

# Sexual Conflict in Humans: Variations and Solutions

MONIQUE BORGERHOFF MULDER AND KRISTIN LIV RAUCH

Growing interest in sexual conflict since the late 1980s reflects several developments within behavioral ecology. These include recognition of females as active participants in co-evolutionary interactions,<sup>1–3</sup> demonstrations of high levels of extrapaternity in many “monogamous” species,<sup>4</sup> remarkable evidence of life-threatening toxic compounds in the sperm of fruit flies,<sup>5</sup> and experimental studies revealing deleterious consequences of arms races for both males and females.<sup>6</sup> Many of the ideas in this new body of work were sparked by Parker’s papers on how sexual conflict shapes physiological and behavioral traits. These ideas were brought to popular attention by Dawkins,<sup>7:140</sup> who posed the question: “If there is conflict of interests between parents and children, who share 50% of each others’ genes, how much more severe must be the conflict between mates, who are not related to each other?” Research into sexual conflict among nonhuman primates is flourishing,<sup>8</sup> but has received less explicit attention in the study of humans, despite cogent arguments that women’s strategies are often constrained by the forceful and manipulative behavior of men and their kin.<sup>3,9</sup> Here we explore new hypotheses for the extent and direction of sexual conflict among humans, both within and between populations, focusing on signaling mate quality, family size preferences, and the marital bond.

Monique Borgerhoff Mulder is at the University of California, affiliated with the Department of Anthropology, the Graduate Group in Ecology, and the Center for Population Biology. In her research she focuses on sexual selection and human life histories, with additional work in the origins of inequality, cultural phylogenies, and conservation. Her primary field sites are in East Africa.

E-mail: mborgerhoffmulder@ucdavis.edu  
Kristin Liv Rauch is a graduate student in human behavioral ecology researching mate selection. Her specific interests include the adaptive significance of assortative mating and the impact of social structure and dominance hierarchies on human mating patterns.  
E-mail: klrauch@ucdavis.edu

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*“It is a long way to school here, all the way from Mahmudabad. Dangerous. An hour at least. A girl shouldn’t go to school if it is so far away. It just shows.”*

*“He followed them ... he jumped out from behind a rock...”*

*“She won’t get a husband after this.”*

*“... the judge told her she has to marry Abbas as soon as they catch him.”*

*“They’ll beat her up at home until she says yes ...”*<sup>10:113–118</sup>

Parker’s<sup>11:124</sup> definition of *sexual conflict* (Box 1) as “a conflict between the evolutionary interests of individuals of the two sexes” is both intuitive and all-encompassing. Sexual conflict occurs in two primary contexts: over mating, where males typically benefit more from mating with multiple partners than do females,<sup>12</sup> and over bi-parental care, where parents can increase their individual fitness by reducing their own efforts if there is compensation from the other parent.<sup>13</sup> Such conflicts

## Box 1. Glossary

**Sexual conflict** — “A conflict between the evolutionary interests of individuals of the two sexes”<sup>11:124</sup>; sexual conflict occurs when the optimal value of a trait differs between the two sexes.

**Conflict (or shared) trait** — Traits that differ in value for the sexes because of sex-specific costs and benefits.

**Sexually antagonistic selection** — Occurs when selective forces act on males and females in different directions.

**Sexually antagonistic coevolution** — A chain of adaptations and counteradaptations during the struggle over sex-specific optimality in a given conflict trait.

**Anisogamy** — Different sized sex cells; i.e., sperm are small, ova are large.

**Phenotypic gambit** — A research perspective focusing on phenotypic adaptation and plasticity geared to local environmental conditions rather than the precise underlying genetic processes.

**Lekking** — The gathering of males for the purposes of sparring or other competitive mating displays.

**Cuckoldry** — The unknowing investment of a woman’s primary mate in the offspring of another man as a result of infidelity.

lead to complex dynamic “unresolvable evolutionary chases.” These are classically portrayed through Parker’s<sup>14</sup> extraordinary descriptions of female yellow

### Box 2. Sexual Conflict and the Theory of Sexual Selection

Exploration of the profound evolutionary conflicts between the sexes, even as mated pairs, has thrown conventional classifications of sexual selection thinking into disarray. This is because rather than building on male competition and female choice, Darwin's two original pillars of sexual selection theory, investigators of sexual conflict models explore a third and different dynamic, the conflict that occurs *between* the sexes. Indeed, some investigators posit this as a third pillar of sexual selection theory.<sup>22</sup> Sexual conflict models entail thinking simultaneously about direct effects (costs and benefits that accrue directly to individuals) and indirect effects (costs and benefits that accrue to individuals through the fitness of their offspring). These dynamics are typically treated as distinct. In many respects, sexually antagonistic selection, in which males benefit from damaging their mates, is a *direct* model, insofar as it typically is the female who benefits from avoiding the harmful behavior of males.<sup>18,105</sup> The classic example here is a female's attempt to avoid mortality-inducing male seminal products.<sup>5</sup> However, indirect effects may also be entailed, effects that compensate females indirectly with genetic benefits for the direct costs of mating with nasty males. For example, Head and coworkers<sup>106</sup> show that female house crickets (*Acheta domesticus*) kept with attractive males have shorter lives but more attractive sons than do females kept with unattractive males.

Another anomaly is that sexually antagonistic coevolutionary models are different from other direct models in that the sign of selection is negative<sup>107</sup> or, in Holland and Rice's<sup>6</sup> terminology, "antithetical." In other words, females are not favoring males with, for example, valuable nuptial gifts, but avoiding males who do them damage. Females can therefore find themselves in an awkward trap as a result either of male coercion<sup>3,9,22</sup> or male seduction.<sup>6</sup> Incorporating the conflict that occurs between the sexes into the study of sexual selection introduces considerably more variability into expected gender roles than hitherto has been appreciated.<sup>19,34</sup>

dung flies (*Scathophaga stercoraria*) drowned in struggles among their male suitors, but also bear some striking similarities to the ethnographic example given earlier. Villagers gossiping about the rape of a young Iranian woman predict that the victim will receive no support from her family or the local judicial system, but rather be coerced into marrying her attacker. Similar themes pervade the nonhuman primate literature, where sexual conflict has been a major focus of empirical work.<sup>15–17</sup>

Evolutionary biologists apply the term "*sexually antagonistic selection*" to situations where selective forces act in different directions on males and females.<sup>6,18</sup> In species where manipulation, experimentation, and even genetic modification are possible, they have studied the chain of adaptations and counter-adaptations, or "*sexually antagonistic coevolution*"<sup>18</sup> that ensues, and

have drawn parallels with the kinds of coevolutionary processes seen in host-parasite interactions. They have also given careful consideration to how sexual conflict relates to conventional models of sexual selection (Box 2). One conclusion to emerge is that the diversity in intersexual dynamics across animals reflects much more than simply *anisogamy* and postzygotic parental care.<sup>19</sup> In our consideration of sexual conflict, we focus less on the history of selection and more on the behavioral plasticity whereby men and women seek to outmaneuver each other. In effect, we are adopting the conventional *phenotypic gambit* of behavioral ecologists.

