Evolutionary Anthropology 24:50–61 (2015)

ARTICLE

An Evolutionary Theory of Large-Scale Human Warfare: Group-Structured Cultural Selection

MATTHEW R. ZEFFERMAN AND SARAH MATHEW

When humans wage war, it is not unusual for battlefields to be strewn with dead warriors. These warriors typically were men in their reproductive prime who, had they not died in battle, might have gone on to father more children. Typically, they are also genetically unrelated to one another. We know of no other animal species in which reproductively capable, genetically unrelated individuals risk their lives in this manner. Because the immense private costs borne by individual warriors create benefits that are shared widely by others in their group, warfare is a stark evolutionary puzzle that is difficult to explain. Although several scholars have posited models of the evolution of human warfare,[1–6] these models do not adequately explain how humans solve the problem of collective action in warfare at the evolutionarily novel scale of hundreds of genetically unrelated individuals. We propose that group-structured cultural selection explains this phenomenon.

What is meant by group-structured cultural selection? First, there is selection; that is, inherited variation in traits and their properties that influence their relative rates of inheritance. Second, these traits are transmitted culturally rather than genetically. That is, the traits are acquired, within or across generations, through social learning.[7] Third, the population is group-structured. A "group" is a subset of individuals in a larger population where interactions regarding the trait in question are different for individuals inside the subset than for individuals outside of it.[8] When warriors from one village recruit a war party to raid a neighboring village, an important group boundary occurs at the village level. Group-structured cultural selection has been referred to as cultural group selection[9] or cultural multilevel selection.[10] We avoid these terms because some scholars find them irredeemably confusing.[11,12]

We posit that the logic of group-structured cultural selection applies to most, if not all groups engaging in large-scale warfare, which we define as involving more than three dozen warriors engaging in combat with a substantial risk of being injured or killed. Alternate theories, such as mutualistic payoffs, costly signaling, cultural rewards, political centralization, and evolutionary mismatch, might be part of a broader explanation, but cannot explain large-scale human warfare without also taking group-structured cultural selection into account.

How does group-structured cultural selection overcome the collective action problem in warfare? Within a group, selection on genes should work against participation in warfare if it carries a high risk of serious injury or death. However, if more participation in warfare within a group increases the overall spread of the genes of group members, genes that favor participation in warfare might spread. For humans, genetic selection at the level of groups is weak because even a little gene flow between groups reduces between-group genetic variation to where it cannot overcome genetic selection against warfare within groups. However, if some process can maintain between-group behavioral variation despite migration, the strength of selection on groups becomes more important. Cultural transmission provides exactly that process.[9,13,14] If migrants learn locally relevant behavior from members of their new group, they will adopt locally prevalent behavior even though they are genetically unchanged. Therefore, migration need not erode between-group variation and, consequently cultural selection can be much stronger than genetic selection on group-beneficial traits such as warfare in a population of highly cultural organisms.

Group-structured cultural selection addresses another vexing empirical pattern that evolutionary theories have not yet tackled satisfactorily: Unlike intergroup violence among other animals, human warfare is extremely variable.

Matt Zefferman is a Postdoctoral Research Fellow at the National Institute for Mathematical and Biological Synthesis. His research focuses on cultural evolution and the origins of large-scale human political complexity.
Email: mrz1@nimbios.org

Sarah Mathew is Assistant Professor in the School of Human Evolution and Social Change at Arizona State University. Her research focuses on the evolutionary origins of large-scale cooperation in humans. She conducts field work among Turkana pastoralists in Kenya, examining how they solve the collective action problem in warfare.
Email: Sarah.Mathew@asu.edu

Key words: collective action; cooperation; lethal violence; norm psychology; peace

DOI: 10.1002/evan.21439
Published online in Wiley Online Library (wileyonlinelibrary.com).

Long before Mead[15] declared that "war is only an invention - not a biological necessity," anthropologists have disagreed on whether war or peace is the natural state of humankind.[16] Some scholars present evidence that prehistoric small-scale societies were predominantly warlike, suggesting that humans have an evolved predisposition for engaging in lethal intergroup violence.[6,17–20] Other scholars sharply disagree, citing numerous societies having little or no evidence of warfare.[21–23] Both sides can marshal ethnographic and archeological examples, and have for decades. However, neither side has adequately explained why there are some societies where peace prevails and others, such as communities among the Turkana, in which 50% of adult male mortality is due to warfare.[24]

We contend that the considerable variation in human warfare is best explained by a psychology that evolved for adopting local cultural norms—a "norm psychology."[25] Norm psychology helps create the necessary conditions for cultural selection in group-structured populations. There is variation in cultural norms and institutions between groups that causes variation in war success, and variation in war success leads to a differential spread of norms and institutions. Thus, both group-structured cultural selection and norm psychology are essential in explaining large-scale human warfare.

HUMAN WARFARE REQUIRES A NOVEL EVOLUTIONARY EXPLANATION

The scale and intensity of human warfare is evolutionarily novel. To illustrate, we contrast humans to two taxa that engage in lethal intergroup conflict that is often compared with ours: nonhuman primates, specifically chimpanzees, and social insects, particularly ants. Unlike chimpanzee coalitional violence, human warfare frequently occurs between large groups of unrelated individuals who are willing to undertake great personal risk. As opposed to intergroup conflict in social insects, which can rival that of humans' in scale, the vast majority of fellow combatants in large human groups are not close genetic kin.

Intergroup Violence in Chimpanzees and Argentine Ants

Chimpanzees, which are closely related to humans, are one of the few mammals that engage in lethal intergroup conflict, leading some researchers to suggest that war's origins predate our most recent common ancestor.[6,26] In a typical chimpanzee raid, a small patrol of males (median size of nine individuals, maximum observed size of 28) enters an area inhabited by a neighboring community.[27] They listen for their neighbors' calls and avoid confrontation with groups of a similar or larger size. Patrols attack and kill members of another group only when they have an overwhelming majority, typically greater than a four-to-one ratio.[26] With persistent raiding, a chimpanzee community can displace and take over some or all of the territory and resources of a neighboring community through attrition.[28]

Although chimpanzee raiding has similarities to small-scale raiding in humans,[26] there are notable differences. First, chimpanzee attackers assume little risk. In the recorded history of chimpanzee raids, no member of an attacking group has been killed or seriously injured.[26,28] Although, at all scales, warring human societies make tactical trade-offs between minimizing their casualties and obtaining military objectives, members of attacking groups, even in prestate human societies, suffer casualties.[18] Second, chimpanzees are patrilocal and raiding parties typically involve related males. Although it is unclear whether genetic relatedness suffices to explain chimpanzee raiding behavior,[29] a dozen chimpanzee males from one community are much more genetically related than hundreds of human warriors drawn from several communities.

Unlike chimpanzees, certain species of eusocial insects rival humans in the scale of their intergroup conflicts. A well-studied example is *Linepithema humile*, the Argentine ant. In many ant species, queens leave their natal nest, mate, and begin new colonies some distance away. However, both male and female Argentine ants mate in or near their natal colonies, building up local genetic relatedness and allowing the ants to form "supercolonies" from multiple nests of closely related queens. Supercolonies are large, spanning approximately a hectare, with individuals in one supercolony being more genetically related to one another than to individuals in neighboring supercolonies. Consequently, there is frequent conflict between supercolonies, with multiple nests from a supercolony joining together in battle.

