaters, people do much better (Cosmides, 1989). Evolutionary psychologists attribute this effect to a "cheater detection module," a circuit or set of circuits in the human brain that evolved to solve recurring social problems. In contrast to HBE, EP argues that mismatches will frequently occur between human psychological adaptations (which are argued to have formed mainly in the remote past, in an Environment of Evolutionary Adaptedness (EEA) when humans all lived as hunter-gatherers), and current human circumstances, which have changed radically due to technological innovations. Thus, people have strong preferences for diets rich in fats and sugars, which promoted improved survival in the EEA. However such diets make consumers in industrialized societies prone to obesity and diabetes, conditions that lead to reduced survival, and presumably reduced evolutionary fitness.

Dual inheritance theory (DIT) proposes that both genetic and cultural evolution are centrally important for understanding human evolution (Cavalli-Sforza and Feldman, 1981; Durham, 1991; Henrich and McElreath, 2007; Richerson and Boyd, 2005). Human behavior depends not only on genetic adaptations, but also cultural adaptations, which evolve in ways that are broadly analogous to biological evolution, though with some important differences. Because cultural traits can be transmitted horizontally as well as vertically, and because new traits emerge and spread through innovation and copying rather than random mutation and gene flow, cultural evolution can occur much faster than biological evolution. Additionally, cultural innovations can dramatically change an organism's ecological context, resulting in gene-culture feedback loops. Thus, stone tools, fire, cooking, and domesticated livestock all originated as cultural innovations, but have had profound effects on anatomy and social behavior, including reductions in chewing and digestive anatomy, increases in body and brain size (Wrangham, 2009; Wrangham et al., 1999), and the evolution of lactase persistence in societies with a sufficiently long tradition of herding and drinking milk (Tishkoff et al., 2007).

Despite differences in emphasis and methods, each of these three research traditions is rooted in the theory and practice of neo-Darwinism, and the approaches are, to some extent, converging. For example, cultural evolution, a focus of DIT, provides a mechanism whereby human populations can become well adapted to their ecological conditions, despite rapid changes in subsistence strategies, technology and social organization. Cultural rules, or strategies, that are maladaptive (leading to reduced fitness) tend to become extinct, whereas cultural rules that are adaptive (leading to increased fitness) tend to become more common. Cultural evolution proceeds much more rapidly than genetic evolution, such that innovations in one area (such as the invention of agriculture, bows and arrows, or smart phones) can be rapidly tracked by innovations in other areas (such as marriage rules, body armor, and social media, respectively) (Perrault, 2014). Thus, while fundamental psychological mechanisms may indeed have been shaped during the Pleistocene, cumulative evolution of cultural rules has enabled individuals to adapt their behavior in ways that provide fitness benefits despite dramatic changes in circumstance. Most evolutionary anthropologists maintain that behavior is the result of complex interactions among genetics, environment, and proximate influences and cannot be attributed to a single genetic source (Laland and O'Brien, 2011; Laland et al., 2001). Similarly, evolutionary anthropologists recognize that humans have behavioral flexibility and that culture is a crucial influence on behavior that interacts with, sometimes overrides, and is sometimes constrained by, biological predispositions.

3. Intergroup coalitionary aggression

Primates live in a variety of societies, ranging from solitary individuals, to troops with stable group composition, to fission-fusion communities and multi-level societies (Mitani et al., 2012). These grouping patterns influence both the likelihood of intergroup conflict and the particular form it takes, which can range from vocal contests, to “battles”, and finally lethal raiding against out-groups. Wrangham (1980) proposed that one of the main benefits primates gain from living in groups is increased competitive ability to gain access to key resources that affect reproductive success such as food, water and shelter. Living in groups may also provide more mating opportunities and improved protection from predators (Koenig et al., 2013; van Schaik, 1983).

In behavioral ecology, aggression is viewed as a strategy by which animals attempt to acquire and defend resources essential to their reproductive success (Maynard Smith and Price, 1973). Animals are predicted to use aggression when the anticipated costs are low compared to the expected benefits (Georgiev et al., 2013; Rusch and Gavrillets, 2017). In competition between groups, larger groups tend to win fights against smaller groups (Crofoot and Wrangham, 2010). Because intergroup dominance provides reproductive benefits to members of successful groups, individuals are motivated to achieve dominance in intergroup contests (Crofoot and Wrangham, 2010). Such benefits of grouping have been documented in other group-living animals. For example, in lions, larger coalitions gain reproductive benefits for both sexes; larger coalitions of males have greater success in maintaining access to groups of females (Bygott et al., 1979), and prides with more females maintain higher quality territories (Mosser and Packer, 2009).

The intensity and lethality of conflict varies with the socioecology of the species, which shapes the costs and benefits of aggression. When animals compete over resources, they often bluff and display rather than engage in direct damaging fights. Nonetheless, fatal fights do sometimes occur among many species, especially when the resources in question are critical to an individual's lifetime reproductive success (Enquist and Leimar, 1990; Hardy and Briffa, 2013), as when male red deer compete for dominance and mating opportunities (Clutton-Brock, 1982). Such fights can be risky to opponents on both sides: individuals value their own lives and will fight intensely to save themselves.

Based on evolutionary game theory, behavioral ecologists argue that fatal fighting should only occur when the benefits are unusually large, the “value of the future” is unusually low (i.e., when an opponent has a short life expectancy anyway, and thus has nothing to lose), or when the attackers experience unusually low costs in the effort to kill (Enquist and Leimar, 1990). In species where groups compete mainly over food, the value of a particular food resource is unlikely to be worth the risk of fatal fighting. In species where intergroup aggression involves competition for access to females, such as among gorillas, fatal fighting can be more common, but this usually involves pairs of opponents, such as the resident silverback gorilla male defending his females against a lone silverback seeking to recruit one or more females to his own group (though recent findings show that coalitionary killing can emerge in gorillas under appropriate circumstances (Rosenbaum, 2016)). In species in which individuals have an evolved motivation for intergroup dominance and costs of aggression are low, proximate triggers such as short-term resource competition are not necessary for intergroup conflict (Wrangham, 1999).

Many primate species live in stable social groups called “troops” within which most members feed, move, and sleep together (Mitani et al., 2012). Intergroup relations vary greatly among troop-living primate species, and even within species, depending on factors such as population density and the distribution of resources (Cheney, 1987). One study of bonnet macaques, for example, found that only 29–30% of intergroup encounters involved aggression (Cooper et al., 2004), whereas among chacma baboons 72% of encounters were aggressive (Kitchen et al., 2004).

Many species of primates use loud vocalizations to advertise territory ownership and/or repel members of rival groups (Cheney 1987). When groups come within sight of one another, they may interact peacefully (e.g., ~70% of encounters in bonnet macaques (Cooper et al., 2004); 28% of encounters in chacma baboons (Kitchen et al., 2004)) or they may engage in escalated fights, which typically involve the exchange of loud vocalizations, chasing, and the retreat of one or both groups. Intergroup killings are generally rare among troop-living species, and when they do occur they are likely to involve infanticide by males attempting to recruit females (gorillas: (Watts, 1989); Thomas langurs: (Steenbeek, 1999)) or take over groups of females (langur monkeys: (Borries et al., 1999); chacma baboons: (Kitchen et al., 2004)), or the killing of lone males that may pose a risk of group takeover or infanticide (white-faced capuchins: (Gros-Louis et al., 2003); gorillas: (Rosenbaum et al., 2016)).