### SEXUAL CONFLICT

#### The Underlying Theory

Iconic studies in this area of theory center on sexual conflicts over fertilization and mating. Such conflicts are

conventionally attributed to sex differences in the maximum rate at which parents can produce offspring if access to mating partners is unconstrained (potential reproductive rates).<sup>20</sup> This is usually higher for males than females because of the small size of sperm compared to eggs and the prolonged parental care typically invested by females.<sup>13</sup> Insects most dramatically demonstrate sexual conflict.<sup>21</sup> In some bedbugs (*Heteroptera cimicidae*, for instance), males have evolved hypodermic genitalia that pierce the female body wall, while females have counter-evolved structures to reduce the costs of traumatic insemination. Attention subsequently moved to fish, birds, and mammals. Similar struggles emerge in nonhuman primates, where in males we see sexual coercion, forced copulations, mate guarding and herding behavior,<sup>16,17,22</sup> as well as a range of female counterstrategies, including the soliciting of extrapair matings and behavior that appears to confuse paternity.<sup>1,15,23</sup> In a recent (companion) paper Stumpf and coworkers<sup>8</sup> examine the extent and significance of sexual conflict in nonhuman primates.

Increasingly, however, the centrality of anisogamy to understanding sex roles in mating and parenting has been rethought. New theory<sup>24</sup> and evidence<sup>25,26</sup> suggest that it is not simply sex differences in pre- and postzygotic investment that affect optimal mating strategies for males and females. A range of additional factors need to be considered, including the sex-specific costs of breeding, variations in mate quality, the distribution and availability of the resources required for successful breeding, and the adult sex ratio.<sup>19,25</sup> For example in a *lekking* African antelope (topi, *Damaliscus lunatus*) females are more eager to mate than males are and compete with each other for matings more than do males, showing a pattern of sexual conflict over mating rates opposite in direction to that predicted by potential reproductive rates.<sup>27</sup> Sperm depletion in males may explain their faltering ardency, while the single-day mating opportunity for females may explain their engagement in lethal competition to get the best mate. Indeed, even in largely monogamous species sexual conflict occurs, as shown dramatically in the behavioral, mechanical, and chemical adaptations in

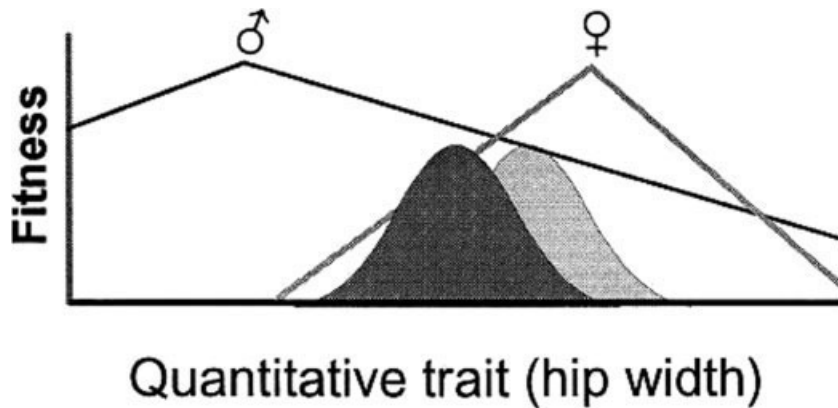


Figure 1. The potential for sexual conflict. Solid lines signify the selective optimal for males and females for the sexually dimorphic trait (hip width) that produces sexually antagonistic selection. Shaded areas indicate the distribution of male (dark grey) and female (light grey) phenotypes resulting from this sexually antagonistic selection. Figure modified from Rice and Chippendale.<sup>32</sup>

insects, where antics range from females eating their mates to males employing mechanical plugs or chemical anti-aphrodisiac compounds to control their mates.<sup>21</sup> Furthermore, where sex occurs for reasons other than reproduction, as proposed by Hrdy more than twenty years ago,<sup>1-3</sup> even more opportunities for conflict emerge. The more general lesson is that optimal mating strategies are driven not only by differences in pre and postzygotic parental care, but also by trade-offs among various options available to an individual.<sup>28</sup> The compromises reached reflect the relative power of either sex, the benefits of winning a conflict, and the relative costs of escalation.<sup>11</sup>

Sexual conflict studies generally spring from the assumption that males are rather more eager to mate than are females. The new theoretical developments allow us to move away from such simple sex-role stereotypes. Furthermore, they have particular relevance in the study of humans, where there is probably more variation in gender roles across and within populations than occurs in any other species. As a result of culturally transmitted knowledge and norms that permit ecological adaptation to a vast array of different environments, we find populations that differ radically in the gendered patterning of sexuality, pair-bonding, and parental care. In a species where some populations uphold women's promiscuity and others their claustration, and where some popula-

tions permit men to marry multiple wives and others require wife sharing, we would expect to find an extraordinarily broad patterning of sexual conflict. For this reason, a theoretical stance predicated on conventional sex differences is unlikely to explain the great variation that we see across human populations.<sup>29</sup>

### Identifying Conflict Traits

Biologists have produced useful frameworks for thinking about sexually antagonistic traits, asking us to think about *conflict (or shared) traits*<sup>30</sup> in which the ideal values for males and females do not coincide. Consider the size of the human pelvis as a conflict trait. Wider hip width benefits women because it allows safer birth of large-brained infants.<sup>31</sup> Men, however, cannot reap this benefit, only paying the costs of decreased locomotor efficiency. For the sake of illustration (Fig. 1), let us assume first that hip width is polygenically controlled and that many of the contributing loci are expressed in both sexes. Second, assume that disruptive selection exists (as outlined) and third, that selection on hip width can be described with a simple linear function, with the female function being twice as steep as that for males, reflecting stronger selection contingent on dangerous childbirth. Pelvis size is therefore a conflict trait.<sup>32</sup> Other can-

didate traits are mating rate and the control of fertilization (primary foci in studies of nonhumans), mate signaling, family size, and pair-bond duration.

There are considerable challenges in the study of sexual conflict. First, to understand the roles of sexual conflict in male-female relations we need data on forces of selection, past and present. The problem is that past conflict is hidden by adaptation. Adaptation followed by counteradaptation makes coevolutionary trajectories difficult to observe, as in any predator-prey or host-pathogen relationship. Recognizing this, researchers have effectively employed various approaches. Some conduct experimental evolutionary studies, as with the arrested-evolution interventions in *Drosophila*.<sup>6</sup> Others investigate how antagonistic traits coevolve, specifically by testing across sister taxa.<sup>33</sup> When such approaches are not feasible, biologists resort to economic studies of the costs and benefits of specific traits. This approach usefully demonstrates conflict, but reveals nothing about the forces responsible for traits.<sup>30</sup>

A second problem is that a researcher looking for human or nonhuman conflict traits is in danger of being too easily deceived by our perceptions of coercion, manipulation, and control. For instance, what looks like male nastiness may not be coercion, but rather an honest signal advertising competitiveness that females (or their male offspring) might benefit from. Similarly, apparently peaceful postcopulatory behavior can conceal bitter conflicts, such as chemical coercion.<sup>18</sup> Indeed, studies of insect genitalia reveal the highly discriminating role of females in selecting sperm for fertilization despite their apparent behavioral passivity. In short, the researcher must appreciate that absence of overt aggression does not imply common interest,<sup>6</sup> just as apparent aggression does not necessarily indicate sexually antagonistic selection.

On account of these difficulties, as studies move from insects to more complex and less manipulatable systems of fish, birds, and mammals, there is growing advocacy among biologists for more emphasis on the *natural history* of sexual conflict, correlative studies, and

empirical searches for repeatable differences in the extent of sexual conflict across ecological contexts.<sup>30,34</sup> Humans, with their enormous intraspecific variation in sexual and reproductive strategies, provide many opportunities for the latter. Furthermore, such studies offer huge opportunities to move the study of sexual conflict away from its conventional focus on mating rates to other domains of social and sexual interactions.

