**Abstract:** Are males more likely to engage in violent forms of competition when mates are limited or abundant? We review the theory behind parental investment and mating market models, emphasizing recent reformulations within sexual selection theory integrating both groups of models. The relationship between sex ratios, the intensity of sexual selection, and parental investment is clarified, particularly regarding violent behavior in human populations. We explore conflicting trends within the evolutionary, sociological and economic literatures, and evaluate empirical evidence for the different models of sexual selection. In short, we find that the "more men more violence" expectation derives from a simplistic interpretation of Trivers' original paper, a failure to appreciate recent theoretical developments, and the very loose use of the term 'competition'.

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**Keywords:** sex ratio, violence, competition, sexual selection, mating market
Dear Dr. Craze,

Please find enclosed our manuscript, “Too Many Men: The Violence Problem?” by Ryan Schacht, Kristin L. Rauch and Monique Borgerhoff Mulder, which we would like to submit for publication as a Review Article in *Trends in Ecology & Evolution*.

In this manuscript we explore the relationship between violence and the sex ratio, focusing primarily on humans. We present conflicting theoretical and empirical trends within the sexual selection literature and show how expectations of higher levels of violence in groups with an excess of males is oversimplistic. We show that violent competition is not the only male response to a shortage of mates and we highlight evidence indicating greater variance in male fitness when males are scarce, not abundant. In sum, because “violence” may be present in both high and low sex ratio conditions, identifying how a particular violent act relates to mating competition is of critical importance for understanding the strength and direction of sexual selection in a particular sex ratio.

We believe our findings would appeal to the readership of *Trends in Ecology & Evolution*.

We confirm that this manuscript has not been published elsewhere and is not under consideration by another journal. All authors have approved the manuscript and agree with its submission to *Trends in Ecology & Evolution*.

Thank you for your consideration of our work. Please address all correspondence to me by email (rnschacht@ucdavis.edu).

Sincerely,
Ryan Schacht

Attached:
Manuscript (including 1 table, 4 boxes)
Highlights
Title: Too Many Men: The Violence Problem?

Authors: Ryan Schacht (1*), Kristin L. Rauch (1) & Monique Borgerhoff Mulder (1-3)

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Abstract (120/120 words)
Are males more likely to engage in violent forms of competition when mates are limited or abundant? We review the theory behind parental investment and mating market models, emphasizing recent reformulations within sexual selection theory integrating both groups of models. The relationship between sex ratios, the intensity of sexual selection, and parental investment is clarified, particularly regarding violent behavior in human populations. We explore conflicting trends within the evolutionary, sociological and economic literatures, and evaluate empirical evidence for the different models of sexual selection. In short, we find that the “more men more violence” expectation derives from a simplistic interpretation of Trivers’ original paper, a failure to appreciate recent theoretical developments, and the very loose use of the term ‘competition’.

Main Text (3500/3500 words)

More men more violence
Recent high-profile cases of violence, such as the notorious 2012 Delhi gang rape case, have the public, journalists and researchers alike all searching for explanations. A popular explanation centers on male-biased sex ratios, with specific examples coming from both India and China where there are growing numbers of extra men (often termed “bare branches”) due to son preferences and daughter-biased infanticide and elective abortion [1]. Because, on average, men are more violent than women it is argued that more men will necessarily lead to more violence. This argument is not new to the scientific literature and has become central to how many understand sexual selection. Essentially, when there are more males than females in a population, males are expected to compete vigorously for the limited number of mating opportunities available. In applying this idea to humans, it is appealing to attribute elevated rates of violent crime to high sex ratios and a shortage of women [e.g., 2, 3]. While this reasoning is intuitive, we question both its underlying theoretical basis and its empirical support. Put plainly, are males more likely to engage in violent forms of competition when mates are limited or when they are abundant? We tackle this issue by focusing primarily on human societies. We explore conflicting trends within the evolutionary, sociological and economic literatures, and in particular we highlight recent
reformulations within sexual selection theory that challenge our intuitions and generate very different predictions, rather more in line with recent empirical findings.

The “more men, more violence” prediction is derived from a long-standing model of sexual selection, laid out by Trivers [4] and developed by Emlen and Oring [5] and Clutton-Brock and Vincent [6], the former with the concept of Operational Sex Ratio (OSR) and the latter with Potential Reproductive Rate (PRR) (see Box 1 for Acronyms Defined). Essentially, according to the traditional parental investment (PI) model, when one sex is tied up with parental care, or more generally with activities that lower its PRR, the other sex competes over this limited resource, leading to the prediction that the sex in abundance competes more intensely for mates than does the rarer sex, and the ancillary expectation that this will generate more violence in the more abundant sex.

