The controversial origins of war and peace: apes, foragers, and human evolution

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Abstract

The role of warfare in human evolution is among the most contentious topics in the evolutionary sciences. The debate is especially heated because many assume that whether our evolutionary ancestors were peaceful or warlike has important implications for modern human nature. One side argues that warfare has a deep evolutionary history, possible dating to the last common ancestor of bonobos, chimpanzees, and humans, while the other views war as a recent innovation, primarily developing with the rise of sedentism and agriculture. I show that although both positions have some support warranting consideration, each sometimes ignores uncertainties about human evolution and simplifies the complex reality of hunter-gatherer worlds. Many characterizations about the evolution of war are partial truths. Bonobos and chimpanzees provide important insights relevant for understanding the origins of war, but using either species as a model for human evolution has important limitations. Hunter-gatherers often had war, but like humans everywhere, our ancestors likely had a range of relationships depending on the context, including cooperative intergroup affiliation. Taken together, the evidence strongly suggests that small-scale warfare is part of our evolutionary history predating agriculture and sedentism, but that cooperation across group boundaries is also part our evolutionary legacy.

1. INTRODUCTION

The debate about the origins of war shows no signs of abating. Researchers on both sides draw on observations of non-human species and hunter-gatherers when debating the evolutionary significance of warfare. Those arguing that war has deep evolutionary roots, possibly extending prior to the origin of our species and even genus (*deep rooters*) point to the fact that many social species, including our close relatives the chimpanzees, have lethal intergroup violence that resembles war. Alternatively, those who maintain that war is a recent development in humans (*shallow rooters*) take the presence of intergroup cooperation and lack of lethal intergroup killings among bonobos as support for a peaceful human ancestor. Deep rooters often look at the extensive occurrence of war among ethnographically documented hunter-gatherers as evidence that war was present in our evolutionary history, while shallow rooters point to the fact that war appears non-existent among some foragers and appears to increase with hierarchy and monopolizable resources. These two examples—the strikingly different behavior of chimpanzees from that of bonobos, and variation in the behavior of hunter-gatherers—illustrate a common trend in the debate about the origins of war: There is often empirical support for both views that needs to be taken seriously, but that each side tends to overlook or dismiss.

The role of warfare in human evolution is among the most contentious topics in the evolutionary sciences. Many believe that the question of whether war was a selective feature in human evolution matters because the answer reveals something critical about human nature, including whether our species is doomed to war. Perhaps because of the importance of this question, the debate has become entrenched, with both sides sometimes overlooking competing evidence, or, in some cases relying on incorrect empirical claims, mischaracterizations of competing positions, and even personal attacks.

In what follows, I focus on the most debated claims made to advance deep or shallow roots perspectives and provide evidence about each claim allowing the reader to evaluate them more critically. Taken together, I hope this approach illustrates that our evolutionary history is more complex than one of selection for war *or* peace; rather, it reflects the complicated lifeways of a highly social and interdependent

cultural species for which both cooperation and war were likely important selective forces.

1.1. What is war?

How we define war determines what we count as evidence for the origins of war. If our definition of war is derived from contemporary human war, sometimes called "war above the military horizon" and defined as requiring centralized leadership, chains of command, advanced material technology (e.g., fortifications or weapons), a high mortality rate, or conflict between unrelated groups (Turney-High 1949), then war is something that our pre-human ancestors are unlikely to have been capable of producing. A definition of war that requires behaviors only recent humans can produce is of little use in evaluating when war emerged evolutionarily or if it occurs in other species.

To study the evolution of a trait, (e.g., war, friendship, social structure, pair-bonds, etc.) evolutionary scholars take care to focus on behavioral characteristics that can be generalizable across multiple species. For war, the most salient characteristic is "*intergroup coalitionary killings*". Groups can be communities, clans, bands, political units, states, or even families. Accordingly, war as defined as *intergroup coalitionary killings* may involve but does not require weapons, fortifications, or multiple victims. This definition is also silent about the motivations; war can be motivated by revenge, dominance seeking, or competition for resources or mates. Intergroup coalitionary killing only requires that individuals as part of or supported by a coalition attempt to attack and kill members of other social groups. Some species of ants, as well as meerkats, banded mongoose, wolves, chimpanzees, and humans all sometimes engage in killing members of other groups as part of a coalition. They may do so with teeth, claws, pinchers, hands, and fists, or, in the case of humans, with simple technologies such as stones or spears, or complex technologies such specialized weapons and structures such as fortifications.

1.2. Approaches to studying the evolution of war.

For species that have intergroup coalitionary killings, we can ask when and why they evolved this capability (just as we can ask why pair bonds, food sharing, mate guarding, or dyadic aggression evolved). Deep rooters typically use one or both of two different evolutionary approaches to understanding the origin of intergroup coalitionary killing: The first, a *phylogenetic approach*, focuses on whether closely related species share a trait, taking shared traits as evidence for a common evolutionary origin from which the trait was inherited. For humans, we may look to our closest relatives, the bonobos and chimpanzees, for evidence that a trait was shared with our ape ancestors, or we may look at all the great apes, all primates, or even all mammals to see how deep in our evolutionary history a trait extends. For example, our great ape relatives the gorillas, chimpanzees, and bonobos are all quadrupedal, while humans are bipedal. This is strong phylogenetic evidence that the last common ancestor of humans, gorillas, chimpanzees, and bonobos was also quadrupedal and that bipedalism evolved sometime after humans split off from the last common ancestor shared with any of these species.

The second approach is *adaptive,* which focuses on identifying the selective pressures that gave rise to a trait and the conditions in which it evolved. For bipedalism in humans, for example, adaptive approaches seek to identify that ecological and social conditions that would have favored a transition to upright walking (such as longer day ranges) and then identify when in our evolutionary history this occurred (such as through analyzing paleoanthropological skeletons). Adaptive approaches often compare across species that share the trait to identify the conditions in which the trait emerges and to assess the associated costs and benefits of it. This is an especially powerful method for revealing the role that social or ecological factors have. For instance, if humans share important traits with bonobos (such as strong female alliances) or chimpanzees (such as high rates of fission-fusion), and these plausibly influence intergroup coalitionary killing, then the shared commonalities may help us understand the conditions which may have favored the evolution of war or peace in our species' history.

In taking an adaptive approach, we often ask whether there are positive fitness consequences for success in that behavior in evolutionarily relevant contexts, i.e., does success in the activity result in producing more offspring through direct or inclusive fitness compared to alternative strategies? If the answer is yes—intergroup coalitionary killing reproductively benefits participants overall compared to alternative strategies, and that occurred over evolutionary time scales—then it becomes possible that lethal intergroup killing (or any other behavior) was a selective force in the evolution of that species. Over evolutionary time scales this would have resulted in an evolved psychology and biology that is predisposed to form and use coalitions for strategic violence when conditions are appropriate.

War does not require a high death rate to be important evolutionarily. Just as predation on a species may be infrequent yet still be a strong selective force, intergroup coalitionary killing can be occasional or even rare and be an important evolutionary factor in shaping a species. Thus, findings that chimpanzee or human communities may go years without lethal raids, or that the rates of death from within-group violence is more than between-group violence, or that there are important ecological co-variates of war in themselves do not reveal anything about the selective importance of war.

In contrast, the perspective most shallow rooters take is that war is a *by-product* of other traits, such as novel social conditions such as greater population density, new forms of social organization, or increased intelligence (Kelly 2000; Kelly 2005; Roscoe 2007). On this approach, traits may arise due to unique ecological or social conditions rather than being evolutionarily inherited from an ancestral species or being adaptations that provide benefits. Many shallow rooters argue that war is not the result of either an adaptation for coalitionary violence or inherited from an ancestor, but rather arose recently in our history when our species faced novel conditions.

2. CONTROVERSIES ON THE EVOLUTION OF WAR

In what follows, I critically evaluate the most controversial claims about the evolution of war. Many of these claims contain important observations that may help us understand the origins of war, but warrant further scrutiny. The primary debate is about whether humans have evolved adaptations for intergroup coalitionary killing. Is this capability something that was adaptive and selected for in our species or in an ancestral species that we inherited it from? Shallow rooters argue no, war is a recent development in our species and a by-product; they argue our species has likely lacked war since the last common ancestor of bonobos, chimpanzees, and humans (Figure 1A). Deep rooters argue that intergroup coalitionary killings have a deep evolutionary history but differ in whether they think it was inherited from a chimp-like last common ancestor (Figure 1B) or evolved more recently sometime after the split with *Pan* perhaps sometime in the genus *Homo*.

In what follows I argue that the strong version of the both the deep and shallow roots position, that humans inherited war or peace from the last common ancestor of bonobos, chimpanzees, and humans is weakly supported. Despite the lack of strong evidence for inheriting war or peace from our distant ancestor with bonobos and chimpanzees, there is better evidence that war and intergroup cooperation are both part of our evolutionary history likely since at least the beginnings of our species *Homo sapiens*.

2.1: Was the last common ancestor of humans, chimpanzees, and bonobos like chimpanzees or bonobos?