### EXTENDING THE STUDY OF SEXUAL CONFLICT TO HUMANS

A variety of interactions among men and women, including spousal violence,<sup>35</sup> rape,<sup>36</sup> and many of the more subtle kinds of intersexual negotiation, strategy, and counter-strategy described in numerous gender-informed social science studies suggest a history of sexual conflict in humans. In a pioneering paper, Smuts<sup>9</sup> catalogued a persistent pattern of both general violence and sexual coercion, examined its parallels with nonhuman primates,<sup>16</sup> and ethnographically explored its variability. Psychological work more generally addresses the potential evolutionary dynamics entailed in intersexual interactions.<sup>37</sup> Our reading of the subsequent literature nevertheless suggests that, with the exception of Smuts' initial paper, the term "sexual conflict" in human studies is often used interchangeably with sex differences and/or sexual selection, and almost never in connection with Parker's definition (Box 3). Only rarely do investigators acknowledge problems in making predictions about sexual conflict contingent on the dynamics of a coevolutionary arms race between the sexes,<sup>38,39</sup> and have thereby gained particular insights into sexual conflict over fertilization (Box 4).

As noted, however, our own species offers extraordinary opportunities for understanding sexual conflict. First, sex-specific costs and benefits to mating in primates are likely to differ from those in insects. As reviewed by Stumpf and coworkers,<sup>8</sup> female primates engage in sex for reasons other than reproduction, such as to establish protective friendships with males whereby they can avoid harassment;

### Box 3. Evolutionary Anthropology and Sexual Conflict Terminology

In the psychological and evolutionary anthropological literature on humans, "sex differences", "sexual selection," and "sexual conflict" are often used interchangeably or assumed to imply each other. Here we emphasize that sex differences may or may not be attributable to sexual selection; that sexual selection can occur without sexual conflict; and that sexual conflict does not necessarily lead to sexually antagonistic selection. Regarding sex differences, these may reflect the operation of natural or sexual selection, as in the debate over whether men hunt to attract social allies or to provide food for their families.<sup>87,99</sup>

Regarding whether sexual selection implies sexual conflict, it is true that anisogamy generally leads to sexual conflict, reflecting the different reproductive rates of the two sexes<sup>20</sup> and the fact that females are effectively resources for males; among mammals with high female postzygotic investment, these conflicts are often acute. However, given the importance of paternal investment in many human societies, the potential for sexual conflict among spouses over parental investment is likely to vary by context, depending on gender-specific provisioning, alternative sources of child care, and other factors.<sup>108</sup>

Regarding sexually antagonistic selection, it is difficult to determine whether sexual conflict leads to sexually antagonistic selection and coevolution. Arguments can only be made from design. For example, Gangestad, Thornhill, and Garver-Apgar<sup>39</sup> examined whether concealed ovulation might have evolved through a female strategy either to ensure male investment (men cannot distinguish their own offspring) or to achieve extrapair copulations (men tire with constant mate-guarding). Distinct design traits are associated with these two hypotheses, are tested with contemporary behavior, and provide more support for the latter claim. Without the experimental evolutionary manipulations or fine-grained phylogenetic work that can be conducted in nonhuman species, such arguments must ultimately rest on plausibility.

to confuse paternity, thereby either lessening risks of infanticide or eliciting support from all possible progenitors; or to obtain immediate benefits. Systematic analysis of the function of multiple mating has barely begun in our own species,<sup>23</sup> although there are now indications that women may mate multiply for a variety of reasons: to garner new sources of investment from men,<sup>40</sup> to broaden social networks in a tight market for employment,<sup>41</sup> to enhance child survival through greater provisioning and solicitude,<sup>42,43</sup> and possibly to replace poorly performing current mates.<sup>44</sup>

Second, whereas in many species sexual conflict occurs between mated pairs, in humans outside parties can play a significant role in influencing outcomes. Smuts<sup>9</sup> used ethnographic reports to link persistent patterns of both general violence against women

and, more specifically, to link sexual coercion to the strength of alliances among men and women in a given population. The expectation is that violence increases with the size and strength of male alliances and decreases with the size and strength of female alliances. In reality, however, the pattern is complicated, in part because men are often married to the sisters of their allies, so their allegiances can be split. As we will see, it is more useful to think about this from the perspective of specific kin who have distinct vested interests in the couple.<sup>45</sup>

Third, there are some broad ideas about how levels of sexual conflict might vary across social systems. First, reviewing ethnographic studies, Smuts<sup>9</sup> proposed that the degree of political or economic inequality among men will influence the trade-offs they

#### Box 4. Conflict Over Fertilization

Elements of the sexual conflict over control of fertilization studied in nonhumans<sup>109</sup> are likely to be observed in humans. Effort to attain a high mating rate can only benefit male fitness if those matings lead to fertilizations. Females also mate multiply<sup>110</sup> and, through the evolution of cryptic mechanisms,<sup>111</sup> can enjoy the benefits of sire choice while, at the same time, avoiding some of the costs of sexual coercion. Sexual conflict therefore arises as males and females try to attain their respective goals.

In humans, female orgasm is one possible mechanism by which postcopulatory selection among the sperm of multiple males takes place. Strong muscular contractions cause the mouth of the cervix to dip into the pool of sperm that has recently been deposited into the vaginal canal.<sup>112</sup> Research has shown that women are more likely to reach orgasm with men who exhibit signals of genetic quality, such as low fluctuating asymmetry<sup>113</sup> or attractiveness,<sup>114</sup> as well as to have more orgasms with extra-pair mates than in-pair mates.<sup>112</sup> By reaching orgasm during intercourse with particular males and not others, females may be able to internally select the sire of their offspring (but see Pound and Daly<sup>115</sup>).

Are there counterstrategies that can lessen the burden imposed by females on male reproductive interests? Selective forces favor competitive sperm that are able to fertilize the egg and therefore salvage their mating effort despite multiple matings by females.<sup>11</sup> Proposed adaptations include adjustment of ejaculate size,<sup>112</sup> increased testes size,<sup>116</sup> human penis shapes that displace prior males' ejaculates,<sup>117</sup> and increased levels of mate guarding.<sup>118</sup>

Conflict traits can be identified in the cultural realm in both the practices and ideologies governing sexuality. Traits such as the use of chastity belts,<sup>119</sup> female genital mutilation,<sup>120</sup> purdah, and other forms of claustration<sup>47</sup> can limit the risk of sperm competition, thereby serving the interests of at least some men. Mate guarding also prevents the opportunity for infidelities. This type of vigilance can take on new forms in the "information age," through, for example, the use of cell phones. While most of these conflicts appear to have been won by men, we suspect that the strategies of women are under-reported<sup>9</sup> or mislabeled.<sup>44</sup>

face in controlling adultery. In highly stratified systems, powerful men can afford the costs of enforcing sanctions against adultery and, at the same time, gain access to the mates of low status men.<sup>46</sup> In egalitarian systems, however, the costs and benefits of controlling women fall equally on all men and are therefore less elaborate. Sexual sanctions on women generally are more elaborate in stratified populations, as in India.<sup>47</sup> In societies at the extreme end of this continuum, such as the honor-and-shame cultures of the Mediterranean and Middle East, men will beat even their own kinswomen for sexual misdemeanours to demonstrate their commitment to chastity, as seen in the opening anecdote on the women of Deh Koh. These

