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The evolution of war: theory and controversy

ANTHONY C. LOPEZ
School of Politics, Philosophy, and Public Affairs, Washington State University, Vancouver, Washington, USA

E-mail: anthony.c.lopez@wsu.edu

The use of evolutionary theory for explaining human warfare is an expanding area of inquiry, but it remains obstructed by two important hurdles. One is that there is ambiguity about *how to build an evolutionary theory* of human warfare. The second is that there is ambiguity about *how to interpret existing evidence* relating to the evolution of warfare. This paper addresses these problems, first by outlining an evolutionary theory of human warfare, and second by investigating the veracity of four common claims made against the use of evolutionary theory for explaining warfare. These claims are: (1) ancestral warfare was not frequent or intense enough to have selected for psychological adaptations in humans for warfare; (2) the existence of peaceful societies falsifies the claim that humans possess adaptations for fighting; (3) if psychological adaptations for warfare exist, then war is an inevitable and universal component of the human condition; (4) modern warfare and international politics is so qualitatively different from ancestral politics that any adaptations for the latter are inoperative or irrelevant today. By outlining an evolutionary theory of war and clarifying key misunderstandings regarding this approach, international relations scholars are better positioned to understand, engage, and contribute to emerging scholarship on human warfare across the social and evolutionary sciences.

Keywords: war; violence; evolution; psychology

The use of evolutionary theory for explaining warfare has received increasing attention in many disciplines such as anthropology, social psychology, and economics (Choi and Bowles 2007; Ginges and Atran 2011; Gneezy and Fessler 2011; McDonald, Navarrete and Van Vugt 2012). Scholars of international relations have also begun to apply an evolutionary lens toward the study of specific aspects of warfare such as territoriality (Johnson and Toft 2014) and aggression (McDermott *et al.* 2009; Thayer and Hudson 2010). However, few specifically generate a framework for an evolutionary theory of warfare *per se*, and those that do tend to leave one component of a pivotal link unexamined: the selection pressures that have shaped a human coalitional psychology for

warfare, or the information-processing structure of that coalitional psychology itself.

For example, Thayer (2004) examines the ancestral selection pressures that would have favored xenophobia and egoism in humans, yet his analysis stops short of examining the psychological mechanisms themselves that render this behavior conditional in specific ways. Rosen (2005) provides an excellent examination of the operation of the physiological mechanisms that regulate certain forms of dominance and competitive behavior, but his analysis tends to focus on individuals and is relatively disembedded from a consideration of the coalitional dynamics within which status competition occurs. These and other contributions have been invaluable in their own right; however, if there is anything that this growing research area has confirmed, it is that warfare is the complex output of a human coalitional psychology that regulates behavior across many domains, from xenophobia and status competition to cooperation and even peacemaking (De Waal 2012). In short, it is now possible to sketch an evolutionary theory of warfare that clearly articulates an evolved coalitional psychology as the link between ancestral selection pressures and modern political behavior.

As in any field of inquiry, research on the evolution of warfare is accompanied by recurrent disagreements relating to definitional or interpretational issues, such whether certain patterns of behavior can be generalized across space and time. Although there has been persistent disagreement about the use of evolutionary theory in the social sciences broadly and in international relations specifically (e.g. see Bell 2006; Lopez, McDermott and Petersen 2011; Lopez 2014; Johnson 2015), this paper identifies and engages four particularly prominent claims against the use of evolutionary theory for understanding warfare. These claims are: (1) ancestral warfare was not frequent or intense enough to have selected for psychological adaptations in humans for warfare; (2) the existence of peaceful societies falsifies the claim that humans possess adaptations for fighting; (3) if psychological adaptations for warfare exist, then war is an inevitable feature of human societies; (4) modern warfare and international politics are so qualitatively different from ancestral social life that any adaptations for the latter are inoperative or irrelevant today.

Importantly, it can be unclear what an 'evolutionary theory' of warfare is in the first place. Clarification is required in two senses. First, an evolutionary theory of warfare examines the set of adaptations in the human brain designed by natural selection in response to a range of ancestral selection pressures related to coalitional living and competition (Gat 2006; McDonald, Navarrete and Van Vugt 2012; Lopez and McDermott 2012). This approach not only examines the myriad ways in

which species-typical adaptations regulate internal physiology and external behavior, but also examines how unique environmental and genetic variation helps to explain the inevitable plasticity of political behavior (Sapolsky 2006).[1] Second, an evolutionary theory of warfare must lay out a set of testable assumptions and predictions regarding a range of behavior relating to warfare. However, in contrast to classic IR grand theory that seeks to explain most if not all behavior under a single parsimonious framework (e.g. neorealism's structural determinants of behavior) an evolutionary theory of war explicitly abandons such parsimony. An evolutionary approach shifts the focus from *structure* to *context*. Humans are creatures of context, and as psychological adaptations were designed in response to specific contexts, we are left with evolutionary *theories* of war, rather than one general framework that explains all behavior, or even all violent behavior. Therefore, a guiding theoretical challenge will be to identify the contexts that activate specific psychological adaptations, and to investigate how those adaptations regulate behavior in those contexts.

This article proceeds in four main parts. In part one, I briefly outline the adaptationist approach, which investigates (1) the selection pressures that are likely to have prevailed throughout our evolutionary history; (2) evidence for psychological mechanisms that are likely to have been designed by natural selection in response to these pressures; and (3) how these psychological mechanisms are designed to condition behavior upon ancestrally recurrent and adaptively relevant cues in the contextual environment. These mechanisms often operate 'facultatively', meaning that behavior is irrevocably context dependent *by design*. In other words, behavior is a conditional response to the environment, and evolutionary theory is a tool for analyzing the innate structure of this conditionality.

Parts two and three use this adaptationist framework to help explain the evolution warfare and explore the range of psychological adaptations that likely exist for navigating situations of coalitional conflict, respectively. This exercise contributes to a fuller understanding of warfare in international relations and reveals that our minds are quite literally designed to interpret international politics and warfare through the lens of adaptations designed for ancestral small-scale coalitional politics. In this regard,

[1] A looser conception of 'evolutionary' theory in international politics exists. For example, some scholars apply evolutionary dynamics more as a metaphorical instrument for modeling historical and cultural change, sometimes referred to as 'cliodynamics' (Thompson 2001; Turchin 2003). Although cliodynamic approaches are not mutually exclusive with the evolutionary framework explored here, ambiguity regarding 'mechanism vs. metaphor' in the application of evolutionary theory can generate unnecessary confusion if not directly acknowledged. This paper employs evolutionary theory only in the stricter sense.

adaptationist research has revealed the psychological underpinnings of issues of central concern to international relations scholars, such as public preferences for leadership type in wartime vs. peacetime; the complex connection between inter-group hostility and within-group cooperation (e.g. loyalty and nationalism); and the plasticity of out-group coalitional framing (ally or adversary?) and resultant motivational effects. The fourth and final section examines the veracity of four common claims made against the application of evolutionary theory for understanding human warfare.

International relations has benefited greatly from the incorporation of theory and method from other disciplines, especially economics, but also sociology and anthropology (Snyder 2002). Given the pace of developments in evolutionary science regarding the nature of human competition, aggression, and warfare, greater interdisciplinary exchange at this intersection can only deepen and improve our understanding of warfare.[2]

Adaptationism

Adaptationism is an approach for investigating the relationship between ancestral selection pressures, the functional design of the brain, and behavior (Williams 1966; Mayr 1983; Cosmides and Tooby 1987; Godfrey-Smith and Wilkins 2008). Researchers outside of political science are increasingly turning to evolutionary theory to illuminate the psychological mechanisms that underlie many areas of interest to international relations and political science as a whole, such as the design of institutions (Alexander and Christia 2011; Boyer and Petersen 2011); the nature of religious belief and its relationship to political violence and extremism (Atran and Ginges 2012); political ideology (Smith *et al*. 2012); and adaptations for warfare (Johnson, Wrangham and Rosen 2002; Choi and Bowles 2007; Wrangham and Glowacki 2012). Pessimism regarding the relevance or utility of evolutionary theory for explaining political phenomena no longer holds sway (Lopez, McDermott and Petersen 2011; Johnson 2015); instead the question is not whether, but how evolutionary theory help to explain political processes. Adaptationism is a framework for addressing this question.

[2] In the first half of 2012, special issues on the evolution of human conflict were featured by three prominent scientific journals: *Science*; *Philosophical Transactions of the Royal Society B*; and *Human Nature*. Despite the fact that the range of themes investigated in these special issues included xenophobia, racism, and warfare, and political scientists were mostly absent among the group of contributing authors in each instance.

Species-typical adaptations and genetic differences

The human brain is a complex structure consisting of both universal and individually variable features. It is beyond dispute that basic substructures of the brain exist that are species typical. For example, neurological structures such as the amygdala and hippocampus can be found cross-culturally, and the dedicated function of these structures, as well as the operation of behavior-regulatory neuroendocrine pathways such as testosterone and cortisol, are species typical (Brown 1991; Pinker 1997; Gazzaniga 2009; Zak and Kugler 2011). Indeed, these structures are adaptations, built by natural selection, and they serve a specific set of functions. Although adaptations such as these generate output (increased testosterone, dominance behavior, etc.) that predictably varies by context, the adaptations *themselves* are universal. All complex biological adaptations have certain hallmark qualities; for example, they are reliably developing and operate in a specialized manner to solve reproductive challenges, or 'adaptive problems', that prevailed over evolutionary time (Williams 1966).