Intergroup dominance can be achieved not only by numerical superiority (Van Belle and Scarry, 2015), but also by the particular group composition such as the number of adult males (Robinson, 1988), or by territorial advantage (Crofoot et al., 2008). While both males and females may participate in intergroup conflict, recent studies have found that for a broad range of species, groups with a greater number of males are more likely to win intergroup contests (chacma baboons: (Kitchen et al., 2004); yellow baboons: (Markham et al., 2012); blue monkeys: (Roth and Cords, 2016); tufted capuchins: (Scarry, 2013)). Males may participate in intergroup fights to obtain access to resources such as food, water and sleeping sites; to defend mates and/or offspring; or some combination of these (Arseneau et al., 2015; Markham et al., 2012).

In theory individuals in groups may benefit from killing members of rival groups, because doing so weakens rival groups and increases the chances of winning key resources in future intergroup fights. Nonetheless, most intergroup fights among primate troops do not result in serious injuries or death, likely because inflicting lethal damage is risky for an attacker, since victims fight back. Additionally, group-level fighting routinely involves collective action problems (Arseneau et al., 2015; Markham et al., 2012; Rusch and Gavrillets, 2017; Willems et al., 2015; Willems and van Schaik, 2015). While all members of a group might benefit from killing members of rival groups, those benefits are shared by all, including non-participants, creating a large temptation to defect (Nunn, 2000).

3.2. Intergroup aggression in chimpanzees

Chimpanzees live in groups called communities, which average around 40–60 members but can contain 200 or more. Unlike troops, in which all group members stay together throughout the day and night, chimpanzees have a fundamentally different social structure and the entire chimpanzee community rarely comes together. Instead, chimpanzees have “fission-fusion” grouping dynamics, in which individuals travel, forage, and rest in subgroups called parties.

Chimpanzees live at low densities and rarely interact directly with members of neighboring communities. Most interactions involve vocal exchanges in which the opponents are separated by hundreds or thousands of meters and do not come within sight of each other (Boesch et al., 2008; Wilson et al., 2012). Chimpanzees also engage in patrols in which parties of mostly males travel to the border areas appearing to seek signs of members of other communities by sniffing the ground or listening (Watts and Mitani, 2001; Wilson and Wrangham, 2003). When parties from two communities do come within visual range, the outcome depends critically on the number of males on each side. If the two sides are evenly matched, the interactions resemble those of troop-living primates, and involve mainly loud calls, charging displays and occasional and chasing. If one side greatly outnumbers the other, however, or if chimpanzees manage to isolate an individual from the rest of its party, severe gang attacks may result. Intercommunity killings in long-term studies across Africa involved a median 8:1 ratio between attackers and defenders and are a significant source of infant and adult mortality (Wilson et al., 2014).

Coalitionary killing of adult conspecifics is unusual and appears limited mainly to social insects such as ants, social carnivores such as lions, wolves, and spotted hyenas, and a few primates, including humans and chimpanzees (Wrangham 1999). The species distribution of such coalitionary killing appears best explained by the *imbalance-of-power* hypothesis (Manson and Wrangham, 1991; Wrangham, 1999). According to this hypothesis, the fission-fusion grouping patterns of species such as chimpanzees create opportunities for attackers to kill victims with very little risk. In troop-living species, intergroup encounters typically involve many individuals on both sides, and attackers rarely if ever have an opportunity to concentrate lethal force on any one individual. In contrast, since members of chimpanzee communities travel in parties that vary in size, from one to dozens of individuals, intercommunity encounters can involve parties that differ greatly in size. Such numerical asymmetries dramatically lower the costs of killing, tipping the balance in favor of fatal attacks, even if there are no resources immediately at stake. In such fights, attackers seldom receive more than scratches, and have never been recorded to be seriously hurt, while the victims are often killed (Watts et al., 2006).

Chimpanzee intercommunity relations generally conform to the predictions of the imbalance-of-power hypothesis. Parties are more likely to travel to the periphery of their range when in parties with more males (Wilson et al., 2007). When chimpanzees hear calls from strangers, they are more likely to approach when in parties with more males, both in playback

experiments (Wilson et al., 2001) and in naturally occurring encounters (Wilson et al., 2012). Several studies have found that winners of intercommunity conflict expand their territory at the expense of the losers (Goodall, 1986; Mitani et al., 2010; Nishida et al., 1985). For example, Mitani et al. (2010) documented a substantial territorial expansion into a region previously occupied by victims of a series of lethal intergroup attacks. Other studies have found that increasing territory size provides reproductive benefits, including increased body mass (Pusey et al., 2005), shorter inter-birth intervals (reduced time between consecutive births) and higher infant survival due to increased access to resources (Williams et al., 2004).

3.3. Discussion of non-human intergroup coalitionary violence

The benefits of intergroup dominance likely play a role in intergroup relations across primates (Crofoot and Wrangham, 2010) and other group-living animals. The imbalance-of-power hypothesis suggests that animals in many species could gain fitness benefits from killing members of rival groups, but that such killings should rarely occur except in species where factors such as coalitionary bonds and fission-fusion dynamics reduce the costs of killing. Relatively few species have these characteristics, but among them are wolves (*Canis lupus*) and spider monkeys (*Ateles* spp.). A long-term study in Minnesota found that attacks by other wolves accounted for 43% of wolf deaths from natural causes (excluding hunting and trapping) (Mech, 1994). Studies at other sites have confirmed the widespread occurrence of intergroup killing in wolves (Cassidy et al., 2015; Mech et al., 1998; Smith et al., 2015). Spider monkeys males form coalitions, and coalitionary killing has been observed within groups (Campbell, 2006). As reported for chimpanzees (Wilson et al., 2007), spider monkeys travel in larger parties when visiting the periphery of their range, where intergroup encounters are more likely (Symington, 1990; Wallace, 2008). Groups of male spider monkeys have been observed to make raids into the territory of other groups, appearing to seek out other groups, and then attacking individuals they encounter (Aureli et al., 2006). Similarly, mountain gorillas have been observed to engage in lethal coalitionary attacks against out-group males when imbalances of power are sufficiently large (Rosenbaum et al., 2016).

The close phylogenetic relationship between chimpanzees and humans suggests the possibility that the similar patterns of intergroup hostility result from shared ancestry. However, bonobos are just as closely related to humans, but they have strikingly different intergroup relationships. Bonobos accordingly present an intriguing challenge for the imbalance of power hypothesis. Like chimpanzees, bonobos defend group territories and have fission-fusion grouping patterns, and would thus be expected to be vulnerable to intergroup raiding. As in chimpanzees, intergroup encounters in bonobos may include exchanges of loud vocalizations, chasing, and charging, but no intergroup killings have been reported, and peaceful mingling sometimes occurs when groups meet (Idani 1990).