dynamics might be amplified by differences among men in their ability to invest in children since, for the high investors, the costs of adultery merit greater control of women's sexuality. In short, as relationships among men become increasingly egalitarian, women gain sexual freedom and reduced vulnerability to spousal aggression.<sup>48</sup> As is also recognized in work on nonhumans, female autonomy is crucial to the avoidance of manipulation and coercion by males.<sup>3</sup> Where females' dependence on men for resources or protection increases, the alternatives to remaining with a coercive male decline, thereby leading to higher levels of sexual conflict, as shown by the association between male control over the

products of female labor and the frequency of wife-beating.<sup>49</sup>

#### CONFLICT TRAITS IN HUMANS

We might expect a population's (or species') mating system to be a critical determinant of the intensity of sexual conflict. With strict lifetime monogamy, female and male interests will diverge over the initial choice of mate, but will generally coincide over subsequent decisions,<sup>6</sup> at least to the extent that outside options are entirely foreclosed.<sup>21</sup> With multiple partners for each sex, interests diverge so that conflicts appear over mating frequency, timing and pattern of fertilization, relative parental investment, female remating behavior, female reproductive rate, and clutch size. Since the very solutions to these conflicts contribute to the observed "mating system," there is some circularity in this observation. Accordingly, we structure our review not by mating system *per se*, but rather around areas of potential sexual conflict in which strategic interference might occur. These include signaling of mate value, family size, and marriage. For each domain, we identify potential conflict traits and develop hypotheses to unravel the extent and causes of conflict.

#### Conflict Over Signaling Attractiveness As a Mate

Signals of mate quality or value can be conflict traits. Insofar as an assortative market process leads to high-quality individuals pairing with each other, leaving lower ranked individuals to pair accordingly,<sup>50</sup> the quality of mate that an individual can attain is based on his or her own quality. There are, therefore, great incentives to deceive potential mates over mate value. This incentive for deception leads to conflict because, when the deception is successful, the deceived partner is swindled out of an optimal match. That partner will have unwittingly settled for less than his or her own quality merits, and this will have costly fitness consequences.

Conflict over signals is an example of sexually antagonistic coevolution, with a set of traits in one sex interacting

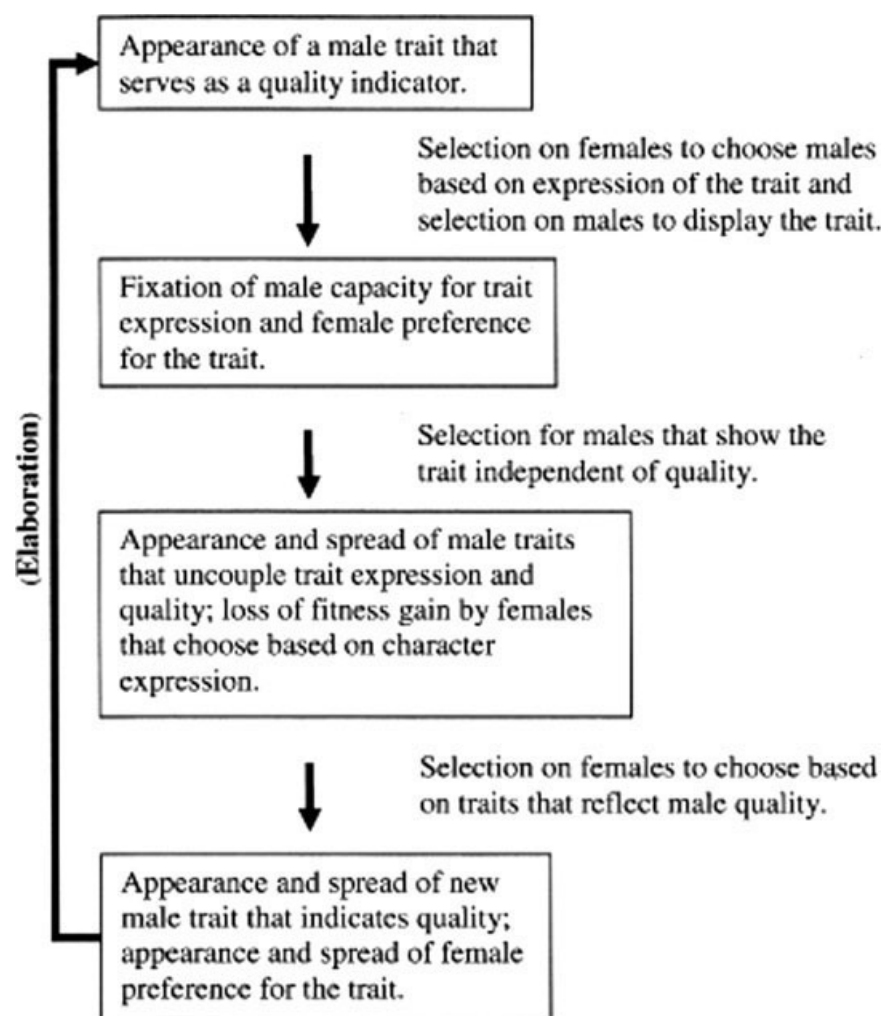


Figure 2. Signal elaboration through sexually antagonistic coevolution. The cycle oscillates between highly reliable costly signals (optimal for receivers, in this case females) and essentially meaningless cheap signals (optimal for signalers, in this case males). Figure reproduced from Hill.<sup>52</sup>

with a different set of traits in the other sex to produce an outcome.<sup>18</sup> In the case of signaling, these suites of traits consist of the honesty and reliability of the signal itself as well as the ability of recipients to distinguish between honest and dishonest signals. Each sex bears both conflict traits because men and women are simultaneously signalers and receivers. However, only opposing traits are involved in any single interaction. For example, male attractiveness signals coevolve with female abilities to judge the honesty of those signals and vice versa.

There is a vast literature on the evolution of honest signals.<sup>51</sup> The general premise is that traits that are more

costly for lower-quality individuals to produce can reliably signal quality. However, selective pressure will act on signalers to find ways of producing the signal without paying the cost. When this happens, counter-selection will act on receivers to guard against counterfeit cues and to find ways of accurately assessing potential mates' quality. Sexual conflict ensues because an optimal trait value in one sex precludes optimality in the corresponding trait of the opposite sex. Costly honest signals are optimal for the receiving sex, while cheap dishonest signals are optimal for the signaling sex. Likewise, choosiness may be beneficial for receivers, but imposes heavy costs on signalers.

The implications of such dynamics for mate quality signaling are considerable (Fig. 2). Note how temporary points during the cycle where the signals are tightly coupled with underlying mate quality give way to periods when some signalers evolve the ability to exhibit the signals regardless of their underlying quality, so that the receivers will pay the costs of being misled.<sup>52</sup> Cycles like this can potentially be in constant flux or they can stabilize. An example of the latter, where deception is forestalled by means of a cultural practice, is the honesty of signaling of menstrual status.<sup>53</sup> Given concealed ovulation in humans, there is intense conflict among men and women over the signaling of menstrual status, with women generally favoring deception and men favoring honesty. For the Dogon of northern Mali, the village "menstrual hut," which women are required to visit during their menses, appears to enforce honest signaling of fertility status. Analysis of urinary steroids showed almost complete compliance with menstrual taboos. If a woman were to deceptively signal fertility status by visiting the hut while already pregnant, she might succeed in confusing paternity. By imposing heavy sanctions against such deception, the men, and maybe older women, have set up an institution that limits married women's ability to solicitously select sires.