For example, evolutionary theorists have argued that in species in which conflict between individuals is commonplace, natural selection should favor adaptations for the assessment of strength in individuals, as well as adaptations that regulate the adaptive use of aggression and violence in such conflicts (Parker 1974; Archer 1988). Subsequently, evolutionary psychologists have tested hypotheses relating to the existence of psychological adaptations in humans and found evidence that humans automatically and cross-culturally detect and attend to ancestrally reliable cues of formidability and strength in others, and that these cues predict propensity toward aggression at both an inter-personal and coalitional level (Sell, Tooby and Cosmides 2009; Sell *et al*. 2009). These results are also consistent with findings that suggest that humans unconsciously track cues in the face and voice that would have ancestrally correlated with threat potential and formidability, and furthermore, that such cues seem to affect leadership preference in wartime and in peace (Puts, Apicella and Cárdenas 2012; Spisak *et al*. 2012). This is an example of adaptationist analysis that examines the existence of psychological adaptations that were favored by natural selection and became species typical in the population because they embodied strategies that produced fitness benefits, on average, in ancestral environments.

However, in addition to complex adaptations in the brain that are species typical in humans, there also exists a tremendous amount of genetic variation among individuals that affects the way these adaptations process information and regulate behavior (Tooby and Cosmides 1990; Buss and

Greiling 1999). For example, although the operation of testosterone in regulating aggression- and dominance-related behavior is a human universal (Archer 2006), genetic differences between individuals may have the effect of setting basal testosterone levels at person-specific levels, making some individuals more or less sensitive to status challenges, for example.

Overall, therefore, we have two important biological features to consider when examining the function of the brain in regulating behavior. First, there are species-typical psychological adaptations designed by natural selection that regulate behavior in response to specific environmental cues. Second, genetic variation among individuals helps to explain some of the individual differences in the operation of species-typical adaptations (Verweij *et al.* 2012). These points help to reveal that an adaptationist approach does not seek to explain *all* behavior as necessarily adaptive (some behavior is clearly maladaptive in modern contexts – as will become clearer below), or even as the product of universal adaptations (some behavior may be better explained by, *inter alia*, genetic variation between individuals). Thus, this approach is distinct from 'pan-adaptationism', which falsely argues that all biological and behavioral traits are adaptive. Pan-adaptationism has been clearly rejected and research has progressed beyond these challenges (Gould and Lewontin 1979; Godfrey-Smith and Wilkins 2008).

Explaining individual differences

The above discussion emphasizes two major biological sources of behavior: species-typical adaptations and individual genetic uniqueness. We can extend this discussion by examining how *both* sources can explain individual differences in behavior.

First, individual differences in behavior can be the result of species-typical psychological adaptations that interact with *unique environments* (Orbell *et al.* 2004). To take a simple example from the aggression system described above, an evolved decision-making algorithm such as 'if bigger than your opponent, advance; if smaller retreat', may generate aggression in certain circumstances by certain individuals, but submission in others (Dawkins 1980). The result is that a species-typical adaptation generates behavioral variation upon interaction with variable environments.

Second, individual differences can be the result of *genetic variation* that affects the operation of species-typical adaptations across individuals. For example, the presence in individuals of a genetic allele dubbed the 'Warrior Gene', in combination with traumatic early life events, enhances aggressive responses to provocation in those individuals (McDermott *et al.* 2009;

Tiihonen *et al.* 2014). This implies that certain thresholds of the species-typical aggression system can vary across individuals as a direct result of genetically heritable variation (i.e. genes or 'alleles' that some individuals possess but others do not, which may make them more or less likely to respond aggressively to threat).

Understanding the interplay of species-typical adaptations and heritable variation is an important theoretical starting point for examining human behavior in the context of evolutionary theory, although typically these two perspectives are examined independently of each other (Lopez and McDermott 2012). There has been growing attention to genetic explanations for political behavior, and these models often utilize theoretical frameworks that focus on heritable variation among individuals (Alford and Hibbing 2004; Alford, Funk and Hibbing 2005; Hatemi *et al.* 2009a, b). There has been relatively less emphasis on adaptationist explanations of political behavior, although this approach is also steadily growing in political science (Sidanius and Kurzban 2003; Thayer 2004; Gat 2006; McDermott, Fowler and Smirnov 2008; Petersen 2009; Thayer and Hudson 2010; Johnson and Fowler 2011; Lopez, McDermott and Petersen 2011). Importantly, both of these approaches reveal that human behavior is at once both deeply plastic and highly malleable not despite, but rather because of this biological inheritance.

Humans as conditional strategists

Although adaptationism as an approach to explaining political behavior is increasingly prominent, many do not directly examine the operation of psychological adaptations as the necessary intermediary between ancestral selection pressures and modern behavior. Instead, the trend has been to infer explanations of modern behavior based on examination of broad evolutionary trends (e.g. Somit and Peterson 1997). Unfortunately, this has left evolutionary-minded social scientists vulnerable to the critique that evolutionary theory is not a useful tool for analyzing social behavior, since applications of evolutionary theory seem to explain a variable (selfishness and altruism) with a constant (evolution). Specifically, for example, some research seems to suggest that our evolutionary history has made us egoistic and selfish (Thayer 2004), while other research suggests that our evolutionary history has made us cooperative and even altruistic (Goodwin 2010). Bell (2006) sees this as evidence of the 'political indeterminacy' of evolutionary theory as a framework for explaining political behavior.

This theoretical challenge is resolved by the recognition that neither evolution nor natural selection affects behavior directly; instead, natural selection builds adaptations, which themselves are the proximate cause of

behavior at the individual level (Symons 1992). Furthermore, an organism does not confront a single reproductive challenge in its environment; rather, the environment is composed of myriad reproductive challenges, each with a potentially unique adaptive solution (Cosmides and Tooby 1994). Given the diversity of adaptive problems in an organism's environment, and given that natural selection designs adaptations that are specialized – and often conditional – solutions to such adaptive problems, adaptationists expect that the human brain contains a diversity of psychological adaptations designed to generate adaptively useful and behaviorally conditional outcomes in specific contexts (Daly and Wilson 1983; Mayr 1983; Barkow, Cosmides and Tooby 1992; Pinker 1997; Buss 2005; Chiappe and MacDonald 2005; Forgas, Haselton and Hippel 2007; Gazzaniga 2009; Morgan *et al.* 2011).

The aggression system described previously is again a useful example: the regulation of conflicts of interest among animals is often resolved through a series of provocative displays in which individuals assess each other and effectively 'decide' whether to challenge or submit (Eibl-Eibesfeldt 1979; Archer 1988; Silverberg and Gray 1992). In the context of agonistic contests, an organism that possessed adaptations instantiated with the strategy 'always challenge' would have been quickly replaced by those that possessed adaptations instantiated with conditional strategies such as 'if bigger, challenge; if smaller, submit' (Dawkins 1980). An analogous situation holds in the domain of exchange and cooperation. For example, one significant adaptive problem that would have faced a social species such as ours would have been choosing whether, and with whom, to cooperate. Evolutionary theorists have argued that if reciprocity and exchange are the products of adaptations designed to regulate behavior in these contexts, these adaptations ought to attend to cues that ancestrally were reliably associated with deception in others and defection-related behavior, as well as the likelihood that the interaction will be repeated (Trivers 1971; Axelrod and Hamilton 1981). Subsequent research by evolutionary psychologists confirmed that humans are surprisingly good at detecting and discriminating against actual and potential defectors, often unconsciously relying on physical cues such as those embedded in facial features to make such determinations (Yamagishi *et al.* 2003; Cosmides and Tooby 2005).[3]

[3] Despite the general statement that adaptations likely exist that equip humans with the ability to detect cooperation and deceit in others, it is manifestly true that humans often make assessment mistakes. Such errors can have many origins. It may be the case that person-specific events in one's life history may have calibrated relevant assessment mechanisms in such a way as to raise or lower one's baseline level of social trust. Or it may also be the case that such individuals

There are several lessons that emerge from careful consideration of adaptationism for the study of political behavior. First, *evolution does not cause behavior; brains do*. That is, adaptations emerged as solutions to specific adaptive problems in the environment, and these psychological adaptations are the proximate cause of behavior. Thus, the functional fit between adaptations and the selection pressures that explain their design should be the starting point of analysis. Second, *psychological adaptations are myriad* and likely exist for many domains, ranging from mating behavior and foraging, to social exchange and warfare. Third, *psychological adaptations often operate according to a specialized conditional logic* because the operational structure of this flexibility correlated with reproductive fitness in ancestral environments. Fourth, *individual differences* can be explained as the product of species-typical adaptations interacting with variable environments, and can also be explained as the product of genetically heritable phenotypic variation between individuals.

The evolution of war

Adaptationist analyses of behavior typically consist of at least two major considerations. The first is to examine, to the extent possible, the character of ancestral selection pressures that may have favored the emergence of the adaptations in question. The second is to apply a task analysis (e.g. with evolutionary game theory) that examines the logical features that a putative adaptation should possess if it is indeed designed for solving a specific adaptive problem. This section ('The evolution of war') will engage the first consideration, while the following section ('Adaptations for warfare') will address the second.

