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Research

Evolution and the psychology of intergroup conflict: the male warrior hypothesis

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The social science literature contains numerous examples of human tribalism and parochialism—the tendency to categorize individuals on the basis of their group membership, and treat ingroup members benevolently and outgroup members malevolently. We hypothesize that this tribal inclination is an adaptive response to the threat of coalitional aggression and intergroup conflict perpetrated by ‘warrior males’ in both ancestral and modern human environments. Here, we describe how male coalitional aggression could have affected the social psychologies of men and women differently and present preliminary evidence from experimental social psychological studies testing various predictions from the ‘male warrior’ hypothesis. Finally, we discuss the theoretical implications of our research for studying intergroup relations both in humans and non-humans and discuss some practical implications.

Keywords: intergroup conflict; sex differences; evolutionary psychology; prejudice; male warrior

1. INTRODUCTION

Intergroup conflict is undeniably pervasive across human societies. Conflicts among human groups have occurred throughout our modern history and range from large-scale conflicts, such as wars between countries, terrorism, racial and ethnic discrimination, and conflict among political parties, to relatively small-scale conflicts involving competition, antagonism and aggression among rival sport teams, gangs and high school cliques [1,2]. Yet, these instances of intergroup conflict may not solely be a modern cultural phenomenon. There are reliable accounts of intergroup conflict in past hunter–gatherer societies—usually via raiding and ambushing—killing substantial numbers of people [3]. A cross-cultural study of the ethnographies for 31 hunter–gatherer societies found that 64 per cent engaged in warfare once in every 2 years, 26 per cent fought wars less often, and only 10 per cent were described as having fought wars rarely or never ([4], p. 75). Furthermore, intergroup conflict has been documented in other social species as well, including hyaenas, wolves, lions and most social primates, therefore suggesting some degree of phylogenetic consistency [4].

It seems that wherever there are social group divisions, there is some degree of conflict. Furthermore, where there is intergroup conflict characterized by violence, injury or death, we find that such acts of aggression are perpetuated almost exclusively by men

[2,5]. In fact, research suggests that men’s tendency to engage in coalitional aggression is manifest in all cultures, modern and traditional, and is therefore considered a human universal [6].¹

In exploring the biological and psychological roots of intergroup conflict, we integrate evolutionary and social psychological perspectives to gain a better understanding of why intergroup conflict is so pervasive, and why men are so often the primary agents and direct targets of intergroup conflict. We also explore the role that women play in intergroup conflict, both in terms of facilitating its perpetuity and in how they respond, cope and adapt to intergroup threat. Finally, we discuss the implications of our research for both theory development and for managing intergroup relations in today’s society.

2. THE ORIGINS AND FUNCTIONS OF INTERGROUP CONFLICT

At an immediate, proximal level of psychological processing, the proclivity for intergroup conflict is shaped by fundamental cognitive processes, such as the tendency for humans to categorize objects and people automatically upon their perception [7]. Given the immense processing benefits that categorization heuristics afford, it is not surprising that humans so quickly recognize individuals as members of groups. Yet, what may be surprising are the positive and negative affective evaluations automatically connected to perceptions of one’s own group (ingroup) versus another group (outgroup). Such ingroup–outgroup biases have been documented widely among both Western and

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One contribution of 12 to a Theme Issue ‘The biology of cultural conflict’.

non-Western populations and they even emerge when such group divisions are based on a random criterion such as the preference for abstract paintings [8,9]. Ingroup–outgroup biases have also been observed in non-human primates such as the Rhesus macaque [10].

The automatic tendency to favour members of one's own group at the expense of members of outgroups, referred to here as tribalism or parochialism, might simply be a by-product of generic cognitive adaptations for classifying the physical world around us. In concert with these cognitive adaptations, however, human tribalism may be rooted more deeply in a human evolutionary history in which groups provided immense survival and reproductive benefits. Group living has afforded benefits such as resource pooling, division of labour, cooperative parenting, protection from predators and territorial defence. Such advantages could have created selection pressure for the evolution of psychological mechanisms favouring sociality, such as our innate desire to cooperate and our need to belong [11].

Such adaptationist thinking can explain why humans have evolved a desire to belong to groups and display ingroup favouritism. However, it cannot readily explain why humans are so fiercely tribal in the sense that they are motivated to engage in discrimination and aggression against members of other groups. Nor can it explain why acts of intergroup aggression, defined as coalition members from one group seeking to inflict physical harm on one or several members of other groups, are perpetrated almost exclusively by men, both now and in the past [2,3,5].

3. SEX DIFFERENCES IN INTERGROUP AGGRESSION: THE MALE WARRIOR HYPOTHESIS

As is the case with interpersonal acts of aggression, there are large potential costs for individuals to engage in coalitional aggression. Yet, across time and cultures, violent intergroup conflicts have been widespread and diverse, ranging from small-scale raiding and revenge killings in hunter–gatherer societies to full-blown warfare between nation states [3,12].