When Argentine ants invaded the Mediterranean climates of North America, Europe, South Africa, and Australia, supercolony sizes were unconstrained by conflict with unrelated neighbors and, as a result, grew much larger than those in Argentina. Although ants from different nests within a supercolony do not fight among themselves, wherever a supercolony encounters another, the scale and lethality of their conflicts is massive. Near San Diego, California, a battle between two supercolonies claims the lives of approximately 30 million ants annually.[30]

Argentine ants fight on a much larger scale and take far greater risks than do chimpanzees because colony members are close genetic relatives. Not only are the thousands of workers in a nest the offspring of a single queen, but the queens within a supercolony are closely related. Conflict arises where there is a discontinuity in genetic relatedness.

Turkana Raiding: A Case Study

Warfare among the Turkana, a pastoral society in northwest Kenya, illustrates some key differences between human warfare and the warfare of chimpanzees or ants. When the Turkana mobilize to raid livestock from neighboring ethnic groups, their war parties have, on

average, more than 300 men.[24] These men are not close associates; instead, they are drawn from many subsections of Turkana society, including, on average, four settlements and three territorial sections. Their mean genetic relatedness is much lower than for raiding chimpanzees; each warrior has, on average, only four of his close kin participating. Warriors risk serious injury and death. One percent of combatants are killed per raid and 50% of the males who survive to adulthood die in warfare. Fifty-four percent of the male deaths in warfare occurred when the Turkana launched raids against other groups; 46% occurred when Turkana settlements were attacked by other groups. Thus, even in egalitarian and uncentralized societies, warriors take substantive risks in large-scale, lethal warfare with groups of genetically distant cocombatants.

If not at the scale of genetic relatedness, at what scale do Turkana wage war? The cooperative unit in Turkana warfare appears to be the cultural, in this case ethnolinguistic, group, encompassing nearly one million people. Mathew and Boyd[24] asked participants from one Turkana territorial section, the Kwatela, their opinions of Kwatela warriors in one of two scenarios. In one scenario, Kwatela warriors raid and steal cows from the neighboring Turkana territorial section, the Lukumong, and drive them back to Kwatela land. In the other scenario, Kwatela warriors raid and steal cows from a neighboring non-Turkana tribe, the Toposa, and drive them back to Kwatela land. Strikingly, even though the Kwatela, who number several thousand people, benefit in both scenarios, participants had extremely different reactions to the warriors' actions. They felt that the warriors who raided Lukumong cattle were very wrong, deserved sanctions, and were undeserving of their help. In contrast, the warriors who raided Toposa cattle were praiseworthy and deserving of help. Thus, Turkana norms discourage warfare within culturally similar groups and promote warfare between culturally dissimilar groups. Consistent with these sentiments, when Turkana raid other Turkana in commercial cattle raids or banditry, these raiders are considered criminals, not good warriors.[31] Mortality patterns show that the norm forbidding warriors to raid other Turkana has a large effect on how Turkana men live and die — 50% of adult Turkana male deaths are the result of interethnic warfare, whereas only 1% are from intra-Turkana lethal violence.[24]

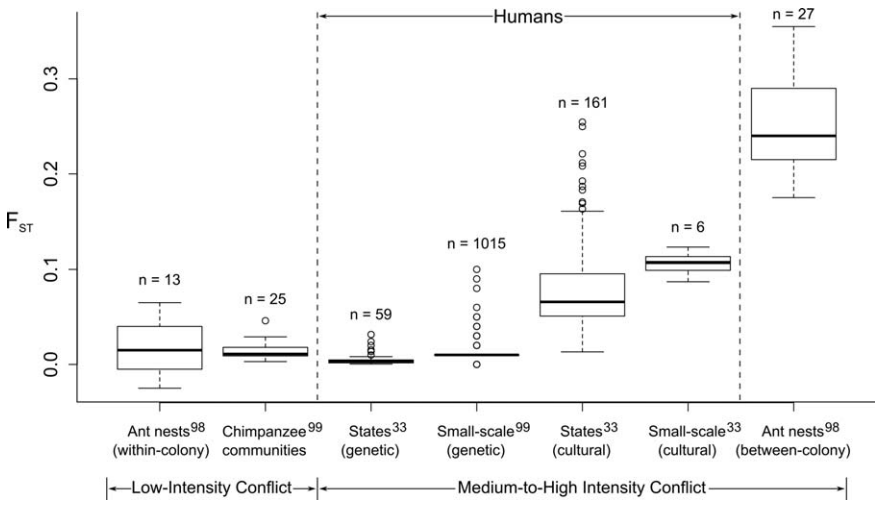

Figure 1. Human genetic F_{ST} between neighboring groups for both small- and large-scale societies is similar to that for chimpanzee communities and within-supercolony Argentine ant nests, whereas human cultural F_{ST} is similar to that for between-supercolony Argentine ant nests. Within-supercolony Argentine ant nests do not engage in conflict and chimpanzees take little risk, suggesting that human genetic F_{ST} is not high enough to support the scale and intensity of human conflict. Argentine ants do engage in large-scale high-risk conflict between supercolonies, suggesting that human cultural variation is more likely to support large-scale human conflict than genetic variation. Data are from Bell, Richerson, and McElreath,[33] Tsutsui and Case,[99] and Langergraber, Schubert, and Rowney.[100]

The Scale of Genetic and Cultural Variation

Whereas chimpanzees and Argentine ants fight at discontinuities in genetic variation, humans, like the Turkana, seem to fight at discontinuities in cultural variation. Mathematical models suggest that a useful measurement of variance between groups is the ratio of between-group variability in traits to the total population variability (F_{ST}). In these models, the higher a population's F_{ST} the higher the cost that individuals bear in intergroup conflict.[9,32] When groups compete for resources, high genetic F_{ST} promotes genetic predisposition for intergroup conflict because these genes become concentrated in specific groups and spread disproportionately as these groups win resources. Similarly, a high cultural F_{ST} promotes cultural predisposition for warfare because, as cultural norms and institutions are concentrated in specific groups they will spread disproportionately as these groups win resources.

We can compare F_{ST} measures across taxa to see how human genetic and cultural F_{ST} compare to those of chimpanzees and Argentine ants. Figure 1 illustrates that human genetic F_{ST} between neighboring pairs of small-scale societies and neighboring pairs of modern countries has the same order of magnitude as that in chimpanzee communities, where chimpanzees take little risk, and that in Argentine ant nests from the same supercolony, where individual ants do not fight one another. This suggests that the genetic variation between any of these human groups is insufficient to generate high-risk, large-scale warfare. However, human cultural F_{ST}, in both modern small-scale societies

and states, approaches the same order of magnitude as genetic F_{ST} for Argentine ants between different supercolonies, which also engage in large-scale intergroup conflicts. Although the techniques for estimating cultural F_{ST} are relatively new and our ability to precisely compare cultural to genetic F_{ST} is an open question, the order-of-magnitude difference between cultural and genetic F_{ST} in humans indicates that cultural inheritance has a potentially greater scope to support large-scale warfare than genetic inheritance.[33]

Gene-based models cannot account for intergroup violence at the scale on which humans fight. In battles and wars involving hundreds to millions of participants, there is simply not enough genetic relatedness among co-combatants to motivate nontrivial risk-taking. Computer and mathematical modeling indicate that genetic variation can support warfare only when group sizes are limited to a few dozen individuals.[2,4,32] Cultural variation more plausibly supports between-group warfare than does genetic variation in humans.

NORM PSYCHOLOGY EXPLAINS VARIATION IN WAR

There is stunning variation across human societies in the prevalence, mode, and scale of warfare. This variation is not adequately explained by either a genetically evolved "war psychology," a motivational system evolved specifically to predispose individuals toward lethal collective violence against out-groups, or a genetically evolved "peace psychology" that predisposes individuals toward not making war. Instead, this variation is better explained by a genetically evolved "norm psychology," or the propensity to recognize and adopt the cultural norms of one's local group.[25] The norm psychology hypothesis for warfare does not require that warfare be intense, persistent, universal, or even common. Norms for war and peace vary within and across societies; they change in response to internal cultural dynamics, strategic action by neighboring groups, resource availability, unification of warring groups, and random factors. Consequently, a genetically evolved norm psychology allows individuals to adapt to this wide variety of local conditions instead of being behaviorally constrained in a single way of war.