As previously explained, it is very difficult to trace the history of a coevolutionary arms race because prior conflicts are masked by subsequent adaptations. However, it is possible to form hypotheses about human sexual conflict over mate-quality-signaling based on patterns of variation in the extent of conflict and in the solutions or corresponding counterstrategies. One key consideration is the sociocultural context in which mate signaling occurs. In small-scale societies, people mostly interact with the same individuals for much of their lives. Foraging or horticulture-based subsistence groups are characteristically close-knit, with face-to-face interactions and limited privacy. These factors make it more difficult to succeed at deceiving fellow community members about one's qualities. In contrast, social interactions in

large, densely populated societies are often impersonal, granting a level of anonymity that would be impossible among most foraging groups. We therefore predict that mate quality deception will be a more successful strategy in larger and more anonymous populations. Solutions in response to mate quality deception will also vary. In small-scale groups, customs like bride service, where men co-reside with and work for their prospective in-laws for an extended period, have a specific function in allowing evaluation of a future husband's (or son-in-law's) quality. In large populations, very different methods are used to assess the honesty of a potential dating partner's signals, perhaps taken to the extreme in the anonymous and uncertain realm of online dating. Both conventional and cyber-daters perform do-it-yourself surveillance (for example, "googling"), criminal background checks, or even lie detection on potential mates (made possible by portable hand-held biometric devices).<sup>54</sup>

An important strategy for receivers to undercut the deception of signalers is to use multiple cues to assess potential mate value.<sup>52,55</sup> A flashy car is not enough to convince a woman that a man is rich. She should also pay attention to his job, schooling, clothes, living arrangements, and spending habits while on dates to decide if there is enough evidence of his underlying mate quality. Similarly, a low waist-to-hip ratio is not enough to assure a male that a female is fertile. He will also consider other cues, such as hair luster, gait, skin clarity, muscle tone, and Body Mass Index. Humans may also use olfactory cues to assess the compatibility and diversity of a potential mate's immune system, specifically the major histocompatibility complex.<sup>56</sup> The prediction is that there will be more deception over mate qualities that are signaled by solitary cues and less deception over traits that can be judged by multiple indicators. Variation in solutions to this conflict will therefore depend on the strategy of the individual. One example of a variable strategy (or counterstrategy) is the length of the courtship period. Lengthy courtships might give receivers the time required to make the most of the various mate-quality cues available to

them. Accordingly, short-term mating might afford deceptive signalers the most success since fake cues are likely to be detected over time. Furthermore, a mixed strategy could also be employed, whereby short-term relationships may serve as a screening process for long-term mates,<sup>37</sup> exemplifying the supreme flexibility in human mating tactics.

Perhaps unsurprisingly, the most frequently investigated aspects of mate-quality deception are based on predictions that follow from Bateman's gradient and the implications of anisogamy. This simplistic characterization of sex differences generates the prediction that men are most likely to

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exhibit deceptive cues about their ability and willingness to invest resources and women are more likely to deceive potential mates about fertility cues such as youth or health. Tooke and Camire<sup>57</sup> found that undergraduate men in the United States were likely to try to deceive women about their level of commitment, displaying false interest in starting a relationship; to appear more friendly, polite, and humble than they really were and to emphasize their ability to acquire resources (misleading dates about career expectations). Women's deceptive tactics were more likely related to their physical appearance (trying to look taller, thinner, or more curvaceous). In a study of

women's counterstrategies against signal deception, Keenan and coworkers<sup>58</sup> found that undergraduate women in the United States expected men to be more deceptive about financial resources (such as exaggerating their current assets, or their current or future job titles), whereas men were less likely to expect women to be untruthful about their financial prospects. On other traits, such as height, weight, or level of physical fitness, no sex differences in expectations about deception were observed.

While interest in the cues of women's fecundity and men's resource holding potential has generated robust empirical findings, we need to move beyond the mating preferences typically derived from Bateman's gradient.<sup>29</sup> In his study spanning 37 cultures, Buss<sup>59</sup> emphasized the gender regularities in mate preferences, with men valuing physical attractiveness in a mate more than women did and women valuing ambition and industriousness in a mate more than men did. However, if the focus is shifted to the cross-cultural variability in Buss's data,<sup>59</sup> one might, contrary to the typical predictions, expect Swazi women to signal ambition more than men do, since this is a preferred trait in women in this population.

It is also important to avoid another assumption based on conventional parental investment theory: that males trade parenting effort for larger investments in mating effort and are therefore primarily signalers, and that females, burdened with obligate parental effort, have little left to invest in mating effort and are therefore primarily receivers of signals. While this assumption may hold for many species, humans exhibit extensive variation in the extent of bi-parental care. This dual investment means that both sexes will compete over mates through signaling and both sexes will be choosy through receiving signals. The fact that humans of both sexes are simultaneously signalers and receivers contributes to the broad variation in conflict and resolutions exemplified in our species' behavioral flexibility. It also presents intriguing questions for further study: Does an increasing ability to discern honest cues bear on the ability to produce convincing dishonest

signals? For the same reasons that a former criminal might make an excellent detective, perhaps the best signal fakers are also superior choosers. Does the co-occurrence of both traits in the same individual therefore accelerate the arms race? All in all, since men and women commonly invest heavily in their offspring (with, of course, great variability within and between populations) the stakes are high when it comes to signaling and deception in the quest for mates, suggesting that signaling and receiving traits are highly prone to sexually antagonistic selection.

### Conflict Over Family Size

The sexual conflict trait here is the *number of children produced* or its correlates, such as interbirth interval or age at first reproduction. Fertility is conventionally viewed as a female trait over which males have little direct influence. Hence, optimal family size will reflect how women trade fertility for offspring survival and future reproduction, as demonstrated in studies controlled for heterogeneity.<sup>60</sup> However, because of sex differences in strength, female mating rates are not necessarily under their direct control. Also, insofar as human females can be subject to strongly sanctioned cultural pressures to reproduce in accordance with local norms or family expectations,<sup>61</sup> there are many reasons to expect sexual conflict in this domain, with typical completed family sizes reflecting some sort of compromise between male and female interests. Here again, the optimality game is not a solitary pursuit.

One reason why men and women might differ regarding optimal family size is that they generally contribute different amounts of parental care and with different physiological and opportunity costs.<sup>13</sup> Men are predicted to favor larger families because the cost of each baby is less to them than to women. Indeed, evidence from a nineteenth-century American Mormon population shows that men's postreproductive survival is less strongly affected by number of children than is that of women.<sup>62</sup> Furthermore, to the extent that women's mate value decreases with age and parity more

rapidly than does that of men, men can replace an exhausted or deceased spouse more easily than can women. In short, fitness-maximizing fertility levels are likely to be higher for men than for women. Demographers have similarly concluded, albeit without evolutionary logic, that because of the initial high investment by mothers in gestation, birth, lactation, and child care, as well as male control over most resources (even those that children produce), the parental cost-benefit ratio is much lower for men than for women.<sup>63</sup>

As might therefore be expected, fertility preferences between men and women differ markedly, with men generally preferring larger numbers of offspring than do women.<sup>63</sup> Demographers recognize spousal conflicts over family size preferences, although these conflicts vary across regions in ubiquity and magnitude.<sup>64</sup> So what accounts for variability in sexual conflict over family size and for how such conflicts are resolved? We can move beyond conventional parental investment theory to develop hypotheses for the answers to these questions.

A first prediction is that intersexual conflict over ideal family size reflects the extent of sex differences in the costs of reproduction. These costs vary enormously across and within populations, depending on context. For example, although paternity was costly in terms of survival in a nineteenth-century Mormon population,<sup>62</sup> in twentieth-century England and Wales only very large families and very early onsets of paternity are associated with negative health and survival outcomes for men.<sup>65</sup> Generally, we would expect greater conflict where the costs of reproduction are less equally shared by the sexes. Using related logic, a subsidiary prediction arises from the fact that sex differences in reproduction change over the life span with, for example, childbirth being most dangerous to women early and late in their reproductive careers. Therefore, we would expect greatest intersexual conflict at these periods.