Scholars often look to bonobos and chimpanzees to understand the origins of human behavior. Both species are the closest living relatives of humans and equally related to us, having shared a last common ancestor or *LCA* 6-9 million years ago (Almécija et al. 2021). The presence or absence of a trait shared between humans and bonobos or humans and chimpanzees is often taken as evidence for that trait's

presence deep in our evolutionary history (Wood 2010). But because bonobos and chimpanzees have radically different social behaviors, scholars typically argue that *either* bonobos or chimpanzees are a better model for the ancestral species of humans. Thus, if one takes chimpanzees as a better model of the last common ancestor (LCA) of the genus *Homo* and *Pan*, the fact that both chimpanzees and humans have intergroup killings is seen as evidence that the last common ancestor of humans, chimpanzees, and bonobos also had intergroup killings. Then during the intervening 6-9 million years, bonobos lost intergroup coalitionary killings. On this account, war among contemporary humans results from our evolutionary inheritance from the last common ancestor of chimpanzees, bonobos, and humans. Similarly, if bonobos are deemed a better model for the LCA, then the fact that bonobos lack lethal raiding and have intergroup cooperation is taken as support for the claim that the origins of human peace lie in our bonobo-like last common ancestor (Figure 1A).

There is little consensus on whether chimpanzees (Muller, Wrangham, and Pilbeam 2017; Pilbeam and Lieberman 2017; Wrangham 2023; Wrangham and Pilbeam 2001) or bonobos (Diogo, Molnar, and Wood 2017; Kano 1992; Zihlman et al. 1978) are a better model for the last common ancestor. Moreover, many scholars argue that the last common ancestral species was substantially different from any of the three species today so using either bonobos or chimpanzees as a model of LCA behavior is of limited use (Almécija et al. 2021; Duda and Zrzavý 2013; White et al. 2015; Hunt 2016; Hunt 2020). Further compounding these difficulties is that radical evolutionary changes can happen in relatively short time scales, making inferences about social behavior deep in our species' evolutionary history tenuous. Bonobos and chimpanzees likely diverged between 1.5 and 2.5 million years ago, yet within this time period they developed dramatic differences in behavior (Gruber and Clay 2016). Among the two most intensively studies subspecies of chimpanzees, striking differences exist in rates of intergroup lethal violence (Wilson 2013; Wilson et al. 2014). Thus, it is uncertain whether and to what extent the behavior of any bonobo or chimpanzee population is a reliable model for the behavior of the ancestral human state prior to our divergence from the other apes (Gruber and Clay 2016).

In addition to the changes that chimpanzees and bonobos have experienced in the intervening 6-9 million years since the LCA, the human lineage has undergone profound changes over this period, shifting what may have been an arboreal ape into a culturally dependent bipedal species living in interdependent multilevel societies with fluid group boundaries (Tattersall 2017). Even if the LCA were largely chimp-like, the intensive changes in the human lineage that have occurred over the last six million years renders the relevance of the LCA for modern human behavior unclear. Our more recent ancestors, the australopiths, who preceded our genus *Homo*, likely did not resemble either bonobos or chimpanzees (Lovejoy et al. 2009; White et al. 2015) and their social behavior was also likely to have been radically different (Wilson and Glowacki 2017). Selection over far shorter time scales, such as thousands of years, can have profound effects on both biology and culture (Fan et al. 2016). The millions of intervening years in our evolution since the LCA makes it difficult to have any confidence in how much of modern human behavior is due to phylogenic inertia and how much is due to selection that has occurred since our split from the other great apes. Given the uncertainty about whether the last common ancestor resembled chimpanzees, bonobos, or neither, inferences locating the origin of human war or peace in the behavior of our last common ancestor are tenuous.

2.1.1: Does the peacefulness of bonobos demonstrate that early humans lacked war?

Bonobos are often used as evidence for the shallow roots of war because they are frequently characterized as peaceful (Clay, Furuichi, and de Waal 2016; De Waal and Lanting 2023; Furuichi 2011), "*renowned for making love instead, not war*" (Barash 2013) and "… *solving power issues through sexual activity*" (de Waal 2013:xii). It is correct that bonobos have much less intense intergroup aggression with other bonobos than chimpanzees do (Furuichi 2011; Gruber and Clay 2016; Wilson et al. 2014) and intergroup killings

have not been reported. Bonobo groups have been documented having sustained periods of intergroup cooperation that involve food sharing and grooming between members of different groups (Samuni and Surbeck 2023). Yet, the study of bonobos is in its infancy compared to the more than 60 years of detailed studies of multiple chimpanzee communities, so our understanding of the species is still developing (Wilson 2021).

The reputation for bonobo peacefulness overlooks the fact that, despite the absence of lethal violence, male-male aggression is more frequent in bonobos than in chimpanzees (Mouginot et al. 2024). When two groups of bonobos meet each other, there is often aggression, with males increasing their rates of aggression (Cheng et al. 2021). At the Lomako bonobo site, 35 percent of intergroup interactions involved physical aggression (Hohmann and Fruth 2002). Although tolerant intergroup interactions have been observed on multiple occasions at the Kokolopori Bonobo Reserve, individuals mostly socialized with members of their own group, not members of the outgroup, and 15% of encounters resulted in physical injuries (Cheng et al. 2022). At the LuiKotale field site, the pattern is similar: During a three-month intensive study period, there were 19 intergroup encounters between different bonobo groups, but the authors note that intergroup encounters "were more aggressive than tolerant" (Moscovice et al. 2022). 47% of the intergroup encounters had "*large-scale coalitionary aggressive events*" often resulting in injuries. "*During one incident, several WBp* [community name] *females targeted an EBp* [community name] *female, May, and hit and bit her repeatedly while she tried to protect her young infant*" (Moscovice et al. 2022).

Shallow roots scholars often accuse prominent deep rooters such as Wrangham and Pinker of "*not consider[ing]*" (Fry 2019b) and "*usually ignor[ing]*" bonobos (Fry 2019a), or hypothesizing about war "*without information about non-raiding bonobos…*" (Fry, Keith, and Soderberg 2020:315). The claim that deep rooters generally ignore bonobos is false. In the heavily-cited book *Demonic Males*, Wrangham and Peterson (1996) devote extensive discussion to understanding why the behaviors of bonobos and chimpanzees are so different. They developed an influential evolutionary account for how differential selection pressure due to foraging competition resulted in lethal violence for chimpanzees and but not bonobos (Wrangham and Peterson 1996). Subsequently, Wrangham's (1999) seminal paper *Evolution of Coalitional Killing* devoted an entire section to explaining bonobo's lack of lethal raiding. Similarly, Pinker's influential *Better Angels of our Nature* (2012) devotes several pages to discussing the lack of raiding among bonobos and the reasons why bonobos may not be a good model for human evolution. In fact, in arguing for a chimpanzee-like LCA, Wrangham and Pilbeam (2001) argue that bonobos can be just as informative about human evolution as chimpanzees depending on the particular question. Scholars can reasonably disagree on whether bonobos or chimpanzees are a better model for the LCA, or whether neither is but the oft repeated claim that deep rooters ignore evidence from bonobos is false.

The reasons why bonobos have cooperative intergroup interactions compared to chimpanzees are unclear. However, bonobos differ from other ape species in having strong female coalitions and stronger reproductive skew among males, which may to inhibit or prevent male coalitions (Clay, Furuichi, and de Waal 2016; Furuichi 2011; Mouginot et al. 2023; Parish, De Waal, and Haig 2000). They also appear to have less feeding competition, and more stable party size than chimpanzees which may result in fewer benefits to be obtained from lethal intergroup aggression (Furuichi 2009; White 1998). Deep rooters argue that the factors that likely shape bonobo peacefulness—strong female coalitions, reduced feeding competition, and larger party sizes were unlikely to be present early in the evolution of our genus and species (Wrangham 2019).

2.1.2. Does chimpanzee intergroup violence demonstrate that humans likely inherited war-like behavior from the Last Common Ancestor?

Chimpanzees are well known for having lethal raiding between communities that can lead to the takeover of territory and the extermination of neighboring groups (Goodall 1986; Mitani, Watts, and Amsler 2010; Wilson and Wrangham 2003). Lethal raiding also appears to provide important fitness benefits for members of successful groups (Lemoine et al. 2020). Comprehensive data from every long-term chimpanzee field site shows that chimpanzee aggression is unrelated to human impacts, including provisioning and habitat change (Wilson et al. 2014). For some deep rooters, chimpanzee intergroup killings are viewed as support for the claim that lethal intergroup aggression began with the last common ancestor of humans and chimpanzees (Meijer 2024; Wrangham and Peterson 1996).

Arguments using chimpanzees as a model for the LCA to understand the evolution of human war often overlook the fact that there appears to be diversity in aggressiveness between chimpanzee populations with "*western chimpanzees appearing more gregarious and less prone to violence than their eastern counterparts*" (Gruber and Clay 2016:248; see also Fuentes 2012; Layton 2014). Chimpanzees in eastern Africa typically have higher rates of lethal intergroup aggression, while in western Africa, chimpanzees at the Tai site have lower rates (Wilson et al. 2014). It is unclear if the observed differences in lethal aggression between eastern and western chimpanzees are due to biological differences or to other factors, such as differences in ecology or the number of males (Wilson et al. 2012; Wilson et al. 2014).