We do not think that a genetically evolved norm psychology is incompatible with a genetically evolved propensity to war or a genetically evolved propensity to peace, only that it better explains variation in modes of human warfare. If primordial propensities for war or peace exist, they seem to be quite readily overwhelmed by local cultural norms, making their adaptive importance unclear. Norm psychology also better explains how the collective action problem in large-scale warfare is solved. Without norms for participation in warfare, enforced by norms of rewarding bravery and punishing cowardice, the adaptive behavior for individuals would be to free-ride on others' participation in large-scale combat.

An alternative hypothesis might be that between-society variation in warfare can be explained by noncultural phenotypic plasticity evolved to elicit particular responses to local ecological conditions. However, this hypothesis does not fully account for variation in warfare because societies that live in similar ecological conditions differ in how they wage war. Also, the prevalence and intensity of warfare within a society can change drastically without corresponding changes in the local ecology.

The Existence of War Varies Across Societies

Some scholars have posited that war was a nearly universal fact of human history.[6,18–20] However, although warfare is practiced by numerous societies, it is not universal. In modern ethnographic surveys, researchers have found that approximately 15% of societies have engaged in warfare only rarely or never.[34–36] An analysis of 31 purely hunter-gatherer subsistence societies found that 10% of them had rarely or never engaged in warfare.[37] Excluding horse-mounted and complex hunter-gather societies, two of 16 societies, the !Kung and Pekangekum, had experienced no warfare in the 50 years before the ethnographic present. This finding includes interpersonal revenge killings and thus may overestimate the prevalence of group-level warfare.[22] Otterbein's cross-cultural survey found that 10% of societies rarely or never engage in warfare; four of these, the Copper Eskimo, Todas, Tikopia, and Dorobo, did not have any level of military organization.[34] In both an analysis of 90 small-scale societies from the Ethnographic Atlas[31] and a comparison of 157 North American cultural units,[36] approximately 15% of the societies rarely or never experienced war. Independently, Fry compiled a list of over 70 nonwarring societies.[22] Even in societies where it has not existed for decades, war can start quickly, without a corresponding change in ecological conditions.

The Mode of Warfare Varies Across Societies

Some researchers have argued that small-scale raiding in decentralized societies follows a typical pattern, specifically one similar to intergroup aggression in chimpanzees. That is, males form small raiding parties and ambush members of other groups while successfully avoiding serious harm to themselves.[6,26] But the mode of combat in warfare, even in politically uncentralized societies, is extremely variable. In Otterbein's analysis of decentralized societies[34] two-thirds of them had hierarchical military organization; a third did not. In societies with military organization, approximately 20% never used a surprise attack strategy. Half of the societies with military organization used surprise attacks exclusively. Otherwise, warriors met and fought in the open. Even among societies with ambush strategies, the tactics varied. Some societies used the "trap" method, in which attackers lie in wait along a trail; others used the "surround" method, with attackers surrounding enemy campsites before attacking. Societies also varied in what fate they meted out to the defeated.[18,34] Some allowed

enemies to surrender, either taking them as captives or freeing them to pay tribute. Others, such as the Iroquois of North America and the Tupi of South America, tortured, killed, and/or ritually sacrificed defeated enemies. For the Shawnee and Fox of North America and the Nuer in East Africa, captured males who withstood torture became family members of victors who had lost men in the fight.

There is little uniformity in the way that attacking parties treated women[34]. Some societies, such as the Tuareg of Sahara and Kapauku of New Guinea, had norms against attacking women; other societies had norms for killing every member of a defeated group regardless of age or gender; still others captured and incorporated females from the losing group.

In most societies, all men participated in combat. In 12% of societies, however, not all able-bodied men joined in combat.[34] In contrast to chimpanzees, the historical record also contains examples of societies that incorporated female warriors.[38] A key characteristic of human warfare is that, unlike chimpanzee intergroup violence, its mode is highly variable.

The Scale of Warfare Varies Across Societies

Humans are the only species in which the size of war parties can range from a few dozen warriors to millions of soldiers living hundreds of miles apart. Among the Yanomamo, egalitarian horticulturalists in the Amazon, raids occur between patrilocal villages of approximately 200 people.[39] Among the Mae Enga, egalitarian horticulturalists of New Guinea, warfare occurs among clans, with clans of the same tribe sometimes forming alliances against clans from other tribes.[40] Hundreds of warriors from several allied clans sometimes join forces to wage ceremonial low-stakes battle against opposing clans. A clan may also undertake lethal raids in which they aim to kill, evict, and destroy another clan. In several East African pastoral groups, large-scale military action occurs between tribes involving thousands of individuals who share an ethnolinguistic identity. For example, in retaliation for an earlier attack, hundreds of warriors from three different territorial sections of the Nyangatom tribe of Ethiopia destroyed a village of the Kara tribe, killing 104 Kara people.[41] Warfare between large territorial states can occur on the scale of millions of people. One engagement alone, the Battle of Stalingrad, involved more than 1.7 million soldiers and resulted in more than 2 million military and civilian casualties.

A Norm Psychology Explains Variation

Given the great variation across human societies in the prevalence, mode, and scale of war, a norm psychology is better suited for individuals than a war psychology or a peace psychology. A norm psychology allows individuals to quickly acquire the appropriate behavior during wartime or peacetime, coordinate with group members on common tactics for fighting wars, and recognize what constitutes the in-group and out-group, which varies substantially between different societies.

A key characteristic of human warfare is that, unlike chimpanzee intergroup violence, its mode is highly variable.

An alternate hypothesis is that variation between societies results from genetically evolved phenotypic plasticity whereby different behavioral strategies are elicited as individual responses to local ecological conditions. However, a society's mode of warfare can change quickly without a corresponding change in ecological conditions. For example, substantial changes have occurred during cultural contact, as ideas and information about warfare spread from one group to another, as in the much-discussed shifts in patterns of warfare among Native American groups after European contact.[42,43]

Another example is the famously peaceful Semai of the Malay Peninsula, who learned to kill from British officers.[18] While the amount of "blood drunkness" felt by the Semai may be overstated,[44] they experienced rapid change as cultural norms of intergroup violence were transmitted to them, not by changes in the local ecology, but by British officers.

Societies that expand and occupy the environments of defeated groups do not shift to the warfare behavior of the defeated group, which is what would occur if ecological conditions elicited the behaviors pertaining to warfare. The Nuer expansion into Dinka territory illustrates this. The Nuer had different war practices and continued to use them even as they began inhabiting Dinka territory.[45,46]

WARFARE MEETS THE CONDITIONS FOR GROUP-STRUCTURED CULTURAL SELECTION

Human warfare meets the two necessary and sufficient conditions for group-structured cultural selection: Variation in cultural traits between groups influences the outcome of warfare and the outcome of warfare influences the spread of these cultural traits. Because both conditions are necessary, group-structured cultural selection is not equivalent to the less restrictive condition that behaviors related to warfare are cultural. To illustrate this difference, consider the Turkana's acquisition of firearms from neighboring groups like the Dodos and Toposa in the 1970s. Individual Turkana herders switched from spears to firearms to better protect their cattle and settlements during attacks. This switch does not require group-structured cultural selection as an explanation because the trait (firearms) could spread to the Turkana regardless of whether the

groups from which they adopted firearms were successful.