A second prediction is that sexual conflict is less acute as family size increases because of the changing relative costs of parental investment to

males and females. This is captured in Smith and Hardling's<sup>66</sup> coevolutionary dynamic model. For males, assuming there is an economy of scale to paternal care, many dependents render paternal care more valuable. For females, the more paternal care their offspring receive, the more offspring they can afford to produce, even if there is not economy of scale.<sup>67</sup> In short, we can expect a coevolutionary relationship between large family size and increasing paternal care,<sup>66</sup> particularly the kinds of care that are nondepreciable, like providing defense or conferring status. Thus, we can predict that discrepancies in men's and women's preferred family sizes will decline as a function of modal family size and the importance of nondepreciable paternal care. For similar reasons, the presence of caretakers (or plentiful sources of family capital) might reduce spousal conflict over fertility. Where paternal care is strongly depreciable, as in some Western economies where "quality" time invested in children's cognitive development evidently is not easily shared,<sup>68</sup> this dynamic may not be observed. It is more likely in economies where siblings help raise each other.

A third factor that might affect male-female discrepancies in fertility preferences is the extent to which an individual's subsequent reproduction is contingent on his or her current spouse's health and survival. This contingency, of course, reflects the mating system, rates of divorce, and extrapair fertilizations. Men will be more tolerant of women's preferences if they have no reproductive options elsewhere, and *vice versa*. These observations suggest predictable relationships with polygyny, rates of divorce, and prevalence of extra-pair relationships. Specifically, where divorce and extra-pair fertility are prominent, men will have much higher ideal fertility levels than women will since exhausted wives are effectively replaceable and since a man might prefer shorter interbirth intervals in order to capitalize on his wife's fertility before losing her to a new husband. Conversely, where polygyny is allowed we might expect the ideal fertility levels of husbands and wives to be more similar. This is because men with multiple wives can, to a certain



### Box 5. Sex Differences in “Ideal Number of Children” for Pimbwe and Kipsigis

“What is the ideal number of children you would like?” Sex differences in response to this question compared across two rural populations in East Africa demonstrate how divergent and how similar men’s and women’s preferences can be. Pimbwe horticulturalists of western Tanzania have unstable marriages, high rates of divorce, and little polygyny, whereas Kenyan Kipsigis agro-pastoralists have very stable marriages and no divorce, but high rates of polygyny. While Pimbwe men generally wanted two more children than did Pimbwe women, Kipsigis men, *when asked for the ideal fertility per wife*, gave values very similar to Kipsigis women.<sup>121</sup> However, when Kipsigis men were asked this question for themselves, their values were, unsurprisingly, much higher than those of women because they were anticipating polygyny. These results (Fig. 1) could be interpreted as Kipsigis men’s tolerance, compared to Pimbwe’s men’s intolerance, of the wishes of their spouses; the former are tied life-long to their wives and have the additional option of polygyny, whereas the latter divorce freely, providing illustrative support for the hypothesis that sex differences in fertility preferences are influenced in predictable ways by the marriage system. Counter-intuitively, in this context polygyny reduces spousal conflict.

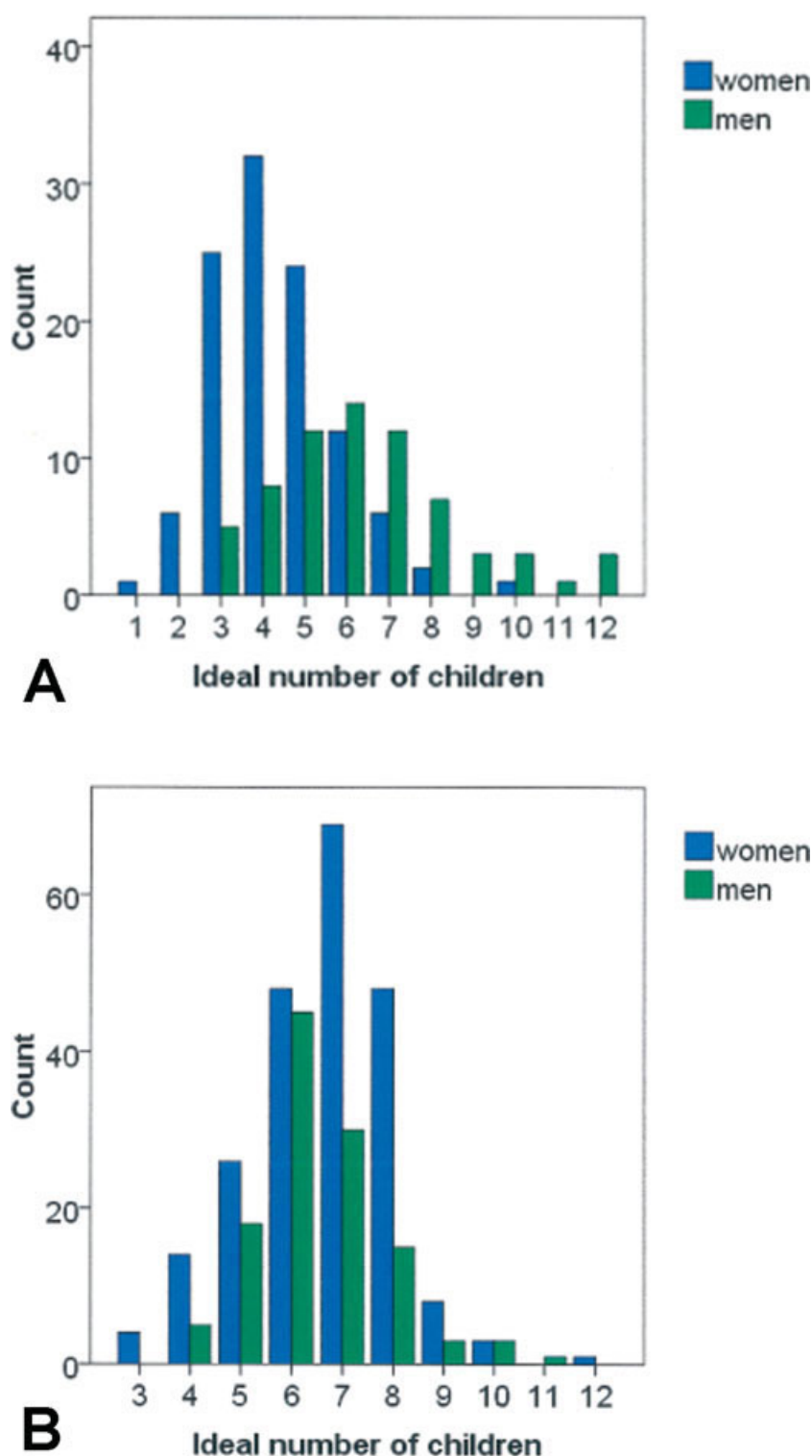


Figure 1. Sexual conflict over ideal number of children in two African populations with different marriage systems, (A) Pimbwe and (B) Kipsigis. (Color figure can be viewed in the online issue, which is available at [www.interscience.wiley.com](http://www.interscience.wiley.com).)

extent, exhaust their capacities for investment in offspring and mate-guarding. Comparative data from two African populations with very different marriage and mating systems illustrate the predicted patterns (Box 5). Indeed, one advantage of polygyny recognized by Kipsigis women is that a husband wanting sexual relations when the wife does not “can be sent elsewhere.” Monogamous women do not have that explicit option.