The underlying causes of the differences between bonobos and chimpanzees remain poorly understood. Wrangham (1999) has proposed that differences in feeding ecology affect grouping patterns, which in turn affect the costs of intergroup killing, not only for chimpanzees compared to bonobos, but also for different chimpanzee populations. The amount of time spent foraging alone varies greatly among populations, and appears highest in eastern chimpanzees, where long dry seasons can result in periods of low food availability. Bonobos and western chimpanzees appear to spend less time feeding alone, and are thus less frequently vulnerable to coalitionary killing (Wrangham, 1999). Comparison of data from long-term studies found that killings occurred most often among eastern chimpanzees, less often for western chimpanzees, and never for bonobos (Wilson et al., 2014). Mathematical modeling suggests that the regular presence of multiple females in foraging parties may be particularly important for deterring raids in bonobos (Pandit et al., 2016). Complementing the ecological ideas, bonobos may have evolved a more peaceful temperament than chimpanzees because of some other factor, such as female strategies that reduce the effectiveness of aggression as a strategy for male mating competition (Furuichi, 2011). In this view, more peaceful intergroup relations may be a byproduct of reduced intensity of mating competition, again made possible by a difference from chimpanzees in social ecology. Detailed, systematic comparisons of data from multiple long-term study sites are needed to test these ideas further.

Whatever the causes, several lines of behavioral and morphological evidence suggest that reduced intergroup aggression in bonobos is a derived trait compared to chimpanzees (Wrangham and Pilbeam, 2001). If this is the case, the occurrence of lethal intergroup aggression in both humans and chimpanzees may result from shared ancestry, rather than convergent evolution.

4. Human intergroup conflict

Evolutionary anthropologists study human intergroup conflict at time scales ranging from prehistory to contemporary societies. Archaeology provides abundant evidence of the cultural evolution of war, including the development of weaponry, fortifications, walled cities, and the emergence of complex societies, which many attribute to arms races among societies, in which larger, better armed societies prevailed (Richerson and Boyd, 2005; Turchin, 2009). Reviewing this large literature is beyond the scope of this paper; here we focus on the question of whether warfare's roots are deep or shallow in human prehistory.

Various trajectories have been proposed for the frequency of war deaths over time. Rousseauians argue that war was rare or nonexistent in the remote past, becoming common only with the rise of settled populations, food storage, agriculture, and/or some other factor (Ferguson, 1984; Fry, 2006; Kelly, 2000). Among the Hobbesians, Steven Pinker (2011) argues that humans share with chimpanzees a deadly past, with rates of death from intergroup aggression declining only with the rise states. Recently, Gómez et al. (2016) compiled mortality data from 600 human societies, including contemporary, historic and prehistoric populations. Although the data must be interpreted cautiously given that they came from a wide set of studies using different methods, data from contemporary societies tended to fit the pattern proposed by Pinker: higher rates of death were reported among hunter-gatherers, while the lowest rates of death were for the contemporary global population, which is dominated by people living in densely settled states. Data from prehistoric populations were more ambiguous; the medians were low, but populations varied greatly.

Archaeological research has the capacity to reveal characteristics of human behavior well before the invention of agriculture or the influence of state-level societies. However, archaeological studies of warfare face many challenges. Evidence of all kinds becomes sparser the further into prehistory we search. Sites from thousands of years ago may preserve buildings, pottery and weapons, but sites from millions of years ago contain at best stone tools and occasional bones. Most evidence consists of fragmented and isolated remains, such that the cause of death is difficult or impossible to determine. For most of human history, the same weapons can be used for hunting game or fighting people, making it impossible to know for sure if weapons were used to kill people, unless they are found lodged in human bone. A final difficulty is determining the cause of death from remains. Many wounds that would have been fatal may not be preserved in the archaeological record because they were located in soft tissue instead of bones. A study of arrow wounds from conflicts in the American West in the 1800's shows that only about one-third of injuries resulted in skeletal trauma. The remaining two thirds of arrow wounds did not damage bone despite the fact that in many cases they were fatal (Milner, 2005). This suggests that inferred incidents of injury and death from violence in the archaeological record trauma are underreported, though the size of this effect will depend on the type of conflict and weapons used.

Despite these challenges numerous archaeological studies indicate that intergroup relationships among archaeological hunting and gathering societies frequently involved violence. The most concrete evidence of intergroup violence among nomadic hunter-gatherers prior to the adoption of agriculture comes from the shores of Lake Turkana dating to approximately 10,000 years ago. At this site, twelve partly preserved bodies were recovered with ten showing evidence that the likely cause of death was due to sharp and blunt force trauma from arrows or clubs (Lahr et al., 2016). In this case, the stone tools that likely killed some of the victims appear to have come from a distant area, suggesting that the victims and attackers had different territories. Similarly, at the Jebel Sahaba site in Sudan, usually estimated to be between 12,000 and 14,000 years old, 58 bodies were recovered, of which 23 showed evidence of having died through violence (Wendorf, 1968). However, given that this area appears to have begun transition to a storage economy, some have argued that it supports the view that warfare results from such transitions, rather than being a feature of pure hunting and gathering societies (Kelly, 2000).

Although these two sites provide evidence of lethal intergroup violence among hunter-gatherers, other sites show little or no such evidence (Nakao et al., 2016). Most diachronic studies that look at extended time spans within a given area find that intergroup violence varies with cultural and ecological factors (Allen and Jones, 2014; Lambert, 2002; LeBlanc, 1999; Martin and Harrod, 2015; Maschner and Reedy-Maschner, 1998; Milner, 1999). One recent study used a large sample of over 6000 burials of hunter-gatherers from central California from 1530 BP to 230 BP. Over 7% of burials had evidence of sharp force or projectile trauma consistent with arrows or spear wounds that occur during intergroup aggression. Rates of violence did not vary with presumed sociopolitical complexity but did vary with estimates of resource scarcity (Allen et al., 2016). Together these studies support the hypothesis that prehistoric societies had lethal intergroup conflicts but their frequency and severity varied due to ecological and social factors.

4.2. Studies of hunter-gatherers

Evolutionary anthropologists also study living populations of hunter-gatherers and other small-scale societies as models to understand how people living in ancestral populations may have behaved. Before the domestication of crops and livestock, all people lived solely by hunting and gathering (foraging) for food. Documented hunter-gatherers lived in a range of societies, from mobile and mostly isolated family groups, such as the Western Shoshoni of the Great Basin, to complex sedentary societies of California and the Pacific Northwest, where storage of foods such as acorns and smoked salmon supported chiefdoms with hereditary social classes and slavery. Which range of this spectrum best represents life in the Paleolithic remains unclear, but ancestral human societies likely varied across different ecological contexts, just as they do today. A ubiquitous feature of human societies, though, is multi-level social structure, in which men and women form stable breeding bonds within larger societies, including bands and ethno-linguistic groups (Chapais, 2010).

