

where males have higher maximum reproductive rates than females. In such species males evolve a set of hormonally mediated competitive traits via sexual selection. Because humans match the predictions of this general evolutionary model, attempts to (re)explain men's aggressiveness in sociological terms are superfluous and misleading.

Archer compares sexual selection (Darwin 1871/1901) and social role theory (Eagly 1987) as explanations for human sex differences in aggressiveness. Archer's empirical claims are grounded, but his case is weakened because he fails to emphasize two related meta-methodological points: the power of the comparative approach and the parsimony it provides. Greater male aggressiveness is neither uniquely human nor universal among animals. It exhibits a particular cross-species distribution, being present in some species and absent in others. That distribution strongly constrains its functional explanation. Unfortunately, social role theory neglects this powerful source of insight. It examines sex differences in aggression in a zoological vacuum, naively treating the human case as unique. As a result of its narrow focus, social role theory fails to shed new light on sex differences in human aggression. Like many models in the social sciences, it is a case of special pleading where none is required.

Darwin (1871/1901) defined sexual selection as an evolutionary process that regularly produces differences between the females and males of a species, and he enumerated the reproductive differentials that drive it. Subsequently, twentieth-century biologists (Andersson 1994; Clutton-Brock & Vincent 1991; Trivers 1972) explained the forces that give sexual selection its polarity. It is this polarity – which sex is more aggressive – that both sexual selection and social role theory seek to explain.

Scientific theories explain relevant variance. Thus, social role theory would have some traction if there were cultures where women are more aggressive than men. For better or worse, no such cultures exist (Brown 1991; Daly & Wilson 1988). So, where is the theory-testing variance? To find it one must escape anthropocentric Durkheimian biophobia and look across species.

Sexual selection theory provides a general explanation of sex differences that applies to all sexual species. It predicts the distribution of sex differences in aggression: which species will evolve greater male aggressiveness, which species will exhibit no such sex differences, and which will show greater female aggressiveness. According to sexual selection theory, aggressiveness is not a function of sex per se, but of sex differences in maximum reproductive rate (Clutton-Brock & Vincent 1991), arising out of sex differences in parental investment (Trivers 1972). To illustrate, because only female mammals gestate and lactate, a male could have many more offspring than a female. Every reproductive venture requires one male and one female; thus the slower sex is in short supply and worth competing for. (In this example reproductive physiology determines reproductive rates but aspects of the mating system may also be important.)

Sexual selection theory's accuracy in predicting the distribution of sex differences across species makes it logically prior to ad hoc explanations of sex differences in any particular species, unless that species fails to match its predictions. Thus, a baseline question for social role theorists is, do humans constitute an exception to sexual selection theory? Men have, and have had for thousands of generations, higher maximum reproductive rates than women. This implies that men will have found women in short supply and consequently evolved a suite of competitive tactics for acquiring mates, including aggression.

What remains for social role theory to explain? Its proponents might say "development." But, whatever ontogenetic influences social scientists imagine for gender roles, their hypotheses will have to contend with a thick cross-species literature on the developmental effects of androgens. Wherever sexual selection has produced more aggressive males, androgens orchestrate the development of that sex difference. As a functional viewpoint would suggest, the very same hormones also shape the anatomical components of the male-competition complex. Compared

to women, men are much stronger and more muscular in the upper body (the region most engaged in physical aggression).

The effect size for these sex differences is approximately 3.0, with 99.9% of women falling below the male mean; individual differences in muscle mass still reliably predict male mating success in the United States (Lassek & Gaulin, in press). Thus, sexual selection simultaneously explains both anatomical and behavioral sex differences and their joint hormonal mediation. Social role theory cannot approach this level of explanatory integration.

But the explanation gap is wider still. The male-competition complex has many evolved manifestations. Bimaturism, sexually differentiated mortality rates, and sex differences in navigational ability are well-described human traits; and again, the cross-species distribution of these traits strongly implicates sexual selection. Delayed sexual maturity of males is limited to species where they have higher reproductive rates than females (Leigh 1992, Leigh & Shea 1995). Controlled within-genus comparisons suggest that searching for mates drives the evolution of male navigational ability, but again, only where they have higher reproductive rates (Gaulin 1992). Both bimaturism and navigational ability are developmentally linked to the same androgenic hormones that organize aggressive structures and behaviors. Many aspects of the male-competition complex entail costs reflected in higher male mortality rates: In both birds and mammals sex differences in mortality are not universal but proportionate to the intensity of sexual selection (Promislow 1992, Promislow et al. 1992). These costs are not limited to combat-related mortality but include higher male susceptibility to infection that: (a) closely tracks the intensity of sexual selection across species (Moore & Wilson 2002), (b) manifests prominently in humans (Owens 2002), and (c) is probably related to androgens' immunosuppressant effects (Folstad & Karter 1992) because castration removes the sex difference in infection rates and hormone replacement reinstates it (Zuk & McKean 1996). It is not the existence of these traits but their patterned, cross-species association that social role theory must confront.

In sum, humans exhibit a suite of traits – elevated male aggressiveness, greater male muscularity and strength, later male maturation, superior male navigational ability, and higher male mortality, all underpinned by an androgen-based developmental system – that they share only with species where male reproductive rates can significantly exceed those of females. The coherent distribution of these traits strongly suggests they were jointly produced by sexual selection. This patterning, revealed by cross-species comparison, supports the causal primacy of sexual selection. In the absence of a significant misfit with the predictions of sexual selection, any attempts to (re)explain men's greater aggressiveness in purely sociological terms constitute unparsimonious exceptionalism and have little scientific promise.

A history of war: The role of inter-group conflict in sex differences in aggression

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Abstract: Human aggression has two important dimensions: *within*-group aggression and *between*-group aggression. Archer offers an

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 intermale *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