

excellent treatment of the former only. A full explanation of sex differences in aggression will fail without accounting for our history of inter-group aggression, which has deep evolutionary roots and specific psychological adaptations. The causes and consequences of inter-group aggression are dramatically different for males and females.

Human aggression takes two very different forms: (1) *intra-group* aggression (between individuals); and (2) *inter-group* aggression (between groups of individuals, such as coalitions, gangs, warriors, armies). Archer argues that observed sex differences in aggression are best explained by sexual selection theory, but this is based on an exclusive focus on intra-group aggression, ignoring the potential explanatory (or confounding) role of inter-group aggression.

We suggest that the inter-group dimension is vital to understanding sex differences in aggression: If inter-group processes explain *some* of the variance in sex differences in aggression, then Archer may have *overestimated* the role of sexual selection in accounting for the observed sex differences, and may also have *underestimated* sex differences in aggression overall (since they may be even higher in inter-group contexts).

Inter-group aggression has arguably been a major force in human evolution. There is evidence that warfare was frequent and severe throughout human history (Gat 2006; Guilaine & Zammit 2004; Keeley 1996; LeBlanc & Register 2003) and has deep roots in human evolution (Alexander 1987; Thayer 2004; Wrangham & Peterson 1996). Warfare has been a significant cause of male deaths (13–15% in the archeological and ethnographic record; Bowles 2006), suggesting a strong selection pressure on adaptations for inter-group aggression.

Studies of warfare differ in many respects but are in agreement on one thing: it is almost *exclusively* a male phenomenon (Potts & Hayden 2008; Wrangham & Peterson 1996). Although women commonly aid in war *efforts* of various kinds, they generally do not participate as warriors. Legends of Amazons and female warriors are so rare (or unsubstantiated) as to serve as exceptions that prove the rule. The introduction of women into *combat* units in modern militaries has also been problematic (Browne 2007). We should, therefore, expect significant sex differences in adaptations to inter-group aggression.

Inter-group aggression introduces at least two complexities to Archer's analysis. First, as noted above, some variance in sex differences in aggression is likely to derive from inter-group processes, not sexual selection. Second, inter-group aggression can often be a cause of *reduced* aggression between males of the *same* group – uniting to fight a common enemy. Indeed, extraordinary cooperation (even self-sacrifice) can emerge in the context of inter-group aggression (McNeill 1995; Rielly 2000). Sex-differentiated aggression in inter-group contexts is as much about inter-male *cooperation* as it is about inter-male aggression.

Empirical evidence supports two key predictions of this “male warrior hypothesis” (van Vugt et al. 2007). First, in situations of *inter-group* threat, men should display more aggression than women. This is a robust finding in both experimental and real-world studies (Johnson et al. 2006; McDermott & Cowden 2001; Wrangham & Wilson 2004). Second, in situations of *inter-group* threat, men should increase their cooperation with the in-group in order to more effectively defend and aggress against the out-group. This is supported by experiments in which cooperation in collective action games increases in the presence of rival groups, but only among men (van Vugt et al. 2007).

An inter-group perspective raises the question of *interactions* between sexual selection and inter-group aggression: what is the impact of sexual selection on aggression between members of different groups? Indeed, inter-group aggression may actually be *rooted* in sexual selection. For example, performance in inter-group warfare may bring status or rewards that increase individual reproductive success (Chagnon 1988). Or, since a primary function of wars in pre-industrial societies is the capture of women (Keeley 1996), warfare may represent competition for reproductive access fought between coalitions rather than

between individuals. Finally, inter-group aggression may even be a method of displacing sexual competition from the in-group to the out-group, serving to minimize within-group conflict (and its associated costs).

An inter-group perspective also raises the question of the role of women in aggression. If women have been beneficiaries and victims of inter-group aggression, we would expect selection pressures on response strategies. For example, there is some evidence that women find military men more sexually attractive, but only if they are observed in battle (Leunissen & van Vugt, unpublished). Women also show an aversion to out-group males at peak fertility in their menstrual cycle (Navarrete et al. 2009). Women might even support inter-group aggression if they (or their offspring and kin) will benefit from the consequences. Keeley reports that among the Apache, “when the meat supply of a band began to run low, an older woman would complain publicly and suggest that a raid be mounted to obtain a fresh supply” (Keeley 1996, p. 135).