Understanding ancestral intergroup relationships through studies of small-scale societies is hindered by changes to their social organization and behavior that occurred due to contact with agricultural and state societies. Throughout most of human evolution, hunter-gatherers bordered other foraging groups who had similar technologies and social organization. However, following the agricultural revolution, farmers and herders took over most of the world, presumably because societies that produce and store food outcompete foragers. As a result, hunter-gatherers have become increasingly rare. Most

foraging groups that have been studied border larger and stronger agricultural or pastoralist groups resulting in asymmetric power differentials that likely altered intergroup relationships (Otterbein, 1989; Wrangham and Glowacki, 2012). State and colonizing forces also affected intergroup relationships among small-scale societies usually resulting in the cessation of hostilities between groups. This is due in part to the fact that states are usually concerned with terminating internal conflict and establishing a monopoly on violence (Pinker, 2011). Sharing borders with more powerful societies, and/or being included within imperial and state boundaries can have a pacifying effect, insofar as the Leviathan of the state enforces laws and prevents war, but colonizers, states, and their representatives also can exacerbate rates of war in various ways, from active persecution of foragers (as in the Indian Wars that accompanied the expansion of the United States) to unintentionally increased violence resulting from access to trade goods such as steel axes and guns (Ferguson, 1992).

One of the first cross-cultural studies on intergroup relationships among hunter-gatherers found that while some hunter-gatherer groups did have peaceful relationships with their neighbors, 90% of societies had war more frequently than “rarely or never” and the majority of pre-state foragers had regular warfare (Ember, 1978). Since then a number of studies have systematically examined intergroup relations in small-scale societies and mostly found similar results supporting the generalization that warfare was a common feature of intergroup relationships among hunter-gatherers (Otterbein, 2004).

The most useful contexts to infer ancestral intergroup relationships come from hunter-gatherer groups that are surrounded by other hunter-gatherer groups without state intervention. There are few records from such societies. Australia presents a unique and important case because until the arrival of Europeans it was a continent of only hunter-gatherers with no domesticated livestock or agriculture. Multiple sources of evidence indicate that lethal intergroup conflict occurred with regularity across Australia prior to the arrival of the English. Ethnographic accounts of early settlers and explores include detailed reports of intergroup violence that predate the arrival of outsiders (Allen, 2014; Gat, 2015; Pardoe, 2014).

Similarly, Wrangham and Glowacki (2012) reviewed intergroup behavior among hunter-gatherers in six regions globally where hunter-gatherers were neighbored by other hunter-gatherers and not by agriculturalists. In all six cases, features of warfare were found including ambushes, shoot-on-sight responses to trespassers, unused border zones near the territory of other groups, and fear of strangers. Although these studies strongly support the claim that warfare among hunter-gatherers was a regular feature of intergroup relationships, humans are also capable of peaceful intergroup relationships. Among hunter-gatherers, groups commonly did have peaceful relationships that could include trade and intermarriage (Fry, 2006; van der Dennen, 1998). Such peaceful relationships were largely limited to relations among bands within larger societies, whereas hostile relations commonly existed between ethno-linguistic groups.

4.3. Patterns of warfare among hunter-gatherers

Warfare among hunter-gatherers or small-scale farmers generally follows a strikingly similar pattern given the wide-variety of cultural variation and ecological habitats humans inhabit. Similar to lethal intergroup aggression in chimpanzees, the most common type of attack among hunter-gatherers is the raid or surprise ambush. A group usually consisting of all men would set out seeking to attack a much smaller group or a lone individual (Gat, 1999). Raiders would attempt to have the element of surprise through attacking at dawn or by ambushing unsuspecting individuals and quickly retreating to safety. These raids were usually low-risk to the attackers, however, injuries sometimes occurred. Chagnon (2009) for example, systematically collected data on scores of raids among a group of lowland horticulturalists living in Venezuela and Brazil called the Yanomamö. He estimated that less than 5% of raids resulted in injuries to attackers, and deaths were very rare. Likewise, data from the Waorani, a lowland horticultural group from Ecuador, show low death rates for aggressors without a single fatality for an attacker (Beckerman et al., 2009). In rare cases, multiple raiders could be killed, usually due to the attacking party being detected before their attack giving the intended victims time to prepare (Wrangham and Glowacki, 2012).

Larger conflicts called “battles” also occurred between hunter-gatherer groups, though they were much more variable than raids depending on features such as geography and social organization. Battles usually consisted of similarly matched groups throwing spears or shooting arrows at each other from a distance and hostilities would cease after one or two casualties. Although battles most often only resulted in just a few injuries or deaths, they could turn into a massacre if one side were greatly outnumbered (Burch, 2005).

Unlike warfare in state societies, hunter-gatherer conflict did not involve chains of command or formal leaders. Although prominent and well-respected persons may plan strategy, there were no mechanisms to compel participation. People were usually free to join or quit as they desired. Success in warfare could bring benefits to the entire population such as access to territory but quantitative data on the relationship between warfare and group benefits is scarce. In addition to group benefits, warriors received private benefits that could include status, captives, or material goods though the receipt of these varies between societies (Gat, 2000; Glowacki and Wrangham, 2013).

There are several key differences between warfare among hunter-gatherers and war among chimpanzees. Unlike chimpanzees, humans use weapons in intergroup conflict including spears, clubs, and arrows. Weapons can amplify power differentials making attackers more dangerous, but at the same time, weapons also make potential victims capable of inflicting serious harm on aggressors (Johnson and Mackay, 2015; Kelly, 2005). In chimpanzee raids, attackers are very rarely injured but among humans aggressors are sometimes killed due to the victims being armed. Human attackers are also able to engage in more complex tactics that including using terrain to their advantage, engaging in deception and lethal treachery and surprise (Wadley, 2003). Attackers may also have revenge as a motive (Boehm, 2011; Walker and Bailey,

2012), something that may not be the case for chimpanzees (though we have no way of knowing for sure). Finally, human groups can also have peaceful intergroup relationships that include trade and intermarriage. Thus while there are important similarities between chimpanzee intergroup aggression and warfare among hunter-gatherers, there are substantial differences.

Most raids and battles in small populations resulted in no more than one or two deaths but over time these numbers could constitute a significant source of mortality. Several studies have compiled mortality rates from small-scale societies that include hunter-gatherers and farmers. Based principally on a compilation by Keeley (1996) the annual mortality rate from intergroup aggression among hunter-gatherers averaged around 165 deaths per 100,000 ($n = 12$ populations), while among farmers the rate was 2–4 times higher (595 deaths per 100,000, $n = 20$ populations) (Wrangham et al., 2006). The majority of the victims were usually men (Beckerman and Lizarralde, 1995). While the total number of victims was typically small, controlling for population size reveals a death rate roughly an order of magnitude higher than typical for industrialized nations (Keeley, 1996; Walker and Bailey, 2012).

