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Conditions Required for Evolution of Warfare Adaptations

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Definition

Describes the ancestral conditions that could allow for the evolution of adaptations for warfare in humans. The evolution of adaptations for warfare is possible when there are low-cost/high-benefit opportunities for violence, and it is also possible even if violence is costly, as long as fitness benefits can outweigh these costs in particular mating contexts. Additionally, in some species such as humans, the existence of warfare adaptations presumes the existence of a coalitional psychology able to track a broader range of group dynamics. In short, the evolution of adaptations for warfare is possible when reproductive benefits can outweigh the variable costs of violence and when those opportunities can be taken advantage of by an evolved coalitional psychology.

Introduction

Warfare is a prevalent feature of human social interaction. Given its significant and recurrent

nature, scholars have sought to explain not only why particular wars are fought but also why humans organize into groups and fight each other in general. Some, such as the anthropologist Margaret Mead, have argued that war is a cultural invention and that it likely developed sometime between the agricultural revolution and the emergence of large sedentary proto-states. These authors claim that our evolutionary history and biological makeup can contribute little or nothing to our understanding of why humans fight. In other words, historical, not biological, explanations for warfare are needed.

Others, however, have argued that group violence in humans is evolutionarily old and that the origins of collective violence can even be traced back to our chimpanzee ancestors, many millions of years ago (Wrangham 1999; Wilson et al. 2014). These authors further argue that the competitive coalitional nature of human evolutionary history had a unique impact on human psychology. Specifically, they argue that due to the fact that coalitional competition had such a significant and recurrent impact on our ancestors' reproductive success, we should expect to see adaptations in the human brain that enable us to reason adaptively in contexts of coalitional competition and violence. These scholars often refer to such adaptations as "adaptations for warfare."

Labels are useful because they help us categorize, define, and understand concepts and dynamics; however, research on the evolution of warfare is one area in which the labels themselves have

been the targets of much dispute. Consequently, many disagreements about whether warfare is evolutionarily old or culturally recent actually hinge on disagreements about what warfare is and how it should be defined.

No consensus exists regarding the definition of terms such as “warfare,” but definitional clarity at least allows one to evaluate the logical coherence of an argument on its own terms. Clearly defining terms such as “warfare” means disagreements about what warfare is can be momentarily put aside in order to ask a more specific question: given a particular definition of warfare, is there evidence that this behavioral pattern occurred ancestrally? This means that different definitions of warfare will result in different conclusions about its prevalence ancestrally and, by extension, different conclusions about the existence of adaptations for warfare. A logical implication is that some forms of warfare probably have no evolutionary explanation, while other forms of warfare probably do. In short, the importance of definitions is not to be overstated and is a necessary starting point.

Defining Terms: “Adaptation” and “Warfare”

What is an adaptation? Like the concept of warfare, there is much discussion on what a biological adaptation is, as well as whether adaptations in the brain should be studied in a fundamentally different way than adaptations in other parts of the phenotype (body). Evolutionary psychologists generally reject the proposition that adaptations in the brain (“psychological adaptations”) require different explanations than adaptations found elsewhere in the phenotype. Thus, evolutionary psychologists argue that the design and function of specific adaptations in the brain can be explained in much the same way as the design and function of adaptations in the liver or heart.

The brain is not one singular adaptation, but rather a collection of specialized adaptations that, broadly speaking, function to regulate the complex behavior of the organism. Indeed, a feature that distinguishes organisms that are capable of

complex behavior from those that are not is the presence of a complex nervous system and brain. Therefore, the specific adaptations that compose the brain are generally designed to regulate some aspect of behavior by processing information from the organism’s environment in specific ways. This is why some evolutionary psychologists will also refer to psychological adaptations as “information-processing mechanisms.”