To begin, an adaptationist explanation for warfare, as a type of coalitional behavior, must begin with the recognition that individual-level aggression is fundamentally distinct from (although related to) coalitional-level aggression. Nevertheless, theory that helps explain individual-level aggression can be a useful starting point for explaining aggression in groups. More precisely, the adaptive problems represented by individual and coalitional aggression are distinct and likely have resulted in distinct adaptations for regulating behavior in these domains, even if the operation of these adaptations functionally overlaps. Indeed, although competition and aggression is not zoologically uncommon between individuals of the same species, it is much less common to observe coordinated aggression

possess a genetic allele that causes them to be overly trusting. The neuropsychophysiology of cooperation and trust is in fact a ripe example of the depth of evolutionary explanations of social behavior. For example, see Zak (2006, 2011).

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among groups (Archer 1988; Tooby and Cosmides 1988). Very few species demonstrate this behavior, which in part suggests that the necessary adaptations that enable such behavior are absent. Warfare, as the output of facultative adaptations for coalitional competition, is necessarily a strategic response to the environment. However, this should not be confused with the claim that, given the right environmental conditions, *any* species can be made to exhibit coalitional aggression. There is no evidence to support this latter claim. The environment cannot 'cause' behavior on its own; rather, behavior is a conditional response to the environment, *and* adaptations necessarily structure the conditionality of this response. Thus, we must interrogate the information-processing structure of those adaptations to gain a deeper understanding of both the prevalence and variability of warfare. I begin with a brief look at adaptations for individual-level aggression and then proceed to explore coalitional aggression and its implications for warfare.

Individual-level aggression

There has been a tremendous amount of research on the evolutionary origins of anger and aggression between individuals, especially in humans and primates. This research has shown that aggression represents the output of adaptations designed to negotiate conflicts of interest (Daly and Wilson 1988; Buss and Shackelford 1997; Wrangham 1999a; Sell, Tooby and Cosmides 2009), and that there are substantial sex differences in the incidence of aggression (Daly and Wilson 1983; Van Vugt 2009). These findings are largely explained using sexual selection theory and parental investment theory, which have proven remarkably successful for explaining the distribution of aggression across a number of species, including our own.

Sexual selection occurs when adaptations are favored by natural selection that aid directly in the competition for mates, and patterns of parental investment in offspring determine the nature and intensity of that competition. In humans, as with most primates and mammals in general, female parental investment in offspring has on average been much greater than male parental investment. The greater the parental investment by one sex, the more the opposite sex competes over access to the sex that invests more (Trivers 1972; Symons 1979). This asymmetry means that each sex faces a unique adaptive problem. From the perspective of the high investors, one must be 'choosy' about the right investment – because once the investment is made, the cost of being wrong (i.e. having chosen a poor investment) is great. The adaptive problem from the perspective of the low investors is to access as many investment opportunities as

possible – because if investing is cheap, you should invest as often as possible. Low investors compete over access to high investors, and the greater the investment asymmetry between the high and low investors, the more intense the competition, and the more selection tends to favor violence and aggression for use in the competition between low investors for access to high investors.

An early obligate investment asymmetry between males and females has been evolutionarily recurrent (e.g. sperm production vs. egg production and 9-month gestation period), and cross-cultural evidence consistently reveals a greater relative incidence of aggression among men than women. As just a few examples, men are more likely than women to be the targets and perpetrators of violence (Daly and Wilson 1988; Van Vugt 2009); to respond to threat with xenophobic reactions to out-groups (Schaller, Park and Mueller 2003); to endorse warfare after being primed with pictures of attractive members of the opposite sex (Chang *et al*. 2011); to 'show-off' via conspicuous self-sacrifice (McAndrew and Perilloux 2012); and to overestimate their chances of success in violent encounters (Johnson, Wrangham and Rosen 2002; Johnson *et al*. 2006). The interaction of sexual selection and parental investment has tended to render aggression relatively more reproductively worthwhile for males than females. Theory also suggests that where aggressive encounters between individuals is a significant adaptive problem, selection should favor adaptations for assessment that adaptively regulate aggression in these contests (Parker 1974; Archer 1988). Subsequently, it has been found that cues in the body, face, and voice of males, but not females, reliably correlates with aggressiveness, and that people are surprisingly good at inferring the formidability of males based on these cues (Sell *et al*. 2009; Haselhuhn and Wong 2011; Puts, Apicella and Cárdenas 2012; Short *et al*. 2012).

Coalitional aggression

Theory and evidence presented above help us to understand the selection pressures that have favored aggression as a reproductive strategy at the individual level that is relatively more 'cost-effective' for males than females. Although the issue of individual-level aggression is certainly not irrelevant for international relations (particularly as it relates to issues of terrorism, for example), this alone does not yet help us understand the nature of *coalitional* aggression. We must begin, however, with the recognition that war, or coalitional aggression, can take a variety of forms. There are two particularly common forms of coalitional aggression that have been well studied: the raid and the pitched battle. The former tends to be characterized by nighttime attacks on rival groups that exploit stealth,

the element of surprise, and quick retreat. Raids can exist in the context of feud spirals or as isolated events. Battles, however, occur when relatively larger groups of 'combatants' from rival groups, that are relatively equal in size, engage each other in attrition-style fighting. Battles are deadlier and less common than raids, and therefore an evolutionary theory of coalitional aggression must take account of this distinction (Johnson, Wrangham and Rosen 2002; Wrangham and Glowacki 2012). Specifically, we must explain how adaptations could evolve that motivate the sort of risk taking necessary to sustain deadly pitched battles.

There are two broad conditions that must be satisfied in order for natural selection to favor adaptations that make coalitional aggression possible – whether raiding or battles. Furthermore, these two conditions also simultaneously help to explain why humans are willing to engage in risky symmetric battles, as well as why such encounters are relatively uncommon among our chimpanzee cousins.

Condition 1: reproductive benefits: First, as a reproductive strategy, the fitness benefits of coalitional aggression must outweigh its significant costs (Wrangham 1999a; Liddle, Shackelford and Weekes–Shackelford 2012; McDonald, Navarrete and Van Vugt 2012). The fitness benefits of raiding have been well studied. Primatologists have shown that the outbreak of chimpanzee coalitional violence reliably occurs in the context of inter-group hostilities where one coalition outnumbers an opposing coalition by an approximate ratio of three-to-one (Manson and Wrangham 1991; Wrangham and Peterson 1996). Coalitional violence in these instances has been reproductively successful because it has correlated with expanded territory, greater probability of success in future contests, and facilitates access to both material and reproductive resources (Mitani, Watts and Sylvia 2010). Chimpanzee coalitional violence occurs almost exclusively in the context of power asymmetries, and in these contexts it is relatively easy to see how an overwhelming victory over a weaker group could be reproductively advantageous. In humans as well, coalitional raiding remains the most common form of violence among groups, and appears to mirror the chimpanzee model surprisingly well (Wrangham and Glowacki 2012). This is further supported by evidence that ancestral coalitional environments may have approximated Lanchester's square law of combat, in which the material and reproductive benefits of successful asymmetric aggression were substantial (Johnson and MacKay 2015).

Although the reproductive benefits of coalitional raiding are clear, human coalitional violence also takes the form of pitched battles of attrition between coalitions of relatively equal size in which victory appears to be more a function of 'fighters left standing' than 'resources gained'. This kind of high-risk/high-loss activity is harder to explain, at first blush, with an

evolutionary lens, and it is certainly inconsistent with the chimpanzee model of coalitional violence. However, a closer look at evolutionary theory reveals that it is indeed possible for natural selection to favor coalitional violence even if 'victory' is purchased at the cost of the death of all coalition members minus one (Tooby and Cosmides 1988; McDonald, Navarrete and Van Vugt 2012). This is because, as mentioned above, male reproductive success is limited only by *access* to mates; therefore, if reproductive resources are zero-sum, the missed reproductive opportunities of the fallen necessarily equal the gained reproductive opportunities of the surviving victors. In other words, a genetically heritable decision rule that motivated participation in these types of coalitional violence would successfully be passed to future generations and spread so long as (1) the coalition is 'victorious' on average; (2) reproductive opportunities are reallocated among the survivors; and (3) the perceived pre-battle distribution of individual risk is effectively random.

Having identified the conditions under which both coalitional raiding and relatively symmetric conflict can evolve, the next logical question is: have these conditions in fact prevailed ancestrally? Although I will return to this question in the final section below, archeological, anthropological, and game theoretic evidence suggests that these selection pressures have indeed endured over human evolution (Manson and Wrangham 1991; Gat 2000; LeBlanc and Register 2003; Bowles 2009; Wrangham and Glowacki 2012). The result is that ancestral coalitional aggression has represented a reproductively worthwhile endeavor in which the average *fitness* benefits (measured over evolutionary time) have tended to outweigh the *somatic* (or immediate, physical) risks. Combined with male overconfidence in warfare, which has been hypothesized to serve the function of bluff delivery in the context of pitched battles (Wrangham 1999b; Johnson, Wrangham and Rosen 2002), it is in fact unsurprising, from an evolutionary perspective, that risk taking, brinkmanship, overconfidence, and symmetric aggression between coalitions seem to be staples of human inter-group conflict. The result of this analysis is to turn the original puzzle on its head: the puzzle is not why *humans* display patterns of pitched battle, but why chimpanzees *do not*. Indeed, part of the answer may be suggested by the second condition necessary for the evolution of coalitional violence.