4.4. Conclusions

Converging evidence supports the claim that lethal intergroup violence was likely common among ancestral hunter-gatherers. However, unlike chimpanzees where intergroup interactions are always hostile, relationships among hunter-gatherers are variable with sustained peaceful relationships possible. The tactical style of human intergroup conflict resembles intergroup aggression in chimpanzees: in both species, killing occurs mainly when a small group of males ambush and kill members of a rival group at minimal risk to themselves. However, advanced cognitive abilities, superior defensive skills and lethal weaponry make warfare an inherently more risky endeavor for human aggressors than for chimpanzee aggressors. Nonetheless, the fundamental similarities in patterns between chimpanzees and humans in small-scale societies suggest a functional continuity in the adaptive significance of intergroup aggression in the two species.

5. Theories of human war

Many scholars have proposed that human warfare emerged primarily as a consequence of cultural changes. Both Lorenz (1966) and Roscoe (2007) have argued that the invention of weapons enabled humans to overcome an innate aversion to killing. Alternatively, Kelly (2000) argued that warfare emerges from increasing social complexity and social substitution (where one group member is substitutable for another). As we elaborate below, however, the invocation of culture as a cause does not provide a free pass from the constraints of natural selection: cultural traits that substantially reduce the inclusive fitness of actors will tend towards extinction, while those that provide fitness benefits will become more common (Durham, 1976; Richerson and Boyd, 2005). In the following, we focus on explanations that are explicitly based on evolutionary theory.

5.1. Behavioral ecology and war

The imbalance-of-power hypothesis predicts that coalitionary killing should occur when species have coalitionary bonds, fission-fusion grouping, and intergroup aggression is tied to increased reproductive success. Mobile hunter-gatherers generally have both coalitionary bonds and fission-fusion societies. The most common type of social organization among foragers is the band (local residential group) where parties subdivide during the day with residents usually foraging alone or in small groups. Many hunter-gatherers societies were territorial and showed hostility to outsiders (Heinz, 1972) with strangers commonly being attacked or killed on sight. Hunter-gatherer conflict usually involved asymmetric party sizes with larger parties attacking smaller groups, and aggressors rarely suffering injuries (Wrangham and Glowacki, 2012).

While the imbalance-of-power hypothesis may be sufficient for explaining the evolution of psychological mechanisms favoring coalitionary killing in humans, by itself it does not explain the full range of behaviors found in human warfare, including the greater risk-taking in human warfare, peaceful intergroup relationships, and the strategic use of alliances and war to advance group functional aims (Wiessner, 2006). Another limitation of the imbalance-of-power hypothesis is that it does not account for how the collective action problem is solved in intergroup aggression. This is especially acute in chimpanzees where the benefits from success in intergroup conflict may take years to accrue (increased reproductive success through access to territory) and go to all group members (including non-participants) while the costs are borne by the individual participants. In chimpanzees there is no evidence that non-participants are sanctioned or participants receive other benefits such as increased dominance rank. However, individuals that stand to benefit most provide the most effort: males with higher mating success (and thus more offspring to protect and feed) participate in boundary patrols more frequently (Watts and Mitani, 2001), and higher-ranking males travel further into potentially dangerous border regions (Wilson et al., 2012). Alternatively, group augmentation theory may explain chimpanzee participation in patrols with individuals bearing the costs of patrolling because doing so may lead to an increase in group size and reproductive fitness through delayed processes (Langergraber et al., 2017).

5.2. Evolutionary psychology approaches

Explanations that use behavioral ecology focus on fitness costs and benefits, rather than underlying psychological mechanisms. Researchers interested in the specific mechanisms contributing to intergroup conflict have proposed a suite of overlapping hypotheses. A comprehensive review is beyond the scope of this paper but we briefly outline some of the major theories. These hypotheses all share the assumption that selection pressures from intergroup conflict resulted in humans having basic psychological mechanisms that influence modern behavior but may be maladaptive today.

Tooby and Cosmides (1988) developed a “risk contract” theory of warfare that focuses on warfare as a coalitional endeavor requiring cooperation among participants. In order for male willingness to participate in coalitional warfare to have evolved, participants must be rewarded on the basis of the efforts and risks they take, while non-participants are punished or excluded. Provided the risk of death is randomly distributed and there is a high probability of success in warfare (low risk of death), then the decision to go to war will pay on average for members of the coalition. This will result in selection for a psychology for males to participate in coalitional aggression when success is anticipated to be likely. One implication of these ideas is that women warriors will be rare (as indeed they are) because they did not experience the same selective benefits for participating in coalitional aggression (Low, 1993).

Van der Dennen (1995) argued that the human pattern of warfare has a limiting set of preconditions that are only found in a few species including coalitions, territoriality, “Machiavellian intelligence, and ‘proto-ethnocentrism’ (van der Dennen, 1995; van Der Dennen, 2002). Because of these preconditions, only a few species are able to evolve coalitional intergroup aggression. Once these conditions are met, however, groups of males can use intergroup aggression and warfare as a facultative reproductive strategy. Warfare provides a way for males to improve their reproductive success through gaining access to resources (such as territory) that improve fitness and access to females themselves.

One of the best-supported hypotheses about the role of warfare in shaping human psychology is the male-warrior hypothesis (McDonald et al., 2012; Van Vugt, 2012). According to this hypothesis, men have psychological mechanisms that facilitate their ability to form coalitions for intergroup conflict against out-groups. Aggression against outgroups functions to protect or acquire reproductive opportunities (McDonald et al., 2012). The male warrior hypothesis makes a number of specific predictions about male psychology. For example, men will engage in greater discrimination and ethnocentrism than women, and they will be more severe against male outgroup members than female outgroup members. Compared to women, men should more easily reconcile following a conflict within the group, as has been found (Benenson and Wrangham, 2016). There are varying levels of support for these predictions but substantial evidence exists that men and women have different coalitional psychologies that appears to have resulted from intergroup aggression (McDonald et al., 2012).

There are several limitations to previous research on the evolutionary psychology of warfare. The majority of research has focused on the effects of warfare on male psychology because men are usually the direct participants but warfare imposes substantial fitness costs on women as well. This is in part because women are often the victims of attacks or taken captive creating fitness costs for them as well. As a result features of female psychology may represent adaptations in response to warfare, though this area of research has been largely neglected (Scalise Sugiyama, 2014).

5.3. Cultural incentive systems and sanctions

Several complementary approaches have focused on understanding the uniquely human aspects of warfare including how the collective action problem in war is solved by focusing on sanctions and incentives for participants. Warfare in small-scale societies creates a collective action problem because there is no formal enforcement to compel participation and prevent desertion during conflict, while warriors face the risk of being killed or injured. Further, many of the benefits from success in war (such as territory) are shared among the group, while the risk is borne by the individual. These explanations focus on how cultural traits can provide mechanisms to overcome the collective action problem inherent in warfare.