A fourth set of predictions about conflict over family size concerns female autonomy. Evidence from a variety of species shows that females who are experimentally prevented from mating with their preferred male produce offspring of lower viability and compensate by investing in the production of greater numbers of offspring.<sup>69</sup> Similar effects are shown for males. Across human cultures, women's opportunities for economic self-sufficiency vary. Where women lack autonomy, their marriages are generally arranged by older representatives of the two families, often with little or no input from the couple themselves; in their husbands' homes, women's position remains one of economic dependency. Under such circumstances, women will favor larger numbers of offspring. Indeed, this preference might be reinforced if their lack of autonomy pushes them, in their later years, into reliance on the support of their sons as in the patriarchal communities of Southern Asia where women typically desire larger families than their husbands do.<sup>70</sup> Conversely, where women enjoy economic independence, they are less constrained in the choice of mates and should accordingly be less concerned with compensating for lower offspring viability. Women with socioeconomic autonomy should also be more successful in realizing their own, rather than their mate's, fertility goals, as shown in several studies.<sup>71</sup> It is not possible to predict that economic gender equality will drive male and female preferences apart (since men's preferences might also shift) but still, it is clear that the extent of women's independent access to the resources needed for reproduction and the trade-offs entailed in capturing these resources will shape both absolute fertility



Figure 3. Responses vary with severity of the offence. From [www.unoriginal.co.uk/cartoons1.html](http://www.unoriginal.co.uk/cartoons1.html). (Color figure can be viewed in the online issue, which is available at [www.interscience.wiley.com](http://www.interscience.wiley.com).)

preferences and their success in achieving these preferences.

We can also make predictions about in whose favor conflicts are likely to be solved. Family systems theorists<sup>61</sup> and evolutionary anthropologists<sup>45</sup> have already shown how in-laws contribute to and even exacerbate spousal conflicts, with a woman's kin having more evolutionary interests in her health and fitness than do her husband's kin. Thus, it is commonly found that cohabiting with or close to the wife's relatives lowers a couples' fertility, whereas cohabiting with or close to the husband's relatives increases fertility, as in The Gambia.<sup>72</sup> A study of the matrilineal Khasi of Northeast India shows that age-adjusted fertility is lowest for divorced women living with their mothers and highest for women living away from their mothers in second marriages.<sup>45</sup> Indeed, Khasi women without mothers appear to be at a disadvantage with respect to leveraging support from men.<sup>73</sup> Issues of causality complicate interpretation of the precise dynamics of the control over reproduction among women, their husbands, and their mothers. However, it is clear from this matrilineal system, and also from patrilineal<sup>74</sup> systems, that

sexual conflicts over the optimal investments in children spill out far beyond the marital bond, as cultural anthropologists studying kinship systems have long recognized.

In sum, although evolutionary theory predicts conflicts among spouses over optimal and, by extension, preferred fertility levels, there is much variation in the extent of this conflict. There are cogent hypotheses about why this is. Conflicts over desired family sizes may vary between and within populations in predictable ways as a function of expected parental contributions, age, resource access, marriage regimes, the presence of relatives, normative values, and other factors.

### Conflicts Within Marriage

Perspectives on marriage are changing as divorce rates escalate worldwide. With data on interpopulation variability in the occurrence and rates of marital breakdown, new theoretical perspectives are revising the conventional view of economists,<sup>75</sup> as well as sociocultural<sup>76</sup> and evolutionary<sup>77</sup> anthropologists. That view saw marriage as a cooperative division of labor in which men share resources with women encumbered with dependent offspring in return for sexual exclusivity, with both partners benefiting equally from the products of this cooperation. Thus, Fisher's<sup>78</sup> claim that divorce rates peak four years after the birth of a child (because this is when a typical forager child is safely through the period of dependence) is replaced with the view that mums and dads at each stage of the reproductive cycle should be considering the benefits and opportunity costs of staying with the same partner.

In light of sexual conflict models, marriage is best understood as a transaction in which love and care, time and money, status and debt, among other things, are exchanged. The great variability in marriage contracts worldwide, with different cultures emphasizing different aspects to this transaction, be they sexual, reproductive, economic, legal, or emotional, complicates this perspective, but does not invalidate it. Once we think about marriage as a contract between two partners (or more, with polygamy), a

suite of conflict traits emerges. First, there is the division of net benefits created in the marriage; effectively, this concerns who works and who enjoys the products of this work. Second, there is the conflict over who, if anyone, transgresses against the contract by, for example, having extramarital affairs or withholding sex or engaging in interpersonal violence, laziness, or theft. Third, intricately related, is the durability of the contract. Finally, though not discussed here, there are conflicts between men and women over how many people to let into a marriage.<sup>79</sup> Accordingly, we can specify a range of conflict traits: how much to work and spend, how much nice behavior to offer or nasty behavior to refrain from and how many of a partner's transgressions to "overlook" before resorting to divorce or worse (Fig. 3).

Sexual conflict in the second and third domains (infidelity and divorce) is, at one level, relatively straightforward. Adultery, especially on the part of wives, is a major precipitating factor for divorce in both cross-cultural<sup>80</sup> and North American<sup>81</sup> samples, reflecting paternal investment that is lost in the case of a cheated-on woman and squandered in the case of a cuckolded husband. This finding is often interpreted as evidence of a deep mammalian concern with paternity confidence. The picture, however, is probably more variable and more interesting; tendencies to divorce are not driven solely by issues of uncertain paternity. One consideration is age. For example it may be to *women's* advantage to initiate divorce early in their reproductive career because they will have greater chances of remarriage, and to *men's* advantage to do so later when they have higher relative reproductive value.<sup>81</sup> Another factor may be the range of variation in mates. With reliable hunting rendered illegal for the Tanzanian Pimbwe, men are now extremely variable in the extent to which they have taken successfully to horticulture. Pimbwe women who raise children with multiple men over their reproductive life spans produce more surviving children than do their monogamous counterparts, suggesting that some women at least may be

replacing spouses who fail to provide.<sup>44</sup> The nature of sexual conflict over infidelity and termination of the marital contract may be more nuanced than earlier studies predicated simply on parental-investment theory have suggested.

To tackle variation in divorce rates, economists use bargaining power models. Building on Becker,<sup>75</sup> they identify a spouse's bargaining power, the well-being Posh can expect without the cooperation of David, and *vice versa*. Differential bargaining power sets each spouse's "threat point,"<sup>82</sup> the contractual arrangement at which Posh or David would be better leaving than staying. Anything that improves an individual's bargaining power with his or her spouse, such as relatively larger earnings, gender-biased divorce laws, or greater chances of remarriage, increases that person's share of the marital pot without risking partner desertion.<sup>83</sup> For example marital stability increases with male income, since high earners are likely to get the highest quality wives the first time round, but decreases with women's income, since richer women have greater utility (and chances of remarriage) outside of marriage.<sup>84</sup> Note too that the partner who is more risk prone and who has a shorter time horizon might also be disadvantaged in bargaining games.<sup>85</sup> The implications of threat points for marital stability, marital assortment, and equilibrial states of the marriage market can be explored with game theory, as demonstrated in models of the "better options" hypothesis for divorce among birds,<sup>86</sup> where divorce rates are shown to decrease with individual quality (fewer "better options," assuming a good first pairing) and age (no time to recoup the costs of divorce). Viewing disruptive behaviors such as relative infidelity rates as conflict traits raises empirically tractable questions. Are men permitted more transgressions than women? Presumably yes, given Betzig's survey.<sup>80</sup> How is this disparity affected by differences in age, income, health, and beauty, as well as legal and demographic aspects of the marriage market? These questions move evolutionary anthropology away from simple models predicated on sex differences in parental investment to more

dynamic studies of conflict over the duration of marriage.