In contrast, group-structured cultural selection is important when group-beneficial traits are costly for an individual to adopt. For instance, if only one Turkana adopted punishment norms for motivating warriors not to be cowards, the punisher would be at a disadvantage relative to other group members. Group-structured cultural selection can, however, increase costly punishment norms if they make groups more successful. This occurs if successful groups expand territorially, grow by attracting migrants or absorbing defeated people, or if they impose their cultural trait on other societies. Alternately, a society as a whole, or its leaders, can decide to adopt the traits of the successful societies.

Group-structured cultural selection also does not depend on how novel traits arise. It describes only the evolutionary dynamics of preexisting traits. Novel ideas, norms, and technology likely originate from a complex suite of innovations and inventions, as well as the fusing of military traditions, ecological variation, and the biases of individual soldiers and warriors. Group-structured cultural selection also does not require that cultural traits persist over many generations or that cultural traditions are deep-rooted in time. Because cultural transmission is not bound by the vertical transmission rules of genetic inheritance, a cultural norm can arise and spread horizontally in a single generation.

How Variation in Cultural Traits Influences War Success

We divide cultural traits that influence war outcomes into three categories. The first category includes advances in technology, tactics, and military organization that directly influence war outcomes. For example, a group with a longer-range bow or a stealthier submarine may be at a decisive military advantage. But technologies can be copied once they have proven their worth in battle, as indicated by the rapid spread of European firearms in the Americas.[47] Therefore, as long as groups have similar abilities to adopt the new technologies, group success due to variance in technological innovation is likely fleeting. In fact, the first group to develop a new technology can be at a disadvantage if other groups free-ride off the innovation costs.[48] However technological variation between groups can be maintained when there are barriers to copying or trade between groups. For example, lack of access to resources may have limited the spread of spears made with stingray spines by the Yir Yoront of Australia.[49]

The second category of traits that influence war's outcome is solidaristic behavior.[50] Cultural norms of cooperation and sacrifice, together with systems of rewards and sanctions that reinforce these behaviors, will increase a group's success in war. The Turkana punish desertion and cowardice with criticism, corporal punishment, and fines.[24] Cowards are more likely to be denied help at a time of need and they are admonished and taught by their age mates about how to become a good warrior.[51] Modern militaries that foster the solidaristic behavior of small-scale societies are more successful. The German army, estimated to have had the highest unit effectiveness in WWII, formed units of soldiers from the same hometown to maximize unit cohesion.[52] In the American Civil War, soldiers serving in more geographically homogeneous units were more effective and less likely to desert than were soldiers serving in geographically heterogeneous units.[53] In both the German and Union cases, military units deployed and were replaced as coherent wholes. In contrast, in Vietnam American soldiers were deployed as individuals and there was little time for them to form solidaristic bonds before battle. This partially accounted for the weak unit cohesion of American military units.[54]

The third category of traits includes those governing political and economic organization. Variation in economic and political organization can indirectly drive group-structured cultural selection through warfare. Agriculturalists can create greater stockpiles of food than herders and thus can feed large standing armies. Differences in the social organization and bride-price systems between Nuer and Dinka societies enabled the Nuer to mobilize larger war parties.[45] Nuer tribes were more likely to defeat Dinka and absorb them into Nuer society, spreading Nuer social organization and bride-price systems. In tenth- and eleventh-century Europe, a new style of economic organization, the territorial state, replaced an amalgamation of feudal kingdoms, city-states, and empires in part because territorial states were better able to raise capital for military engagements.[55,56]

War Success Influences the Spread of Cultural Traits

Success in warfare influences the spread of cultural traits through multiple mechanisms that may operate simultaneously. One mechanism is the selective retention of groups, which occurs when militarily successful groups, either through decisive victory or attrition, kill the members of a less successful group, thus wiping it out. The ethnographic and historical record of New Guinea is one context in which this mechanism can be observed. Small, isolated groups were frequently at war, creating ideal conditions for rapid group formation and extinction to occur. But measurements of the actual extinction rate of groups here suggest that it would require 500-1,000 years for group-beneficial traits to spread.[57] It seems that the selective retention of groups might be important in small-scale societies over long periods of time, but is likely unimportant either in small-scale societies over short period of time or in large-scale societies over any time period.

A more important mechanism for cultural selection in large-scale societies is the absorption of members of a losing group by a winning group. Successful empires, such as the Romans, annexed entire polities after defeating them in battle. Members of these polities, often beginning with the local elite, eventually became

culturally assimilated into the rest of the empire.[58]

Military success leads to the spread of cultural traits when territorial expansion increases the carrying capacity and, thereby, the population size of the winning group. Two centuries ago, the Turkana were part of a small cultural complex in eastern Uganda referred to as the proto-Karimojong group.[59] Today they occupy an area close to 100,000 square kilometers in northwest Kenya and have a population close to one million. The Turkana came to occupy much of their current territory through successful cattle raids. Although livestock is the immediately apparent benefit of cattle raids, large-scale raids by Turkana led to noticeable expansion of their territory, as members of attacked settlements retreated from areas that the Turkana subsequently occupied.

Group-structured cultural selection can also occur through selective emulation, whereby groups copy the norms or institutions of a militarily successful group. Selective emulation can operate quickly because the emulating group need not experience defeat firsthand.[60] If one group defeats another in battle, a third group can observe the results and adopt the traits of the winners. This type of selective emulation is evidenced by the "Westernization" of the Japanese military during the Meiji restoration. In less than two decades, the Japanese sought out the world's most militarily successful nations and imported their military organization and tactics wholesale.[61] After identifying the British Navy and French Army as the most successful in the world, they sent Japanese officers to train in those countries and enlisted British sailors and French soldiers to "Europeanize" Japanese military institutions. However, after France's defeat in the Franco-Prussian war, Japan quickly switched to patterning its army after that of the Prussians.

Military success leads to differential spread of cultural traits through selective recruitment, which can be either coercive or voluntary. Recruitment differs from absorption in that it occurs by obtaining individuals instead of annexing entire groups. For instance, the Comanche raided neighboring Native American groups, such as the Apache, and took women and children as slaves. Depending on these slaves' age and gender, they were integrated into Comanche society and, after a generation, become no different from non-slave Comanche. Raiding helped the Comanche not only to expand their empire through the exploitation of slave labor, but also served to replace the portion of the Comanche population lost to disease or armed conflict.[62]

Voluntary recruitment can occur when individuals choose to join more successful groups.[63] It is unclear how important success in warfare is to voluntary recruitment in small-scale societies, since immigration is often constrained by ethnic identities that can be especially salient in times of war. However, this "bandwagonning" can be important in large-scale conflicts when combatants compete for recruits from neutral parties with flexible identities.[64]

The mechanisms we describe are not mutually exclusive. For example, during the Nuer-Dinka raids, the Nuer enjoyed a four-fold increase in territory at the Dinka's expense.[45] Victorious Nuer raiding parties often stayed on land from which the Dinka fled and based their next military campaign from the new territory, allowing deeper forays into Dinka land. Dinka settlements were also burned and destroyed by the Nuer. The Dinka subsequently experienced food shortages and famine. Dinka women and boys were frequently taken captive and incorporated into Nuer society.[45,46] The Nuer also recruited Dinka brides by offering higher bride wealth than their competing Dinka suitors.

We have described mechanisms whereby variation in cultural traits can lead to variation in war outcomes, and mechanisms by which military success can lead to the spread of the winning group's cultural traits. These mechanisms, in any combination, are necessary and sufficient conditions for group-structured cultural selection.