Condition 2: cognitive adaptations for *n*-person cooperation: If the first condition that must be satisfied for the evolution of war in humans is that it is reproductively beneficial, the second is that, as a cognitive task, coalitional aggression as a collective action requires sophisticated information-processing systems in the brain that allow the simultaneous tracking of *n*-person variables, such as the level of others' participation, distribution of risk, formidability of out-groups, and the probability of

success (Tooby and Cosmides 1988; Tooby, Cosmides and Price 2006). In other words, given that coalitional aggression is reproductively worthwhile, its execution assumes and requires the presence of a host of adaptations necessary to perform the associated cognitive tasks of cooperation and coordination. Do such adaptations exist? Indeed, research in social psychology, biosocial anthropology, and cognitive neuroscience increasingly demonstrates that humans have been equipped by natural selection with a reliably developing evolved 'coalitional psychology' (Kurzban, Tooby and Cosmides 2001; Wagner, Flinn and England 2002; Navarrete *et al*. 2004; Cosmides and Tooby 2005; Kurzban and Neuberg 2005; Schaller, Simpson and Kenrick 2006; Forgas, Haselton and Hippel 2007). I have elsewhere explored many of the components of human coalitional psychology relevant for international relations (Lopez, McDermott and Petersen 2011), and the rest of this discussion below will illuminate to those aspects of coalitional psychology that help explain human behavior in war.

The preceding discussion establishes two important evolutionary conditions necessary to explain the unique pattern of coalitional aggression demonstrated by humans. However, some evolutionary theorists argue that warfare, particularly human warfare, poses a very special kind of selection pressure that is distinct from orthodox natural selection that shapes adaptations for the benefit of individual organisms. This alternative is known as group selection. Once this approach is discussed, we can then turn to analysis of the products of these evolutionary processes – adaptations for warfare themselves.

The role of group selection: Adaptationist analyses of warfare examine the evolved mechanisms in the human brain that were designed by natural selection in response to the ancestral selection pressures relating to inter-group conflict. However, the above discussion has mostly taken for granted that these adaptations were shaped by natural selection occurring at the level of the individual. This means that heritable traits are passed to future generations and spread to the extent that they generate relative fitness benefits for the *individuals* that possess them.[4] In this case, we would say that adaptations are designed to operate 'for the benefit of the individual'. However, it is theoretically possible that psychological adaptations exist that operate for the benefit of the group. These adaptations would be built by natural selection operating at the level of the group, or simply, by

[4] Strictly speaking, all adaptations benefit the genes that code for them; however, it is convention to operate under the assumption that adaptations exist 'for the benefit of the individual' as it is the differential survival and reproduction of individuals that affects gene frequencies in future generations. Thus, the *unit* of selection is always and inevitably the gene, however, the *level* at which selection operates tends to be the level of individual organisms.

'group selection'. Although these processes are clearly not mutually exclusive, they are analytically distinguished by the following question: are adaptations built by natural selection because of the benefits they confer to the individuals that posses them, or because of the benefits they confer to the groups within which individuals live? Or, alternatively, what is determining directional change in gene frequencies across generations – the success of individuals (individual selection), or the success of groups (group selection)?

Group selection was originally offered by Darwin and Wynne-Edwards to help explain certain forms of altruism that seemed puzzling or difficult to explain as a function of genetic self-interest. These are cases in which individuals accept a net cost to themselves in order to confer a benefit on another individual within one's group (Wynne-Edwards 1962). By the middle of the 20th century, however, game theoretic models had demonstrated that the conditions that must hold in order for group selection to occur are uncommon (Hamilton 1964b; Williams 1966; Maynard Smith 1976). Simultaneously, research on inclusive fitness and reciprocal altruism helped explain how certain forms of altruism could indeed be explained by individual-level selection (Hamilton 1964b; Williams 1966; Trivers 1971; Krasnow *et al*. 2013). Nevertheless, by the late 20th century, group selectionists argued that these restrictions had been overstated (Wilson 1997; Sober and Wilson 1999). Apart from the often-intense scientific turf battles this debate has generated, this resurgence has in fact led to a greater degree of useful nuance among evolutionary approaches for explaining aspects of warfare.

One example of this productive nuance is the emerging distinction between 'genetic' group selectionists and 'cultural' group selectionists. Genetic group selectionists continue to argue that ancestral warfare was frequent and intense enough to have selected for biological adaptations in individuals that regulate behaviors for the benefit of the group even though they may be individually disadvantageous, such as forms of heroism, extreme risk taking in battle, or other forms of within-group altruism (Choi and Bowles 2007; Lehmann and Feldman 2008; Bowles 2009). 'Cultural' group selectionists focus on explaining the content and distribution of social norms as a cultural by-product of inter-group warfare (Ginges and Atran 2011; Mathew and Boyd 2011). These scholars argue that in the context of intense and repeated coalitional conflict, groups that cultivated social norms of sacrifice, sharing, and pro-sociality would have prevailed in conflict over other groups whose ability to cooperate was hindered by the absence of such norms. Thus, for 'genetic' group selectionists, warfare exerts a biological selection pressure for pro-social psychological adaptations in the brain, while for 'cultural' group

selectionists, warfare operates through 'cultural selection' to select for pro-social cultural norms. Importantly, these approaches are not mutually exclusive, and warfare is often the independent variable, not the dependent variable.

A second example of this nuance among evolutionary approaches is the greater attention given to the plausibility of multi-level selection, or, natural selection operating at more than one level simultaneously. Although space limits a full consideration of this paradigm here, it is sufficient to note that in effect it represents a tactical retreat from classical arguments that insist on the necessary prominence of selection pressures operating at only one level. From this perspective, the task for understanding the design of a given adaptation, is to identify which levels operate and what their relative impact is on changing gene frequencies (Lopez 2014).

Having now explored the ancestral selection pressures that help to explain the emergence of warfare in humans, we can turn now to an investigation of the products of those selection pressures; namely, the design and operation of psychological adaptations for warfare.

Adaptations for warfare

Warfare, or coalitional aggression generally, is first and foremost a collective action problem. Even simpler examples of stealth raiding entail collective action problems such as labor recruitment and enemy targeting that are often resolved and directed by an individual of disproportionate influence in the group (Glowacki and Wrangham 2013). Thus, to the extent that ancestral inter-group violence posed a set of selection pressures that have favored adaptations for warfare in humans, the general prediction is that modern contexts of inter-group violence continue to activate a host of evolved psychological heuristics regarding the 'proper' solution to collective action problems in those contexts.[5] In other words, our modern-day social, moral, and political intuitions about how people ought to behave when our group or country is threatened are likely the product of adaptations that were designed to facilitate adaptively successful collective action in response to out-group threat in ancestral environments.

From this general proposition, we must proceed to identify the specific ways in which collective action problems must have been solved in ancestral contexts in order to successfully prevail in, or prevent, inter-group violence. The result of this analysis is to outline the architecture of coalitional

[5] One critique of this theoretical claim might be to accept, *prima facie*, the proposition that such adaptations exist, but then to refute that they continue to operate in a relevant way in modern contexts. I will return to this below.

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motivation in warfare, which represents the set of psychological adaptations that exist to solve evolutionary challenges related to the outbreak of war (*ante bellum*), the conduct of fighting (*in bello*), and post-conflict relations (*post bellum*). For the sake of scope, I will focus on the first two sets of challenges, while also noting that research on the psychological challenges and strategies of post-conflict forgiveness and reconciliation is well underway (McCullough 2008; Burnette *et al*. 2012; McCullough, Kurzban and Tabak 2013).

Psychologie, ante bellum

Although there is extensive debate on the causes of war, a useful point of departure is the bargaining theory of war in international relations (Wagner 2000; Reiter 2003). In addition to offering the most prominent set of explanations for the outbreak of war, it is also particularly useful because it offers a taxonomy within which to incorporate psychological motivations for warfare. Lake, for example, argues that psychological and rational approaches to warfare are indeed 'compliments, not substitutes' (2010, 10). Thus, I will briefly explore the rationalist explanation for war, and provide examples of how an adaptationist approach to psychology and behavior can expand upon it.

According to Fearon (1995), given that wars are costly, if bargains short of war exist that will allow states to arrive at their goals without paying the cost of fighting, states should be able to identify and agree to these terms and avoid a costly war. If war erupts, therefore, it is necessarily a bargaining failure, which can occur for at least three reasons. First, anarchy may undermine the ability of self-interested actors to commit to war-avoiding bargains in the long run, which by extension undermines the success of any agreement in the present (Powell 2006). Second, even though war is costly, rational actors also wish to do well in the pre-war bargaining phase; thus, they face strong incentives to misrepresent their capabilities and interests to their adversaries in order to prevail in negotiations, which can inadvertently eliminate the range of war-avoiding options available to states. Third, when rational actors deliberate over issues that they perceive to be indivisible, the 'bargaining space' over which they might compromise is effectively eliminated, and warfare is the result of this bargaining failure.