So what may be the adaptive benefits of joining aggressive coalitions, particularly for human males? One possible explanation relies on the evolutionary theories of sexual selection, parental investment and group selection [13–19]. Sexual selection and parental investment theory attribute sex differences in social behaviour to different selective pressures producing distinct female and male reproductive strategies [20]. In most mammalian species, male reproductive fitness is limited by access to fertile females, whereas female fitness is limited by physiological and energetic constraints. Thus, men may enhance their fitness by monopolizing reproductive access to a large number of mates, whereas women do not profit to the same extent from increased access to mates. This asymmetry results in striking differences in within-sex reproductive variance outcomes, inducing relatively strong intrasexual competition among men in particular [20].

Such competition may take the form of men fighting other men individually, as evidenced by documentation

suggesting that male-to-male violence is the leading cause of homicide in the United States [21]. Alternatively, men may form coalitions with other men to extract reproductive resources from members of other groups. This competition need not take the form of direct contests for instances of sexual access, but may include conflicts over foraging territories, sleeping sites and more intangible resources such as social influence, power and status—resources that can be readily converted into reproductive opportunities. This is because such resources may (i) directly attract females who need more than they individually consume due to child-rearing obligations, (ii) increase the survivability of relatives, or (iii) allow victorious males and their coalitions to drive out or eliminate same-sex competitors [21,22].

The logic underlying the evolution of male coalitional aggression is nicely captured in the risk contract theory of warfare as developed by Tooby & Cosmides [23]. In their analysis, they note that in lethal intergroup conflicts, the marginal gains to a group's average reproductive success will be much lower for each additional male survivor compared with each additional female survivor, owing to the biology of reproduction (e.g. one male can impregnate 10 females). Male deaths are therefore less detrimental to the average success of the group than female deaths. So, although the potential costs are quite high for males who join a coalition, because existing and acquired reproductive resources would be reallocated among the male survivors, the benefits bestowed upon victorious males could be immense.

This theory is consistent with data from many disparate sources in anthropology, history, political science and sociology suggesting that men have been the most likely perpetrators as well as casualties of intergroup aggression [5]. Furthermore, although it is difficult to obtain reliable evidence for warfare among ancestral hunter–gatherer bands—the societies in which early humans evolved—recent estimates suggest that the mortality rates due to intergroup conflict may have been substantially large as to create reasonably strong selection pressures on social behaviour [3].

(a) *The male warrior hypothesis*

Evolutionary psychologists make the reasonable assumption that selection pressures operating in our evolutionary past may have shaped basic psychological mechanisms for solving a wide range of adaptive problems including obtaining access to mates and managing conflicts within and between groups. We therefore argue that for understanding the basic social psychological processes underlying intergroup conflict it may be useful to adopt an evolutionary perspective (although this does not preclude the role of culture [24]).

A first implication of this emerging perspective is that humans, particularly men, may possess psychological mechanisms enabling them to form coalitions capable of planning, initiating and executing acts of aggression on members of outgroups (with the ultimate goal of acquiring or protecting reproductive resources). We refer to this as the male warrior hypothesis [25]. However, this hypothesis does not preclude individual

variation in the male warrior psychology. As such, the development of such a psychology may depend on one's traits and abilities, such as body size, fighting ability and aggressive tendencies. The male warrior hypothesis also argues that humans may calibrate their responses to outgroup males based on an assessment of the strength of, or threat posed by, a male coalition. For instance, male coalitions perceived as more physically formidable may evoke more avoidance-oriented strategies than aggressive approach-oriented strategies. In addition, the male warrior hypothesis argues that humans are likely to possess mechanisms to cope with the potential dangers posed by warrior males, especially those belonging to an outgroup. For instance, ingroups might be more suspicious and fearful of male rather than female outgroup members and have a greater desire to dominate, punish or socially exclude them—referred to as the outgroup male target hypothesis [26]. Finally, men and women might respond differently to outgroup males. Whereas ingroup males might respond with anger and aggression towards outgroup males, it might be more functional for women, given the costs of an unwanted pregnancy or infanticide, to be fearful and avoidant of outgroup males. In the remainder of the article, we present evidence for the male warrior hypothesis and its specific predictions about the psychological significance of intergroup conflict and the differential reactions of men and women.

4. RESEARCH SUPPORT FOR THE MALE WARRIOR HYPOTHESIS

The male warrior hypothesis implies that if men's psychology is designed in ways that facilitate success in intergroup conflicts, evidence for the workings of the mechanisms should be apparent in the thoughts, emotions, motivations and behaviours relevant to intergroup conflict among men in modern societies. For example, as a proximate psychological motivator of warriors in aggressive intergroup conflict, one might expect men to exhibit heightened animus towards and derogatory beliefs about outgroups (i.e. prejudice), a strong preference for between-group social hierarchies, a bias towards protecting and supporting one's ingroup (particularly when intergroup conflict is salient), a lowered threshold for engaging in intergroup aggression, and greater engagement in actual discriminatory behaviour—including competitive and violent actions against outgroups. Across broad domains of research, we find evidence consistent with this expectation.