There is however a different model for thinking about mate competition – the mating market model – that emerged within the social sciences decades before the traditional parental investment model [e.g., 7, 8]. Its roots lie in the supply and demand models of economics. Becker [9] argued that an increase in the sex ratio raises the demand for wives, giving women greater bargaining power and requiring men to invest more efficiently in the traits that make them attractive as long-term partners [see also 10, 11]. Mayr [12] first raised this idea in biology, in his discussion of sex ratios and mating systems in birds, and Noë & Hammerstein [13, see also 14] reintroduced these ideas into behavioral ecology.

These two perspectives have coexisted for over four decades yet make strikingly different predictions, under many conditions, regarding the mating strategies of the more numerous sex. Given the apparent logic, utility and empirical support for both perspectives, the persistent disconnect between these approaches is troubling.

This paper will review the theory behind PI and mating market models and evaluate empirical (primarily human) evidence for both. We outline innovations in sexual selection theory [15-18], which offer promising ways to integrate the two groups of models and develop a sharper understanding of the relationship between sex...
ratios, the intensity of sexual selection, and parental investment, with a view to shedding more light on the occurrence of violence in humans.

**Parental Investment Models**

Building on Bateman’s [19] demonstration of greater sexual selection in males than females, Trivers [4] proposed that the relative PI of the sexes is a key variable controlling the operation of sexual selection. The higher-investing sex becomes a limiting resource for the sex that invests less, leading to escalated levels of mate competition in the latter. Often, and especially for mammals, females invest more in parental care than do males, therefore males face higher levels of competition for access to the limited number of females.

Emlen and Oring [5] added the concept of OSR. The OSR is the ratio of sexually active males to sexually receptive females and is highly influenced by patterns of parental investment. Higher investment by females decreases the amount of time they are ‘receptive’ to fertilization. Such sex differences in the availability of gametes skew the OSR towards males leading to the claim that males face a greater intensity of sexual selection on the traits that make them competitive for relatively scarce females. Insofar as relative PI is typically an important factor contributing to variations in OSR between species and/or populations, Clutton-Brock and Vincent [6, see also 20] proposed that PRRs of males and females can be used to predict patterns of competition between the sexes.

According to this perspective, when males are in abundance they are expected to compete vigorously for mating opportunities, often with the implications of intense physical struggles and violence. Insofar as some males are more successful than others in monopolizing these opportunities as a result of heritable traits [e.g., 21], this is expected to lead to intensified levels of sexual selection on males.

**Mating Market Models**
Mating markets operate by the principle of supply and demand. The rarer sex has more bargaining power in the marketplace than the more common sex, and can leverage their scarcity to realize their preferred mating strategies. The more common sex, as a consequence of their abundance, must cater to the preferences of the rare sex in order to acquire a mate.

Economists and sociologists regularly employ mating market theories. While much of their research is not explicitly based on sexual selection it is, nonetheless, consistent with evolutionary reasoning. In a famous book entitled “Too Many Women” Guttentag and Secord [11] draw from historical accounts and quantitative analyses to demonstrate how sex ratios affect the many aspects of the relationships between men and women. They show that in societies with a surplus of women, men find themselves in demand and can leverage their scarcity, behaving promiscuously and offering little parental investment; whereas when women are in short supply, marriage and a commitment to family are highly valued. A more recent example comes from Colombia [22], where high male mortality rates in some regions have led to an abundance of women, decreased marriage rates and high incidences of men involved in concurrent relationships. Much cross-cultural work corroborates these findings and has shown that female-biased sex ratios are associated with lower levels of male parental investment and higher rates of female headed households [23]. Conversely, when there are too many men the nature of relationships change. For example Angrist [24] found that among immigrants to the U.S., high sex ratios had a large positive effect on the likelihood of female marriage and a large negative effect on female labor force participation due to higher rates of male investment. In general, male biased sex ratios are associated with less promiscuity [23] and greater conjugal stability [25].