An inter-group perspective is also important for Archer's analysis of *intersexual* (male on female) aggression. Archer focuses primarily on aggression among *partners*. However, differences in male and female aggression is likely to be highly dependent on group membership. As noted above, a common objective of pre-industrial warfare is the capture of women, and the occurrence of rape in wartime is widely documented even among modern societies (Naimark 1995; Potts & Hayden 2008). Therefore, male aggression against women is likely to be significantly underestimated if we look only at data on partners – men and women who typically chose to be together in the first place, or at least come from the same in-group.

An inter-group perspective does at least support Archer's rejection of social role theory. Briefly, differences in inter-group behavior between boys and girls also appear at a young age and follow a fairly stable developmental trajectory across contexts (Ellis et al. 2008), suggesting an evolutionary explanation. For example, boys more often play team games involving larger groups and have more transient friendships, whereas girls have more exclusive friendships. Boys are also angrier about rule-breaking behavior in such games.

To summarize, inter-group aggression might seem to have little bearing on Archer's core claims – perhaps just representing a different research question. However, we suggest that the omission of an inter-group dimension is significant, because: (1) it underestimates *overall* sex differences in aggression; and (2) *observed* sex differences in aggression may derive from some third factor *other* than sexual selection – in particular inter-group psychology. Thus, even if the evidence that Archer examines is correct, we cannot tell whether it derives from an evolutionary history of sexual selection or from an evolutionary history of inter-group aggression (or some combination thereof). Sex differences in aggression between groups remains an important research area for the future with implications for understanding, predicting, and intervening in human aggression within both domestic and international contexts.

Suspicious of female infidelity predict men's partner-directed violence

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Abstract: Archer's argument regarding sex differences in partner violence rests on a general account of between-sex differences in

reproductive strategies and in social roles. However, men's partner-directed violence often is predicted by perceived risk of female infidelity. We hypothesize that men's partner-directed violence is produced by psychological mechanisms evolved to solve the adaptive problem of paternity uncertainty.

Archer presents a comprehensive account of between-sex aggression from an evolutionary perspective built on sexual selection theory. We appreciate Archer's argument that sex differences in reproductive strategy are responsible for sexual conflict and for between-sex aggression. Sexual selection explains sex differences in aggression, in general. We contend, however, that there is a particular area of work that deserves more attention in research on violence in intimate relationships. There is a large body of research investigating men's partner-directed violence as an evolved solution to the adaptive problems of female infidelity and paternity uncertainty.

Over the course of human evolutionary history, men have faced the adaptive problem of female sexual infidelity and subsequent cuckoldry – or the unwitting investment in genetically unrelated offspring. The reproductive costs of cuckoldry, including loss of time, energy, resources, and alternative mating opportunities are potentially so great that men are hypothesized to have evolved psychological mechanisms that function to motivate anti-cuckoldry tactics. The problem of paternity uncertainty is hypothesized to have selected for the emotion of male sexual jealousy, which in turn motivates men's anti-cuckoldry tactics such as nonviolent and violent mate retention behaviors. Considerable evidence indicates that men's perceptions of their female partner's infidelity predict men's partner-directed insults, sexual coercion, and partner-directed violence.

Male sexual jealousy is one of the most frequently cited causes of men's partner-directed violence, both physical and sexual (e.g., Buss 2000; Daly & Wilson 1988; Daly et al. 1982; Dobash & Dobash 1979; Dutton 1998; Frieze 1983; Gage & Hutchinson 2006; Russell 1982; Walker 1979). The frequency with which men perform nonviolent mate retention behaviors predicts the frequency with which they inflict physical violence against their partners, arguably because both classes of behavior are outputs of sexual jealousy (Shackelford et al. 2005a). Men who directly accuse their partners of sexual infidelity also are more likely to inflict partner-directed violence (Kaighobadi et al. 2008).