Fearon admits that issue indivisibilities should not exist in a rationalist world, since any material object is, in principle, subject to division. Thus, upon closer inspection, this third category of rationalist explanations for war in fact opens the door to several non-rational motivations for war.[6]

[6] This is not to say that there is no room for evolutionary insight in the other two rationalist explanations. For example, anarchy has been an enduring force not just in international relations,

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The result is an expanded taxonomy that incorporates both rationalist and non-rationalist explanations for war. Adaptationist approaches to the outbreak of war suggest at least two ways in which issue indivisibilities spark the flames of war: sacred values and territory. Furthermore, an adaptationist lens reveals that another assumption of the rationalist framework for war may be violated more often than acknowledged: the assumption that war is costly. I discuss each in turn.

Sacred value and territory: According to Tetlock, sacred values are treated as 'possessing transcendental significance that preclude comparisons, trade-offs, or indeed any mingling with secular values' (2003, 320). Although the issues, objects, and symbols that groups hold as sacred vary tremendously across space and time, the nature of sacred values and people's reactions to the violation of these values are cross-culturally universal. In other words, the adaptations that shape these intuitions are universal, even while their output across space and time is predictably variable. According to the sacred value protection model, individuals react to violations of sacred values with a combination of moral outrage and moral cleansing – the former meant to target violators with a range of punitive sentiment and behavior, and the latter meant to reaffirm sacred values and strengthen the bonds of within-group solidarity (Tetlock *et al.* 2000). Sacred values need not be religious, but when they are, the predicted consequences are all the more dangerous, as is witnessed by the Danish cartoon depictions of Mohammad in 2005 and the proposed burning of the Quran by Terry Jones in 2010.

Sacred values are particularly significant when they are imbued in territorial claims. Territory, by its very nature, should easily lend itself to rationalist division. Indeed, great powers have historically found the problem of territorial division as easy as drawing lines on a map, such as during the Berlin Conference of 1885 or the division of the Middle East under the 1916 Sykes–Picot agreement. Yet, these foreign territorial divisions often remain a source of incredible tension, particularly under two conditions: when rival inhabitants each view themselves as long-time residents (Johnson and Toft 2014), and when they view the land as sacred. In these instances, the perceived indivisibility of territory thwarts movement toward war-avoiding bargains, by at best foreclosing their existence, and at worst sparking outrage and aggression at even the prospect of such a division. Such outrage could not be predicted if the issue were merely that the land is perceived as indivisible for some reason having to do with its

but also especially throughout the vast majority of human evolution on the lawless Pleistocene. Its impact on our evolved psychology cannot be underemphasized (Gat 2009).

material properties alone (and not because it is sacred). In other words, if the problem were merely that an object by its nature precluded division, there would be no reason that the consideration or proposal of its division would ignite hateful outrage. Instead, the prospect of dividing the indivisible would simply be received as puzzling and illogical. Thus, knowing simply that rational actors may somehow stumble upon issue indivisibilities offers a necessarily incomplete explanation of both the causes and contours of the problem.

War is costly … but revenge is sweet: The human drive for revenge represents an undoing of a central assumption of the rationalist framework for war; namely, that war is costly. This undoing is partially demonstrated by the fact that the experienced motivation for revenge seeking is not the future benefit of deterrence, but merely the imposition of harm and suffering for its own sake in the present (Schelling 1966; Löwenheim and Heimann 2008). Revenge seeking against an aggressor can be favored by natural selection because its effect, when successful, is to reverse the fitness benefits gained by the aggressor from exploitation or theft, for example (Barash and Lipton 2011; Boehm 2011). Successful revenge can also indirectly solve the adaptive challenge of deterrence by inspiring caution in would be aggressors through the establishment of a reputation for engaging in costly retaliatory violence (McCullough, Kurzban and Tabak 2013). In this sense, a motivation to seek revenge operates as a commitment device (Frank 1988), designed specifically to overwhelm considerations of cost and future deterrence for the sake of returning suffering upon an enemy. Thus, although revenge can evolve because it in part solves adaptive problems of deterrence, its operation generates a desire to cause harm for its own sake, independent of any expected deterrence value.

Apropos, neurological evidence has revealed that the prospect of inflicting retaliatory punishment triggers pleasure centers in the brain, suggesting that, at least when revenge is the motivation, violence may be perceived as a benefit rather than as a cost (de Quervain *et al*. 2004). At the very least, it suggests that the war-is-costly assumption merits revision by examination of the contexts in which adaptive heuristics operate to endogenously incentivize behavior that may otherwise appear irrational to *homo economicus*. Importantly, revenge is not merely in the error term; rather, it remains among the most common motivations for violence cross-culturally and continues to be particularly salient among states and non-state actors (Barash and Lipton 2011).

Hitler's rise to power is a well-known example of the ability of revenge to compel great power behavior, but it would be false to imagine that revenge might only be relevant for non-democratic states captured by despotic elites. Churchill, for example, was persuaded by the opposite opinion, and

proposed that 'democracy is more vindictive than Cabinets [sic]. The wars of peoples will be more terrible than those of kings' (Levy 1988, 659). Indeed, Gaddis argues that in fact the very foundations of American identity have been shaped by its reaction to surprise attacks on its homeland, such as the attack on Pearl Harbor as well as the terrorist attacks of 11 September 2001. The latter is particularly emblematic of the central characteristics of revenge, such as enhanced xenophobia and indiscriminate targeting of individuals that fit out-group profiles (Michener 2012), as well positive jubilation at the discovery that the suspected mastermind of the terrorist attacks had been killed (Adams 2015).

The desire for revenge is often at the heart of intractable conflicts that remain hot, such as the Arab–Israeli conflict, and it can also remain at the heart of conflicts that remain frozen, where it festers in cultural narratives of defeat and in the minds of resentful elites (Holbrooke 1999). Therefore, although the consequences of revenge have been well studied, its antecedents are equally important to recognize, particularly the role of national humiliation. For example, in the context of the 1973 Yom Kippur War, Kissinger recognized the need to 'allow the Arabs a limited victory, even if largely mythical. Such action was meant to relieve them of enough shame and humiliation to allow for making peace' (Harkavy 2000, 348). Savvy elites may occasionally recognize the potential for conflict-escalating events and act to forestall or mitigate them, such as in this episode. However, a deeper understanding of the role of humiliation and revenge in international relations can only broaden this understanding and even provide policymakers with clearer guidance during times at which our psychology is specifically designed to cloud rather than clarify cost-benefit analysis.

Psychologie, in bello

The bargaining theory of war has provided scholars with a useful set of propositions about the conditions under which bargaining failures may lead to war. Adaptationist perspectives on psychology and behavior broaden our explanations of war in novel ways by, for example, explaining the origin and nature of issue indivisibilities as well as explaining why and when the war-is-costly assumption of rationalist models may not be ecologically valid. Another feature of rationalist models of war has been their tendency to treat actors as unitary (Lake 2010). Although a unitary actor assumption for international relations is not always invalid (Lopez, McDermott and Petersen 2011), we certainly deepen our understanding of war by interrogating the within-group dynamics that may sustain or mitigate inter-group violence. It is to these dynamics that we now turn.

Rally 'round the group': All politics, from the local to the international, is a story of group identity. There is significant evidence that humans instinctively categorize themselves and others according to socially relevant groups with associated identities, and these identities are active in shaping behavior across levels of analysis, and perhaps most dramatically in the case of inter-group violence (Lopez, McDermott and Petersen 2011; Pietraszewski *et al.* 2015). Some of these dynamics have been explored through the application of social identity theory to international relations, which has made important contributions regarding warfare and co-operation (Mercer 1995; Curley 2009), and scholars have applied an evolutionary perspective on social categorization to explain the intensity and recurrence of inter-ethnic conflict (Alexander and Christia 2011; Crisp and Meleady 2012).

Although these within-group biases are powerful determinants of motivation and behavior in the context of warfare, the nature and scope of group boundaries are exceedingly plastic. Yet, despite the plasticity of social and political group borders, the presence of inter-group conflict itself is reliably sufficient to trigger a host of motivational and behavioral effects, such as increased levels of cooperation within groups (Puurtinen and Mappes 2009; Burton-Chellew, Ross-Gillespie and West 2010), a particular eagerness to punish those who do not cooperate, as well as a heightened sense of shame and guilt among non-participants (Gneezy and Fessler 2011). In other words, these instinctual categorizations adaptively direct the magnification of in-group loyalty and cooperation in the context of out-group conflict, in which expediency of action and solidarity of purpose were pivotal determinants of success (Cikara, Botvinick and Fiske 2011; Mahajan *et al.* 2011).

The link between within-group cooperation and inter-group conflict is a useful illustration of the way in which natural selection has built adaptations that are designed to activate a set of cognitive and motivational systems upon detecting one powerful cue in the environment: inter-group conflict. Although the motivational output of these systems is an important determinant of behavior, humans are also particularly good at manipulating the operation of these emotions in others for personal or political gain. For example, emotional motivators such as shame play a powerful role in shaping beliefs regarding the urgency and value of participation in coalitional violence – even in modern warfare. One particularly poignant example of the role of shame (and its manipulation) in warfare is illustrated by the Order of the White Feather in Great Britain during World War I. As it became clear the war would drag on longer than anticipated, the Order sought to manipulate the shame of non-participating service-age males into participating by having females publicly bestow white feathers upon them

(Hochschild 2012). Participation in collective violence against an adversary involves the manipulation of many positive as well as negative emotional motivations, and investigation into the evolved machinery that structures such motivations can illuminate debates regarding public support for warfare as well as questions regarding the recruitment patterns and tactics of terrorist organizations.