**A Reformulation with implications for violence and sex ratios**

In a recent model Kokko and Jennions [18] implicitly integrate the two veins of thought, by including both the importance of PI and the frequency-dependent nature of mating strategies. Accordingly, the adult sex ratio (ASR) becomes a key predictor of sex-differentiated behavior. For example, due to poor odds of remating in a
crowded market, a male-biased ASR discourages male desertion in search of additional matings and instead favors increased male care [18] and less intense sexual competition [26]. According to this reformulation the intensity of sexual selection is driven by intrasexual variability in quality [16], paternity certainty [15, 17], and crucially for our argument here, the relative abundance (or shortage) of either sex [18], such that when one sex is in oversupply both sexes respond by strategically altering their preferences and behavior, as in a mating market [14]. Central to understanding this shift in thinking is the reevaluation of several variables and their relationship with the intensity of sexual selection (Box 2), including the concept of OSR which has until recently structured our understanding of sexual selection [26].

While some of the empirical findings consistent with the traditional model are recovered in the reformulated model, albeit by employing the new logic, [27], in general predictions are strikingly different. All else being equal (to which we return), traditional models predict an abundance of men to lead to greater sexual competition, violence, crime and paternal absenteeism, while reformulated models, in general, contradict these expectations. According to the reformulated perspective men, when they are in abundance (and not therefore in demand), will cater to women’s preferences for investment and fidelity in order to attract and retain limited mating opportunities.

**Turning to humans**

To obtain a clearer understanding of how mate competition varies within species we need to know about the relationship between sexual selection and ASR. To take an empirical approach to this question in humans we worked through two networks of anthropologists [28, 29], using both published sources and personal communications, to examine across 15 populations the relationship between ASR and the opportunity for sexual selection ($I_s$; Box 3). The relationship between the $I_s$ of males and sex ratio of the mating pool is negative, suggesting greater sexual competition among men in female-biased than in male-biased populations. Clearly this is a preliminary empirical demonstration, of primarily illustrative significance, but it does raise the
possibility that, across this small subsample of human populations, when men are scarce they show greater variance in fitness than when they are in abundance.

How does this relate to the patterning of violent competition across societies? We turn now to an examination of the relationship between the sex ratio and different forms of behavior that might be seen as indicators of competition to determine whether or not they are negatively associated, as the reformulated model would predict. As is quickly observed from Table 1, the results are mixed. In some cases male-biased sex ratios are associated with higher rates of violence and crime and in some cases with lower. Why might this be? While methodological differences play a role (see notes in Table 1), this table reveals there is no simple pattern of violence in relation to mating competition.

A closer look at ‘competition’ and how it varies with ASR

Given the variety of forms that mate competition can take (see Box 4), it is incorrect to assume that violent competition is the only male response to a shortage of opposite sex mates – both theoretical [a male-biased ASR favors male care; e.g. 18] and empirical [male mate guarding in response to mate shortage; e.g. 30] findings counter this assumption. This is perhaps the most fundamental reason why violence is not necessarily attributable to “too many men”. More generally, competition is used with a variety of distinct meanings, both in the human and nonhuman sexual selection literature, and it is often unclear how it relates to mating effort (e.g., are males competing to be selected as long-term or short-term mates?). Clarifying this relationship is key to our understanding of the role of sexual selection and for making predictions of patterns of violence and criminal activity.

We can venture explanations for some of the variable patterning of violence with sex ratio shown in Table 1. In line with the reformulated model, comparative studies in the US and cross-nationally find an abundance of males associated with lower rates of rape and sexual assault [31, 32], and a shortage of men associated with
higher rates of male-male homicide victimization [33]. On the other hand, female homicide victimization rates seem to counter predictions of the reformulated model: there is a positive relationship with ASR in the U.S. [34, 35]. However, when women have the advantage in the mating market this may favor female sexual strategies, such as mate sampling [36], that lead to male sexual jealousy [37]. Mate guarding, in response, is one strategy used by males when in abundance to ensure paternity certainty [30, 38] and may be carried to extremes in some cases. These examples highlight a key point - not all violence is due to sexual competition, mate retention strategies may also be violent. Therefore, “violence” may be present in both high and low sex ratio conditions, making identifying a particular violent act and how it relates to mating competition of critical importance for understanding the strength and direction of sexual selection in a particular ASR.