The process of natural selection explains the existence and design of biological adaptations (Williams 1966; Maynard Smith 1993). When some heritable trait emerges in a population, it can be favored by natural selection if it has a positive effect on reproductive success and when that effect is recurrent over evolutionary time. Resultant adaptations will tend to have certain characteristics; broadly, their design will represent a specialized solution to some reproductive challenge or opportunity faced by the organism. With some exceptions (e.g., frequency-dependent selection and “drift”), heritable traits that have a positive impact on the organism’s reproductive success over evolutionary time will tend to spread in the population and become universal or near universal in the population.

As information-processing mechanisms, adaptations in the brain are often designed to produce a range of output (e.g., altered hormone levels) contingent upon a range of input from the environment (e.g., having won or lost a contest). The conditional – or “facultative” – nature of adaptations suggests that if there are adaptations that shape the way humans reason about fighting, then variation in the incidence of fighting across a population will not be evidence that adaptations for fighting are not universal or don’t exist. Rather, it is possible that this variation merely reflects the contingent logic of the universal adaptation.

What is warfare? A voluminous range of definitions of warfare exists, and there is no “right” definition of warfare, only myriad sets of behaviors that can justifiably be referred to as involving violence of some kind among groups. Consequently, much depends on one’s area of interest and expertise. Scholars of modern warfare, such as those who make use of the massive Correlates

of War database, will (appropriately) define warfare as “sustained combat, involving organized armed forces, resulting in a minimum of 1000 battle-related fatalities within a 12-month period.” However, if this is our starting point, then the question of whether warfare has evolutionary origins must be “no” since no one would argue that this form of mechanized combat is anything but historically recent and evolutionarily novel.

Consider an alternative definition of war: “relationships in which coalitions of members of a group seek to inflict bodily harm on one or more members of another group” (Bowles 2009; Wrangham and Glowacki 2012). This conceptualization opens up the possibility that “war” is an evolutionarily old human practice, which, in turn, opens up the possibility that adaptations for “warfare” exist. Whether one agrees that this is the correct definition of war is ultimately less important than whether a form of coalitional violence can be identified that *did* exist ancestrally, enabling specific inferences about how adaptations designed in response to those specific ancestral challenges structure our beliefs and motivations in modern environments.

Conditions for the Evolution of Warfare

Given the above perspective on adaptation, and using the broader definition of war (i.e., Bowles 2009), a specific question can now be asked: what conditions must have held ancestrally in order for natural selection to favor psychological adaptations in humans that guide motivation and behavior in the context of warfare?

Reproductive Benefits

The first condition is simultaneously the least satisfying (due of its general nature) but also the most important. That is, the reproductive benefits of fighting in groups must have outweighed its related costs. This can be difficult to identify in the case of aggression – coalitional or otherwise – because of the significant physical costs involved in violence (Allen and Jones 2014). In other words, it is often easier to see the substantial risks and physical costs of coalitional

violence than it is to see the benefits. However, there are two types of costs to consider in the context of violence: somatic costs and reproductive costs.

The somatic costs of violence refer to the physical damage that an individual or group sustains as a direct and immediate consequence of fighting, such as the loss of limb or the loss of life. In contrast, the reproductive costs of warfare refer to the reproductive opportunities lost as a consequence of fighting. In other words, one cannot reproduce if they are dead. An evolutionary analysis of warfare must attend to the question of its reproductive costs and benefits. Specifically, the reproductive benefits of warfare must outweigh the costs of participation in violence.

The fact that warfare can result in loss of life means that the theoretical challenge is to explain what reproductive benefits could make up for the costs of warfare when such costs entail loss of life and by extension a corresponding possibility of lost reproductive opportunities for the individual. There are two pathways by which the reproductive benefits of collective violence can outweigh these costs. The first pathway intuitively occurs when both the somatic and reproductive costs of warfare are actually quite low relative to the reproductive benefits. The second pathway occurs somewhat counterintuitively when, despite very high somatic costs to the individual, the reproductive benefits of violence are even greater.