Of course, most instances of war are not examples of perfect within-group solidarity, and therefore we are left with the necessity of explaining why, for example, some are compelled to fight while others resist participation and even rebuke the effort. Although this is a complex puzzle with many dimensions, evolutionary theory may help to explain one component of this puzzle. First, recall that not all forms of coalitional violence are equal – two particularly common forms are raids and battles. However, it may also be the case offensive and defensive coalitional violence have been important and ancestrally recurrent types of coalitional violence, each with their own sets of reproductive costs and benefits (Tooby and Cosmides 1988). One important difference between the two forms of violence is that defensive coalitional violence may have generated benefits in the form of public goods more often than offensive coalitional violence (Lopez 2010). Therefore, one prediction would be that the framing of conflict as either offensive or defensive would trigger distinct patterns of support for the coalitional action, leading to wider support for defensive rather than offensive warfare.

Using this distinction, one could predict a very broad pattern of within-group coalitional unity and the resultant distribution of emotions such as shame among non-participants simply by identifying the predominant framing of the conflict along the single dimension of offense vs. defense. In other words, we might hypothesize that while support for defensive action is expected to be relatively wide and deep, support for offensive action would be greatest among (1) those it benefits directly, and (2) those who misperceive the offensive action as defensive. It is perhaps no surprise, therefore, that much political haggling and arm-twisting revolves around the rather parochial question of 'who started it?' Elites and political leaders play a prominent role in framing the answers to these critical questions.

Rally 'round the leader': The above discussion illustrates that many coalitional dynamics within one's group are triggered and shaped by important and adaptively relevant contextual features such as the existence and nature of out-group threat. At the center of these coalitional dynamics, of course, is the issue of political leadership. Experimental evidence suggests that individuals possess psychological adaptations that evolved in response to the challenge of identifying

effective leadership for coalitional action (Van Vugt and Ahuja 2011; Price and Van Vugt 2014). Indeed, leadership can dramatically reduce the cost of coalitional aggression by providing focal points and enhancing coordination. Although people are often willing to defer to leaders and to allow them to keep a share of the group benefits (Hooper, Kaplan and Boone 2010), people remain sensitive to the prospect of leadership exploitation (Smith *et al.* 2007). This indicates that an evolutionary arms race likely existed between leaders and followers in which selection favors leadership as a solution to collective action problems, but there is a counter-selection pressure in which follows resist the tendency of leadership to drift toward despotism and undermine collective action (Van Vugt and Ahuja 2011).

Of course, as mentioned above, all collective action is not equal, and different individuals – by virtue of their personality or formidability – may prove to be more effective leaders in wartime than in peace. To the extent that this has proven true over evolutionary time, we would hypothesize that adaptations exist that lead individuals to prefer particular types of leaders contingent upon the immediate context. Indeed, Spisak *et al.* (2012) show that support for specific leaders depends on cues in the face that ancestrally correlated with success and failure in specific coalitional environments. Regardless of the sex of the prospective leader being evaluated, people tended to prefer masculine faces in wartime, and people tended to prefer feminine faces during peacetime. In a related study, age was also a significant predictor of support for a prospective leader in wartime. Spisak (2012) hypothesized that, if it was the case ancestrally, all else equal, that greater age tended to correlate with greater status and dominance leadership, then during wartime, individuals should be especially supportive of older candidates. Experimental evidence confirmed these expectations even when controlling for the actual and perceived political experience of the candidates.[7]

The link between within-group cooperation and inter-group conflict, as well as the challenge of leadership, are two broad domains that allow us to think more clearly about what adaptations ought to exist to regulate behavior in wartime, and specifically how natural selection builds adaptations that are designed to operate facultatively upon the detection of a range of contextual cues specific to the occurrence of inter-group hostilities.

[7] Importantly, as Spisak (2012) clarify, the hypothesized ancestral relationship between age and status is likely quadratic, as at very extreme old age, for example, there must have been an inverted relationship between age and dominance-related status.

Grand theory in international politics?

The architecture of coalitional motivation sketched above has one major implication for grand theory in international politics: it must either be built upon a model of the mind that is not ecologically valid, or grand theory is simply not possible. Specifically, grand theories of international politics that seek to explain a range of behavior across a multitude of domains by reference to only a few structural or cognitive principles are likely to be theoretically hamstrung by their failure to recognize and incorporate the motivational plurality that actually drives behavior and its exquisite sensitivity to context. Adaptationism is a framework for uncovering the range of contexts, or 'domains', that trigger evolved adaptations, as well as for uncovering the ways in which evolved adaptations are designed to respond to context, as presented above. What we are necessarily left with are *theories* of warfare, and the tools for expanding our understanding of the coalitional psychology that shapes inter-group violence in many contexts. Neither realist anarchy nor the enlightened self-interest of liberalism is sufficient to explain the range of behavior of interest to international relations scholars. Constructivism is similarly incomplete to the extent that it fails to acknowledge the material properties of the mind that are active in producing and responding to social values and norms, which, for example, is necessary in order to explain why some norms seem to be more 'sticky' than others (Adler 1997; Lopez and McDermott 2012).[8] Previous attempts at grand theorizing in international relations have generated useful middle-range insight into important dynamics, such as alliance formation and neoliberalism's solutions to the prisoner's dilemma (Milner 1992). However, future research must incorporate and build upon these specific insights while abandoning the quest for a single grand theory of international politics.

Now that the theoretical framework for explaining and exploring the evolution of coalitional aggression, or warfare, has been established, we can turn to a closer examination of four critiques that are often levied against evolutionary approaches to warfare.

Fighting fallacies

There are four prominent claims against the application of evolutionary theory for understanding warfare. Although the fallacious nature of these claims should now be largely transparent given the preceding discussion,

[8] This trend is experiencing reversal as constructivists increasingly turn to psychology to solve this problem. See, for example, Shannon and Kowert (2011).

these claims deserve to be singled out because they are particularly enduring and forceful. Consequently, I engage them here in order to expose their assumptions and evaluate their merit.

Ancestral warfare was not frequent or intense enough to have selected for psychological adaptations for warfare

Adaptationist analyses depend in large part on our ability to survey and understand ancestral environments. When experimental results fail to verify hypotheses regarding the design of adaptations, it can be due to the fact that we are incorrect regarding the structure of ancestral selection pressures (e.g. such pressures are either misspecified or non-existent), or it can be due to the fact that the logic that links the psychological design or 'form' of adaptations to their ultimate ancestral purpose or 'function' is flawed (Confer *et al.* 2010).[9]

Consequently, there are two forms of evidence upon which to rely when evaluating the prevalence of ancestral warfare: we can survey the current state of research on direct and indirect evidence of ancestral coalitional warfare, especially in fields such as archeology, paleoanthroplogy, and primatology (Tooby and DeVore 1987), and we can survey current experimental evidence with modern humans to examine the extent to which hypotheses regarding the structure of psychological adaptations for warfare are verified given a set of ancestral selection pressures. As I have discussed above, there is substantial laboratory and cross-cultural evidence that humans seem to be endowed with a coalitional psychology, and that such adaptations are specialized for the regulation of behavior, motivation, and cognition in the context of warfare. However, what is the state of knowledge regarding direct and indirect evidence of coalitional warfare in ancestral environments?

Primatology: Primate studies have mostly revealed that if there is an evolutionary origin of human violence, it can be traced back at least to the hominid–chimpanzee split (Manson and Wrangham 1991; Wrangham and Peterson 1996; Wrangham 1999a). There are clear selection pressures favoring coalitional violence, and the fitness benefits of such activities have been measured and replicated (Mitani, Watts and Sylvia 2010; Wilson *et al.* 2014). Chimpanzees appear equipped with psychological mechanisms that adaptively regulate the expression coalitional aggression based on cues such as relative power differentials between groups.

[9] This theoretical dynamic is not entirely dissimilar from rational choice models, in which it is possible to backsolve from revealed preferences to the structure of underlying decision-making mechanisms.