THE INADEQUACY OF ALTERNATIVE MODELS OF HUMAN WARFARE

Although scholars from the social and evolutionary sciences have proposed explanations for human warfare, none have adequately explained both how the collective action problem of large-scale warfare is overcome and the variability in human warfare.

Alignment of Individual and Group Interests

Some scholars have posited models of warfare in which individual and group interests are sufficiently aligned that cultural norms or institutions are not needed to motivate combatants. Defection is not a problem in these models because the direct benefits of participating in warfare outweigh its direct costs.

It is tempting to deem raiding for loot as a situation in which group and individual interests are aligned. In one model, a successful group gains enough reproduction-enhancing resources from raiding that a participating raider has higher reproductive success than a non-raider.[4] However, a closer inspection of raiding behavior indicates that individual and group interests are not sufficiently aligned to adequately motivate combatants.

First, even in raiding, cowardice can result in higher relative returns than bravery. For example, in Turkana cattle raids, some men can lag behind until after their opponents are overcome, participating fully only when it is time to drive the cattle. Their net gains will be higher than those of braver warriors who have been killed, injured, or distracted by fighting. Thus, in the absence of second-order cultural institutions of punishment and social sanctions, shirkers would be more successful than full participants.

Second, many rewards of victory, such as territorial expansion, deterrence, protection of property, and territorial expansion, are nonexcludable; for instance, in the wars of the Wappo, a hunter-gatherer group in California, against the Pomo, the

Pomo abandoned border territory, allowing the Wappo to expand their territory and enjoy a larger buffer zone that protected them from attacks[18] Wars of revenge may also have nonexcludable benefits. As Wiessner and Tumu note,[40] the Mae Enga consider failure to take revenge to be a sign of weakness. A clan with the reputation of retaliating against enemies who attack them is less likely to be attacked than are other clans.[40]

Third, if warriors require persuasion to participate in combat, it shows that the incentive to participate is not entirely provided by war's direct material benefits. In one well-documented case of warfare, Chagnon[39] reported that great effort was spent to prevent Yanomamo warriors from turning back once a raiding party had departed. There are similar social pressures on Dodoth warriors[65] and Turkana.[24] If mutualism explains warfare, there should be no need for such extensive persuasion.

Costly Signaling

One reason why a person may behave altruistically is because such acts are honest, costly signals of having an underlying desirable quality.[66,67] If so, altruistic acts can evolve through direct fitness benefits. Costly signaling, which has been proposed to explain large-game hunting[68,69] and heroism,[70] is consistent with Chagnon's controversial finding that Yanomamo warriors who have killed more enemies have higher reproductive success.[1] However, costly signaling can stabilize any signal when the marginal cost of producing the signal is lower for higher-quality individuals and the recipient benefits from pairing with higher-quality individuals. Given the set of all possible costly signals, those that are most likely to be selected for will have high broadcast efficiency.[67–69] Costly signaling plausibly explains why males hunt large game and share conspicuously: Such sharing is both readily observable to other group members and readily attributable to a single individual.

However, bravery in warfare is not as easily attributed to the individual. Offensive warfare is a joint venture, often occurring out of sight of the signal recipients. Consider raiders who have gone into enemy territory and return after a few days with loot.[45] The cost of their contribution to the public good — how bravely they fought — occurred far from signal observers. When the raiders return, the information about who was brave and who was a coward is impossible for those who stayed home to reconstruct unless that information is conveyed by the raiders themselves. However, in the costly signaling payoff scenario, returning warriors are rivals competing for access to signal recipients and will be tempted to distort information about themselves and others who were part of the raiding party. The classic literature on signaling suggests that under such conditions, signal recipients will evolve to ignore the signal.[71]

The sentiments toward cowards in Turkana raids further challenge the costly signaling hypothesis.[51] The Turkana believe it is wrong to lag behind others and not fire one's weapon, but they do not negatively judge an unskilled warrior who tries, suggesting that free-riding, not an evaluation of underlying skill, is key. Furthermore, warriors who are reproductive rivals criticize, advise, coax, and discipline cowards with the goal of correcting their behavior. This behavior would be surprising if an individual's bravery relative to that of others was key to reproductive success. Finally, this cajoling indicates that private gains from signaling are not sufficient to make warriors undertake the desirable level of risk for the success of the raiding party.

The costly signaling model works better if it is embedded in group-structured cultural selection. If members of different groups coordinate on different costly signals, group-structured cultural selection should preferentially select for signals that are group-beneficial.[67] Group-structured cultural selection might also help solve the second-order collective action problem of misinforming signal recipients about one's own exploits and those of others.

Exogenous Institutions

Other proximate hypotheses presuppose the existence of institutions that constrain individual choice. Recent examples include the "cultural rewards war-risk hypothesis," which suggests that humans participate in warfare because they are likely to be rewarded by members of their group, and the "punitive sanctions hypothesis," which suggests that humans participate in warfare because they are otherwise likely to be punished by members of their group.[3,72] Rewards might include increased status, material wealth, or access to mates. Punishment might include decreased status, physical beatings, social sanctions, banishment, or death. If the rewards or punishment are sufficiently high, they may motivate participation in warfare by offsetting the individual's cost of fighting.

Institutions of rewards and punishment are important proximate explanations for human warfare in many groups. However, the hypotheses of cultural rewards war-risk and punitive sanctions are incomplete in that they do not explain the existence of the institutions of reward and punishment. Both rewarding participants and punishing shirkers in war is costly; this cost must be paid by members of a warrior's group. Thus, in attempting to resolve the collective-action problem of participation in warfare, these models create either the collective-action problem of cultural rewards or that of social sanctioning, which are so-called "second-order" dilemmas of collective action. A recent attempt to solve second-order punishment posits that punishment pays for itself by allowing cooperators to extract resources from free-riders.[73] This argument does not adequately address the second-order problem because it assumes that only cooperators are capable of forcibly extracting resources from other individuals. Second-order and n^{th}-order collective action problems can, however, be

solved by group-structured cultural selection.[9,74]

Centralized Political Institutions

It seems obvious to some that either centralized political institutions or contact with societies having centralized political institutions explains large-scale warfare. However, as we have described, politically decentralized societies like the Turkana are fully capable of coordinating large-scale warfare. Archeological and ethnographic records also indicate that war occurs in numerous societies without formal centralized political institutions.[17–19] Warfare has been documented among horticulturalists of New Guinea,[40] East African herders,[31,46,65,75] agriculturalists in Africa,[76] Plains Indians of North America,[77] and hunter-horticulturalists in South America.[78] Lethal warfare occurred before agriculture, sedentary living, or Western contact, as shown by the oral histories of many cultures,[40,76,79] the remains of fortified settlements,[80,81] a 500-person massacre in pre-Columbian North America,[82] a 12-14,000-year-old mass burial in the Sudan,[83] and a trophy head collection at a Mesolithic hunter-gatherer site in Germany.[84]

Ethnographic and early historical evidence of warfare demonstrate that hunter-gatherer societies could engage in large-scale warfare.[85,86] A large-scale battle over water wells occurred between the Walbiri and Waringari, egalitarian mobile hunter-gatherers of the central Australian desert.[87] Lethal intercommunity raiding was common among the Murngin, sedentary hunter-gatherers in northern Australia, whose population of 3,000, over 20 years, sustained 100–200 deaths.[88] In one incident, approximately 100 people were killed by a warrior party of 50–60 men.[89] The Unangan, complex sedentary hunter-gatherer of the Aleutian islands waged war on the neighboring Kodiak. Ethnographic and oral historical accounts have described raiding parties of 200 and 340 warriors at the time of European contact. One raid the Unangan made on the Alutiiq resulted in five Unangan men being killed, indicating that members of the offensive party assumed substantial risks too, unlike in chimpanzee raids.[90]

Even in modern states,coercive institutions typically are not soldiers' primary motivation for fighting. During World War II, for example, more than 140,000 of United States service members died in combat, but of 20,000 deserters only one was executed — the only U.S. service member executed for desertion since the Civil War. Cohesion within small units is the more important motivation especially if there is an effort to ensure within-unit cultural similarity.[91] Toward the end of World War II, Japanese troops not only engaged in suicide attacks using aircraft, small boats, and human torpedoes, but also committed suicide to avoid capture. The massive 4,000-person suicide charge at Saipan was carried out only after the Japanese commanding officers had committed suicide, leaving no one with the coercive authority to punish those that would surrender.[92] The Japanese soldiers' sacrifice resulted from a mix of nationalism and small-unit cohesion, not coercion from centralized political institutions. Centralized political institutions are not a necessary or sufficient condition for warfare because decentralized societies fight wars, and coercion is rarely the primary motivating factor, even in politically centralized societies.