Pathway 1: Reproductive benefits of low-risk raiding. Collective violence can evolve in coalitional environments in which low-risk/high-benefit aggressive opportunities exist. When these opportunities exist, selection can favor raiding behavior between coalitions. Such behavior has specific characteristics and is well explained by the imbalance-of-power hypothesis (Wrangham 1999). Absent weaponry, success in aggressive encounters is often determined by relative strength, and thus, all else equal, the greater the size asymmetry between coalitions, the more likely the larger coalition is to prevail at low cost to its members. In combination with the element of surprise, the attacking coalition can virtually guarantee a low-cost, high-benefit outcome.

The low costs of asymmetric warfare for the attacking party are clear. However, what are the benefits? The first benefit is a direct consequence of the violence – the rival coalition loses one or more of its members, which constitutes a relative power loss. In an environment in which coalitions are small to begin with, the loss of even one individual would not be trivial. A loss of coalition strength can result in increased attacks from neighboring coalitions and an inability to defend the territory controlled by the coalition. Thus, not only is the rival coalition weakened, but the winning coalition can also obtain greater territory and with it the resources that it contains – both material and reproductive. The material and reproductive benefits of low-risk raiding have been well studied and measured (Wilson et al. 2014).

This “chimpanzee model” of warfare (Wrangham and Glowacki 2012) is a clear illustration of one set of conditions under which coalitional violence can evolve via natural selection, namely, where low-risk/high-benefit aggressive opportunities exist. This pattern can be seen in humans, although with important differences. Human raiding, like chimpanzee raiding, occurs by stealth, is increasingly likely as the imbalance of power reaches a ratio of 3:1, and is accompanied by non-negligible material and reproductive benefits such as expanded territory (Johnson and Toft 2014). Unlike chimpanzee raiding, however, human raiding can be somewhat more risky due to the presence of weaponry and the cycles of revenge.

It may be the case that chimpanzee warfare offers a glimpse at the ancient “roots” of human warfare. However, while some aspects of human warfare resemble the chimpanzee model, other aspects do not. In a comprehensive review and comparison of chimpanzee and human warfare, Wrangham and Glowacki (2012) argue that there are two problems with the comparison of chimpanzee and human warfare. First, relations among human coalitions can range from hostile and violent to peaceful and cooperative. Second, human warfare seems to entail greater risks to attackers than the chimpanzee model, which returns us to the initial question of how evolution could explain

psychological adaptations that motivate high-risk violence. Each is discussed briefly in turn.

The first problem (i.e., cooperative as well as combative coalitions) is not evidence that human raiding is not motivated by psychological adaptations that operate to seize low-risk/high-benefit aggressive opportunities. Rather, it suggests that this “raiding psychology” is part of an evolved coalitional psychology that is equipped with a broader toolkit of coalitional interaction. To oversimplify, one could say that humans have psychological adaptations not only for coalitional violence but also for inter-coalitional (as well as intra-coalitional) cooperation and alliance. This issue must be put aside and returned to in a subsequent section on coalitional psychology. For now, however, what can be said is that the conditional logic of psychological adaptations for intergroup violence in humans likely operates within a wider or at least different set of variables than it does in chimpanzees, encompassing opportunities for aggression as well as alliance and trade.

The second problem (participation in high-risk violence) must be engaged by careful reconsideration of the reproductive costs and benefits of coalitional violence. The resolution of this second problem reveals the second pathway by which the reproductive benefits of warfare can outweigh its potentially significant costs.

Pathway 2: Reproductive benefits of high-risk battles. Collective violence can evolve despite the existence of significant somatic costs – even individual death – when reproductive resources in the coalition are subject to zero-sum distribution (Tooby and Cosmides 1988; McDonald et al. 2012; Lopez 2016). To understand this argument, the reproductive success of the gene or suite of genes that would benefit from the risk-taking behavior of its host must be examined.