Based on the available data, the variation in lethal violence between chimpanzee populations limits our ability to make confident inferences that ancestral chimpanzees would have had lethal raiding. In fact, the differences between western and eastern chimpanzees are so profound that some researchers hypothesize that "*bonobos may thus appear more similar to western than to eastern chimpanzees*" (Gruber and Clay 2016:248). As a result, shallow-rooters stress that there is an over-reliance on eastern chimpanzees in understanding human warfare, while neglecting the more peaceful western chimpanzee communities (Ferguson 2011; Fry 2013; Sussman and Hart 2015). Arguments that use the behavior of chimpanzees as a model for war since the LCA, would be strengthened by demonstrating that eastern chimpanzees are a better model for the last common ancestor than western chimpanzees.

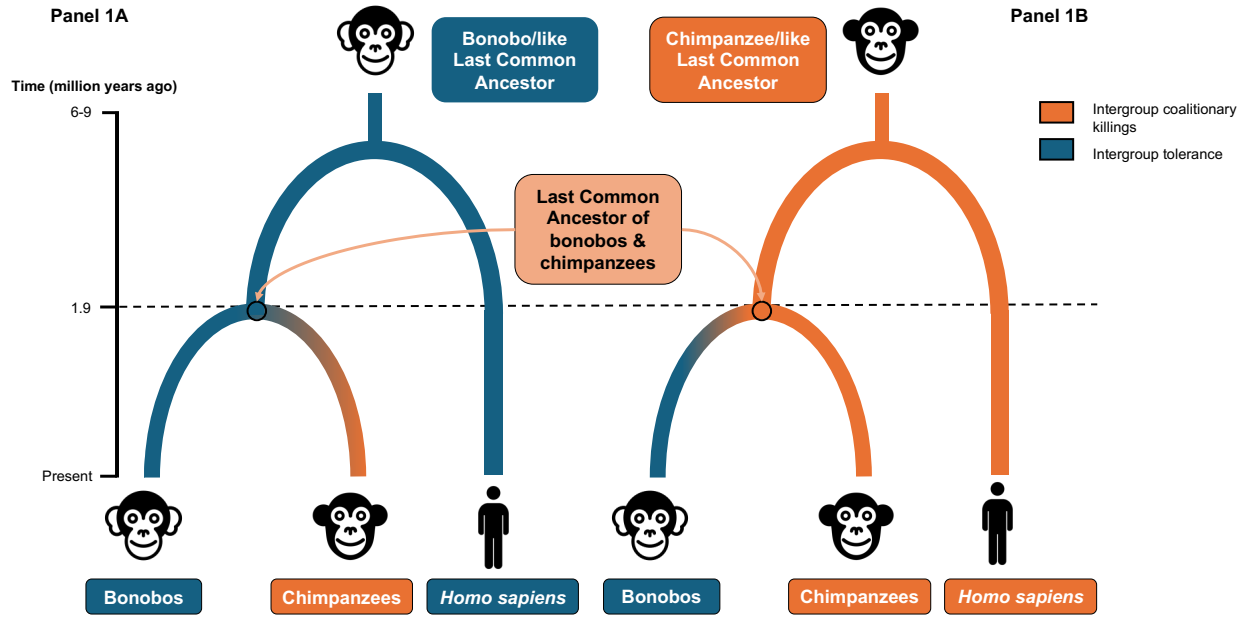

Figure 1: Depicts evolutionary trajectory of war and peace since the last common ancestor according to the bonobo (Panel 1A) and chimpanzee (Panel 1B) models of human evolution. There continues to be debate about whether the last common ancestor was more like chimpanzees and bonobos. Dates approximate.

2.1.3. The importance of chimpanzees and bonobos as models for the adaptive significance of war and peace

Deep rooters generally agree that adaptive approaches are a valuable way to understand the origins of coalitionary intergroup killing. Adaptive approaches examine how the benefits that result from a behavior can select for that behavior. To do so, they typically compare across species to understand how factors shared between different species can give rise to similar traits. For example, similar ecological conditions or social structures may select for similar behaviors in different species. To understand why humans and chimpanzees both have intergroup coalitionary killings, adaptive approaches often focus on social organization and foraging ecology to assess whether they result in costs and benefits that shape intergroup killing. This approach is extremely powerful because it makes predictions about the conditions in which a trait is expected to emerge that can then be tested by quantifying costs and benefits, and examining a range of species that satisfy those conditions.

Adaptive approaches are valuable for understanding peace, as well as war. For instance, adaptive approaches can identify the conditions that selected for strange males to affiliate with each other without aggression, a critical component of peace that is lacking in chimpanzees but present in bonobos and humans (Pisor and Surbeck 2019; Samuni, Langergraber, and Surbeck 2022). Similarly adaptive approaches can identify features that allow intergroup cooperation to evolve, such as risk pooling, protection from predators, or benefits from interdependence (Robinson and Barker 2017).

Adaptive approaches have provided key insights into the evolution of aggression including why bonobos and chimpanzees have such radically different intergroup behaviors, though the mechanisms are still being unraveled (Crofoot and Wrangham 2010; Wilson and Wrangham 2003). Wrangham, for example, argues that differences in foraging ecology between bonobos and chimpanzees alters the payoffs between the two species such that chimpanzees intergroup aggression is adaptive, while in bonobos intergroup aggression provides fewer benefits (Wrangham 1999; Wrangham 2023), while others identify the key differences as being due to female coalitions or territorial defense (Furuichi 2011; White 1998; White, Waller, and Boose 2013). As such, adaptive approaches that use the behavior of chimpanzees, bonobos, and other species may be the most promising avenue to understand why and how humans evolved the capacity for war, and the ability to make peace.

2.2. Are recent nomadic foragers good models to understand the evolution of human war?

Both deep and shallow roots proponents rely on recent hunter-gatherer (forager) populations as models for understanding how ancestral humans behaved. They both typically agree that the hunter-gatherer societies that best reflect our evolution are those societies that lack complex social structures, but instead are organized into residential groups called *bands* that are based loosely on marriage, kinship, and friendship. These groups generally lack significant food storage, have strong norms for egalitarianism *within* age and sex, and are often mobile, moving camps on the basis of resource availability (R. L. Kelly 2013; Woodburn 1982). This is called the *nomadic-egalitarian model.*

Despite agreement between deep and shallow rooters that nomadic foragers are generally useful models to study human evolution (though see below for important critiques of this model), there is still debate about which specific societies are appropriate for understanding the evolution of war. The deep rooters, for example, often include horticultural societies such as the Yanomamo in discussing the evolution of war (Keeley 1996; LeBlanc and Register 2003; Pinker 2012). While deep rooters recognize that these groups

are not nomadic foragers, they are often included because they are like mobile foragers in many important respects, such as having a heavy dependence on hunting and gathering, high mobility, and little social stratification. Lee (2014; 2018), Ferguson (1992; 2013), and others (e.g., Fry and Söderberg 2014) have argued that nonetheless the inclusion of horticulturalists is dubious for inferences about human evolution not just because of their reliance on horticulture, but also because of the impact that states and other colonizers have had on them.

By contrast, shallow rooters typically rely on recent 20th century band level foraging groups such as the San (Bushmen), Mbuti, Batek, and Semai to argue that foragers generally lack war (Fry and Söderberg 2013; Lee 2018). However, many of these groups have been significantly impacted by outside forces or were incorporated into state societies often resulting in profound changes to their social systems (Helbling 2006; Service 1971). The !Kung San who are often held up as a model for a peaceful society live in an extremely dry desert with little permanent surface water (Lee 1979). They have a long history of interaction with farming and pastoralist neighbors. Lee himself writes "*most of the men had experience of herding cattle at some point of their lives…many men had owned cattle and goats in the past…the !Kung were no strangers to agriculture*" (Lee 1979:409). The San's long history with pastoralists and state societies leads some to argue that they lost important features of their social structure, including raiding (Lee 1979), kin-based corporate groups, and more significant forms of leadership once they began interacting with agricultural neighbors (Singh 2021; Wilmsen et al. 1990). Other groups, such as the Mbuti, inhabit dense rainforests which, while high in plant matter, are low in carbohydrates. Thus, many Mbuti form critical trade relationships with neighboring farming groups to obtain food (Turnbull 1965); in some cases 60% of their calories come from these relationships (Ichikawa 1983). Other groups categorized as peaceful foragers, such as the Sirionio, have a heavy reliance on crops they grow themselves in addition to being semi-sedentary (Holmberg 1950; Rival 1993)[1].

The effect of state societies on recent foragers are so profound that Marvin Harris writes that it is a "*serious error… to suppose that contemporary band-organized hunting and gathering societies are representative of the great bulk of paleolithic hunting and gathering groups. Almost all of the ethnographically classic cases of band-organized hunters and gatherers are marginal or refugee peoples driven into, or confined to, unfavorable environments by surrounding groups of more advanced societies*" (Harris 1968:156). For this reason they are sometimes called "*defeated refugees*" (Keeley 1996) or "*the helpless people or the defeated people*" (Service 1971:35).

A further challenge to the nomadic forager model to study the evolution of war is that there is an emerging perspective that argues that our foraging ancestors during the late and possibly middle Pleistocene would have lived in more resource-abundant areas, such as river valleys, flood plains, and coastal regions (Compton 2011; Finlayson 2014) than 20th century nomadic foragers. Foragers in these resource-abundant regions would have faced much less resource shortage and would have been able to live in higher population densities with increased sedentism (Graeber and Wengrow 2021; Roscoe 2013; Roscoe 2014; Singh and Glowacki 2022). For example, at Kalambo Falls, Zambia, interlocking logs joined by a cut notch have been dated to 476kya suggesting the construction large combined structure such as a dwelling or fishing platform (Barham et al. 2023). This suggests that the hominins at this site who were previously "perceived as mobile foragers with limited technological diversity" may have had "*sustained occupation*" "*creating a built environment*" (Barham et al. 2023:111). Hunter-gatherers such as these would better resemble more recent semi-sedentary hunter-gatherers, rather than mobile hunter-gatherers. Recent semi-sedentary foragers commonly had warfare, although rates of violence varied substantially across time and space (Roscoe 2006; Roscoe 2014).