Evolutionary Mismatch

Evolutionary mismatch hypotheses posit that the psychological mechanisms that motivate humans to fight evolved genetically in small-scale human societies and "misfire" in a modern context. In small-scale societies, if group members were primarily genetic kin, individuals would have evolved a psychology to participate in warfare to increase their inclusive fitness.[5] In addition, if fellow combatants were familiar individuals who were likely to interact with one another again, they would evolve a psychology motivating them to cooperate to maintain their reputation as cooperators within the community.[93] Although, in the past, these mechanisms conferred genetic fitness benefits, they are maladaptive in modern contexts in which we regularly interact with nonkin and strangers because they do not increase our genetic fitness.[93]

Choi and Bowles[2,32] have developed theoretical models in which psychological mechanisms, parochialism, and altruism evolve genetically through lethal conflict between groups of agents. They suggest that these mechanisms might underlie the evolutionary origins of human warfare. However, in these models parochial altruism evolves only when groups are small (and, therefore, mostly close genetic kin) and group extinction rates are high (maximizing the cost of losing a conflict). As group size increases to more than a few dozen individuals, warfare disappears. In these models, because genetic predispositions for warfare are selected against, no "evolutionary mismatch" evolves as group size increases.

Another problem for the evolutionary mismatch hypothesis is evidence against the premise that foragers lived in bands of close kin. Data from two contemporary hunter-gather societies, the Ju/Hoansi and Ache, show that approximately three-quarters of a band are not close genetic kin.[94] Turkana live in settlements that disperse and regroup seasonally, like hunter-gatherer bands. If they had a psychology cued to band-like groups, we would expect the Turkana to cooperate on the scale of a settlement. Turkana warriors report that in large-scale raids with participants coming from different settlements, age groups, and territories, there are some participants they know, but many others they do not.[24]

Even if warfare did evolve through genetic kin selection in small forager bands, mismatch models do not explain how mechanisms that evolved for cooperation in small bands would be misapplied to large groups, particularly because people are capable of discriminating kin from nonkin and transient interactions from reputationally

consequential interactions.[25] We suggest that to explain the transition from low-risk, small-scale territorial raiding to high-risk, large-scale warfare, we must recognize that humans evolved for living with group-structured cultural norms and institutions.

OPEN QUESTIONS

The Extent of Gene-Culture Coevolution

Group-structured cultural selection and norm psychology seem necessary to explain the scale and intensity of human warfare, but are they sufficient? Might there have been feedback between human genes and culture that led to a coevolved war psychology — a motivational system that facilitates cooperation with members of our cultural group specifically in the context of warfare? A coevolved war psychology might have occurred if warfare was consistently maintained by group-structured cultural selection for large periods of our evolutionary history.[95] But evidence of these conditions is mixed.

The archeological record does not provide much evidence of warfare in Pleistocene forager societies. Outside of the Gebel Sahaba Paleolithic cemetery in Sudan, dated 10,000–12,000 BC,[83] there is no strong evidence of intergroup conflict until the Mesolithic period (approximately 10,000 BC) in Europe and the Near East.[21] While several ethnographically known hunter-gatherer groups engaged in warfare, it is difficult to assess whether such warfare was persistent enough over the course of human evolution to generate a genetically evolved predisposition toward acquiring norms for making war.

The archeological record suggests that warfare became widespread over a brief period in the early Neolithic. There is evidence that many human genes underwent rapid selection around this time, although the functions of these genes remain unknown.[96] Although this period also coincided with the spread of other cultural innovations, including agriculture, it is possible that some of this selection may have favored alleles that predisposed humans to participate in warfare with other cultural group members. Empirical studies to assess the existence of a culturally mediated war psychology would have to show that local norms regarding warfare are learned and put into practice with relative ease compared to norms that regulate novel aspects of social life for which humans are unlikely to have a dedicated psychology.

Warfare at Scales Other Than That of Cultural Variation

The group-structured cultural selection hypothesis is most clearly applicable to large-scale warfare. Whether stealth-raiding in small-scale societies can be explained without group-structured cultural selection and norm psychology is an open question. Warriors in small-scale raiding are more likely to be kin or close associates and the mode of stealth raiding, with a few warriors ambushing opponents with little risk of injury or death, is fairly similar across societies.[17,72] Better measures of genetic and cultural variation and the costs of combat in small scale societies might resolve this issue.

A coevolved war psychology might have occurred if warfare was consistently maintained by group-structured cultural selection for large periods of our evolutionary history.

Our hypothesis best applies to warfare between groups that vary in norms and institutions, such as different ethno-linguistic groups or states. However cross-cultural analyses show that some societies engage in internal warfare, in which seemingly culturally similar units, such as clans or the residents of territories within an ethnic group, wage war against one another.[34,37] However, there are few measures comparing cultural similarity within and between the warring parties. It is unknown whether these groups would, given the opportunity, prefer waging war against more culturally dissimilar groups.

Our view is that several factors determine the costs and benefits of warfare at different scales. There are many reasons to wage war on neighboring settlements that are culturally similar: Conflicts are most likely to arise among people who interact frequently and share resources. Nonmobile people with land will benefit most from acquiring additional territory adjacent to their own; captured women from culturally similar groups may be preferred as wives; and captives who know the local ecology and subsistence mode might make more productive slaves. There is less cost involved in traveling to the next village than to a faraway foreign territory. Moreover, mechanisms that solve collective action problems at small scales compete with group-structured cultural selection. There is a correlation between patrilocal residence and internal warfare, suggesting that in societies where related males live together they will fight culturally similar but unrelated individuals.[37] It is surprising that internal warfare is not the *de-facto* state of warfare, and it requires an explanation.

Alliances and peace-making institutions between ethnic groups do occur. The Comanche had a sophisticated foreign policy in which some groups were enemies and others allies.[62] The California Indians were notable for being relatively peaceable.[97] The Northern Shoshone were allied with the Bannock in their long-running conflicts with the Blackfeet, whereas the Blackfeet were allied with other tribes. The Southwestern Pueblos maintained a tight alliance against raiding by hunter-gather tribes and Spanish, Mexican, and American domination. Although the literature on ethnocentrism suggests that ethnic groups

dislike one another, the facts suggest that different ethnic groups have a wide range of attitudes toward one another; ethnic boundaries may also be peaceable.[98] Furthermore, if gene-culture co-evolution has acted on a norm psychology rather than a "war psychology," people may be motivated to converge on norms and institutional arrangements such as alliances and peace treaties, which would aid the success of their cultural group via war or peace.