All biological adaptations arise initially as a consequence of a random genetic mutation that is maintained in a population because of its positive effects on the organism’s ability to reproduce. Taken to the fullest extreme, therefore, Dawkins quips that “a chicken is only an egg’s way for making another egg” (Dawkins 1976). Put simply, natural selection describes the processes whereby

a gene arises that has some effect on the body of its host, and when this effect causes more copies of that gene to make it into subsequent generations, this gene is under positive selection. Thus, natural selection can favor maternal altruism in part because a mother's offspring is likely to share a significant fraction of her own genes (Hamilton 1964). Despite the fact that the "vehicle" in which the gene finds itself absorbs a cost to confer a benefit on another vehicle, the reality is that the genes in one vehicle are able to help copies of themselves in other vehicles. So what appears to be altruism at the level of the organism or "vehicle" is actually selfishness at the level of the gene (Dawkins 1983). This perspective can help to reveal the underlying genetic benefits of what often appear to be somatically costly behaviors, that is, behaviors in which one organism absorbs great personal costs to benefit another.

With this "gene's eye perspective" it is possible to reexamine the reproductive benefits and somatic costs of warfare, beginning with some assumptions. First, assume a polygynous system in which male parental investment is relatively low and in which the primary limiting factor for male reproductive success is access to females (Trivers 1972). Second, assume a world of two male coalitions that are roughly equal in size. Third, assume that these coalitions fight, resulting in the death of all males in the losing coalition, as well as the death of every male except for one individual in the winning coalition. Fourth, assume that reproductive resources and opportunities are allocated in a zero-sum fashion within the coalition. This means that the reproductive opportunities lost by the fallen equal the reproductive opportunities gained by the victorious survivors (Tooby and Cosmides 1988), which is made possible by the polygynous nature of the system. The result is that the reproductive benefits to the winning coalition are not diminished by its high mortality, but, rather, are reallocated among the survivor(s). The "last man standing" is therefore able to reap tremendously great reproductive benefits from this instance of coalitional aggression, despite the great somatic costs of the effort.

As Tooby and Cosmides argue, this situation therefore means that natural selection can favor a

gene that motivates participation in somatically costly high-risk battles. Even if many individuals die from the effort, the zero-sum allocation of reproductive opportunities within the coalition means that the average fitness payoff to the members of the victorious coalition is not diminished by the death of one or even most of its members, assuming the above conditions are met. And since natural selection operates to favor strategies that are successful *on average* over evolutionary time (i.e., despite individual fitness reversals), a heritable propensity for participation in high-risk battles can spread in the population. Thus, even if the result is occasional death, the on-average reproductive benefits can outweigh serious and even fatal somatic costs to individual coalition members. This may be particularly true when a "veil of ignorance" exists regarding the prebattle distribution of risk among the coalition members.

The Strength and Existence of Selection Pressures. What has been shown is that it is possible for the reproductive benefits of risky battles to outweigh their related costs. The theoretical possibility on its own by no means implies that adaptations for warfare exist or that if they do exist, they must be explained in this fashion. It is merely to suggest that adaptations for warfare can indeed be explained by natural selection operating at the level of the gene and the individual. The concluding section briefly engages the question of whether natural selection operating at other levels (e.g., the group) can explain the evolution of warfare adaptations.

First, however, a related question arises: given the possible ancestral existence of conditions that would have favored warfare adaptations, how strong must this selection pressure be in order for such adaptations to emerge? Recall that in order for selection to build adaptations, there must be some challenge or opportunity in the environment that is both recurrent and has fitness consequences for the organism. Thus, one common critique against the existence of adaptations for warfare is that even if there may be fitness benefits associated with coalitional violence, such behavior was actually extremely infrequent or even nonexistent ancestrally. In other words, one cannot claim that adaptations exist in

response to an environmental event that was rare or nonexistent.

This challenge leads to two questions: (1) Did our ancestors engage in coalitional violence? (2) How frequently did they engage in coalitional violence? Unfortunately, the evidence does not allow a conclusive answer to either of these questions, forcing researchers to engage in methodological triangulation and to make educated guesses about the possibility and prevalence of ancestral coalitional aggression. Direct evidence of warfare, such as fossilized bone indentations, mass graves, and weaponry, is exceedingly rare and ultimately nonexistent as one peers further and further back in time.