Our consideration of how violence is patterned in relation to ASR points to three things. First, the patterning is complex, and likely reflects multiple interacting factors not yet modeled by theoreticians. Key factors may be the degree of intrasexual variation in quality, and the shape of the Bateman gradients that capture the marginal returns to agonistic competition [39]. Second, violent crime statistics need to be more precisely disaggregated in order for the ideas suggested above to be testable (e.g., avoid combining multiple measures). We need to know, for example, whether a particular type of crime, or specific violent act, is: sexual effort or competition over resources for parental care [e.g., higher rates of property crime when men are in abundance, 40]; an exemplification of within or between sex conflict; restricted to certain sectors, or socioeconomic brackets, of the population. For example one man might commit theft and another man may go to the office, with both gaining the resources to attract a mate; similarly some men might display their good genes through violence, others through artistic expression. In both examples, the motivation and outcomes may be the same, but the context can impose constraints on behavioral options and influence patterns of crime. Third, social scientists have not yet properly delineated the behavioral options available. For example, in response to high ASR, unmarried men might migrate to regions with more women, patronize prostitutes, resort to polyandrous marriage, or even set up bachelor households and “bachelor villages” as reported for contemporary China [41].
In short, our understanding of how men compete for women, how women’s reproductive strategies vary, and how these are affected by sex ratio, is greatly under-theorized. It is clear, however, that the uncritical acceptance of the “more men, more violence” expectation of traditional theory is unwarranted.

**More theory to the rescue**

Modelers have already anticipated the variation in the relationship between sex ratio and violence we see in Table 1, and from them we can identify potential avenues towards a more precise understanding of the patterning of violence across human societies. First, Kokko & Jennions \[18\] show that, counter intuitively, a particular behavior may be selected for even when it increases mortality rates. This is because frequency dependent selection selects against care in the rarer sex, and mortality patterns will influence which sex is rare. So, if competition entails a higher risk of mortality, then the competing sex will remain the rare one, favoring competition among those who survive. If caring (whether as a form of mate competition or not) brings a higher mortality risk, the caring sex will become the rare sex and thus the opposite sex is now abundant and favored to provide care due to poor odds in the mating pool \[27\]. Thus empiricists committed to explaining the patterning of human violence should be quantifying the relative mortality costs associated with caring and mate competition across different human societies, a difficult task to be sure.

Second, modern sexual selection theory identifies two additional factors other than ASR that influence male strategies, therefore complicating simple (“all else equal”) predictions about the effect of ASR on violent behavior: the extent of variation in quality among males and females, and paternity certainty \[15\]. Where there are differences in male quality that affect the future likelihood of mating, paternal care may be unlikely for two reasons. First, already mated males are likely to desert because they face very good odds of remating by virtue of the qualities that gained them mating success in the first place. Second, unmated males have no choice but to remain in the mating pool since they have no offspring to care for. Similarly where males have low paternity
certainty, even at high ASR high paternal care will not be favored. These factors can vary independently of ASR between populations, and can interact, as when low paternal care favors female strategies that reduce paternity certainty.

The third important factor that intersects the relationship between ASR and male violence is the criteria on which females choose mates. If females choose males on their provisioning qualities, and provisioning does not entail violence, then consistent with Kokko & Jennions’ [18] model the lowest levels of violence would indeed be observed at highest ASRs. However, if successful provisioning depends on the control of resources, and resource access entails physical competition, high ASRs may indeed be associated with violence. Furthermore, male violence might be selected even at high ASRs if females choose mates based on indirect benefits to offspring, affording their sons a potential advantage in violent competitive environments [42, see also 43].

Finally, much of the above reasoning assumes that females are able to exercise choice. Model predictions about levels of violence must be modified accordingly when females are not able to express their mate preferences [44]. Additionally, recent findings have shown that assuming a tradeoff between parenting effort and mating effort is problematic [45]. Indeed, parental care can be a mate competition strategy [two-spotted goby, Gobiusculus flavescens; 46].

**Conclusion**

Humans are a good species in which to investigate how violent competition and other traits are related to sex ratio because we have such variable mating systems, from harem polygyny attained through violence among men against women [e.g., Yanomamo, 47], through resource defense polygyny attained through economic competition among men who are chosen by women or their kin [e.g., Kipsigis, 48], to situations where men and women choose each other on the basis of individual qualities [e.g., Tsimane, 49]. This review has suggested that violence is not structured according to simple predictions from the traditional parental investment model, nor intuitive reasoning. A major reason is that measures of violence are simply proxies for what the models are
actually trying to gauge: the intensity of sexual selection. When we measured the intensity of sexual selection directly (using $I_s$), the findings assembled in Box 3 are in line with reformulations in sexual selection theory, pointing to the importance of ASR as a predictor of the relative opportunities for sexual selection.