CONCLUSION

We have outlined a group-structured cultural selection theory of warfare with five arguments. First, although genetic selection might plausibly explain the scale and intensity of intergroup conflict in nonhuman species, human warfare, in which potentially large numbers of genetically unrelated individuals participate and risk their lives, requires a different explanation. Second, centralized political institutions and genetic selection alone cannot explain large-scale warfare because noncentralized groups, such as the Turkana, engage in warfare on scales than cannot be explained by genes alone. Third, there is substantial variation between groups in the existence, mode, and scale of warfare; this is best explained by a genetically evolved norm psychology rather than either a war psychology or a peace psychology. Fourth, human warfare meets the minimally sufficient conditions for group-structured cultural selection: Existing cultural variation between groups influences war outcomes, and war outcomes influence the differential spread of cultural traits. Fifth, competing models of the origins of human warfare are, by themselves, inadequate to explain human warfare without the addition of group-structured cultural selection. We conclude by offering a challenge to future research in this area: Given that group-structured cultural selection is necessary to explain human warfare, what additional processes, including patterns of gene-culture coevolution, underlie its origins and development?

ACKNOWLEDGMENTS

We thank Peter Richerson, Richard McElreath, Kyle Joyce, Emily Zefferman, and our anonymous reviewers for their comments on earlier drafts of this manuscript. This work was funded, in part, by a block grant from the University of California, Davis, Graduate Group in Ecology and partly done at NIMBioS, sponsored by the NSF and the U.S. Departments of Homeland Security and Agriculture through NSF Awards EF-0832858 and DBI-1300426, with additional support from the University of Tennessee.

REFERENCES

1 Chagnon N. 1988. Life histories, blood revenge and warfare in a tribal population. Science 239:985–992.

2 Choi JK, Bowles S. 2007. The coevolution of parochial altruism and war. Science 318:636–640.

3 Glowacki L,Wrangham R. 2013. The role of rewards in motivating participation in simple warfare. Hum Nat 24:444–460.

4 Lehmann L, Feldman M. 2008. War and the evolution of belligerence and bravery. Proc R Soc B 275:2877–2885.

5 Tooby J, Cosmides L. 2010. Groups in mind: the coalitional roots of war and morality. In: Høgh-Olesenn H, editor. Human morality and sociality: evolutionary and comparative perspectives. New York: Palgrave MacMillan Press. p 91–234.

6 Wrangham R, Peterson D. 1996. Demonic males: apes and the origins of human violence. New York: Houghton Mifflin Harcourt.

7 Boyd R, Richerson P. 1985. Culture and the evolutionary process. Chicago: University of Chicago Press.

8 Sober E, Wilson D. 1999. Unto others: the evolution and psychology of unselfish behavior. Cambridge: Harvard University Press. p 92–98.

9 Henrich J. 2004. Cultural group selection, coevolutionary processes and large-scale cooperation. J Econ Behav Org 53:3–35.

10 Turchin P, Currie T, Turner E, et al. 2013. War, space, and the evolution of Old World complex societies. Proc Natl Acad Sci 110: 16384–16389.

11 West S, Griffin A, Gardner A. 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. J Evol Biol 20:415–432.

12 van der Dennen, JMG. 1995. The origin of war. San Rafael: Origin Press.

13 Boyd R, Richerson P. 2010. Transmission coupling mechanisms: cultural group selection. Philos Trans R Soc B 365:3787–3795.

14 Richerson P, Baldini R, Bell A, et al. n. d. Cultural group selection plays an essential role in explaining human cooperation: a sketch of the evidence. Behav Brain Sci. In press.

15 Mead M. 1940. Warfare is only an invention - not a biological necessity. Asia 40:402–405.

16 Crook P. 1994. Darwinism, war and history. Cambridge: Cambridge University Press.

17 Gat A. 2006. War in human civilization. Oxford: Oxford University Press.

18 Keeley L. 1996. War before civilization: the myth of the peaceful savage. Oxford: Oxford University Press.

19 LeBlanc S, Register K. 2003. Constant battles: why we fight. New York: Macmillan.

20 Smith DL. 2009. The most dangerous animal: human nature and the origins of war. New York: Macmillan.

21 Ferguson RB. 2013. The prehistory of war and peace in Europe and the Near East. In: Fry DP,editor. War, peace, and human nature: the convergence of evolutionary and cultural views. Oxford: Oxford University Press. p 191–240.

22 Fry D. 2007. Beyond war: the human potential for peace. Oxford: Oxford University Press.

23 Fry D, Söderberg P. 2013. Lethal aggression in mobile forager bands and implications for the origins of war. Science 341:270–273.

24 Mathew S, Boyd R. 2011. Punishment sustains large-scale cooperation in prestate warfare. Proc Natl Acad Sci USA 108:1091–6490.

25 Chudek M, Henrich J. 2011. Culture-gene coevolution, norm-psychology and the emergence of human prosociality. Trends Cogn Sci 15:218–226.

26 Wrangham R. 1999. Evolution of coalitionary killing. Am J Phys Anthropol 110:1–30.

27 Wilson M, Boesch C, Fruth B, et al. 2014. Lethal aggression in Pan is better explained by adaptive strategies than human impacts. Nature 513:414–417.

28 Mitani J, Watts D, Amsler S. 2010. Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. Curr Biol 20:R507–R508.

29 Wilson M, Hauser M, Wrangham R. 2001. Does participation in intergroup conflict depend on numerical assessment, range location, or rank in wild chimpanzees? Anim Behav 61:1203–1216.

30 Thomas M, Payne-Makrisa C, Suarez A, et al. 2006. When supercolonies collide: territorial aggression in an invasive and unicolonial social insect. Mol Ecol 15:4303–4315.

31 McCabe J, Terrence J. 2004. Cattle bring us to our enemies: Turkana ecology, politics, and raiding in a disequilibrium system. Ann Arbor: University of Michigan Press.

32 Bowles S. 2009. Did warfare among ancestral hunter-gatherers affect the evolution of human social behaviors? Science 324:1293–1298.

33 Bell A, Richerson P, McElreath R. 2009. Culture rather than genes provides greater scope for the evolution of large-scale human prosociality. Proc Natl Acad Sci USA 106: 17671–17674.

34 Otterbein K. 1985. The evolution of war: a cross-cultural study. New Haven: HRAF Press.

35 Ross M. 1983. Political decision making and conflict: additional cross-cultural codes and scales. Ethnology 22:169–92.

36 Jorgensen J. 1980. Western Indians. Freeman Press.

37 Ember C, Ember M. 1992. Resource unpredictability, mistrust and war: A cross-cultural study. J Conflict Resolution 36:242–262.

38 Goldstein J. 2001. War and gender. Cambridge: Cambridge University Press.

39 Chagnon N. 1983. Yanomamo: the fierce people, 3rd ed. Holt, Rinehart and Winston.

40 Wiessner P, Tumu A. 1998. Historical vines: Enga networks of exchange, ritual and warfare in Papua, New Guinea. Washington DC: Smithsonian Institute Press.

41 Tornay S. 1979. Armed conflicts in the lower Omo Valley, 1970–1976: an analysis from within Nyangatom society. Osaka: Senri Ethnological Studies National Museum of Ethnology. p 97–117.

42 Secoy F. 1953. Changing military patterns of the Great Plains Indians. Lincoln: University of Nebraska Press.

43 Ross JB. 1984. Effects of contact on revenge hostilities among the Achuara Jivaro. In: Ferguson RB, editor. Warfare, culture, and environment. Orlando: Academic Press. p 83–109.

44 Robarchek C, Dentan R. 1987. Blood drunkenness and the bloodthirsty Semai. Am Anthropol 89:356–365.

45 Kelly R. 1985. The Nuer conquest: the structure and development of an expansionist system. Ann Arbor: University of Michigan Press.