Thus in general 20th century nomadic foragers are poor systems for studying intergroup relationships in human evolution in part because their social systems have been radically transformed through contact with powerful farming neighbors and incorporation into state societies (Bird-David 1992; Haas and Piscitelli 2013; Solway et al. 1990). While no human society is an ideal model for studying human evolution, hunter-gatherer societies surrounded by other hunter-gatherers with minimal reliance on farming or trade with state societies, such as in pre-colonial Australia, the Andaman Islands, or parts of North America may provide better insight into conditions approaching those present during human evolution (Allen 2014; Dye 2013; Hames 2019; Pardoe 2014). Warfare appears to have occurred in all of these cases, including Australia which was an entire continent of hunter-gatherers prior to colonization (Allen 2014; Lourandos 1997; Wrangham and Glowacki 2012)

2.3. Did nomadic hunter-gatherers lack war?

Many shallow rooters claim that nomadic foragers lacked war in any meaningful sense. They observe that some recent foraging groups did not practice war, that the egalitarian social organization makes it difficult to mobilize large number of persons for war, and that evidence for war substantially increases with the emergence of social hierarchy and sedentism. For example, Sponsel (2010:20) asserts it is "*fiction*" that hunter-gatherers had war and that they "…*epitomize… attributes of a non-killing society*" (Sponsel 2017:38). Fry and Söderberg state that it is "*nonetheless false*" (Fry and Söderberg 2014:259) that hunter-gatherers in our evolutionary had war and claims to this effect are "*merely mythical caricatures detached from the data*" (Fry and Söderberg 2014:263). Giorgi (2010:93) concludes that "*nonkilling cultures have been the norm since the emergence of Homo sapien*s".

Several scholars have complied lists of multiple societies who appear to lack war, including the San, Semai, Mbuti, and other recent foragers (Baszarkiewicz and Fry 2008; Fabbro 1978; Fry 2007). It is correct that, in the 20th century, many of these foraging groups lacked war. However, as we have seen in section 2.2, recent foragers, especially those living surrounded by state societies or other powerful neighbors, are poor proxies for understanding intergroup relationships in human evolution. The Semai, for example, are perhaps the most famous example of a peaceful foraging society (Dentan 1968). Yet they are surrounded by more powerful neighbors whom they appear fear, and this seems to be an important reason for their lack of intergroup violence (Dentan 1978; Dentan 2004). Similarly, the peaceful Semang and Sirionio appear to have been driven from their homes and adopted retreat and fleeing as a strategy for survival (Holmberg 1950; Schebesta 1932). Thus, while it is perfectly reasonable to point to peaceful foraging societies to illustrate that human communities can live in a state of peace, the surrounding context, especially whether they are bordered by powerful agricultural societies or are incorporated into state society, should be carefully considered in making inferences about whether foragers during human evolution had war.

Nonetheless, many scholars have still tried to reconstruct how recent hunter-gatherers behaved through systematic reviews of ethnographic materials from multiple foraging societies. Most cross-cultural surveys of recent hunter-gatherers find that warfare occurred, though it may be intermittent. Ember (1978) found that 90% of foragers had war more often than "rarely or never", while Wright (1942) found that 92% of 216 societies had war. Wrangham and Glowacki's (2012) study of six world regions of hunter-gatherers surrounded by other hunter-gatherers found evidence of war in all of them, such as ambushes, raids or unused border zones, but did not report data on the frequency or intensity of war.

Cumulatively, the evidence is overwhelming that most documented hunting and gathering groups had war at least occasionally (Allen and Jones 2016; Hobhouse, Wheeler, and Ginsberg 1915; Standen et al. 2023; van der Dennen 1995; Wrangham and Glowacki 2012; Wright 1942). In some of these, war appears to have been frequent and a significant source of mortality, while in others it may have been

infrequent or rare, and within any society was likely to change over time. It is also clear that some 20th century mobile foraging groups living adjacent to powerful agriculturalist neighbors such as the Semai and Mbuti lacked warfare, demonstrating that hunter-gatherers can peacefully co-exist with their neighbors. But the claim that hunter-gatherers generally lacked war appears to be a fiction rather than a claim grounded in ethnographic evidence.

2.3.1 A critical evaluation of an influential paper

A frequently-cited paper published in the distinguished journal *Science* examined ethnographies of twenty-one mobile forager societies searching pre-selected ethnographic texts for specific descriptions of individuals killed by lethal violence (Fry and Söderberg 2013). The authors then coded the context of the death for variables including if there was more than one attacker and whether attackers were ingroup or outgroup members. Thus, each society received a numerical value for the number of deaths due to warfare that can be compared against deaths due to other types of violence. Crucially, if an ethnographic text did not discuss a *specific* death due to war, then that society was coded as having *zero* deaths due to war. The inference is that societies with zero reported war deaths lacked war. This is a potentially useful method to assess the proportion of deaths from intergroup violence compared to ingroup violence but is of limited utility in assessing the importance of war among hunter-gatherers. For war to be an important force in human societies, the deaths from war do not have to exceed those from withing-group violence. War can occur sporadically and still be an important force with selective consequences.

From these 21 societies, Fry and Söderberg (2013) coded a total of 148 accounts of violent deaths, with lethal violence occurring in all but three societies. Of these 148 killings, 34 percent are from intergroup conflict. The authors use a restrictive protocol excluding 13 cases that many consider examples of aggression between different social groups—if these cases are included, it brings the percentage of intergroup killings up to 43%. Similarly, a reanalysis that removed unclear cases showed that 50.8% of deaths are were due to between-group violence (Hames 2019). Based on these results, Fry and Söderberg infer that their study "*contradict[s] recent assertions that [mobile foragers] regularly engage in coalitionary violence against other groups*" and instead asserts that foragers "*are not particularly warlike*" (Fry and Söderberg 2013:272).

There are substantial concerns with the sampling framework Fry and Söderberg use. Their sample includes many groups that were living within state society or are better described as enclaves or refugees such as the Mbuti, Vedda and Semang, rather than hunter-gatherers surrounded by hunter-gatherers. Secondly, by only recording the number of deaths, but not data on the time frame or size of the population, it is impossible to make meaningful comparisons among different populations.

More alarmingly, their coding scheme *excludes descriptions of war* that did not provide an unambiguous count of the number dead. By excluding these accounts of war, Fry and Söderberg effectively treat societies with explicit descriptions of practicing warfare but that fail to report a specific number of dead from an event as supporting the absence of war (effectively coding them as a 0 rather than an N/A). There are strong *a priori* reasons to think that specific numbers of deaths from warfare may not be reported by the ethnographer even when they write about war. Many of the ethnographies they used were written decades after the society had been incorporated into state society, so the ethnographer would be more likely to report on general practices rather than specific deaths (such as a chapter on tactics and rituals around war), or the specific number of deaths may not have been reported to the ethnographer. In other cases, the ethnographies they code are not extensive so it would be surprising if they reported on specific cases of war deaths, any more than they may report on specific cases of death due to disease or animal attack.

Consider the North American group in their sample known as the Slave. The short 33-page ethnography that is their primary source material begins by noting that "***of the truly aboriginal condition… there is no knowledge****. In even the earliest reports it is evidence that the contact situation had already wrought changes in the aboriginal way of life*" before proceeding to discuss wars of the past (Macneish 1956:131–132). Despite the fact that the ethnography they use is not comprehensive, clearly states that there is no knowledge of the traditional pre-contact way of life, and then proceeds to discuss warfare (while not reporting a specific number of deaths due to war), the Slave are inferred to lack war. The case is similar for the Paiute. The coded text consists of a single 100-page ethnographic text *on the role of sorcery published in 1950* (Whiting 1950). Although the Paiute are inferred by Fry and Söderberg to lack war the ethnography they code describes traditional Paiute life where men wear armor for protection and states that "*raids made it dangerous for families to wander alone,*" describing Paiutes raiding against other groups and "*tak[ing] scalps*" (Whiting 1950). The Fry and Söderberg coding scheme accurately does not report any specific instances of war deaths based on these two short ethnographies. However, claiming these societies lack war is inaccurate and misleading based on the ethnographic texts themselves

The Yukaghir are an even more dramatic example. They are reported as lacking war, with only one lethal incident (cannibalism due to starvation). However, the ethnography Fry and Söderberg code contains extensive discussions of war, including that "*The Yukaghir did not undertake armed expeditions against one another, as they did against the Tungus, whom they hated as a people. The Yukaghir…were always on the lookout for the Tungus or Koryak,* ***in order to kill them***" (Jochelson 1926:126) Villages utilized a watch system because of the threat of raids. In one at least one incident, attackers "*kill[ed] a watchman and the sleeping warriors and… seized the camp*" (Jochelson 1926:383), while "*girls used to be taken as captives and distributed among the warriors*" (Jochelson 1926:133). This would surely count as war to most unbiased readers.