The belief that violence and crime are exacerbated in human populations by an excess of males is oversimplistic. We show in Table 1 that the patterning of violent crime shows no simple association with the sex ratio, the patterning is complex. We discuss reasons why current understandings of sexual selection are as yet inadequately articulated to deal with a number of the critical intervening factors we have identified. We also recognize that empiricists have failed to quantify some of the key parameters needed for such modeling, such as the relative costs of care competition and the role of violence in attaining mates. Finally, we point to a need for a much richer ethology of human violence – the data is primarily drawn from police reports and/or national statistics that, for the most part [for a remarkable exception see 50], combine inter and intra sexual attacks, crime directed at people and property, and crime emanating from different sectors of the population.

The simple message to take from this review is that the often related claim that when males are more numerous than females (high ASR) males will create a potential social problem [e.g., 51], rests (as we can now see) on a very specific set of assumptions about the nature of male-male competition and the extent to which females can make choices over mating. There are policy applications of this research, with serious practical implications for people’s lives. Recommendations that a low sex ratio will alleviate problems of male violence, while well-intentioned, could actually exacerbate the problem [e.g., attempting to reduce bullying by lowering a classroom’s sex ratio, 52]. Likewise, “tough on crime” policies that incarcerate increasing numbers of men may actually be contributing to rates of violence, rather than alleviating them, through the resulting sex ratio imbalance in highly policed communities [e.g., 53]. Similarly appeals to abolish polygyny because of the dangerous emergence of a class of unmarried men rely on equally flawed logic [2]. In short, the “more men
more violence” expectation derives from a simplistic interpretation of Trivers’ original paper, a failure to appreciate more recent theoretical developments, and the very loose use of the term competition.

Acknowledgements

For financial support we thank the University of California, Davis (RNS) and the Wissenschaftskolleg zu Berlin (MBM); for discussions and comments on the manuscript our colleagues in the HBE and Cultural Evolution labs at UCD, and for secondary data the generous anthropologists whose populations are included in Box 3.
**TABLE 1. Sex ratio and violence: a literature review**

<table>
<thead>
<tr>
<th>Reference</th>
<th>Sample</th>
<th>Sex Ratio Measure (1)</th>
<th>Measure of violence (2)</th>
<th>Relationship SR/Violence</th>
</tr>
</thead>
<tbody>
<tr>
<td>[33]</td>
<td>100 countries; UN</td>
<td>Complete sex ratio</td>
<td>Homicide</td>
<td>Negative</td>
</tr>
<tr>
<td>[34]</td>
<td>U.S.; FBI</td>
<td>Men and Women (18+)</td>
<td>Female homicide victimization</td>
<td>Positive</td>
</tr>
<tr>
<td>[32]</td>
<td>70 countries; INTERPOL</td>
<td>Men and Women (15-64)</td>
<td>Murders, rapes &amp; violent assaults</td>
<td>Negative</td>
</tr>
<tr>
<td>[54]</td>
<td>Review</td>
<td>Mixed</td>
<td>Historical accounts</td>
<td>Positive</td>
</tr>
<tr>
<td>[37]</td>
<td>U.S.; FBI</td>
<td>Men (18+)/Women (18-34)</td>
<td>Male-on-female partner violence</td>
<td>Positive</td>
</tr>
<tr>
<td>[56]</td>
<td>India; Government data</td>
<td>Complete sex ratio</td>
<td>Homicide</td>
<td>Positive</td>
</tr>
<tr>
<td>[40]</td>
<td>China; Government data</td>
<td>Men and Women (16-25)</td>
<td>Violent and property crime</td>
<td>Positive</td>
</tr>
<tr>
<td>[57]</td>
<td>HRAF</td>
<td>Complete sex ratio</td>
<td>Warfare mortality</td>
<td>Negative</td>
</tr>
<tr>
<td>[58]</td>
<td>Review</td>
<td>Mixed</td>
<td>Historical accounts</td>
<td>Positive</td>
</tr>
<tr>
<td>[59]</td>
<td>U.S.; State data</td>
<td>Complete sex ratio</td>
<td>Homicide &amp; suicide rates</td>
<td>Mixed</td>
</tr>
<tr>
<td>[60]</td>
<td>56 countries; WHO &amp; UN</td>
<td>Complete sex ratio</td>
<td>Homicide</td>
<td>Negative</td>
</tr>
<tr>
<td>[61]</td>
<td>45 nation sample; WHO &amp; UN</td>
<td>Complete sex ratio</td>
<td>Homicide</td>
<td>Negative</td>
</tr>
<tr>
<td>[31]</td>
<td>U.S.; Census &amp; FBI</td>
<td>Five-year groupings</td>
<td>Rape</td>
<td>Negative</td>
</tr>
<tr>
<td>[62]</td>
<td>India; Crime in India database</td>
<td>Complete sex ratio</td>
<td>Homicide</td>
<td>Positive</td>
</tr>
<tr>
<td>[63]</td>
<td>46 nations; WHO &amp; UN</td>
<td>Complete sex ratio</td>
<td>Homicide</td>
<td>Negative</td>
</tr>
<tr>
<td>[64]</td>
<td>46 nations; World Values Survey</td>
<td>Men and Women (18+)</td>
<td>Homicide</td>
<td>Negative</td>
</tr>
<tr>
<td>[65]</td>
<td>U.S. Counties; FBI &amp; Census</td>
<td>Unmarried men &amp; women (18-44)</td>
<td>Homicide</td>
<td>Unassociated</td>
</tr>
<tr>
<td>[35]</td>
<td>U.S. Cities (n=217); FBI</td>
<td>Complete sex ratio</td>
<td>Female homicide victimization</td>
<td>Positive</td>
</tr>
<tr>
<td>[66]</td>
<td>Chinese Cities (n=37); community level data</td>
<td>Men (17-23), women (15-21)</td>
<td>Forced sex</td>
<td>Positive</td>
</tr>
</tbody>
</table>
We performed a literature search for violence and sex ratio in humans on Web of Science (April 3, 2013, n=64). Some search results were excluded due to redundancies, lack of empirical data (e.g. book reviews), or irrelevance to the question at hand (e.g. studies looking at the sex ratio of criminal offenders without reference to the population sex ratio). This table summarizes the results of the remaining papers (n=21), highlighting inconsistencies in the relationship between the sex ratio and violence as well as critical methodological differences.