In most small-scale societies, warriors obtain private benefits from their participation that are mediated by culture and these can provide powerful incentives for participation (Gat, 2000). The “cultural war-risk” hypothesis posits that the additional risk-taking in human warfare is explained by individual-level private incentives that alter the payoffs from participating in risky combat (Goldschmidt, 1994; Wrangham and Glowacki, 2012). While all members of a successful group gain access to collective goods such as territory, through cultural institutions private incentives are available to those who participate in conflict. The types of incentives vary across cultures but commonly include status, increased reproductive opportunities, and allies. By altering the payoffs from participation in warfare, private incentives give warriors reason not to defect in spite of risks from conflict. While it is difficult to quantify relative risk and private incentives, cross-cultural data from hunter-gatherer and farming groups has been used to test this hypothesis. Using independent estimates of the relative riskiness of warfare, Glowacki and Wrangham (2013) found that cultural incentives for warriors are positively associated with increased risk-taking in warfare providing initial support for this hypothesis.

Several case studies have focused on specific pathways by which warriors may benefit reproductively. Chagnon (1988) compared the reproductive success of Yanomamö men who had participated in killing an enemy and received a title of *unokai* with non-*unokai* (men who had not participated in killing an enemy) finding that *unokai* had more wives and children than non-*unokai*. A recent analysis showed that the most likely pathway driving this association was that men used raiding as an opportunity to form strategic alliances with other men that they could leverage to obtain additional marriage partners (Macfarlan et al., 2014). Similarly, among pastoralists along the Ethiopian–South Sudanese border raiding over a lifetime

raiding was associated with having more wives and children. In this case, the pathway for increased reproductive success by raiding was through the acquisition of livestock that were then converted into bridewealth, allowing the raider to obtain additional marriage partners (Glowacki and Wrangham, 2015). These findings parallel research in contemporary societies showing that decorated soldiers have more children than other soldiers (Rusch et al., 2015).

Alongside incentive systems that promote participation in warfare through providing private benefits to warriors, sanctioning systems also serve to deter free-riding (Boyd et al., 2010; Boyd and Richerson, 1992). While many small-scale societies use gossip (Wiessner, 2005) and reputation (Macfarlan and Lyle, 2015) to encourage prosocial behavior, there has been little research on the use of sanctions in conflict. Mathew and Boyd (2011) conducted the first systematic assessment of the role of sanctions in solving the free-rider problem in small-scale conflict. Using data on defection in livestock raids among the pastoralist Turkana in Kenya, they found that sanctions involving gossip, deprivation of property, or physical beatings had a role in maintaining cooperation on raiding parties. They argue that such sanctions are crucial for maintaining cooperation in the face of risk of death on raids.

Cultural systems explanations for warfare that include positive incentives and sanctioning have attempted to explain the variation in severity of war as well as understanding how collective action in warfare is sustained. However, they have largely been silent on the causes of variation in cultural systems. If warfare creates group level benefits, why do some societies provide more incentives for warriors than others? Why do some societies handicap themselves, for instance, by not adopting common incentivizes for participation (such as through forbidding female or slave capture)? More systematic, comparative data is needed to answer these questions but there are few opportunities to collect such data.

5.4. Group selection and warfare

A central issue motivating the advances in evolutionary theory in the 1960s was skepticism towards group selection theory. Williams (1966) argued that selection acted mainly on the level of the gene, rather than the individual or the group. As discussed above, the theoretical insights resulting from taking the gene's-eye view of evolution proved inspirational for the founding of the evolutionary social sciences. More recently, however, group selection has experienced renewed interest concerning both genetic and cultural group selection. Enthusiasts of group selection have long focused on warfare, both because it provides a mechanism for group extinction, and because it involves potentially self-sacrificing behavior that seems difficult to explain through individual-level selection. Though this topic remains contentious, many evolutionary biologists consider it to be a largely semantic argument: “kin selection and new group selection are just different ways of conceptualizing the same evolutionary process. They are mathematically identical, and hence are both valid” (West et al., 2007).

5.5. Genetic group selection

In the current wave of enthusiasm for group selection, several research teams have proposed that group selection can explain the evolution of psychological traits such as heroism and bravery. These studies follow on Darwin's (1871) observation that tribes with courageous and helpful members would be more likely to win wars than tribes with cowardly and spiteful members. Choi and Bowles (2007), for example, used game-theoretical modeling and agent-based simulation to account for human propensity to sacrifice themselves on behalf of in-group members (altruism) and hostility towards outsiders (parochialism) showing that groups in which individuals were altruistic towards group members and hostile towards other groups would be more successful in war. Bowles (2009) used archaeological and ethnographic data from 23 societies to test the hypothesis that warfare may have contributed to the evolution of parochial altruism via group selection. His model focused on the extent of genetic differences between populations in conflict (winners and losers) and how an increasing number of in-group altruists would affect success in conflict. Using sources of mortality from warfare taken from archaeological sites and ethnographic societies, Bowles found that rates of death were consistent with a model in which warfare drove the evolution of altruism towards in-group members and hostility towards out-group members. These models have generated interest in the role of warfare in the evolution of prosocial emotions and the possibility of multi-level selection on human behavior. Group selection has been argued to be a mechanism by which humans may have evolved a psychology not just for parochial altruism but for warfare more specifically (Van Vugt, 2012).

Group selection arguments for the evolution of parochial altruism face challenges in explaining why an extraordinary degree of altruism would develop in humans but not in other species with similar levels of intergroup violence, such as chimpanzees, lions and wolves. Since rates of intergroup killing (Wrangham et al., 2006) and levels of genetic differentiation between subsistence-level groups appear similar between chimpanzees and human hunter-gatherers (Langergraber et al., 2011), intergroup killing alone seems insufficient to explain the extraordinary prevalence of prosocial behavior in human societies. Additionally, given that hunter-gatherers (like chimpanzees) seek out low-cost opportunities to kill enemies, it is not clear that extraordinary mechanisms are needed to explain participation in hunter-gatherer warfare. Finally, the occurrence of parochial altruism can in theory be explained as a result of social dynamics occurring entirely within groups, without the need to invoke warfare (Boehm, 2012).

5.6. Cultural group selection

The renewal of enthusiasm for group selection extends also to cultural group selection. In certain respects, cultural group selection may be a more plausible mechanism than genetic group selection, given the potential for massive horizontal transmission of cultural traits following the conquest and absorption of peoples. Whether “cultural group selection” is a helpful or confusing term for this process continues to be debated.

As social complexity increases, war practices among humans become more variable, more dangerous, and frequently involve larger groups sometimes including thousands of individuals. Cultural group selection arguments make the point that evolved psychological approaches to explain human warfare have difficulty accounting for the extreme variability in war practices, which range from low-risk raids to high-risk battles, and the maintenance of high-risk cooperation among large-parties of unrelated individuals (Zefferman and Mathew, 2015).

Cultural group selection models seek to solve these problems. Via cultural transmission, the traits of successful groups are copied within and between groups (Richerson et al., 2016; Zefferman and Mathew, 2015). Norms and behaviors surrounding warfare are modified in response to cultural pressures, such as the threat of conflict from other groups. Costly institutions for enforcing within-group cooperation (such as police and armed forces) and otherwise ensuring the smooth functioning of larger-scale societies (such as bureaucracies) may only emerge when they provide net benefits in competition among groups (Turchin et al., 2013). Cultural traits that impose substantial costs at the genetic and individual levels can nonetheless make groups more effective at intergroup competition.