The Kaska are reported by Fry and Söderberg as lacking intergroup violence, while the ethnographic text extensively describes them as practicing war. After detailed descriptions of pre-raid preparations "*fighting started as soon as enemies were encountered… Men were not spared for capture. As victims fell warriors wielding stone knives detached scalps by cutting above the ears… The bodies of the dead received obscene treatment… Women captives became wives who initially had to be carefully watched or tied less they seek to escape*" (Honigmann 1954:94).

Similarly, the Andaman Islanders are reported as lacking lethal intergroup violence. This ignores that the ethnography Fry and Söderberg code describes raiding parties in detail. "*Attacks were generally made… at early dawn when everyone would be asleep. The attacking party would rush the camp and shoot as many men as they could. Though the aim… was to kill the men, it often happened that women or children were killed. The whole fight would last only a few minutes… Such attacks and counterattacks might be continued for years. More usually, after one or two such fights peace would be made*" (Radcliffe-Brown 1948:85). The Micmac are also reported as lacking war in the Fry and Söderberg sample, but the sources they code paint a very different picture of life: "*If we investigate the motives and the particular causes which have inspired these peoples* ***in going to war****, we find… a desire to avenge an injury… or, more often, the ambition to make themselves feared and dreaded… [they] wait… behind some tree—all in order to find opportunity to surprise, fight, and vanquish their enemies, to remove their scalps, and to return to their own country loaded with these cruel spoils.*" (Le Clercq 1910:265).

Taking the Fry and Söderberg paper at face value would lead the reader to believe that the Yukaghir, Micmac, Andamanese, Kaska, and Slave lack war while the ethnography they code describes a very different reality in which these societies all practiced war. The Fry and Söderberg study is correct that war may be intermittent and occasional in foragers, but the conclusions are blatantly misleading. Most foragers around the world are reported in primary ethnographic texts as having participated in warfare at

least occasionally. Many of the most notable exceptions involve hunter-gatherers surrounded by agricultural, pastoralists societies or living adjacent to or within state society.

2.4. Resources, Population Density, and War

Both deep and shallow rooters often view population density and competition for resources as key factors in the emergence of war. Typically they both agree that when humans approached the carrying capacity of their landscape or became more sedentary, this would have led to war (c.f. Haas and Piscitelli 2013; LeBlanc and Register 2003). However, they disagree about whether this occurred when our species developed agriculture, or earlier with mobile hunter-gatherers. For example, one prominent deep rooter argues that "*foragers were at their carrying capacities almost all the time*" (LeBlanc 2014:41), while Kelly writes "*war appears when mobility is not an option*" (2013:156). In contrast, I argue that there is conflicting evidence for a relationship between warfare, population density, and resource stress. As a result of cultural and ecological variation, it is unlikely that there is a simple causal relationship between resource competition, population density, and warfare.

2.4.1. The relationship between resource competition and war is likely to vary by context

Despite decades of research attempting to demonstrate a connection between competition for natural resources and war, the evidence in support of a clear relationship is mixed. Some studies suggest that increasing resource competition is associated with warfare. For example, Allen and colleagues (2016) examined the relationship between blunt and sharp force skeletal trauma using a dataset of over 7,000 skeletal remains from central California hunter-gatherers dating from 1,530 to 230BP, a period of over a thousand years. Sharp force trauma is much more likely to be lethal than blunt force trauma. Rates of blunt force trauma changed little over the period while rates of sharp force trauma were greater in regions that had lower contemporary net primary productivity (NPP), which was used as proxy for resource scarcity. But crucially, it is unclear whether the current values of resource productivity the authors use reflect prehistoric levels of competition.

Due to the difficulty of estimating ancestral resource competition directly, more research has focused on population density and population pressure as a proxy for resource competition. Using a sample of 19 forager societies, Kelly (2013, Table 9.3) finds a correlation between the rate of internal war (war between communities of the same society) and population pressure. Using a sample of 30 foragers, Fry and colleagues (2020) find that war is associated with population density, but not population pressure. Although we confine our discussion to foragers, multiple studies among non-foragers have shown similar relationships between increasing population measures and warfare (Ember et al. 2012; McCool et al. 2022; Nakagawa et al. 2021; Snyder and Haas 2023).

Yet, many other studies fail to find a clear relationship resources and war. A study using a cross-cultural sample of 87 different societies found no correlation between population density and warfare (Keeley 1996; Table 8.3). Similarly, for Aboriginal Australia both Pardoe (2014) and Allen (2014) fail to find any relationship between population density and warfare. An important recent study examined all excavated human burial sites in the Nile Valley with skeletal remains from between the terminal Pleistocene ranging to the early Holocene evaluating signs of violent trauma in the skeletons (n=382) (Brukner Havelková et al. 2023). They found that the earlier and less dense Pleistocene populations had more traumatic injuries from violence than later populations. This difference is remarkable because later Holocene populations had significantly higher population densities in this region. Similarly Chatters (2014) found higher rates of interpersonal violence among early Paleoamericans at extremely low population densities compared to later populations. The lack of a clear relationship between war and population density leads Keeley to write that "*Groups with densities of less than one person per square mile are just as likely to engage in warfare… as groups whose densities are hundreds of times higher*" (1996:118).

Some scholars are skeptical of a strong connection between competition for natural resources and warfare because groups can respond to increased competition through the development of cultural institutions to promote trade or cooperation or technologies to improve environmental productivity. For example, the decline of violence in the Nile Valley between the Paleolithic to the Holocene despite the higher population density of Holocene populations may have been driven by new cultural innovations to better resolve and prevent conflicts, potentially including male exogamy and inter-group risk-reducing alliances (Brukner Havelková et al. 2023). Similarly, among prehispanic Pueblo farmers in the American Southwest in the period from 1100 AD until the arrival of the Spanish several centuries later, the population size increased yet violence declined alongside this population increase likely due to development of larger polities and intergroup sodalities (Kohler et al. 2014).

No simple generalization about the relationship between resource stress, population density, and warfare is likely to capture the complexity of human intergroup relationships in the face of increasing resource stress. War may be one possible response but societies may also respond to resource stress through expanding trade and sharing networks, intergroup marriage, or altering their subsistence patterns.

2.4.2. Was the population density too low and were resources too scarce for war in the Pleistocene?

The myth that war requires large populations fuels the idea that our foraging ancestors lacked war. Fry, for example, states about our foraging ancestors that the *"population density is so low that it's hard to get enough people together to have a war… What would they fight over?... they don't have much to fight over. It's not like they have a lot of stocks and bonds or even a food supply…so there is nothing to plunder and pillage really"* (Fry 2019b). This view is echoed by Sarah Hrdy (2009:18) who writes "*how much sense would it have made for our Pleistocene ancestors eking out a living…to fight with neighboring groups rather than just moving?*" Haas and Piscitelli (2013:176) argue that "*low population densities obviated all the proposed biological or cultural reasons for warfare and intraspecific conflict."*

It is correct that the ability to monopolize valuable resources is often associated with higher rates of warfare, which may be reason why farmers, pastoralists, and complex hunter-gatherers appear to have higher rates of warfare (Ember and Ember 1997; Fry, Keith, and Soderberg 2020; Hames 2019; Kelly 2000; Knauft 1991; Wrangham, Wilson, and Muller 2006). However, the central claim is that the population densities of hunter-gatherers were too low to support war and that the potential benefits from warfare were too few to promote warfare. Neither of these claims is supported by strong evidence. Although many groups of hunter-gatherers were at low population densities, lethal coalitionary intergroup aggression still occurred. Chimpanzees are sometimes at even lower population densities than many forager groups (median density 3.3 chimpanzees/ km^2 (Wilson and Glowacki 2017) compared to a median density of 6.6 for foragers (Based on Table 9.3 in R.L. Kelly 2013) and yet have rates of death from intergroup violence that approach or exceed those of some hunter-gatherers (Wrangham, Wilson, and Muller 2006). While higher population densities may facilitate warfare by putting more potential co-participants in close proximity, low population density does not prevent its occurrence.

Unlike pastoralists or farmers who can capture food and livestock from war, these potential benfits are were generally not available to hunter-gatherers (Glowacki and Wrangham 2013; Manson et al. 1991). However, many hunter-gatherer groups did capture women and children in war and took trophies from victims that increased their status (Allen and Jones 2016; Gat 2000).

Despite claims about hunter-gatherers having too low of a population density or that the lack of resource competition that inhibits war, it is clear that many mobile hunter-gatherers practiced warfare. In doing

so, they often gained status and took captives, especially women and children, and such results appear independent of group size or resource competition.