Nevertheless, two factors complicate our ability to infer a clear evolutionary link between chimpanzees and humans. The first is the existence of relative peace among bonobos, which genetic tests reveal are nearly as similar to humans as are chimpanzees (Prüfer *et al.* 2012); the second is the fact that humans exhibit a form of warfare that chimpanzees do not – sustained battle between coalitions of roughly similar size. Although genetic tests have revealed that bonobos are as closely related to humans as chimpanzees, we do not yet know the substance of that relationship. Indeed, humans share many similarities with *both* bonobos and chimpanzees (Rilling *et al.* 2011; Boehm 2012b). Furthermore, real differences between chimp and human coalitional aggression do not contradict the empirical fact that among both chimps and humans, the most common form of coalitional aggression is the lethal raid (Gat 2006; Wrangham and Glowacki 2012). Lastly, regarding the fact that chimps do not engage in large-scale coalitional aggression, recall that the evolution of warfare in humans requires both reproductive benefits and unique cognitive adaptations for *n*-person cooperation and coordination. Given the cognitive requirements for sustaining and operating large *n*-person coalitions, it would in fact be more puzzling if chimpanzees *did* engage in large coalitional battles but humans did *not*. In short, coalitional aggression is reproductively worthwhile for both chimps and humans, but it is likely that unique cognitive abilities in humans allow greater coalitional maneuverability and provide the space for cultural innovations to sustain such coalitions. Indeed, this divergence between the chimp and human pattern of warfare is to be expected, and not an anomaly. Taken together, this supports the conclusion that human coalitional violence has roots in our primate past, but also that this is not the end of the story; we must investigate aspects of the coalitional environment that have been unique to human evolutionary history after the hominid split in order to fully understand the design and structure of putative adaptations in these domains.

Anthropology: The prevalence, intensity, and frequency of hunter-gatherer warfare has been a topic of intense debate, in part because the character of warfare in this context is believed to offer a partial window into our evolutionary past as a species. What is certain is that warfare is not a perfect human universal, strictly speaking; depending on measurement techniques, there are usually a handful of cultures that scholars can point to as existing relatively free of coalitional violence for certain periods of time. However, despite the absence of perfect universality in the strictest sense, it is nevertheless also the case that the overwhelming majority of cultures surveyed do indeed experience some form of coalitional violence (Ember 1978; Keeley 1996; LeBlanc and Register 2003; Gat 2006).

Not surprisingly, at the heart of disagreements over the *prevalence* of warfare are questions regarding the *definition* of warfare, since the latter necessarily affects one's conclusions regarding the former (Palmer 2006). If it is a useful window into ancestral environments, the character of modern hunter-gatherer warfare does seem to suggest that coalitional violence was prevalent in some form during our evolutionary history, but definitional disagreements will likely prevent any conclusions on the matter.

Definitional disagreements, however, do not hinder our understanding of the existence of adaptations for warfare; they merely force us qualify our arguments, which can be useful rather than debilitating. For example, the Correlates of War (COW) project defines war as 'sustained combat, involving organized armed forces, resulting in a minimum of 1000 battle-related fatalities within a 12 month period'. If we go by this definition, then it is clear that there can be no adaptations for warfare of this type, since this type of warfare was only possible well after the dawn of agriculture and is evolutionarily recent. Clearly, no adaptations exist for the quick and effective maneuvering of an M1 Abrams battle tank or phalanx troop columns. However, if we take a broader definition of warfare, the implications are predictably different. For example, Levy and Thompson (2011) define war as 'Sustained coordinated violence between political organizations'. Similarly, Bowles (2009) defines war as 'Relationships in which coalitions of members of a group seek to inflict bodily harm on one or more members of another group'. Defined in this way, it is indeed likely that warfare existed ancestrally, and this perspective can assist the search for evidence that can test this claim.

This is not to say that the COW definition of war is wrong, or that broader definitions of war somehow capture its 'true' essence; rather, definitional disagreements only reveal that warfare can take many forms, and that only a particular form or forms of warfare existed ancestrally that likely shaped adaptations for motivation and behavior in these contexts. Whether or not one wants to call the occurrence of this ancestral activity 'warfare' is really beside the point. The challenge, therefore, is to explore how adaptations for a form of coalitional behavior that prevailed ancestrally operate in a modern environment in which the instruments and scope of this activity have changed drastically. Just as our visual adaptations do not cease their relevance or operation in the context of modern instruments that allow the viewing of celestial objects, adaptations for coalitional violence remain relevant even in the modern world of mechanized battle.

Archeology: The archeological evidence of ancestral warfare is again hotly debated, and in this case, the central issue has been the existence of 'direct' evidence of warfare (Ferguson 1997; Otterbein 2004; Fry 2007).

Direct archeological evidence of warfare consists of bone and skull indentations and fractures caused by weapons such as spears or other stone-based instruments, as well as evidence of fortifications. However, these types of material innovations only occurred within the last 30,000–40,000 years, and the building of fortifications was only possible after the transition to sedentary lifestyle once the agricultural revolution had occurred about 12,000 years ago (Ferguson 1997). Nevertheless, as archeologists LeBlanc and Register have noted, 'The world was hardly peaceful until someone in China or Mesopotamia hammered out the first bronze sword' (2003). Therefore, as we evaluate such evidence, we must be careful not to confuse the *instruments* of war with the *occurrence* of war; weaponry and forts are not prerequisites of coalitional violence, and it is therefore false to infer the absence of the latter based on the absence of the former alone.

Warfare is not the only form of social behavior that leaves a fossil trail that is open to multiple interpretations. For example, evolutionary scientists have begun active and productive investigations into the human penchant for storytelling (Gottschall 2012), as well as religious belief and behavior (Boyer 2002; Atran and Ginges 2012), as products of underlying psychological adaptations. Both of these phenomena represent forms of social behavior that would likely not have left direct fossil evidence of, for example, an ancestral history of telling stories or religious belief. However, the absence of literary instruments or religious artifacts from the ancestral fossil record alone is not sufficient to disprove the possibility that adaptations exist that are designed to regulate these forms of behavior. Similarly, it makes little sense to assert that religion or religious belief emerged only as early as we can find religious artifacts in the fossil record, and it would be clearly false to argue that humans could not possess an adapted talent for storytelling merely because writing utensils or books are relatively modern inventions. To take the case of chimpanzees, although there is no fossilized evidence of weapon-related fractures, fortifications, or mass graves among these primate cousins, there is nevertheless clear and overwhelming evidence that adaptations in chimpanzees exist for the adaptive regulation of coalitional aggression (Wilson *et al.* 2012; Wrangham and Glowacki 2012).

Problematically, it is inevitably the case that evidence from primatology, anthropology, and archeology considered in isolation of each other are necessarily incomplete regarding the ancestral presence of coalitional violence. However, when considered together, the overwhelming evidence does suggest that inter-group conflict was a prevalent and reproductively significant feature of ancestral environments, based on evidence of chimpanzee coalitional aggression, the near universality of hunter-gatherer

warfare in humans, and direct evidence of warfare as far bask as the preservation of its instruments allows. Furthermore, experimental research that investigates the existence of psychological adaptations for warfare only continues to expand and generate new and novel hypotheses regarding evolved coalitional aggression, which would also seem to suggest that warfare was ancestrally recurrent, especially as many of the hypotheses generated from this framework mentioned above (e.g. overconfidence and brinkmanship; heroism and self-sacrifice in battle; perception of and support for leaders based on facial cues) are unintelligible absent this assumption.

The existence of peaceful societies falsifies the claim that humans possess adaptations for fighting

The most prominent recent example of this argument comes from Fry in his book *Beyond War: The Human Potential for Peace* (2007). Fry relies in part on evidence of the non-universality of warfare to argue that humans could not possess adaptations for warfare. Is the existence of 'peaceful' cultures evidence against the existence of adaptations for warfare?

As mentioned above, to the extent that psychological adaptations exist that regulate behavior and motivation in domains of social interaction, it should also be the case that these adaptations are facultative, rendering behavioral and motivational output a conditional response to environmental circumstances. In his analysis of adaptations in chimpanzees for coalitional aggression, Wrangham writes that, 'selection has favored a tendency among adult males to assess the costs and benefits of violence, and to attack rivals when the probable net benefits are sufficiently high'. Also, regarding human coalitional violence, McDonald, Navarrete and Van Vugt write: 'humans may calibrate their responses to out-group males based on an assessment of the strength of, or threat posed by, a male coalition' (2012, 672). Similarly, Tooby and Cosmides argue that putative psychological adaptations for warfare in chimpanzees and humans are designed in order to 'observe, assess, and to regulate the appropriate pattern of response towards several different males structured into a coalition' (1988).

This is a far cry from previous models, such as the 'killer ape' hypothesis, which asserted the existence of a latent and persistent passion for war and aggression, which perennially fueled the fire of inter-group conflict (Lorenz 1966). From this antiquated perspective, the existence of variation in the incidence of warfare is indeed confusing. However, given the innate conditionality inscribed by natural selection into the design of facultative adaptations for warfare, it is not surprising that cross-cultural variation exists in the occurrence of warfare. Indeed, this is exactly what an

adaptationist perspective would predict. Claims of universality in adaptationist models refer narrowly to the psychological adaptations themselves, and not the behavior they generate and regulate. To argue that warfare does not represent the operation of underlying psychological adaptations merely because warfare is cross-culturally variable is to confuse the *variable output* of adaptations with the *species typicality* of the adaptations themselves.

If psychological adaptations for warfare exist, then war is a necessary and inevitable component of human societies

There are (at least) two reasons why the existence of adaptations for warfare does not render war inevitable.