Cumulative culture changes the dynamics for humans by creating essentially open-ended variation in the relative competitive ability of different societies. In chimpanzees, communities vary little in their competitive strategies. The outcome of intercommunity encounters depends mainly on demography and local ecology (i.e., whether current food availability permits individuals to travel in parties with many males): whichever side can recruit the most males to the melee wins. In contrast, in humans, even hunter-gatherers, substantial variation in intergroup competitive ability depends on cultural traits. Archaeology and history have chronicled repeated cases in which military innovations have enabled early adopters to sweep away their rivals and establish empires, including horses, chariots, crossbows, gunpowder weapons, and the like (Morris, 2014). In addition to weapons technology, social institutions, such as socialization for pugnacity, cultural rewards for warriors, and sanctions for defectors, can dramatically influence the relative competitive ability of societies.

Worldwide, humans increasingly live within densely urbanized societies, following ultra-social norms, interacting peacefully and trustingly with other citizens despite neither knowing them nor being closely related to them. To address the puzzle of how such large-scale societies emerged, Turchin et al. (2013) constructed an agent-based simulation focusing on cultural multilevel selection via the elimination of groups through warfare. They assumed that ultra-social norms are costly at the local level but beneficial at large-scales of social organization (such as the state); thus if groups break into smaller units they risk losing these ultra-social norms. They ran their model in a geographically explicit model of the Old World from 1,500 BCE to 1500 CE, and compared their results to a dataset of empires that actually emerged in the area. They found that costly social institutions spread with success in warfare. Innovations in war technologies diffused and intensified war; only societies that also evolved costly social institutions managed to survive and expand. Warfare, under this model, is responsible for the rise of complex societies, including the ultra-social norms that characterize our own. Thus, as with Darwin (1871) and Bowles (2009), they argued that within-group altruism is closely linked to inter-group hostility.

Despite the appeal of cultural group selection in accounting for the variability of human warfare, there is limited empirical evidence in support of it as a mechanism of cultural change. Among the few such empirical tests was one conducted by Soltis and colleagues (Soltis et al., 1995) who examined data from New Guinea on rates of group formation and extinction and between-group variation. They found that group selection was a plausible mechanism for rates of change on the order of 500–1000 years, but that different mechanisms were needed to explain cultural change that takes place on faster timescales. This raises the question: given that many documented cases of cultural evolution take place on a more rapid timescales, is cultural group selection generally too slow and weak to be a generally important mechanism? More such explicit, empirical tests of cultural group selection and alternative explanations are needed.

6. Discussion and future directions

Evolutionary anthropology has had success in explaining interspecific patterns of conflict among non-humans and hunter-gatherers, yet important challenges remain (Table 2). Substantial controversy still exists over the role of evolution in shaping a psychology for warfare (Lopez, 2016). Many anthropologists continue to argue that biology has little role, and instead view warfare as solely the product of culture. Thus one of the most important challenges remaining is to distinguish between features of human psychology that were selected for as a result of warfare and those that arise from the unique characteristics of modern social organization and culture.

The unique features of human warfare not found in other species, such as our increased risk-taking and ability to solve the high-risk collective action problem inherent in war, require better explanation. An emerging body of research has focused on within-group heterogeneity and leadership as a means to achieve collective action, especially in war (Gavrilets, 2015; Gavrilets and Fortunato, 2014; McAuliffe et al., 2015; Von Rueden et al., 2015). Recent empirical research in humans provides some support for these hypotheses. Using data on raiding party composition for pastoralists in Ethiopia, Glowacki et al. (2016) found that low-risk raiding parties depended on heterogeneity in social network structure with well-connected

Table 2

Main explanations for coalitionary intergroup aggression and war.

Hypothesis	Key Features and Predictions	Species/Population	References
Intergroup Dominance	Groups compete over key resources, access to which provides reproductive benefits. Aggression is commonly not lethal.	Group-living species where fitness depends on access to key resources. Includes many primates, social carnivores, and social insects;	Crofoot and Wrangham (2010); Wrangham (1999)
Imbalance of Power	Killings occur when numerical advantage enables attackers to kill at low cost to themselves	Species with fission-fusion grouping dynamics that create imbalances between groups. Includes humans, chimpanzees, bonobos, and wolves.	Manson and Wrangham (1991); Wrangham (1999); Wrangham and Glowacki (2012)
Evolved Psychology for War	Evolutionary history of intense intergroup aggression selected for psychological mechanisms such as parochial altruism and xenophobia	Humans and possibly chimpanzees where reproductive benefits from intergroup aggression primarily accrue to males.	McDonald et al. (2012); Tooby and Cosmides (1988); van der Dennen (1995); van Vugt (2009)
Cultural Incentives/Sanctions	Human patterns of warfare, especially risk-taking, require private incentives or sanctions to solve the collective action problem.	Humans. More common in cultures with greater risk-taking and elaborate cultural institutions and complex social organization.	Gat (2000); Glowacki and Wrangham (2013); Goldschmidt (1994); Mathew and Boyd (2011)
Cultural Group Selection	Variation in war practices reflects cultural group selection. Features of more successful groups spread within and between populations.	War practices will vary between populations. Warfare can enable the rise of ultrasocial norms and complex societies.	Zefferman and Mathew (2015); Turchin et al. (2013)
Genetic Group Selection	Groups that contain more individuals willing to behave altruistically towards in-group members, and act parochially towards out-group members may achieve greater success in warfare driving the evolution of human parochial altruism.	Species in which self-sacrificial behavior in war is associated with improved group outcomes.	(2009); Choi and Bowles (2007); Smirnov et al. (2007)

nodes serving a crucial function in initiating raids. Varying the social network properties including the number of initiators can create population-level effects contributing to the spread or decrease of conflict (Isakov et al., 2016). High-risk battles create a more severe collective action problem, depending upon leaders who take both greater organizational responsibility and greater risk than ordinary participants so much that dying in combat is a realistic possibility (Glowacki and von Rueden, 2015). These results are similar to research in chimpanzees showing a key role in collective hunting for a small number of “impact individuals” who appear to galvanize the group to hunt by taking more risky roles (Gilby et al., 2015). This emerging research suggests that important group-level behaviors can result from internal social dynamics rather than evolved species-level psychological propensities.

Going forward, given the increasing rise of decentralized conflicts, including terrorism, future research will identify correlates of individual and cultural variation seeking to understand the mechanisms that amplify and dampen conflict. Given the profound consequences intergroup conflict has on the world, few questions are more important.