2.4.3. Does the egalitarian and flexible social composition of nomadic hunter-gatherers hinder warfare?

Mobile foragers typically lack hierarchal leadership and social structures that make coordinating large numbers of persons difficult. For these reasons, it is sometimes claimed that they were unable to organize for warfare (Fry 2012; Fry and Söderberg 2013; Giorgi 2010; Sponsel 2010). Fry, for example, claims that *"the nomadic forager type of social organization makes the waging of war very difficult*" (Fry and Söderberg 2013 SI), while Sponsel (1996:107) states that "*warfare would be absent… if one considers that they… lack sufficient food surplus to sustain a military organization… and do not have political leadership and organization to direct warfare.*"

As these quotations correctly illustrate, the social organization of a society can limit the types of organization it can achieve. Likely because of this, hunter-gatherer warfare typically did not involve structured fighting units and chains of command but generally consisted of loosely organized raiding parties engaging in ambushes and surprise attacks (Gat 1999; Keeley 1996). Battles, in which multiple participants faced off, appear less common than in other kinds of social organization but are ethnographically reported in some mobile foraging societies (Burch 2005; Meggitt 1962). Understanding how acephalous decentralized groups like hunter-gatherers or even chimpanzees wage warfare is a major area of research (Glowacki and McDermott 2022; Glowacki et al. 2016; Mathew 2017; Pandit et al. 2016; Zefferman and Mathew 2015) but regardless of the absence of centralization it is clear that foragers can and often do wage war.

While mobile hunter-gatherers generally have flexible group boundaries, in many societies, there are strong divides between groups. Among the Andaman islanders, groups kept closely to their home range because of the risk of attack by outside groups: "*Whenever two parties of them met by any chance, the larger party would attack the others.*" (Radcliffe-Brown 1948:86–87). Early ethnographic reports among the San document both territoriality and aggression in response to violations of a group's territory such that "*Men who hunted in the land of their neighbors are said to have been killed by them*" (Heinz 1972:412). So strong were the group divides that "*Though [the] band[s] live as neighbors there had been no exchange of marriage partners for some 15 years. This struck my attention because I knew that boys and girls were available on both sides*" (Heinz 1972:411).

These examples illustrate that the social structure and egalitarian ethos of foragers does not prevent war. Even the most radically egalitarian nomadic hunter-gatherers such as the San appeared to have engaged in at least occasional lethal intergroup coalitionary violence prior to colonization. As Lee himself notes "*raiding expeditions had occurred in the distant past, during the youth of the grandparent generation of the oldest living people*" (Lee 1979:382), and some groups of San mounted intensive armed resistance against colonial incursions (Guenther 2014; Wright 1971). But it is also correct that increasing hierarchy, leadership, and social stratification is often associated with more intense warfare, likely due to the ease of mobilizing participants (Fry and Söderberg 2014; Fry, Keith, and Soderberg 2020).

The fact that many foragers had intergroup violence is contrary to the noble savage stereotype put forth by Fry, Sponsel, and others that raiding was "*runs counter to the ethos of egalitarianism*" (Fry and Söderberg 2013:271). Egalitarian hunter-gatherer groups, like humans elsewhere, sometimes engaged in warfare that including killing their opponents. However, forager warfare was likely limited in scale and intensity compared to war among larger sedentary populations due to the difficult of organizing and mobilizing participants.

2.5. Did nomadic hunter-gatherers make peace?

Deep roots proponents sometimes appear to assume that intergroup cooperation between hunter-gatherer groups was rare and that war was the most common type intergroup interaction (Keeley 1996; LeBlanc and Register 2003). LeBlanc, for example, writes about hunter-gatherers in human evolution "*Warfare was pervasive, constant, and deadly*" (2014:42). This view may be because ethnographers are more likely to write about war than the absence of war, or interest on the part of researchers. It may also be due to numerous well-known studies from Oceania and Papua New Guinea where warfare was often intense and chronic contributing to the perception that incessant warfare was extremely common among foragers in other regions (Koch 1974; Meggitt 1977; Pospisil 1994). Most of these populations were sedentary horticulturalists rather than mobile foragers, but this distinction is often not clear to non-anthropologists. Whatever the reasons, hunter-gatherer intergroup relationships are more varied than just hostility and often include cooperation, trade, marriage, and peace (Fry 2009; Fry, Keith, and Soderberg 2020; Glowacki 2024).

While it is difficult to reconstruct the lifestyles of hunting and gathering groups prior to agriculture and colonization, a consensus is emerging that intergroup cooperation extended into the Paleolithic (Boyd and Richerson 2022; Fry 2012; Fuentes 2004; Glowacki and Lew-Levy 2022; Glowacki 2024; Hames 2019). Marriage was likely an important source of intergroup exchange and many hunter-gatherers appeared to practice bilocality where they could live with kin of either spouse and often moved between them (Kramer 2021; Marlowe 2005). Paleo-archeological evidence demonstrates that intergroup trade extends deep into our evolutionary history. Stone tool trade dates to at least 300,000 thousand years ago (Brooks et al. 2018). In southern Africa, there is extensive evidence of long-distance trade of eggshell beads across a distance of *more than 3,000 kilometers* over a period of nearly 20,000 years beginning 50,000 years ago (Miller and Wang 2021). Similarly, archaeological remains of hunter-gatherer populations around the world show extensive evidence of the exchange of goods across group boundaries (Bennyhoff and Hughes 1987; McBryde 1984; Oka and Kusimba 2008). These findings are consistent with ethnographically recent hunter-gatherer groups who often cooperated and traded across strong group boundaries that could span hundreds of miles and multiple languages (Bird et al. 2019; Fry et al. 2021).

Many hunter-gatherer groups appeared to work to avoid or minimize intergroup conflict (See Fig 3). In the Andaman Islands, notorious for intense intergroup warfare, societies developed mechanisms to resolve conflicts and renew relationships positively that was institutionalized in a peacemaking ceremony. Members of two enemy groups would come together with the party who committed the last offense hosting the ritual. The visitors would give expression to their anger through "*mak[ing] expressive gestures at the end of which they sit down and weep together,*" exchanging weapons, giving gifts, and remaining camped together for a few days (Radcliffe-Brown 1948:134). "*The whole purpose of the rite is to abolish a condition of enmity and replace it by one of friendship*" (Radcliffe-Brown 1948:242). Among the Walbiri in western Australia, despite long simmering feuds with their neighbors, groups would often work to quell hostilities as "*between the raids there were occasional inter-trial meetings for totemic rituals and for trade*" (Meggitt 1962). Among the Ona in Terra del Fuego, there was a "*traditional ceremony called Jelj [which was an] ancient way of ending blood feuds and was performed only when all were agreed that strife was must end*" (Bridges 1948:404). It included a dramatic event where members of each hostile group had an opportunity to shoot blunted arrows at members of the other group, afterwards renewing "*friendly intercourse*" between the formerly hostile groups. Boehm (2013) reviews multiple cases using a sample of hunter-gatherer societies deemed appropriate as models for late Pleistocene societies and documents a range of behaviors foragers employed to facilitate peace, including peace meetings and formal truces [see also (van der Dennen 2014; van der Dennen 1998) for thoughtful discussion of peace among hunter-gatherers].

These examples illustrate that even though intergroup conflict may have been an important aspect of intergroup relationships, it does not mean that hunter-gatherer societies were perpetually at war. Indeed, it would be strange to imagine human groups who were incapable of tolerantly interacting or cooperating with their neighbors, especially when it would have provided benefits such as tools, information, new allyships, or access to reproductive partners. The potential benefits from trade and cooperation with other groups creates the opportunity for evolution to act on the ability to build extended cooperative relationships across group boundaries.

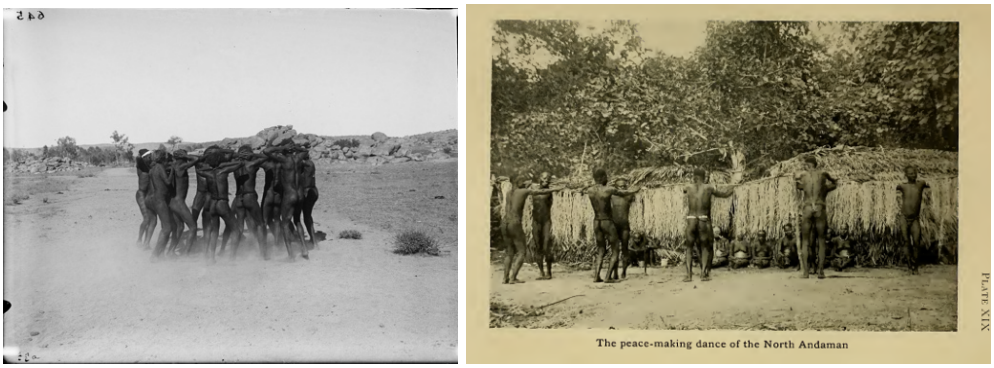

Figure 3: *Left panel*: A group of Arunta men in Australia dancing in preparation before a raid against a distant group (Spencer and Gillen 1904). *Right panel*: In the Andaman Islands, making peace involved a ritualized dance between hostile groups that displayed aggressive feelings before culminating in an exchange of weapons (Radcliffe-Brown 1922).

2.6. Is there really no evidence of war before approximately 10,000BP?

Critics of the deep roots view of lethal intergroup coalitionary violence point to the lack of unambiguous archaeological evidence of warfare prior to approximately 10-14,000 years ago. According to Giorgi (2010:93) "*direct violence and war appeared only in large settlements of the Late Neolithic*" while Fry claims the "*earliest evidence of warfare anywhere on the planet is 10,000 years ago, not more than that*" (Fry 2019b). If unambiguous skeletal evidence of massacres were truly necessary to demonstrate the existence of warfare deep in our evolutionary history, then this absence would represent a formidable challenge. However, the claim that there is a lack of evidence for war before 10,000bp is misleading for two reasons.