(a) *Prejudice and discrimination against outgroups*

Across cultures, time and samples, self-report survey research has consistently demonstrated that, on average, men display more xenophobic and ethnocentric attitudes than do women [27–34]. Men also display a tendency to use danger-relevant stereotypes about outgroup members when faced with ambiguously threatening situations, such as when primed by ambient darkness [35]. Men are also more likely than women to dehumanize outgroup members, such as by describing them using animal-typical words [2], which may help ease the psychological discomfort

that might otherwise be associated with harming others during violent intergroup conflict.

Research on discrimination against outgroups using a punitive allocation task shows that men are willing to endure greater sacrifices by their own group in order to exact a greater punishment on an outgroup, but as predicted by the male warrior hypothesis, only when the outgroup is composed of men. By contrast, women tend to equalize punishment across the ingroup and outgroup and do not show evidence of discrimination based on gender [26]. This provides further evidence that men tend to be more discriminating against outgroups than do women, but also suggests that intergroup bias is primarily directed at men, particularly when it is framed as a competitive enterprise.

(b) *Men's preference for intergroup hierarchies*

Research suggests that men tend to exhibit much greater preferences for group-based systems of social hierarchy than women. Research on social dominance orientation (SDO) examines the extent to which individuals desire to establish, maintain and justify dominant–subordinate relationships among social groups [36]. Across a variety of different cultures, research has demonstrated that men consistently score higher on SDO than do women, suggesting that men have stronger preferences for group-based hierarchy. These results were confirmed in a recent meta-analysis of 74 studies examining gender differences on SDO [37].

Importantly, scores on SDO tend to be positively associated with a wide variety of social attitudes and ideologies that tend to legitimize existing hierarchical systems, including social conservatism, racism, patriotism and the explicit endorsement and support for wars of aggression [36]. In a related theme, research suggests that men may more strongly identify with their tribal group memberships than do women. For example, men are more likely to associate their favourite colour with an ingroup, such as their favourite sports team or their country's flag [2], and are also more likely to complete the statement 'I am...' with a group membership role, such as indicating that they are a member of a fraternity [38, p. 644]. This strong identification with one's ingroup may serve to facilitate men's motivations to dominate outgroups.

(c) *Supporting the ingroup*

The male warrior hypothesis implies that men may be more motivated to support and defend the ingroup. This should be particularly true when faced with threats from another group, given that ethnographic and primatological evidence supports the notion that throughout our evolutionary history, human societies had stronger kinship ties among men, rather than women (reviewed in [4]). This would make it such that men should have stronger solidarity with the ingroup, particularly when threatened. Recent research has explored this idea by asking whether men's voluntary cooperative contributions to their group increase when the group is faced with an external threat [25]. In a series of studies, researchers gave groups of participants a monetary endowment that they could keep or donate to a group fund, with the incentive that if at least four of the six

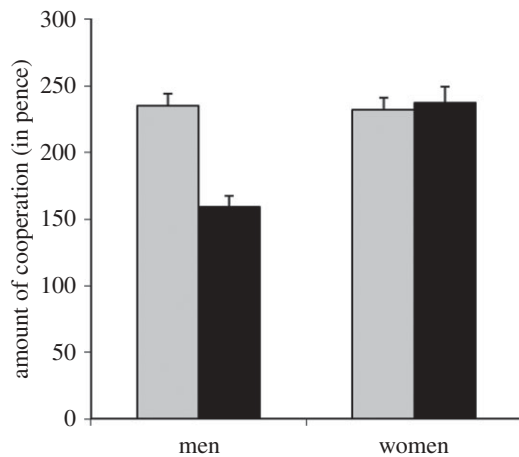


Figure 1. Altruistic group contributions increase among men during intergroup conflict. Black bars, individuals; grey bars, groups. Adapted with permission from Van Vugt *et al.* [30].

group members donated to the group they would all receive a larger individual endowment. In one condition, participants were told that the researchers were concerned with their individual performance whereas in the other condition participants were told that they were interested in how their group performance compared with that of local (rival) universities.

Across three studies, results demonstrated that men were more likely to make donations to the group when in competition with other universities, whereas women's likelihood of donating was largely unaffected by the group manipulation (figure 1). Also of interest was the finding that men's self-reported identification with their group was greater in the competition condition than in the individual condition (not true for women), and that identification with the group mediated the association between competition and cooperative donations to the group (figure 2). These results suggest that men are willing to put aside selfish motivations when the status of their group is at stake. These findings are also consistent with the model proposed by Choi & Bowles [39] in which intergroup aggression requires intragroup cooperation, which then reinforces the reproductive stakes and payoffs from engaging in conflict. In facilitating these functions, men may be equipped with psychological mechanisms (e.g. such as increased identification with the ingroup) that foster cooperative motives when one's group is under threat.