(1) Measures of sex ratio vary widely, and there is no evidence that the scale of the sex ratio measurements (ranging from national level to village level data) is appropriate to capture the relevant mating pool.

(2) Measures of violent crime range quite widely: in some cases all homicides are included, some just female victims and others include a mix of physical assault and property crime.
**BOX 1: Acronyms and Definitions**

- **Operational Sex Ratio (OSR):** the ratio of sexually active males to sexually receptive females in a population.
- **Potential Reproductive Rates (PRR):** the hypothetical maximum number of independent offspring produced by males and females per unit time.
- **Adult Sex Ratio (ASR):** the ratio of adult males to adult females in a population.
- **High sex ratio:** more males than females in a population.
- **Low sex ratio:** more females than males in a population.
BOX 2. Changing the direction of the causal arrow between parental investment and sexual selection

The traditional PI model has been influential in the development of sexual selection theory but it is logically flawed. The reasoning goes that because females produce large, costly eggs, male fitness is constrained by access to mates, producing (in most cases) female-biased care and male-biased competition. However, shortly after Trivers [4] presented this argument, criticisms of the model began to mount. (I) Sex differences in PI cannot be taken as a determinant of the intensity of sexual selection as this entails committing the faulty logic of the “Concorde Fallacy” [18, 67]. Past investment alone is irrelevant to decisions about future behavior. (II) As with Maynard Smith’s [68] classic model relating parental care evolution to sex differences in mating opportunities, Trivers’ verbal model lacks internal consistency, violating the requirement of equal average fitness for females and males and effectively making females exogenous to the model [16]. While males do have higher PRRs [6], it is actual and not potential rates that matter in terms of selection [69]. To make the model self-consistent the additional paternity of deserting males must be accounted for, and comes at a cost to the paternity of other males [i.e. the extra mates of successful males must come from somewhere; 17]. (III) In the traditional PI model a male-biased-OSR leads to more intense intrasexual selection and greater competition among males due a shortage of females [5]. However, male biased OSRs do not necessarily lead to greater intensity of sexual selection. Klug et al [70] show how OSR only accurately predicts sexual selection under a limited set of circumstances, most specifically when mate monopolization is strong. In fact a wise strategy for a male who may face a long wait time in between reproductive events if he were to desert would be to instead stay with his current partner [18]. Thus the OSR can equally be thought of as a frequency dependent mechanism that selects for care in the sex that is in abundance.