6.1. The roots and future of war

As discussed above, anthropologists continue to debate whether war’s roots are deep – extending back millions of years to earlier species, perhaps as far back as the common ancestor of chimpanzees and humans – or shallow, extending back only 10,000 years or so. Resolving this debate is made challenging – and perhaps impossible – because of the sparse and fragmentary nature of the archaeological and paleoanthropological record, and the many ways in which contemporary hunter-gatherer societies have been impacted by powerful neighbors and invaders, including pastoralists, farmers, and states. For several commenters on war (Ferguson, 2011; Fry, 2006; Horgan, 2012; Sussman and Marshack, 2010), assessments of the evidence for war appear to be greatly influenced by the concern that a deep roots view of warfare has pernicious implications because it may be used to justify war and violence. In our view, however, there is no reason to see a “deep roots” view of warfare as pernicious, fatalistic or pessimistic. All manner of undesirable things have deep roots, and yet can be remedied by advancing our understanding of them. Our ancestors suffered from exposure to harsh weather conditions, predation, infectious disease, and food shortages. Despite the deep roots of such conditions, many people throughout the world now live in climate-controlled houses, encounter dangerous predators only in zoos and game reserves, and have access to modern medicine and reliable (even super-abundant) food supplies. Just because war is in some sense natural does not mean that it is good, justifiable, or inevitable.

Commentators on all sides of the debate recognize that war is ubiquitous in human history and occurs worldwide today, in a broad range of societies. This fact about the historical and contemporary world is true whether war has deep or shallow roots, whether war originated with some ancestor of both humans and chimpanzees, or more recently, after the lineages of humans and chimpanzees diverged, or whether war (in humans) is entirely the result of more recent cultural processes. Whether important components of war psychology are somehow in our genes or not, warfare is certainly present in a great

many of our societies. Nonetheless, despite the ubiquity of war, people have also discovered a number of mechanisms for making war less common and less destructive. Debate continues over the relative importance of different mechanisms, but researchers have variously found that warfare is less common among states that are democratic (Doyle, 1995; Hobson, 2011; Joas, 2012; Russett, 1993) and have economies that are market-based (de Soysa and Fjelde, 2010) and contract-intensive (Mousseau, 2013) and/or regularly trade with one another (Gelpi and Grieco, 2008). Nonetheless, while interstate war has become less common in many parts of the world, other regions, particularly sub-Saharan Africa through the Middle East and Central Asia, remain chronically prone to war and terrorism (Morris, 2014). Why regions vary in the frequency of warfare should be a central topic for a fully developed anthropology of warfare.

The debate between Rousseauans and Hobbesians, between Doves and Hawks, between those favoring shallow versus deep roots of war, hinges on the meaning attributed to key terms, including “adaptive,” “instinct,” and “innate.” Ferguson (2011), Fry (2006) and Horgan (2012) reject the proposition that warfare can be adaptive. We disagree with this view, but we also do not view warfare as something that is invariably adaptive. If by “adaptive” one means “a trait that, over average, promotes reproductive success,” then the degree to which war is adaptive clearly varies across different conditions. This is a separate question entirely from whether war is ‘an instinct’ or ‘innate,’ since complex traits can result not just from biological evolution, but also cultural evolution, or some combination of the two.

For example, Ferguson (2011) and Fry (2006) acknowledge that warfare is prevalent among pastoralists, mounted foragers (like American Indians of the North American Plains and the South American Pampas in the 19th Century), and sedentary societies with food storage (like Northwest Coast Indians). Why did such societies have war? Presumably because war was adaptive in that context: people who teamed up to take resources aggressively from others, and who collectively defended their own resources, did better than people and groups who did not fight.

Given that warfare is widespread in some societies, it is likely to be adaptive in those contexts—otherwise it would have ceased to exist. This argument does not require any differences in the genetic predispositions of people in war-like versus pacific societies. Instead, cultural traits, including social institutions such as warfare and the socialization of boys to be either warriors or peace-leaders, affect the survival and reproductive success of people adopting those cultural traits. If war tended to decrease the reproductive success of participants (and their close kin), war would become extinct. This would be the case whether war is the result of biological evolution, cultural evolution, or some mix of these.

War may be adaptive under some conditions, but not others. Under certain conditions, warfare clearly does not pay. Changes in political structure, economics, and technology have all reduced the payoffs for the small-scale warfare that once prevailed across much of the world. An important goal of the behavioral ecology of warfare would be to identify the conditions under which war does not pay, which could lead to efforts to expand those conditions.

Warring behavior clearly does not represent a single instinct, coded for by one or a few genes. Instead, war is likely an emergent property that results from people having a number of different evolved psychological predispositions. The precise set of such evolved psychological mechanisms remains to be determined, but may include tendencies towards xenophobia, parochial altruism, a desire for intergroup dominance, aptitude for numerical assessment, and a motivation to seek out low-cost opportunities to attack rivals.

Evidence from studies of the male warrior complex (McDonald et al., 2012) support the view that humans – and particularly men – have psychological adaptations specific to the context of war. It is also clear, however, that many aspects of war involve cultural evolution (Zefferman and Mathew, 2015). In humans, cultural evolution is rapid and has profound effects on societies (Richerson and Boyd, 2005). Even if such evolution is purely cultural, it still follows the basic rules of selection. As evolutionary game theorists have made clear, the success of any particular strategy depends on what strategies others are using. Accordingly, evolutionary studies of conflict have relied heavily on the game theory concept of the Evolutionarily Stable Strategy (ESS), a strategy that if adopted by a population cannot be invaded by another strategy (Maynard Smith, 1974). Whether a given strategy is an ESS does not depend on whether it is encoded in genes or cultural traditions. Strategies that promote their own replication become more common; strategies that impede their own replication become extinct. For example, the adoption of agriculture appears adaptive in some ecological contexts (e.g., where there is sufficient, reliable rainfall); agricultural populations thus have replaced hunter-gatherers throughout most of the well-watered parts of the world (Diamond and Bellwood, 2003). But in regions not suitable for agriculture, other subsistence strategies are more successful, such as pastoralism in drier grasslands and cold tundras. Agriculture is an ESS in well-watered landscapes; societies that don’t adopt it are quickly replaced by societies that do adopt it, once agricultural technology reaches an area. (To be really effective, agriculture might need additional help, such as effective rule of law, property rights, and protection from invaders and raiders (Bowles and Choi, 2013)). Nobody supposes that agriculture is a genetic adaptation in humans (though it does result in genetic evolution, such as lactase persistence). But it is adaptive in the sense that in appropriate ecological settings, people who adopt this strategy will outcompete people who don’t.

Similarly, warfare appears to be an ESS under a broad range of ecological conditions. The patterns of warfare in agricultural empires that emerged in different parts of the world (e.g., the Andes, Meso-America, China, Indus Valley, Mesopotamia, etc.) are strikingly similar. In our view, this reflects evolved psychological predispositions – for example, warriors are mainly men in all these societies. But even if we suppose these patterns are entirely the result of cultural evolution, warfare still appears to be an ESS under a wide range of conditions. If warfare were not adaptive as a cultural strategy, it would disappear. And indeed, under some conditions, warfare does disappear, as among tribes such as the Semai (Kelly, 2000), and among friendly neighboring nations, such as within the EU.

Part of the job of a state is to monopolize violence, pacifying the land within its boundaries, and pushing the zone of war out to the international borders. In regions of friendly nations, the zone of peace may be expanded further, as in much of Europe and the Americas. The success of peacemaking institutions gives hope that the zone of peace could one day encompass the entire planet.

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