First, adaptations for coalitional aggression are facultative, which means that framing and context are fundamental determinants of inferential, motivational, and behavioral outcomes. For example, although out-group threat indeed often triggers hormonal responses that are associated with dominance reactions and aggressiveness, escalatory responses are not inevitable. Anthropologist Flinn *et al.* have demonstrated that the hormonal responses (particularly testosterone) to coalitional competition depend critically upon whether the mind receives cues that one's opponent is an out-grouper or an in-grouper (Wagner, Flinn and England 2002; Flinn, Ponzi and Muehlenbein 2012). In other words, the severity of conflict can be affected by one's perceptions regarding the coalitional identity of the other group. Relatedly, despite the well-known studies in which amygdala response is heightened when subjects are shown pictures of members of other races, there is also research that shows that this common xenophobic reaction can be muted through even as simple an exercise as travel through other cultures (Sapolsky 2006). In short, humans are groupish and we incessantly define socio-political interactions along group boundaries (Ridley 1997; Kurzban, Tooby and Cosmides 2001). These boundaries affect the way we respond to threat and the prospect of cooperation; however, these boundaries are also plastic and subject to extensive manipulation.

Second, the existence of adaptations for coalitional aggression does not preclude the existence of adaptations for pro-social behavior, such as cooperation and conflict management (Hamilton 1964b; Trivers 1971; Axelrod 1984; Dugatkin 1997; Cosmides and Tooby 2005). For example, research has demonstrated evidence for adaptations that regulate cooperation and social exchange (Fehr and Schmidt 1999; Cosmides and Tooby 2005; Nowak 2006; Aktipis 2011), altruism toward strangers (Boyd and Richerson 2009; Delton *et al.* 2011), and inter-personal and

group-level trust (Zak 2006; Zak and Kugler 2011). McCullough, Kurzban and Tabak (2013), for example, find that humans possess evolved psychological mechanisms not only to seek revenge, but also to rebuild relationships and seek forgiveness. These findings collectively suggest that humans are equipped with reliably developing psychological machinery designed to navigate the *many* challenges of social living – from conflict to cooperation. We are armed with the phenotypic weapons of inter-personal and coalitional competition, yet we also possess sharpened moral intuitions and cooperative inclinations that enable and facilitate peacemaking and conflict resolution (Boehm 2012a; De Waal 2012).

As the history of human civilization reveals, humans are adept at the creation and manipulation of cultural innovations that expand the reach of social and political institutions (Wright 2000). Despite the fact that the in-group/out-group distinction is a social categorization that appears deeply ingrained (Mahajan *et al*. 2011), humans are also noteworthy in our ability to manipulate the boundaries of these categories, widening social inclusivity in meaningful and lasting ways (Sapolsky 2006). War is not inevitable, but peace is not easy.

Modern warfare and international politics is so qualitatively different from ancestral politics that any adaptations for the latter are inoperative or irrelevant today

This view has its roots in classic arguments made by Turney-High (1949) and Wright (1983) in their early and authoritative examinations of 'primitive warfare'. Turney-High, for example, argued that war below the 'military horizon' was qualitatively distinct, and indeed bore little resemblance at all, to war above the mechanized horizon of modern warfare. According to this view, below the horizon is the domain of ritualistic contests, ignited for impractical goals, and in a relatively harmless fashion. In contrast, war above the military horizon is the realm of organization and rational policymaking, and it is exceedingly lethal. Although there can be no doubt that primitive and modern warfare are differentiated by a great degree of coordination and political organization, subsequent studies have demonstrated that many of the goals and tactics of warfare both above and below the military horizon remain similar regardless of innovations in logistical complexity or command and control structures (Keeley 1996; LeBlanc and Register 2003; Gat 2006; Gat 2009).

As the psychological adaptations we continue to possess today were designed in response to recurrent environmental challenges over evolutionary time, to understand their modern impact in any given case, we must ask at least two questions: to what extent do

modern contexts mirror ancestral contexts, and what happens when they don't?

Modern contexts trigger ancestral logics: To the extent that modern international conflict mirrors domains of ancestral inter-group conflict, we should expect these situations to tap into and trigger these adaptations as if modern warfare is played out in the ancestral environments that these adaptations are designed to expect. For example, as mentioned above, the mere presence of inter-group conflict is sufficient to trigger various forms of within-group pro-sociality, such as a greater willingness to reward cooperators and punish non-cooperators (Puurtinen and Mappes 2009). Importantly, these lab results have been complimented by field experiments in the context of actual political violence (Burton-Chellew, Ross-Gillespie and West 2010; Gneezy and Fessler 2011). Ginges and Atran (2011) find that decision making in a modern scenario of military intervention often operates independently of rational expectations regarding the likelihood of war to achieve its aims, and Johnson, Wrangham and Rosen (2002) show that states and their leaders may actively self-deceive regarding their chances of victory in modern strategic environments. It seems clear that these quick and reliably operating heuristics actively shape the quality of modern warfare, even if at times their operation appears puzzling from a rationalist framework, which leads to the next point.

Modern 'mismatch' helps to explain irrational or surprising behavior: Adaptations for coalitional behavior affect the shape and character of international politics even when the latter presents environmental novelties that adaptations are not designed to expect. In other words, there may be a 'mismatch' between the environment the adaptation 'expects' and the environment it actually encounters. For example, our adaptations for coalitional behavior were designed in small-scale environments that lacked strong institutionalized hierarchies, where leadership was often informal and unstable. As discussed above, effective leadership could provide significant reproductive benefits in the context of coalitional competition in which quick and coordinated action is critical (Kurzban and Neuberg 2005; Van Vugt and Kurzban 2007), and there is evidence that individuals' decisions to support a given leader is contingent upon adaptively relevant cues such as facial features and the status of coalitional conflict (Spisak *et al.* 2012). Given the ancestral importance of personal leadership for many coalitional endeavors, it is unsurprising that one of the most remarkable challenges faced by developing countries is that of building trust in institutions and the 'rule of law'. Democratic transitions the world over are frustrated by regression to authoritarianism or 'superpresidentialism', and often dominated by cults of personality that privilege personal relationships over trust in state-level institutions (Ishiyama and Kennedy 2001;

Barany 2008). Although institutional trust is challenging to develop for many reasons, the ultimate reality is that state-level institutions are an evolutionary novelty to the mind's eye. Combined with the fact that people tend to prefer stronger leaders in times of inter-group conflict, developing countries face an uphill battle against built-in biases that generate preference for powerful and charismatic personalities over impersonal and diffuse institutions.

These dynamics are apparent not only in the case of democracy and institutions, but also in warfare. For example, historically, large armies have systematically tended to overestimate their chances of victory, often undervaluing aspects such as the will to fight by local insurgents. Ancestrally, relative numbers was indeed a critical variable, perhaps *the* critical variable that would have determined the outcome of coalitional conflicts. In such environments, groups were relatively nomadic, and an adaptive response to invasion by a larger coalition would have been to flee and surrender territory. However, in modern environments where political groups are generally tied to territorially fixed nation-states, flight is less of an option, which may inadvertently magnify the will to fight of cornered adversaries, such as entrenched insurgents.

The study of warfare from an evolutionary perspective is still young, and research at this point remains focused on identifying adaptations that may exist and investigating their operation. As this research progresses, it will become increasingly necessary and central to investigate the question of how such adaptations interact with evolutionarily novel aspects of the modern environment. Adaptationists who study human behavior have proven remarkably successful at explaining various aspects of coalitional behavior and have demonstrated that these mechanisms continue to operate even in evolutionarily novel environments, such as many aspects of international politics.

Conclusion

The study of international politics has matured in no short measure as a consequence of its ability to integrate its own perspectives with those of other disciplines, especially economics, and also social psychology (Mercer 1995) and anthropology (Snyder 2002). Although the scientific study of warfare is expanding at great pace in the evolutionary sciences, scholars of international relations have been relatively slow to acknowledge and integrate such findings. Two reasons for this reluctance are uncertainty regarding the proper application of evolutionary theory toward the study of warfare, as well as uncertainty regarding the proper interpretation of modern and ancestral evidence of warfare.

I focus attention on the evolution of warfare for three reasons. First, the ancestral recurrence of inter-group conflict has posed significant selection pressures that yield a range of unique hypotheses regarding the resultant structure of evolved mechanisms for coalitional competition. Second, research on the evolution of war has already yielded substantial findings, such that the state of research is ripe for interdisciplinary integration (McDonald, Navarrete and Van Vugt 2012; Wrangham and Glowacki 2012). Third, international relations, as the natural 'home field' for the study of warfare, ought to take the lead in this interdisciplinary integration. Although there has been some movement toward integration by international relations scholars (Johnson, Wrangham and Rosen 2002; Gat 2006; Thayer and Hudson 2010; Lopez, McDermott and Petersen 2011; Johnson 2015), there is much room for gainful exchange.

An adaptationist perspective provides scholars of international relations with the tools necessary to generate and test evolutionary hypotheses of behaviors relevant not only to warfare but also to other domains of interest, such as the design of institutions (Boyer and Petersen 2011). This perspective dispatches the false notion of an innate passion for violence and replaces it with the understanding that we are endowed with a strategic coalitional psychology. Adaptationism provides opportunities for reconciliation with rationalism by helping to explain apparently irrational proclivities such as the stubborn persistence of issue indivisibilities, and may also support constructivist frameworks by helping to explain why certain social forms may appear more appealing or intuitive to the mind's eye than others.

Adaptationism has established itself as an effective framework for illuminating the information-processing structure of our evolved coalitional psychology. As research on the evolution of war continues apace, international relations scholarship is well positioned to benefit from and contribute to this interdisciplinary merger.

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