For human remains from the Pleistocene to offer insight into whether warfare occurred requires both enough remains to form generalizable samples, and that the remains are in satisfactory condition to be able to infer the cause of death. However, there are vanishingly few intact archaeological remains from African Pleistocene populations before approximately 15,000 years ago. Grine (2016) systematically reviewed hominin remains in Africa from the Late Pleistocene over the last 200,000 years (MIS 6-2) finding "*a notable paucity of human remains*" with "*only a dozen or so [sites] providing particularly informative or interesting evidence spanning this period of nearly 200 kyr*"(Grine 2016:323). The vast majority consist of teeth or isolated fragments of bone, not articulated skeletons, making inferences about the presence or absence of war impossible (see Table 1).

Thus, the claim that war did not occur because there is little skeletal evidence demonstrating injuries from coalitionary violence is dubious because the evidence to test it (numerous intact skeletons from multiple sites) is exceedingly rare. We assume that humans in Pleistocene populations in Africa sometimes died from wildlife encounters (attacked by elephants or buffalo, or were predated upon by carnivores for example), or during childbirth, and that the population pyramid generally consisted of more children than

753 adults. Yet, the skeletal evidence to support these almost certainly true claims is lacking. However, we do
754 not use the lack of physical evidence for animal attacks or deaths in childbirth to claim that these did not
755 happen during human evolution. Rather, we predict a lack of skeletal remains due to preservation issues,
756 and not the underlying absence of childbirth, animal attacks, or lack of children. Because there are so few
757 skeletons sufficiently intact to infer the cause of death, the lack of skeletal evidence is not strong support
758 for the lack of war. The lack of skeletal evidence is a key reason why anthropologists often look to more
759 recent foraging groups to reconstruct human life histories.
760

Site/ Specimen	**Site age in thousands of years**	**Human remains found**
Omo (Kibish Formation)	195,000	Cranium; fragmentary skull and partial postcranial skeleton.
Kébibat	200,000 – 130,000	Skull fragment
Twin Rivers	178,000 – 139,000	Humerus fragment
Mumbwa Caves	172,000	Two teeth; two radius fragments; possible femoral diaphysis
Jebel Irhoud	160,000	Two crania, juvenile mandible; fragmentary postcrania
Herto	160,000 – 150,000	Cranium; fragmentary cranial remains of five individuals
Singa	145,000 – 133,000	Calvaria
Border Cave	170,000 – 156,000	Postcranial fragments
Ngaloba Beds	129,000	Cranium
Blind River	124,000 – 112,000	Femur
Klasies River	115,000 – 58,000	Multiple cranial, mandibular and postcranial fragments
Sea Harvest	110,000 – 71,000	Manual distal phalanx, tooth
Grotte des Contrebandiers	110,000 – 92,000	Cranial fragments
Dar es-Soltan II	125,000 – 92,000	Incomplete skull; cranial fragments
Eyasi	104,000 – 92,000	Partial cranium; mandibles; cranial fragments; teeth
Equus Cave	103,000 – 30,000	Eight teeth
Aduma	105,000 – 80,000	Cranium; cranial fragments
Pinnacle Point	162,000 – 90,000	Parietal; tooth
Blombos	102,000 – 70,000	Nine teeth
Ysterfontein 1	130,000 – 50,000	Three teeth
Witkrans	100,000 – 50,000	Three teeth
Plovers Lake	89,000 – 62,000	Postcranial fragments
Haua Fteah	80,000 – 68,000	Two mandibular fragments
Mumba Shelter	78,000 – 60,000	Teeth
Porc-Épic	78,000 – 36,000	Mandibular fragment
Die Kelders	74,000 – 59,000	24 teeth; mandibular fragment; 2 phalanges
Klipdrift Shelter	72,000 – 52,000	Isolated tooth
Sibudu	77,000 – 38,000	Phalanx; distal fibula
Diepkloof	61,000 – 48,000	Two toe bones; tooth
Mugharet el ‘Aliya	57,000 – 27,000	Juvenile maxilla; isolated teeth
Nyamita	55,000 – 45,000	Partial humerus

Magubike Rock Shleter	42,000	Six teeth
Nazlet Khater	38,000	Skulls and postcranial skeletons
Hofmeyr	36,000	Cranium
El Harhoura I	41,000 – 26,000	Mandible; tooth
Ishango 11	26,000 – 20,000	Fragmentary crania and postcrania
Taramsa 1	70,000 – 24,000	Child skeleton
Leopard's Hill Cave	24,000 – 21,000	Isolated parietal
Lukenya Hill	24,000 – 22,000	Partial calotte
Tuinplaas	<20,000 – 11,000	Skull and partial postcranial skeletons
Deir El-Fakhuri (E71K1)	18,000	Two partial skeletons
Taza Cave I	16,000 – 14,000	Skull
Afalou-bou-Rhummel	15,000 – 11,000	63 partial crania and skeletons
Gebel Silsila 2A	14,000 – 13,000	Isolated frontal bone
Jebel Sahaba (117)	14,000 – 12,000	58 partial skeletons (many show evidence of death due to violence)
Wadi Halfa (6b28 & 6B36)	14,000 – 10,000	Mandible (6B28); 37 partial skeletons (6B36)
Ifri n'Baroud	17,000 – 11,000	Single postcranial skeleton
Bushman Rock Shelter	13,000 – 12,000	Single infant mandible
Mlambalasi Rock Shelter	13,000 – 12,000	Partial postcranial skeleton (? in situ)
Grotte des Pigeons (Taforalt)	13,000 – 11,000	200 skeletons in various states
Iwo Eleru	13,000 – 11,000	Incomplete skeleton and calvaria
Nataruk*	10,500 – 9,500	27 skeletons, 12 articulated (ten show evidence of lethal trauma)

Table 1: Based on Grine (2016 Table 17.2) reproducing all African sites with hominin remains from MIS 6 until 10,000 BP.* The Nataruk cite was excluded from the Grine's data because of late publication.

Preservation issues are compounded in the archaeological record because lethal wounds often inflict little or no damage to the skeleton. Milner (2005) examined skeletal remains of victims from the wars between federal troops and Native Americans finding that only one out of three arrows damaged bone, even though many of these were lethal wounds. Elsewhere Lambert (1997) notes that only one out of four stone points are clearly embedded in the bones of victims leading some scholars to expect only 25% of injuries from stone tipped projectile weapons leave skeletal injuries. If these estimates can be applied to the Pleistocene it suggests that potentially up to 75 percent of deaths due to war would not be attributed to lethal trauma. Thus, whatever paleoarchaeological evidence there is for war, the record likely vastly underestimates the actual incidences of lethal aggression.

The second reason this argument is misleading is that for Pleistocene populations it is virtually impossible to distinguish homicide from warfare as the skeletal signatures are nearly identical. The primary type of war among mobile hunter-gatherers is a raid that targets a lone individual through ambush, thus leaving a single victim usually away from their residential camp (Gat 1999). Similarly, homicide due to in-group conflicts typically leaves a single victim, making it nearly impossible to distinguish war from homicide in the paleolithic record (Kissel and Kim 2019; Martin and Harrod 2015). Thus using skeletal evidence alone will be of limited use in making inferences about Pleistocene social behavior (Kim and Kissel 2018).

Despite the lack of skeletons, several sites at the end of the late Pleistocene include strong evidence of lethal violence. Naturuk, in Kenya, is the most dramatic of these (Lahr, Rivera, Power, Mounier, Copsey, Crivellaro, Edung, Fernandez, et al. 2016) dating to 10,500 - 9,500 BP. The remains of 27 individuals were found, including 12 articulated skeletons, ten of which showed lethal injuries such as blunt-force trauma and arrow wounds, in addition to several specimens appearing to be bound (Lahr, Rivera, Power, Mounier, Copsey, Crivellaro, Edung, Maillo Fernandez, et al. 2016) suggesting a massacre. The mass cemetery at Jebel Sahaba dating to more than 13,000 years ago, contains the remains of at least 61 individuals, 41 of whom have traumatic injuries (healed, unhealed, or both) (Crevecoeur et al. 2021). A full 75% of the adults at the site, and half of the youth have one or more signs of skeletal trauma. For example, two children aged approximately 4 and 5 years age were found together with five stone artifacts (ie, projectile points) with the body of one child showing many unhealed traumatic injuries including projectile impacts and blunt force trauma. The authors hypothesize that this site shows "*episodes of recurring violent events such as raids or ambushes… [which] have taken place on a short time scale*" (Crevecoeur et al. 2021:8)

Wu and colleagues (2011 SI) collected records of all traumatic lesions that have been found prior to the Last Glacial Maximum approximately 14,000 years ago. They identified sixty-one skeletons with evidence of traumatic lesions, but it is impossible to say whether these injuries resulted from interpersonal violence such as homicide, coalitionary intergroup violence such as war, or from another reason (See Table 2 of Kissel and Kim 2019 for the most interesting of these cases). Fry and Söderberg's (2013) research suggests that between 34 to 50% of deaths due to violence among mobile hunter-gatherers are from *intergroup* violence. Assuming this estimate captures the approximate proportions of deaths due to intergroup and intragroup violence among early hunter-gatherers and that war in human evolution followed a similar pattern, then of the 61 injuries on skeletons Paleolithic skeletons with traumatic lesions around 20-30 of the injuries could be inferred to have come from intergroup violence. This is an extremely rough estimate, but whatever the exact percentage, it is likely that at least significant number of the 61 bodies with skeletal trauma were victims of intergroup coalitionary killing.