(d) Intergroup competition and aggression

Greater variance in reproductive outcomes for men creates an incentive structure in which men are willing to accept more risk in competition for valued resources. Given this, we expect to find that men are less inhibited to engage in aggressive intergroup behaviour. In accordance with this, men tend to report experiencing more competitive intergroup interactions than women [40]. Research also suggests that men are more likely to engage in 'pre-emptive strikes', without provocation, in simulated war games with countries interacting with one another [41]. In a recent experimental study [42], researchers found that men, but not women, were more likely to endorse statements supporting war after they had been primed with attractive members of the opposite sex relative to unattractive members of

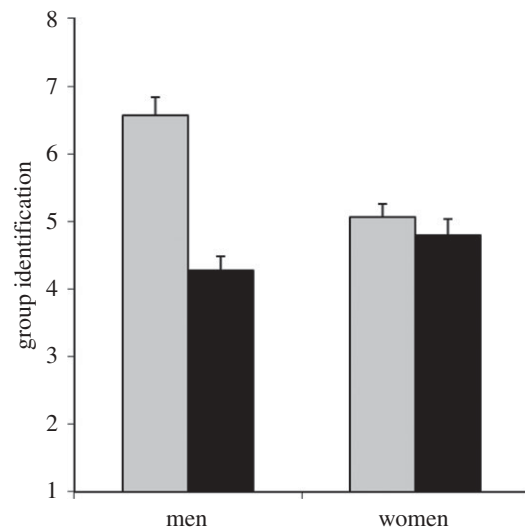


Figure 2. Group identification increases among men during intergroup conflict. Black bars, individuals; grey bars, groups. Adapted with permission from Van Vugt *et al.* [30].

the opposite sex. These results are consistent with the notion that, for men, intergroup conflict may serve the ultimate purpose of securing reproductive resources.

Given a reduced threshold for intergroup aggression, it is not surprising that men are more likely to engage in actual instances of aggressive intergroup conflict. Support for this notion is readily apparent in boys' preferences for competitive war-like games, the fact that nearly all street gangs are composed of men, and that large-scale conflicts between countries are largely initiated, escalated and negotiated by men [4,22,43–47]. Incidentally, a similar pattern is found among Gombe chimpanzees, such that the males often patrol the boundaries of their territory looking for chimpanzees from neighbouring groups that have strayed too far. When a female is found, she may be persuaded to emigrate into the home troop, but when a male is found he is likely to be brutally beaten and possibly killed [4].

Overall, this collection of findings is consistent with the male warrior hypothesis. We have provided evidence that men, more so than women, exhibit greater prejudice against outgroups, a stronger preference for group-based social hierarchies, strong motivations for protecting and supporting one's ingroup (even at an individual cost), a lowered threshold for engaging in intergroup aggression, and a greater tendency to self-select into situations of intergroup violence and competition, both in the real world and in the laboratory.

5. FEAR AND PREJUDICE AGAINST OUTGROUP MALES

If we take as true the assumption that men have been the primary agents of intergroup conflict and aggression throughout humans' evolutionary history, it is likely that selection has favoured psychological systems to adapt to the unique threat posed by outgroup men. In accordance with this, theories of prepared learning have argued that the neural circuitry underlying associative learning can be 'prepared' to learn fear or arousal in response to stimuli that have posed a significant threat to an animal's safety over evolutionary time.

Recently, researchers have used a fear conditioning paradigm to explore the persistence of fear responses towards members of racial outgroups. Cognitive experiments have demonstrated that anxious responses conditioned to danger-relevant stimuli (e.g. poisonous animals or predators) resist extinction, whereas responses towards danger-irrelevant stimuli (e.g. butterflies) are more readily extinguished [48]. Such domain-specific learning biases are said to be 'prepared' towards agents to whom humans and other primates have had sufficient exposure over evolutionary time. This evolved psychological system produces adaptive 'fight-flight' responses such as avoidance or extermination of stimuli to which one has had aversive experiences, thereby reducing one's risk of future harm [49].

For example, Olsson *et al.* [50] demonstrated that conditioned fear (measured via skin conductance response) towards facial displays of individual exemplars of racial outgroups resist extinction, whereas conditioned fear towards ingroup exemplars readily extinguish. Navarrete *et al.* [51] extended these findings by demonstrating that conditioned fear towards faces of outgroup exemplars resists extinction solely when the outgroup targets are male and not female, which is consistent with the male warrior hypothesis.