In sum, the relative abundance of gametes (i.e. more sperm than eggs) generates the conditions for sexual selection. If selection occurs, patterns of care and competition are an outcome [15]. Therefore, sexual selection is not an outcome of patterns of PI as posed in traditional models, but instead the arrow of causality must be flipped [69].
BOX 3. The Sex Ratio and Opportunity for Sexual Selection across 15 populations

We calculated the opportunity for sexual selection ($I_s$) of males against the sex ratio of the mating pool for each population, selected from the work of human behavioral ecologists working in non-industrial societies. The $I_s$ is a standardized measure of variance in reproductive success (RS) and is calculated by dividing the variance in RS by the squared mean of mating success [71-73]. It represents the upper limit of the potential strength of sexual selection in a given population (importantly, not the actual strength of sexual selection on specific traits).

The $I_s$ is useful for cross-population comparisons because it is standardized by mean fitness and describes the variation in mating success that drives sexual selection within a population. The $I_s$ provides a valuable summary statistic to describe mating systems [74] because it offers a concise description of the distribution of fertilizations [75] and does not rely on vague descriptions of variation in the distribution of matings that labels such as ‘monogamy’ and ‘polygyny’ often do [76]. Below we show how the opportunity for sexual selection is associated with the sex ratio of the local mating pool across 15 populations.
The regression line (calculated using maximum likelihood estimation) shows a negative relationship between the sex ratio of a population’s mating pool and the $I_s$ among males (dashed line) and the 95% confidence limits (displayed in pink for female-biased sex ratios and blue for male-biased sex ratios). The slope is negative, suggesting that traditional assumptions regarding a positive relationship between the abundance of males and the intensity of sexual selection is flawed. Rather, as the sex ratio decreases the opportunity for selection among males increases [see also (77) for a similar conclusion for human populations but based on normative mating system categorizations].
BOX 4. Empirical Ambiguities: The Term ‘Competition’, and ‘Violence’ as Proxy

The specific form that mate competition takes is central to the question of sex ratios and violence. Here we propose a working taxonomy:

(1) *Demographic competition*: In a simple demographic sense, there is ostensibly a higher degree of mate competition among the more common sex when sex ratios are imbalanced; this is indeed the inference from OSR. The term “competition” here is used simply to depict the fact that, under most conditions, not all individuals find a partner due to the number of competitors. Note that the term is neutral with respect to competitive behavior, and with respect to the implications for the intensity of sexual selection (Box 3), even though it corresponds to OSR (see Box 2).

(2) *Courtship competition*: These behaviors are usually directed at opposite sex individuals, and are “competitive” due to mate selection. Females in some species (including humans) have considerable autonomy with respect to their choice of mates [see 78]. Accordingly competition among males may take the form of providing what females and their relatives want [e.g., a bridegroom’s labor 79], and among females in providing what males want [chastity, 80]. This might entail accumulating resources [48], advertising paternal proclivities and abilities [81], or demonstrating genetic fitness [82].

(3) *Agonistic competition*: This type can, of course, also occur behaviorally among and between both sexes irrespective of ASR. Focusing here just on males it can take many forms, as in bellowing displays in bison [83], fighting over the control of breeding or nesting territories as in red-winged blackbirds [84], or forced copulations as in orangutans [85]. In humans this kind of competition might entail physical attacks to eliminate (or character attacks to denigrate) male competitors [86], direct sexual attacks on women [44], or property crimes [40]. In many cases this type of competition is directed at same sex individuals, but not always, as in rape and sexual assault [87].
It is clear from these simple categories and examples that not all mate competition is violent, and not all violence is mate competition – a problematic reality for empirical analyses that use violence as a proxy for the intensity of sexual selection. For instance, a female shortage might decrease violence by favoring more courtship competition among males. Similarly, a male shortage could increase violence by diminishing the influence of female choice for caring males.
References


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Highlights

(1)
We explore the relationship between violence and the sex ratio in humans

(2)
Conflicting theoretical and empirical trends within sexual selection are reviewed

(3)
Evidence indicates more variance in male fitness when males are scarce, not abundant

(4)
We show that violent competition is not the only male response to a shortage of mates

(5)
The expectation that violence is higher in groups with excess males is oversimplistic