The lack of intact skeletons from African Pleistocene populations is of limited utility in estimating the presence or frequency of warfare. However, the fact that evidence of multiple victims consistent with massacres does not appear until the late Pleistocene/ early Holocene is consistent with an evolutionary history where warfare largely consisted of occasional and unpredictable ambushes with one or two victims at most such as found at the Jebel Sahaba site.

2.7: If war was important in human evolution, is it inevitable?

Shallow roots proponents sometimes claim that if warfare was important in human evolution, then our species will always have war, or worse, that an evolutionary history of war will be used as a justification for war. Horgan cautions "*many people think that if war is ancient and innate, it must also be inevitable*" (Horgan 2016b), while Sponsel claims deep rooters "*champion the assumption that humans are innately, instinctively, genetically, or biologically programmed to be aggressive, and, therefore, that war is an inevitable manifestation of human nature*" (2010:22) with an "*absolutist, universalist, and essentialist posture*" (2010:22). Fry characterizes the deep roots argument as being plagued with a fallacious inevitability" "*We have always been this way, we will always be this way*" (Fry 2019b). If war has deep evolutionary roots, then this "*justifies militarism. If natural selection produced a human primate with a tendency to attack neighbors… well let's forget the negotiating table and arm to the teeth. Let's stick it to them before they stick it to us.*" (Fry and Söderberg 2014:263). Sapolsky, for example, writes "*if war is natural, there is little point in trying to prevent, reduce or abolish it*" (Forward to Fry 2007:5). Ironically, many of these same authors have argued elsewhere that interpersonal aggression (between ingroup members) was likely important in human evolution and that we can use the knowledge gained by studying it to reduce the likelihood of aggression

in the world today (Horgan 2016a; Sapolsky 2017). If interpersonal aggression has a biological and evolutionary basis and we can use our scientific knowledge to reduce it, then the same should be true of war.

Most evolutionary anthropologists would disagree with the bleak assessment offered by Sapolsky, Horgan, Fry and others that a biological propensity for a behavior means that it is inevitable (Nettle et al. 2013; Smith 2011; Smith 2013). The superficial caricatures they provide of deep roots proponents as fatalistic or justifying war are misleading and often false. Many of the most ardent proponents for the deep roots of warfare acknowledge that although war may have a biological basis, social and cultural institutions can drastically reduce it. Pinker (2012), for instance, documents how exceptionally labile war is, with large-scale historic changes in the severity and intensity of war that correspond with cultural and social changes ultimately leading to a dramatic reduction in war and other forms of violence. Wrangham writes "*while war is not inevitable, conscious effort is needed to prevent it… Abundant evidence shows that* ***violence is socially influenced and socially preventable****. History, after all, has long told us that* ***societies can be at peace for generations****. Evolution of a behavioral tendency does not mean that the behavior has to be inevitable, inflexible, or in some other way independent of human will*" (Wrangham 2019:251–254). Glowacki and colleagues argue that although warfare results from "*evolved psychological predispositions*" the "*success of peacemaking institutions gives hope that the zone of peace could one day encompass the entire planet*" (Glowacki, Wilson, and Wrangham 2020:977–978). Such quotes directly contradict the fatalistic claims that Sponsel, Fry, and others attribute to deep roots perspectives.

Further, many deep roots scholars attempt to use the scientific knowledge of war to consider how and why peacefulness arises. Wrangham, for instance, argues that by minimizing a "*high likelihood of cost-free success [in war]… people can live for long periods at peace* (Wrangham 2019:254). Wilson and Wrangham (2022) use the evolutionary study of war to suggest areas of study that might promote peace, stating, "*the challenge of preventing major wars is mainly undertaken by politicians and lawyers, but we think that every contribution might help,*" and then outline a series of questions intended to provide insight into preventing war including what is "*the point at which leaders… perceive the benefits of peace as outweighing the costs of war? Or how [do] individuals categorize others as friend or foe?*". Rather than being afraid that a biological basis for war may justify or lead to fatalism about war, we could follow the lead of evolutionary scholars themselves, who argue that "*an understanding of warfare rooted in [evolutionary biology] seems likely to point the way towards a better understanding of the contexts that support peaceful intergroup relationships*" (Wilson 2013:382–383). Nothing about a biological or evolutionary basis for war as it is currently understood makes war inevitable or justifies it.

3. DISCUSSION

Human warfare is a complex social behavior resulting from the interaction of culture, social structure, and our evolved psychology and biology. It should therefore be unsurprising that the evidence for the origins of war is complex and sometimes ambiguous. Our close cousins, the chimpanzees and bonobos, provide evidence for and against the claim that we inherited war from the last common ancestor, if one assumes that either species is a good representative of the LCA 6-9 million year ago. Bonobos and humans both have female alliances and intergroup affiliation, while chimpanzees and humans have intergroup raiding and high rates of fission-fusion. It is also reasonable to argue that simplistic phylogenetic approaches using the last common ancestor of bonobos, chimpanzees, and humans are not a useful way to study the evolution of war due uncertainty about the LCA and the radical changes in the human lineage since our separation from the other apes. Overall the evidence suggesting that war or peace was inherited from a chimp or bonobo-like last common ancestor depends on how good of a model either species is for the LCA. This debate is unlikely to be resolved soon and both species as models of the LCA have serious challenges.

The behavior of recent foragers also fails to clearly resolve the debate about the origins of war. Most foragers appear to have had at least occasional war, especially in the form of small raids that are low risk for attackers. Yet for some foraging societies, war was infrequent and unpredictable, and some recent foragers seem to have lacked war altogether suggesting our foraging ancestors were capable of intergroup cooperation and peace. Still, given the near universal presence of at least occasional intergroup coalitionary killings among pre-state foragers it would be surprising if our foraging ancestors lacked war altogether. However, for war to be important in our evolutionary history (or that of other primates), not every group needs to have practiced war and war does not need to occur with the severity or frequency found in agricultural societies nor have a dramatic mortality rate. It only needs to have fitness consequences for participants. Given the lethality of war it would be surprising if it lacked these.

The paleo-archaeological record is similarly complex. There are a significant lack of intact human remains from the Pleistocene, limiting our ability to rely on skeletal materials to date the origins of war. The intact remains there are provide evidence that lethal aggression occurred but was variable in time and place, although it is unclear whether it is war or interpersonal violence. The skeletal evidence for war begins to clearly emerge in the last 15,000 years, and then generally increases with the development of agriculture, hierarchy, and increased availability of intact human remains at most sites. But this does not imply that war did not exist before agriculture or that sedentism explains war. One of the most intriguing findings comes from Paleolithic hunter-gatherers in the Nile Valley where violence declined as groups became more sedentary and population density increased. Even if wars in the Paleolithic had low mortality rates, war could still be an important factor in human evolution. What matters is not whether the rates of death from war were high during the Pleistocene but whether there are positive fitness consequences for that behavior compared to alternative behaviors. Even an occasional and rare behavior with high fitness consequences can create a strong selective pressure.

Despite the many misconceptions about the origins of war and peace, we are coming closer to understanding their origin. Increasing but still sparse evidence from the Paleolithic is demonstrating that war predates agriculture, but as many shallow rooters have argued, the presence of violence profoundly varies across space and time. Long-term field studies of bonobos, chimpanzees, and even gorillas reveal that both lethal violence and cooperation can be natural features of primate species. Based on evidence that includes research on socioecological conditions that favor intergroup violence, evidence from other species, the presence of skeletal injuries from violence among paleolithic populations, and the near ubiquity of war among recent hunter-gatherers, it appears that intergroup coalitionary killing is likely to have been part of our evolutionary history. If war is part of our evolutionary history, then there was likely selection for psychological adaptations to facilitate it, such as ingroup/ outgroup biases, coalition formation, and the strategic use of aggression.

However, this does not mean was the primary or most important selective force in our species history. All human societies appear to have the capacity to flexibly respond to their neighbors through war or peace. The flexibility of contemporary societies as well as ethnographically documented foragers suggests that tolerance and cooperation were likely to have also been important selective features in human evolution alongside the strategic use of coalitionary violence. Just as relationships between societies today can include aggression and cooperation, it is reasonable to expect the same to be true of our foraging ancestors once benefits for cooperation or aggression appeared. To assume that intergroup relationships in the evolution of *Homo sapiens* were predominantly warlike or peaceful is to ignore the complexity of human societies and the differing motivations of individuals—and the fact that both cooperation and aggression can pay but which strategy dominates depends on the context, including the behavior of others.

Taken together, these findings converge on an evolutionary history that is more exciting and complex than just one of war or peace. Our ancestors almost certainly experienced lethal intergroup violence but also cooperated across group boundaries. Due to their important fitness consequences, both war and intergroup cooperation were likely to have been important selective forces in the evolution of modern humans. Recognizing that the capacity for both war *and* peace may be an outcome of our evolutionary history better explains how our species today can create durable peaceful relationships among societies that encompass billions of individuals but at the same time petty grievances and disputes can precipitate war with little provocation. We carry their evolutionary legacy today in our own struggles to create a more peaceful world, but one in which we all too often turn to violence.

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ENDNOTES

[1] Special thanks to Will Buckner for curating and making available many resources on this topic. See this Twitter thread for more insights into recent foragers: https://twitter.com/Evolving_Moloch/status/1083514455802109952