Participants were shown images of black and white faces that were either male or female (manipulated between subjects) while skin conductance responses were recorded during the presentation of each stimulus. During the fear acquisition phase, one face from each group (the reinforced conditioned stimulus, CS+) was paired with an electric shock as well as a white noise blast (the unconditioned stimuli, US), and one face was not paired with US (the non-reinforced conditioned stimulus CS-). To determine the fear response, participants' skin conductance responses towards the CS- were subtracted from the response towards the CS+ to control for pre-existing differences in fear response towards the group category. After the acquisition phase, conditioned fear was allowed to extinguish by presenting all faces without the US. Resistance to extinction was assessed by averaging the conditioned response across the last five trials of extinction separately for ingroup and outgroup targets. Results indicated that participants' fear response resisted extinction when the targets were outgroup males, but not when the targets were ingroup males, ingroup females or outgroup females (figure 3).

Such findings are consistent with the prepared learning perspective [48] in which an evolutionary history of coalitional violence perpetrated by outgroup males has selected for psychological mechanisms that are *prepared* to learn fear towards outgroup males and subsequently resist extinction of that fear. As such, these results lend support to the male warrior hypothesis in that they are consistent with the notion that it has been primarily men who have acted as the agents of intergroup conflict.

6. THE OUTGROUP MALE TARGET HYPOTHESIS

The male warrior hypothesis argues that the ultimate purpose of intergroup conflict is to gain access to fitness-enhancing resources, such as food, territories

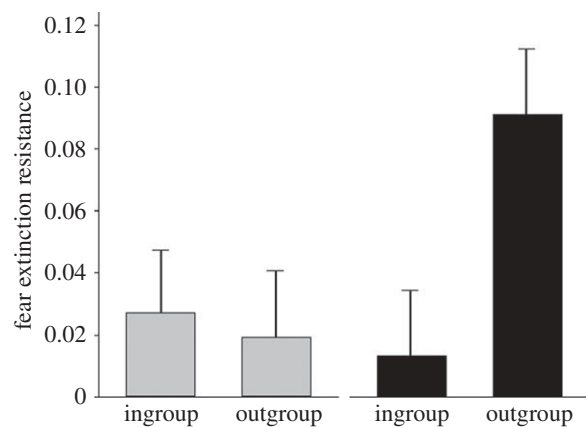


Figure 3. Fear-extinction resistance by target gender and target group. Higher values denote greater resistance to extinction of a conditioned response, as measured by skin conductance. Zero values denote complete extinction, and error bars indicate standard errors. Black bars, male target ($n = 84$); grey bars, female target ($n = 83$). Adapted from Navarrete *et al.* [51].

and mates. From this perspective, women are a reproductive resource to be competed for (rather than against). This implies that males should not only be the agents of intergroup conflict as we have suggested above, but also the direct targets of intergroup conflict in terms of prejudice, hostility and aggression (the outgroup male target hypothesis). As evidence for this, the United States Bureau of Justice reports that across all types of violent crime except rape/sexual assault, males experience higher victimization rates than females. Between 1980 and 2008, 77 per cent of murder victims were males [52]. Although these crimes are not specific to intergroup violence, they are consistent with the prediction that men tend to target other men, not women, when the action is of a violent, non-sexual, nature. In studies of racial discrimination, there is also abundant evidence that it is primarily men of the minority or lower status group, not women, who bear the largest burden of discrimination. For example, on average Blacks earn lower wages than Whites do, but this discrepancy is larger among men than women [53–55]. Black men also experience more discrimination in the retail purchasing market than Black women, as was demonstrated in a series of field-audit studies of automobile purchase negotiations [56–58]. Similar patterns of discrimination have been observed with criminal sentencing [59,60]. These results provide preliminary support for the notion that men are generally the direct targets of intergroup conflict whereas women are more likely to experience the negative effects of intergroup conflict indirectly or incidentally. In addition to these indirect effects, and crucial to our understanding of how women's psychology of intergroup conflict may differ from men's, we posit that such conflict also affects the reproductive interests of women as the victims of sexual aggression.

7. THE ROLE OF WOMEN IN INTERGROUP CONFLICT: AVOIDING SEXUAL COERCION

If the threat of sexual coercion was a persistent problem throughout women's evolutionary history, then one

would expect women to be equipped with mechanisms for protecting themselves [61]. This is because sexual coercion eliminates a woman's reproductive choice, which is a key component of most female mammalian mating strategies. Given that women do not benefit to the same extent as men from mating with many partners, they tend to adopt a quality-focused mating strategy in which they are particularly choosy about their mates. This provides women a greater opportunity to select a mate of optimal genetic quality and/or a mate who is willing to invest in their shared offspring. As such, sexual coercion represents a serious threat to women's reproductive interests.