Proponents of the evolution of warfare, however, point out that the absence of such evidence is not evidence of the absence of warfare; rather, the absence of direct evidence of warfare is instead the absence of the *instruments* of warfare, not of warfare itself. In that sense, the labeling of such evidence as “direct” is unfortunate and imprecise, since such evidence is actually indirect, not direct. Swords, mass graves, and fortresses, for example, are not requisites for coalitional violence, and therefore their absence from the fossil record after a certain time period does not allow us to conclude that ancestral warfare was nonexistent. As Leblanc and Register wryly note: “The world was hardly peaceful until someone in China or Mesopotamia hammered out the first bronze sword” (2003).

This author has elsewhere engaged the question of the likelihood of ancestral violence, and it is a debate that has been vigorously argued on all sides (Pinker 2011; Allen and Jones 2014; Lopez 2016). However – and somewhat disappointingly for both sides in the debate – the very strongest claim that can be made regarding the existence of ancestral coalitional violence is that the evidence does not allow us to conclude that it did not exist. What seems clear is that unless it can be concluded (which it cannot) that ancestral coalitional violence was nonexistent, even the infrequent recurrence of coalitional violence could very well have provided enough of a selection pressure to favor adaptations for warfare. As has been well explored elsewhere, what appear to be

quantitatively small selection pressures at one point in time can sum to very large impacts over evolutionary time (Dawkins 1986). Thus, claims that chimpanzee coalitional violence is not recurrent enough for selection to favor adaptations for warfare fail both theoretically and empirically. In theory, they underestimate the power of natural selection to operate on even the slightest fitness differentials. Empirically, clear evidence demonstrates that the rate of chimpanzee coalitional violence is sufficient to yield significant reproductive benefits (Wilson et al. 2014).

Coalitional Psychology

The previous section explored the structure of reproductive opportunities that could lead selection to favor the emergence of adaptations for warfare. However, in addition to the existence of opportunities, the right equipment is necessary in order to take advantage of such opportunities. Coalitional aggression is fundamentally a collective action problem, and participation in warfare therefore requires a degree of cognitive design for navigating a host of coalitional challenges. In short, adaptations for warfare presume the existence of an evolved coalitional psychology that is designed to solve problems relating to the building, maintaining, and enforcement of within- and between-group relationships (Lopez et al. 2011).

The complexity of this task is not to be underestimated and requires cognitive mechanisms that perform a range of tasks, such as the following: identify and punish free riders; respond and yield to leadership; and regulate the distribution of resources. In short, collective action for aggression presumes cognitive machinery that quickly and reliably solves a range of related but distinct n-person challenges.

One characteristic of the inseparable link between the unique challenges of warfare and the broad toolkit of coalitional psychology is the immediate and reliable way in which the former triggers the latter. Experimental research in the lab and in the field has repeatedly and powerfully demonstrated the effect of intergroup conflict on within-group cooperation. Specifically, the prospect or actuality of intergroup violence is sufficient to trigger a host of within-group dynamics

such as an increase in the overall level of cooperation, greater desire to reward participants and to see noncooperative individuals punished, as well as the associated emotional displays of within-group solidarity and shame or guilt among bystanders (Gneezy and Fessler 2011).

The effect of intergroup conflict on within-group collective action is twofold. First, warfare operates as an “effect multiplier” by enhancing many of the dynamics necessary for the prosecution of collective action in general, such as punitive sentiment toward free riders. Second, warfare triggers a unique set of psychological mechanisms designed specifically for intergroup competition and aggression, such as the tracking of in-group/out-group membership (Kurzban et al. 2001) and relative coalitional formidability (Parker 1974). These two effects of warfare on collective action dynamics mean that researchers must be careful to distinguish between those adaptations that are uniquely designed for warfare and those that are designed for collective action but triggered in the context of coalitional violence. The two sets of adaptations are necessarily integrated yet distinct.