Sexual coercion also is hypothesized to function as an anti-cuckoldry tactic (Lalumière et al. 2005; Thornhill & Thornhill 1992; Wilson & Daly 1992; see also Goetz & Shackelford 2006). Instances of forced in-pair copulation (FIPC) have been documented in avian species that form long-term pair-bonds (Bailey et al. 1978; Barash 1977; Birkhead et al. 1989; Cheng et al. 1983; Goodwin 1955; McKinney et al. 1984). FIPC is hypothesized to be a form of post-copulatory male-male competition – that is, a sperm-competition tactic (Barash 1977; Cheng et al. 1983; Lalumière et al. 2005; McKinney et al. 1984), because it often follows a female partner's extra-pair copulation or intrusions by rival males (e.g., Bailey et al. 1978; Barash 1977; Birkhead et al. 1989; Cheng et al. 1983; Goodwin 1955; McKinney et al. 1983; McKinney & Stolen 1982; Valera et al. 2003). Sperm competition occurs when a female copulates with and is inseminated by more than one male in a sufficiently brief period of time (Parker 1970). Thus, by forcing the female to copulate shortly after the increased risk of insemination by a rival, males place their sperm in competition with any sperm deposited into their partner by a rival male (Birkhead et al. 1989; Cheng et al. 1983).

Observations of sperm competition in nonhuman species offer a framework with which to consider similar adaptations in humans, who also form long-term socially (but not genetically) monogamous pair-bonds. Recent evidence suggests that sperm competition has been a recurrent feature of human evolutionary history and that men have physiological and psychological mechanisms that may have evolved to solve related adaptive problems (Baker & Bellis 1993; Gallup et al. 2003; Goetz et al. 2005;

Kilgallon & Simmons 2005; Pound 2002; Shackelford & Goetz 2007; Shackelford & Pound 2006; Shackelford et al. 2002; 2005b; Smith 1984). It has been hypothesized that, by forcing their partners to have sex, men who are suspicious of their partner's infidelity introduce their own sperm into their partner's reproductive tract and thereby decrease the risk of cuckoldry. Thornhill and Thornhill (1992) argued that women who resist or avoid copulating with their partners might thereby be signaling to their partners a recent sexual infidelity; hence, forced copulation might function to decrease men's paternity uncertainty. And the fact that rape of a woman is more likely to occur during or after a breakup (when men's concerns about women's infidelities are greatest) may provide preliminary support for this hypothesis (see Thornhill & Thornhill 1992). A number of studies have documented a positive relationship between men's sexual jealousy and men's sexual coercion of their partners. For example, Frieze (1983) and Gage and Hutchinson (2006) found that men who sexually coerced their wives are more sexually jealous than men who did not. Previous research has found a direct positive relationship between men's suspicions and accusations of partner infidelity and men's sexual coercion of their partners (Starratt et al. 2008). In two studies securing data from men's self-reports and women's partner-reports, Goetz and Shackelford (2006) found that men's sexual coercion correlated positively with women's past and future likelihood of engaging in sexual infidelity.

We recognize that sex differences in intimate partner violence can be explained by sex differences in reproductive strategies and by social roles, as Archer argues; however, men's partner-directed violence can be more specifically predicted by perceived risk of female infidelity and male sexual jealousy. A large body of empirical evidence supports the hypothesis that men's partner-directed sexual coercion and violence might sometimes be a product of evolved psychological mechanisms designed to prevent or punish female infidelity. The relevant evolved mechanisms interact with stable dispositions and situational factors to produce manifest behavior. Future research might benefit by using an evolutionary perspective to build models of intimate partner violence that include stable dispositions such as personality traits, environmental factors such as social roles, and situational factors such as perceived risk of partner infidelity.

A quantitative genetic approach to understanding aggressive behavior

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Abstract: Quantitative genetic studies of human aggressive behavior only partly support the claim of social role theory that individual differences in aggressive behavior are learnt rather than innate. As to its heritable component, future studies on the genetic architecture of aggressive behavior across different contexts could shed more light on the evolutionary origins of male-female versus male-male aggression.

Archer's review explores the extent to which human sex differences in aggression can be explained by (1) sexual selection theory versus (2) social role theory. From the perspective of a behavioral ecologist and evolutionary geneticist this seems like a highly unequal comparison. While sexual selection theory