To protect oneself from the threat of sexual coercion, women may avoid targets or situations that threaten their reproductive interests. Given that individuals not belonging to one's ingroup are perceived as having fewer social controls over their behaviour, particularly during intergroup conflict, women may assess outgroup men as having an elevated risk of sexual assault. Throughout history, intergroup conflicts have provided greater affordances for sexual coercion of women, especially for men of the conquering group. Given that violent intergroup conflict may have been even more common in prehistoric societies than has been the case in modern or historical societies [62], women may have faced a considerably higher probability of sexual assault by outgroup men in intergroup contexts. So although both ingroup and outgroup men may have engaged in sexually coercive mating tactics, because women spent more of their time with men of their own group, outgroup men may have been a more probable threat for assault after controlling for the amount of time that women would have spent in proximity to each [26]. Examples of the association between intergroup conflict and sexual assault have been documented during wars among modern societies and in warfare among primitive tribal groups, [4,63].

As a result of the threat posed by outgroup men, women may be expected to display greater bias against outgroup men than ingroup men. Yet this type of vigilance can be costly in terms of the energy expenditure required to constantly monitor one's environment, as well as costly in terms of lost opportunities for foraging and mating if substantial time is spent avoiding potential threats. Given these costs, women's bias against outgroup men may be calibrated in its expression so that it is most pronounced at times when threats to women's reproductive choice are most costly, that is during the periovulatory phase of the menstrual cycle when conception is most likely.

Research examining women's attitudes and behaviour during the fertile window of the menstrual cycle is consistent with the notion that women may be equipped with psychological mechanisms for protecting themselves against sexual assault. For example, fertile women have been shown to display increased strength after being exposed to cues of sexual coercion [64], are more likely to avoid activities that put them at increased risk of sexual assault [65,66], and exhibit a greater tendency to infer coercive intent among strangers [67].

Although these examples point to more generalized mechanisms for protecting against threats to one's

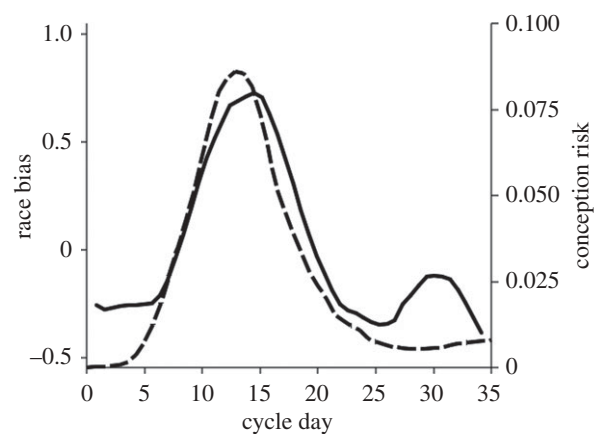


Figure 4. Mean composite race bias (solid line) and conception risk (dashed line) across the menstrual cycle. Curves reflect a smoothed local average. Adapted with permission from Navarrete *et al.* [68].

reproductive choice, recent research has suggested that women may be equipped with mechanisms for avoiding sexual threats from outgroup males specifically. Navarrete *et al.* [68] found that White women evaluated Black men more negatively as a function of their increased risk of conception across the menstrual cycle (figure 4). Furthermore, the association between conception risk and evaluations of Black men was moderated by women's self-appraised vulnerability to sexual coercion, such that White women who reported feeling more vulnerable to sexual coercion evaluated Black men more negatively as a function of increased conception risk.

Recent research has taken this notion a step further by showing that women's perceptions of the formidability of outgroup males may be important [69]. Although there are potential costs associated with interacting with outgroup men, for women there are also some potential benefits. Assuming that coalitional groups tended to mate selectively with other ingroup members, ingroup members would be genetically more similar to one another than to members of other groups. Given that diverse genetic profiles can confer resistance to disease and decrease the likelihood of inheriting recessive genetic disorders, intergroup mating may have influenced reproductive fitness positively by increasing the genetic variability of offspring. In accordance with this, research suggests that fertile women prefer the scent of men that have *major histocompatibility complexes* (which play an important role in immune function [70]) that differ optimally from their own.

In the light of the conflict between the potential costs and benefits associated with intergroup interactions, selection may have favoured psychological mechanisms that evaluate the level of threat that an outgroup member poses prior to enacting approach or avoidance behaviours. One potential indicator of threat may be the extent to which men of the outgroup are perceived as physically formidable, as these traits would increase the effectiveness of a man's attempts to physically overpower and constrain a woman's behaviour. Research in support of this has found that evaluations of outgroup males become more negative

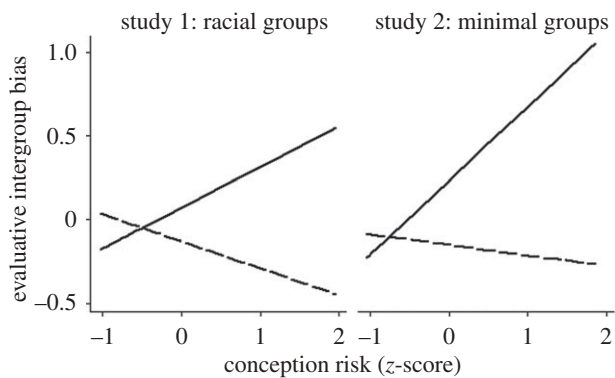


Figure 5. Evaluative intergroup bias against men in racial and minimal group contexts as a function of conception risk and high (solid lines) and low (dashed lines) physicality associations. Adapted with permission from McDonald *et al.* [71].