As one example of the integrated nature of adaptations for collective action and adaptations for warfare, Tooby and Cosmides (1988) outline the “risk contract of war,” which outlines the psychological conditions that must be met in order for coalitional violence to be initiated against an out-group. The risk contract consists of two broad components: first, regulation of the individual’s decision to participate and, second, the enforcement of the agreement (or risk contract) on others. The individual decision of whether to participate is regulated by variables such as formidability, the degree of perceived risk, and its expected distribution within the group, as well as the expected distribution of spoils antebellum. The enforcement of the risk contract on others depends on an individual’s ability and willingness to pay costs to reward and/or punish others for the sake of labor recruitment and alliance maintenance. Thus, while the main challenge of the first component is one’s own willingness to participate, the main challenge of the second component is to manipulate the willingness of others.

In short, adaptations for warfare presume the existence of an evolved coalitional psychology that enables solutions to the complex coordination problems posed by intergroup violence. Taken together with the previous section, the overall discussion so far has explored the evolutionary feasibility of both low- and high-risk coalitional aggression, the power of even weak selection pressures to build complex adaptations for warfare, and the role of coalitional psychology for facilitating intergroup violence.

Auxiliary Observations Regarding the Uniqueness of Human Warfare

The above discussion outlines some general conditions that make the evolution of warfare adaptations possible. These conditions alone do not explain or attempt to describe the full range of psychological adaptations that possibly exist in humans for engaging in coalitional violence. Doing so would be the next logical step and requires careful adaptationist analysis of specific reproductive challenges that is beyond the scope of this brief and general inquiry (McDonald et al. 2012; Lopez 2016). Nevertheless, some brief observations should be made that necessarily complement the preceding adaptationist inquiry into warfare.

Research on the evolution of war and its related psychological adaptations should not blind researchers to the very real and powerful “other half” of the story, namely, the evolved human capacity for peace. The existence of adaptations for warfare does not undermine the case for adaptations for cooperation, alliance, or reconciliation. Indeed, the psychology of cooperation and forgiveness among groups is well studied (McCullough 2008). The most fruitful way forward in these respective areas of research (on war and cooperation) is to examine the ebb and flow of motivations and dynamics related to each. For example, when and why do conflicts escalate or deescalate? Such a question can only be answered by acknowledging both the human capacity for violence and the human capacity for cooperation.

Researchers must also carefully examine sex differences in aggression. There is tremendous evidence of reliable and cross-cultural differences in the way males and females reason about and engage in warfare (Van Vugt 2009; McDonald et al. 2012). The theories of sexual selection and parental investment (Trivers 1972) provide a basis upon which to explain the distribution of sex differences within and between species, and these theories have also been used to successfully explain a range of sex differences in humans, particularly regarding individual and coalitional aggression (Van Vugt 2009). Importantly, the evidence does not show that females never fight; rather, the relevant distinction is to be found in the conditions under which males and females fight (Brooks and Valentino 2011; Lopez et al. 2011).

Research Note: The Levels of Selection Problem

The above discussion has focused on the fitness costs and benefits of warfare for individuals and genes. For instance, under certain conditions, genes that code for behavior-regulatory mechanisms that motivate participation in warfare can spread either because of the associated benefits that accrue to the individual or *despite* significant costs – even death – to the individual. In the latter case, a gene can spread despite costs to the organism when the on-average result is genetic selfishness. This process is known as genetic selection and can result in patterns of behavior as seemingly dissimilar as maternal altruism and battlefield heroism. In the former case, however, a gene can spread simply because it produces direct positive fitness consequence for the organism in which it finds itself. This is known as individual selection and is the more commonly understood level of selection in evolutionary theory.

In addition to genetic and individual level selection, however, it is theoretically possible for a gene to spread in a population because of the benefits it generates for the *group* of organisms in which it finds itself. This is known as group selection. This is significant for the current discussion because warfare can be thought of as a process by which some groups survive and expand while others

withier and perish. Warfare is, at least in this superficial sense, a process of group “selection.”