Bargaining models can be used to look at another set of conflict traits within marriage: who does the work and who benefits from the produce. This, of course, has been a focus of evolutionary anthropological debate since Hawkes<sup>87</sup> and others<sup>88</sup> followed up behavioral ecologists' observations that males might use paternal investment to impress prospective mates rather than to protect offspring. With the "show-off" model, Hawkes ventured that things men do apparently for their children, such as hunting, herding, and direct care, are nothing of the sort. Ensuing studies to determine whether "male provisioning" is parental or mating effort showed, perhaps unsurprisingly, that there are elements of both in modern<sup>89</sup> and traditional<sup>90,91</sup> populations. Bargaining-power models allow us to move from the "yes it is/no it isn't" dialogue to predictive models of how spousal allocations within a marriage are affected by relative earning power, attractiveness of alternatives to marriage, the ratio of men to women, and the availability of substitutes such as nannies or kin helpers.<sup>92,93</sup> In short, the benefits of marriage are reaped disproportionately by the partner with the highest bargaining power.

Anthropologists' terminology differs from that of economists, but they find patterns that fit with these models. For example, there is clear evidence that relative earning power shapes marital expenditures. In developing countries, increases in men's income is associated with more spending on alcohol and clothes, while transfers to women are spent on education, health, and household services.<sup>94</sup> Similarly, in a United States panel study, a 1% increase in the adult sex ratio raises transfers from husbands to their wives by around \$2,500 per year.<sup>93</sup> In a cross-cultural sample, Quinlan and Quinlan<sup>95</sup> observed that divorce is more common in populations where only one sex contributes heavily to household production and where bargaining power presumably is unbalanced. Not only relative earnings, but relative power is important in affecting bargaining power. Thus, Jones and Ferguson<sup>85</sup> reveal how, in Colombian

couples, spousal violence rises with dyadic power asymmetries. In particular, factors that lessen a woman's bargaining power relative to that of her mate, such as having a low level of education, or being much younger than he is, increase her likelihood of experiencing violent or otherwise controlling behavior from her mate. Bargaining power also is affected by the sex ratio, insofar as this constrains outside options. Members of the sex in greatest abundance will have more difficulty finding mates than will members of the rarer sex. For instance, in the United States in 1910, men in states with male-biased local sex ratios had to have more wealth to marry than did men in states with less biased sex ratios.<sup>96</sup> Similarly in a comparison of four foraging groups, the Ache, Hiwi, Hadza, and !Kung, Blurton Jones and coworkers<sup>97</sup> found that the best predictor of divorce is *fertility units per male*. This ratio of reproductive-aged females to males, weighted by total fertility rates, gauges men's opportunities for new matings. Fewer fertility units per male mean more stable pair bonds, because strong male-male competition over a few outside options can be a deterrent to desertion.

With all this evidence of the importance of bargaining power in adjudicating tensions in marriage, we should not lose sight of the fact that marriages also entail cooperative elements. Winking and coworkers<sup>98</sup> investigated whether, among the Bolivian Tsimane, bargaining power influences commitment to a marriage. The expectation was that men allocate more effort to extra-pair matings as their reproductive value increases relative to that of their wives. However, no support was found for this prediction. Indeed, further analysis shows that while the gains and costs of marriage are not spread equally among Tsimane men and women, marriage still provides favorable and efficient outcomes for *both* partners insofar as men and women both value work effort in their partners, their marital labor contributions are complementary, and spousal work effort is correlated.<sup>99</sup> In sum, whether we are interested in cooperative behavior within marriages, disruptive actions, or the duration of the marital bond, it is use-

ful to focus on conflict traits. These are typically patterns of production, consumption, and sexual exclusivity, and result from a tense interplay of each partner's interests.

### CONCLUSIVE RASH THOUGHTS ON WHO WINS

Parker<sup>11</sup> argued that the sex that wins the conflict (that is, the value of the shared trait coincides with their sex-specific optimum) will be the sex that has the stronger selection pressures operating on it. Long trains will be selected if the mating benefit to the peacock exceeds the predation cost to the peahen. On this logic, given anisogamy, Parker saw males as the ultimate winners, as female attempts to resist male control cannot yield fitness benefits as strong as those accruing to males. As we learn more about the huge diversity of gender roles,<sup>2,26,29,100</sup> the simplicity of this logic dissolves. And as our review has shown, predicted outcomes are shaped by many factors other than sex differences in postzygotic investment in offspring.

More fundamentally, of course, the identification of winners and losers is a flawed pursuit. There are winners and losers in each sex. Peacocks pay a high cost for their fancy feathers. Evolutionary equilibrium will be reached when marginal fitness gains or losses are equal for the average male and average female. Furthermore, the costs and benefits of mating systems are not distributed homogeneously within each sex; some males are big winners and others are big losers. Earlier, we mentioned Kipsigis women who adroitly chose the man offering the most land, irrespective of whether or not he was polygynous.<sup>101</sup> Are they the winners? Yes and no. Kipsigis women would be much happier to own the land and cows themselves, but their choices in that respect are highly constrained. Yet, compared to Tanzanian pastoral Datoga<sup>79</sup> and Dogon,<sup>102</sup> they do rather well out of polygyny by accepting a married man only if he is rich; thus they "partially compensate" for the costs of polygyny in Searcy and Yasukawa's terms.<sup>103</sup> Perhaps because divorce is not an option and they are so dependent on men's resources, Kipsigis

women, or their parents on their behalf, chose among men particularly carefully. Other subtle counterstrategies women successfully use to mitigate the costs of polygyny include picking sisters as cowives<sup>104</sup> or bringing a dowry into the marriage.<sup>79</sup> Here it is easy to quip that men have "won," but women pursue successful counterstrategies even in highly patriarchal communities, as might be predicted from our deeper evolutionary lineage.<sup>23</sup>

What we learn here is that answers to the question of who wins must be restricted to specific conflict traits or, in other words, how close each sex comes to its preferred control of resources, marital preferences, optimal family size, and other conflict traits discussed here. Winning in one domain does not ensure winning in another. Kipsigis women lose in resources but gain in marriage; Datoga women, with their dowries, have more control over their resources, but apparently less control over their marriages.

Generally, we should think of sexually antagonistic contests as dynamic and ongoing. In this view, neither sex "wins," at least not for more than a short spell. This is because selection simultaneously favors male control of female reproductive decisions and female control over (or resistance to) males. Which set of traits is under stronger selection will oscillate over time. In fact, an important consequence of sexual-conflict thinking is the recognition that sexual selection produces winners and losers *within each sex*, winners being individuals who are particularly successful not only in manipulating or controlling the behavior of the other sex, but in competing with their own sex.

Building on new developments within sexual selection theory, specifically between-population variability in sex-specific costs of reproduction, variations in mate quality, and the adult sex ratio, we have proposed new hypotheses for the highly variable gender roles that we see in our species. In this way, we have tried to move away from a focus on stereotypical gender roles and to draw attention to a new framework for the systematic study of such variability. To make our case, we discussed three conflict traits: signal-

ing between potential mates, fertility schedules, and the establishment of long-term relationships. There are many other potential conflict traits that require both theoretical modeling of their potential coevolutionary trajectories and empirical investigations of their sex-specific optima. This work remains for the future.

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