as a function of heightened conception risk, but only for women who associate the outgroup with physical formidability [69]. These findings were replicated in a second study where the intergroup context was defined using an arbitrary categorization scheme based on colour preferences (figure 5). This implies that the mechanism by which women's evaluations of outgroup men become more negative as a function of conception risk does not depend on a specific racial context (e.g. Black versus White). Instead, the mechanism likely relies on more basic categorization processes that respond to even minimally bifurcated cues of group membership. This is consistent with the idea that the mechanism evolved during a time in our evolutionary history when groups were not defined by race, but by differences in language, accent, social customs and rituals [72,73].

Overall, these results suggest that women may be equipped with flexible psychological mechanisms designed to protect reproductive choice by avoiding individuals who have historically posed the greatest reproductive threat and who are perceived as being most capable of effectively constraining one's reproductive choice—formidable outgroup males. Thus, although women are unlikely to be direct targets of intergroup conflict in its most lethal forms, the potential threat of sexual aggression may have uniquely shaped their psychology of prejudice, and this may subsequently contribute to the perpetuation of intergroup conflict.

(a) *Sex-specific motives underlying intergroup bias*

From the research outlined above, it is clear that although both men and women play a role in perpetuating intergroup conflict and aggression, the motives that underlie men and women's intergroup biases are distinct. As such, Navarrete *et al.* [26] hypothesized that the persistence of a conditioned anxious response towards outgroup male faces may be motivated by different underlying systems for men and women. Given the assumption derived from the male warrior hypothesis that (i) males have historically been the primary agents of intergroup aggression in humans and (ii) the potential for harm present in the stimulus

prepares the fear system for functionally specialized behavioural outcomes, such as counter-attack [48,49], Navarrete *et al.* [26] expected that men's responses might be associated with traits related to aggression and dominance. These traits would include those expected to be of some utility in generating retaliatory responses to violent provocation in intergroup contexts, such as a personal history of fighting, angry outbursts, and social dominance ideation. In contrast, given the evidence suggesting women's bias against outgroup men functions to protect reproductive choice by avoiding sexual threats, it was expected that women's conditioned responses would be more likely to be predicted by their self-appraised vulnerability to sexual coercion. Results confirmed these predictions, demonstrating that resistance to extinction of a learned fear towards outgroup males was predicted by an interaction of social dominance motives and aggression for men, but fear of sexual coercion among women.

Given that recent neurophysiological studies have implicated the amygdala in the expression of race bias [69], such results raise the question as to whether prepared learning in an intergroup context engenders a response among men that can be described as fear or some other kind of agonistic emotional state associated with amygdala activity physiologically priming the body for aggressive conflict. For many individuals, an aversive encounter with a formidable agent (such as a large predator) may lead to fear and avoidance. However, for those with a penchant for agonistic social encounters—primarily aggressive and physically formidable males—such encounters may evoke the motivation to retaliate, aggress against and eliminate the offending target. This phenomenon has its analogues in many animal societies, where agonistic solutions to threats such as chasing away or dispatching strangers or predators are often the purview of the more formidable adult male members of the group [74,75]. As such, these results highlight the importance of individual differences among men in reactions to an intergroup threat. Given the large potential costs associated with intergroup conflict, it makes sense that it may primarily be men with the goal of group dominance and a history of aggressive behaviour who engage in conflict—not all men are suited to be warriors.

8. CONCLUSIONS AND IMPLICATIONS

Conflict between human groups is a pervasive social problem, to which a solution remains elusive. One potential reason for this difficulty may be that our evolutionary history has shaped the human mind in ways that tend to perpetuate intergroup conflict. The male warrior hypothesis argues that, for men, intergroup conflict represents an opportunity to gain access to mates, territory and increased status, and this may have created selection pressures for psychological mechanisms to initiate and display acts of intergroup aggression. For women, intergroup conflict substantially increases their risk of being sexually assaulted by outgroup men, and may have therefore created selection pressure for psychological mechanisms that bias women against outgroup men. We have presented findings from various research programmes that

provide much support for predictions derived from our evolutionary hypothesis. Still there is much work yet to be done in terms of integrating our findings with the anthropological and biological literatures.