As a rough illustration, if a heritable trait emerges within the individuals of a group that has the effect of making that group more likely to win battles, then these genes would prosper, while alternative genes in the individuals whose group was vanquished would disappear. The result would be that directional change in gene frequencies is driven by its effects on group success, not individual success. This conceptualization led early critics of group selection to claim that this process can only work when there is no migration between groups and when the rate of group extinction is high (Maynard Smith 1976). Later proponents of group selection argued that both early conceptions of group selection and restrictions offered by critics were excessive or imprecise (Sober and Wilson 1999; Nowak et al. 2010). More recently, scholarship has focused on the possibility that the evolution of warfare has occurred via the simultaneous interaction of multiple levels of selection.

Game theoretic evidence has modeled the viability of warfare evolving via group selection given what is known about the likely prevalence of ancestral intergroup conflict (Choi and Bowles 2007). Nevertheless, critics of group selection continue to make two points in particular. First, the conditions are rare or absent that would be necessary for group selection to build complex adaptations, and modern genetic data are inconsistent with predictions from group selection (Langergraber et al. 2011). Second, although group selectionists argue that behaviors such as “prosociality,” heroism, and other forms of social altruism can only be explained by group selection, critics argue that these are adequately – and more parsimoniously – explained by natural selection operating at the individual or genetic level (Williams 1966; Price 2012).

Conclusion

The foregoing discussion is an attempt to outline a set of conditions that may facilitate the evolution of adaptations for certain forms of intergroup

violence. After defining the relevant terms, this effort consists of several components. First, it is necessary to carefully identify the reproductive costs and benefits of fighting and to identify the conditions under which the benefits of warfare would have outweighed its related costs. Second, if current or subsequent research can demonstrate that these conditions held ancestrally, then support is greater for the possibility that some features of human warfare can be explained as products of human adaptations for intergroup violence.

Adaptations for warfare can evolve when coalitions are faced with recurrent and reproductively significant opportunities for low-risk/high-benefit violence. Resultant adaptations should carefully monitor relevant variables such as relative coalition size, the element of surprise, and opportunities for escape – the ancestral analogue of the “exit strategy.” Indeed it is known that in chimpanzees such opportunities exist and are reproductively beneficial, and the pattern of raiding behavior conforms to this adaptive conditionality (Wrangham 1999; Wilson et al. 2014). Raiding in humans does not perfectly conform to the chimpanzee model due to the fact that human raiding can entail higher physical risk to participants, and inter-coalition relationships are characterized by peaceful as well as agonistic relationships.

Adaptations for warfare can also evolve even in the face of steep somatic and reproductive costs, as long as the fitness benefits of coalitional violence are even greater. This is possible in a world in which reproductive resources and opportunities are allocated within the victorious coalition on a zero-sum basis. Although a high-casualty war of attrition between two large coalitions results in sizeable fatalities for both coalitions, the zero-sum allocation of reproductive resources for the winners means that the surviving victors stand to reap tremendous reproductive benefits. When selection is operating at the level of the gene, the result can be adaptations that motivate what appear to be individually irrational and even reckless participation in violent conflict. In other words, selfish genes can motivate risky behaviors in individuals when the reproductive benefits over evolutionary time outweigh the fact that such behavior can occasionally lead to individual death.

Warfare is a collective action problem and therefore presumes the existence of cognitive machinery that enables individuals to solve complex coalitional coordination problems. Thus, in order for warfare to evolve via natural selection, the reproductive benefits must outweigh the related costs of warfare, but individuals must also be able to navigate complex coalitional landscapes in the first place.

In addition to an elaboration of the conditions for the evolution of warfare and the search for ancestral evidence that such conditions existed, future research should continue to dissect the information-processing structure of adaptations designed for warfare by examining the adaptive logic of related motivations such as revenge, intergroup anger and reconciliation, xenophobia, morality and sacred values, and sex differences in aggression. Last, but not least, researchers must continue to develop models of multilevel selection to understand the complex interplay of selection pressures that operate not only at the level of the gene but also at the level of individuals and groups.

Cross-References

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