46 Evans-Pritchard E. 1940. The Nuer: a description of the modes of livelihood and political institutions of a Nilotic people. Oxford: Oxford University Press.

47 Worcester D, Schilz T. 1984. The spread of firearms among the Indians on the Anglo-French frontiers. Am Indian Q 8:103–115.

48 Horowitz M. 2010. The diffusion of military power. Princeton: Princeton University Press.

49 Sharp L. 1952. Steel axes for stone-age Australians. Hum Org11:17–22.

50 Turchin P. 2003. Historical dynamics: why states rise and fall. Princeton: Princeton University Press.

51 Mathew S, Boyd R. 2014. The cost of cowardice: punitive sentiments towards free riders in Turkana raids. Evol Hum Behav 35:58–64.

52 Richerson P, Boyd R. 1999. Complex societies: the evolutionary origins of a crude superorganism. Hum Nat 10:253–289.

53 Costa D, Kahn M. 2008. Heroes and cowards: the social face of war. Princeton: Princeton University Press.

54 Gabriel R, Savage P. 1978. Crisis in command: mismanagement in the army. New York: Hill and Wang.

55 Tilly C. 1992. Coercion, capital and European states. Hoboken: Wiley-Blackwell.

56 Spruyt H. 1996. The sovereign state and its competitors. Princeton: Princeton University Press.

57 Soltis J, Boyd R, Richerson P. 1995. Can group-functional behaviors evolve by cultural group selection? Curr Anthropol 36:473–494.

58 MacMullen R. 2008. Romanization in the time of Augustus. New Haven: Yale University Press.

59 Gulliver PH. 1966. The family herds: a study of two pastoral tribes in East Africa: The Jie and Turkana. London: Routeledge.

60 Farrell T, Terriff T. 2002. The sources of military change. In: Farrell T, Terriff T, editors. The sources of military change. Boulder: Lynne Rienner. p 3–20.

61 Westney DE. 1987. Imitation and innovation: the transfer of Western organizational patterns to Meiji, Japan. Cambridge: Harvard University Press.

62 Hämäläinen P. 2008. The Comanche empire. New Haven: Yale University Press.

63 Boyd R, Richerson P. 2009. Voting with your feet: payoff biased migration and the evolution of group beneficial behavior. J Theor Biol 257:331–339.

64 Kalyvas S. 2008. Ethnic defection in civil war. Comp Pol Stud 41:1043–1068.

65 Thomas E. 1981. Warrior herdsmen. New York: Norton.

66 Zahavi A. 1977. The cost of honesty (further remarks on the handicap principle). J Theor Biol 67:603–605.

67 Gintis H, Smith EA, Bowles S. 2001. Costly signaling and cooperation. J Theor Biol 213: 103–119.

68 Hawkes K, Bird RB. 2002. Showing off, handicap signaling, and the evolution of men's work. Evol Anthropol 11:58–67.

69 Smith EA, Bird RB. 2000. Turtle hunting and tombstone opening: public generosity as costly signaling. Evol Hum Behav 21:245–261.

70 Iredale W, Vugt MV, Dunbar R. 2008. Showing off in humans: male generosity as a mating signal. Evol Psychol 6:386–392.

71 Smith JM, Harper D. 2003. Animal signals. New York: Oxford University Press.

72 Wrangham R, Glowacki L. 2012. Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers. Hum Nat 23:5–29.

73 Okada D, Bingham P. 2008. Human uniqueness-self-interest and social cooperation. J Theor Biol 253:261–270.

74 Henrich J, Boyd R. 2001. Why people punish defectors: weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas. J Theor Biol 208:79–89.

75 Fukui K, Turton D. 1979. Warfare among East African herders. Osaka: National Museum of Ethnology.

76 Fadiman J. 1982. An oral history of tribal warfare: the Meru of Mt. Kenya. Athens: Ohio University Press.

77 Willey P. 1990. Prehistoric warfare on the Great Plains. New York: Garland

78 Patton J. 2000. Reciprocal altruism and warfare: a case from the Ecuadorian Amazon. In: Cronk L, Chagnon N, and Irons W, editors. Adaptation and human behavior: an anthropological perspective. New York: Aldine Transaction. p 417–436.

79 Lamphear J. 1976. The traditional history of the Jie of Uganda. Oxford: Clarendon Press.

80 Lambert P. 2002. The archaeology of war: a North American perspective. J Archaeol Res 10: 207–241.

81 Bamforth, D. 1994. Indigenous people, indigenous violence: precontact warfare on the North American Great Plains. Man 29:95–115.

82 Gregg J, Zimmerman L. 1986. Malnutrition in fourteenth century South Dakota: osteopathological manifestation. N Am Archaeol 7:191–214.

83 Wendorf F. 1968. Site 117: a Nubian final Paleolithic graveyard near Jenel Sahaba, Sudan. In: Wendorf F, editor. The prehistory of Nubia, Vol 2. Dallas: Southern Methodist University Press. p 954–995.

84 Frayer D. 1997. Ofnet: evidence for a Mesolithic massacre. In: Martin DL, Frayer DW, editors. Troubled times: violence and warfare in the past. Oxford: Gordon and Breach. p 181–216.

85 Wheeler G. 1910. The tribe and intertribal relations in Australia.London: Murray.

86 Morgan J. 1980. The life and adventures of William Buckley. Canberra: Australian National University Press.

87 Meggitt M. 1962. Desert people. Sydney: Angus and Robertson.

88 Warner WL. 1930. Murngin warfare. Oceania 1:457–494.

89 Strehlow T. 1970. Geography and the totemic landscape in central Australia: a functional study. In: Berndt RM, editor. Australian aboriginal anthropology: modern studies in the social anthropology of the Australian aborigines. Crawley: University of Western Australia Press. p 92–140.

90 Maschner H, Katherine RM. 1998. Raid, retreat, defend (repeat): the archaeology and ethnohistory of warfare on the North Pacific. J Anthropol Archaeol 17:19–51.

91 Shils E, Janowitz M. 1948. Cohesion and disintegration in the Wehrmacht in World War II. Public Opin Q 12:280–315.

92 Reiter D. 2007. Nationalism and military effectiveness: post-Meiji Japan. In: Brooks R, Stanley E, editors. Creating military power: the sources of military effectiveness. Stanford: Stanford University Press. p 28–54.

93 Krasnow M, Cosmides L, Pederson E, et al. 2012. What are punishment and reputation for? PLoS One 7:e45662.

94 Hill K, Walker R, Boievi M, et al. 2011. Co-residence patterns in hunter-gatherer societies show unique human social structure. Science 331:1286–1289.

95 Richerson P, Boyd R. 2001. The evolution of subjective commitment to groups: a tribal instincts hypothesis. In: Nesse RM, editor. The evolution of commitment. New York: Russell Sage. p 186–220.

96 Richerson P, Boyd R, Henrich J. 2010. Gene-culture coevolution in the age of genomics. Proc Natl Acad Sci USA 107:8985–8992.

97 Sturtevant W, Washburn W, editors. 1988. Handbook of North American Indians: history of Indian-white relations, Vol. 4. Washington DC: Government Printing Office.

98 Fearon J, Laitin D. 1996. Explaining interethnic cooperation. Am Political Sci Rev 90: 715–735.

99 Tsutsui N, Case T. 2001. Population genetics and colony structure of the Argentine ant (*Linepithema humile*) in its native and introduced ranges. Evolution 55:976–985.

100 Langergraber K, Schubert G, Rowney C, et al. 2011. Genetic differentiation and the evolution of cooperation in chimpanzees and humans. Proc R Soc B 278:2546–2552.