First, there is some controversy about the intensity of intergroup violence and aggression in prehistoric societies. Some anthropologists have argued that intergroup aggression was virtually non-existent due to low population densities [76]. Yet, others have argued that during the Late Pleistocene and Holocene, competition for resources intensified and intergroup aggression might have been fairly endemic with estimates of between 10 and 25 per cent of adult men being killed in intergroup conflicts, which would have constituted a fairly strong selection pressure [3,62]. This is backed up by archeological evidence of mass graves containing predominantly male skeletons with damage owing to the force of weapons, such as spear points [3]. Although it is difficult to get reliable estimates of raids and wars in our ancestral past, these findings add some credence to the idea that humans have an evolved psychology for intergroup conflict.

Second, more comparative research on the male warrior hypothesis is also needed. There is evidence from one of our closest genetic relatives, the chimpanzee, for the formation of aggressive male coalitions to conduct border patrols. Unfortunately, we do not know enough yet about the social behaviour of bonobos, our other closest genetic relative. Bonobos display dramatic reductions in violence among the sexes, between ingroup males and across communities. Yet, there are anecdotal reports that in the rare encounters between two communities the females are more peaceful than the males [4,77]. Yet, it is also true that in some other species, such as hyaenas, coalitional aggression is primarily observed among females rather than males [4]. This suggests that there may be ecological and social factors which influence whether it is easier for males or females to form coalitions [78].

Third, and related, we suggest that there are important cultural and individual variations in the phenotypic expression of male warrior traits that must be further investigated. For instance, in patrilocal societies the men have stronger genetic ties and this might facilitate the formation of male coalitions to defend their group and attack other groups. Ecological and social pressures such as the competition for territories, food resources and sexual mates (e.g. locally distorted sex ratios) might also increase the propensity for male warrior behaviours. Finally, there is likely to be individual heritable variation in male warrior behaviour. Research suggests that physically formidable men anger more quickly and exhibit more aggression [79]. Furthermore, as we have seen, females calibrate their fear responses based on the perceived formidability of outgroup males. This suggests that the individual propensity to engage in intergroup aggression may be influenced by traits such as one's body size or hormones, as well as life-history factors such as past fighting success.

Fourth, in terms of female response to outgroup males, we have looked at the potential threat of sexual coercion only. Yet it is possible that reaction towards outgroup males might also be triggered by concerns about the safety of their offspring. Infanticide by

outgroup males is commonly observed among the animal kingdom and this might have also been true for prehistoric societies. Psychological research suggests that women might display a tend-and-befriend response in coping with threats [80]. Thus, in interactions with outgroup males mothers of young offspring might exhibit (i) a protective response towards their offspring, possibly combined with (ii) an affiliative response towards the outgroup male to ensure that he is not causing any harm towards the children.

Fifth, although there may have been some benefits to intergroup conflict in our evolutionary past, today the costs can be immense in terms of social and economic losses. The male warrior hypothesis makes various suggestions for interventions to improve intergroup relations. When outgroups pose a coalitional threat, interventions might be targeted specifically at male-to-male interactions because they are the most likely perpetrators and targets of intergroup prejudice and aggression. In terms of their objectives, interventions will be particularly successful when they eliminate the sense of threat associated with particular outgroups altogether. Attempts must be made to individuate members of such outgroups, for instance, by accentuating their individual needs, ambitions and goals rather than those of the cultural groups they represent. A second aim of interventions is to alter the perceptual cues that elicit threat responses towards men of particular outgroups, such as new immigrant groups in society. Cultural artefacts, language, rituals, norms and public behaviours serve as tribal markers, now and in our evolutionary past. Reducing the salience of these cultural cues, or generating more inclusive cues that cut across ethnic and racial groups may decrease the likelihood of outgroup members being perceived as threats. Third, interventions might focus on changing the specific cognitive and affective responses towards outgroup males. Yet, if it is true that these responses are evolved, then the link between threat and response might be difficult to inhibit or extinguish. Nevertheless, we suspect that mere exposure and frequent positive interaction will reduce prejudice and hostility over time. The famous Jigsaw classroom experiment [81] demonstrates that intergroup conflict can be reduced by inducing cooperative relations among school children of different ethnic groups.

The social psychological literature on intergroup conflict is rich and diverse. Yet it has been mute about the evolutionary and biological roots of intergroup aggression and it cannot easily explain sex differences in intergroup behaviour. Here we have offered a novel theory, the male warrior hypothesis, inspired by recent findings in evolutionary psychology, social psychology, biology and anthropology, explaining how a deep evolutionary history of intergroup conflict may have shaped the social psychologies and behaviours of men and women. Although these sex-specific responses could have been adaptive in ancestral times, they might not be functional in modern times and are often counter-productive. Nevertheless, understanding why male outgroup members elicit particularly negative emotions, cognitions and behaviours is the first step towards a sensible policy to improving intergroup relations in modern societies.

END NOTE

¹This is not true for all species; in some, such as the hyaena, the females engage in coalitional aggression. One possible reason for this is that female hyaenas have stronger coalitional bonds and therefore work together more easily than do the males [4].

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