



## Research

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# What do men want? Re-examining whether men benefit from higher fertility than is optimal for women

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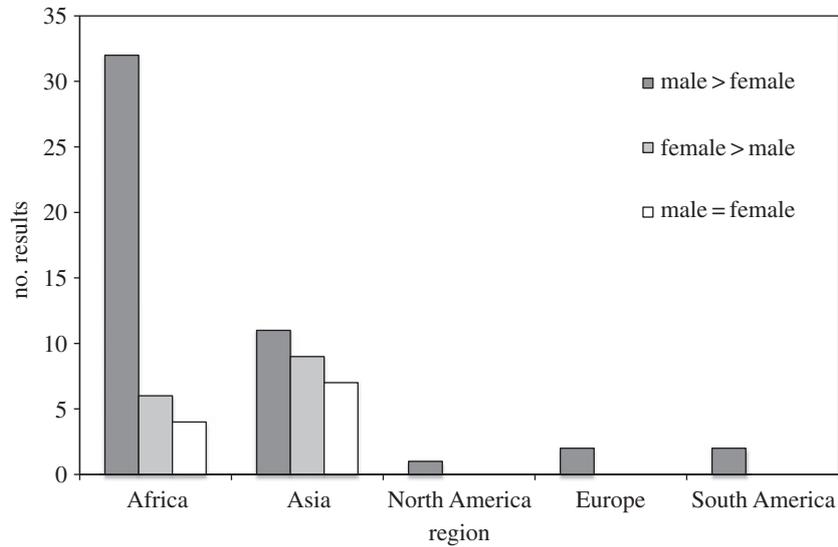
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Several empirical observations suggest that when women have more autonomy over their reproductive decisions, fertility is lower. Some evolutionary theorists have interpreted this as evidence for sexual conflicts of interest, arguing that higher fertility is more adaptive for men than women. We suggest the assumptions underlying these arguments are problematic: assuming that women suffer higher costs of reproduction than men neglects the (different) costs of reproduction for men; the assumption that men can repartner is often false. We use simple models to illustrate that (i) men *or* women can prefer longer interbirth intervals (IBIs), (ii) if men can only partner with wives sequentially they may favour shorter IBIs than women, but such a strategy would only be optimal for a few men who can repartner. This suggests that an evolved universal male preference for higher fertility than women prefer is implausible and is unlikely to fully account for the empirical data. This further implies that if women have more reproductive autonomy, populations should grow, not decline. More precise theoretical explanations with clearly stated assumptions, and data that better address both ultimate fitness consequences and proximate psychological motivations, are needed to understand under which conditions sexual conflict over reproductive timing should arise.

## 1. Introduction

There is a large demographic literature on gender and fertility which broadly shows that societies where women have more autonomy also have lower fertility (though within very low fertility societies, greater gender equality is often associated with higher fertility) [1]. This is commonly interpreted by social scientists as women exercising their preferences for smaller families than men when they have the power to do so ([2–5], but see [6] for a more nuanced understanding). While female autonomy and empowerment are operationalized in diverse ways, their definitions share an emphasis on women being able to act in their individual interests with limited social coercion.

Evolutionary social scientists are also interested in gender relations and their impact on fitness-relevant outcomes such as fertility. This interest stems from the theoretical expectation of sexual conflicts of interest, and has led to many parallel conclusions to those of the conventional demographic literature. Thus, observations that women often report wanting fewer children than men do [7–10] and that cultural institutions that reduce women's reproductive autonomy (e.g. patrilocality, polygyny and patriarchal norms) are associated with higher fertility [11–15] have been interpreted as evidence that natural selection has favoured lower fertility, and specifically longer interbirth interval (IBI), reproductive strategies for women than for men [11,16,17]. Sexual conflicts of interest arise if males or females can pursue reproduction with more than one mate. For example, one individual may benefit from extracting parental investment from their partner, while this partner would benefit more from pursuing other mates. Nearly all human societies allow individuals of at least one gender to remarry, minimally



**Figure 1.** Literature review of gender differences in desired fertility. The number of effects showing males with higher fertility preferences than women are shown in dark grey, those showing a higher fertility preference for women are in light grey, and those with no difference are in white. These are sorted by geographical region. See the electronic supplementary materials for a full listing of the referenced effects.

upon the death of their spouse, which can decouple the spouses' reproductive interests and thus increase conflicts insofar as this increases men's or women's outside options. However, humans have also experienced selection towards long-term monogamous pair-bonding that should lower such sexual conflicts [18]. In these long-term pair bonds, a man suffers from his partner's costs of reproduction—e.g. if she suffers higher mortality risks that lower the number or survival of her children, then his fitness will also be adversely affected because her children are also his. Husbands' and wives' fitness are therefore typically closely tied in humans [19].

In this paper, we draw attention to some of the assumptions in the evolutionary literature on human sexual conflicts over reproduction, and question whether the empirical patterns result from differing optimal strategies for men and women. To do so, we first review some of the empirical evidence that men and women disagree on fertility decisions. Next, we consider some of the problematic assumptions in evolutionary work that interprets this literature in the light of sexual conflicts of interest. Such work has tended to rely on verbal arguments rather than formal theoretical models. So in §2, we use simple models to illustrate the importance of formalizing intuitions when drawing conclusions about sex differences in this regard. We also use these models to draw some simple predictions about the ways that mating systems and individual differences affect sexual conflicts of interest over reproductive pace, a proxy for fertility. These models are not intended to be comprehensive or conclusive determinations of whether sexual conflicts of interest are of great importance to fertility, but rather as illustrations that several conditions influence the degree of sexual conflict and whether it will be expressed as men or women desiring faster reproduction. Our results suggest that universal sex differences in optimal strategies are unlikely to account for the empirical patterns described in §1a. In §3, we return to the empirical observations and discuss alternative explanations for these.

### (a) Does the empirical literature show that men want higher fertility than women do?

Because actual fertility outcomes depend on both male and female behaviour, and may therefore represent compromises

made between reproductive partners, ideal family size (IFS) has been used to compare the private reproductive preferences of men and women [17]. Several reviews of the empirical evidence on differential desired fertility in developing countries suggest that men and women usually agree on IFSs, but that when discrepancies do occur, men are more likely to favour larger families than women are, though female preferences for larger families are also observed [6–8]. We have reviewed the literature on sex differences in IFS and show in figure 1 that this discrepancy varies by world region (see the electronic supplementary material for sources used in this review). These sex differences in desired family size have been highlighted in the evolutionary literature [16,17,20] and are explicitly, or implicitly, interpreted as reflections of different fitness-optimizing strategies.

Cross-cultural comparisons of fertility across societies with varying degrees of female autonomy provide another tactic for examining the private reproductive preferences of women relative to men. Researchers have noted that women living patrilocally (i.e. with, or near, their in-laws) often have higher fertility than women living matrilocally. A recent review suggests that a greater proportion of studies examining the effects of a woman's in-laws show positive effects (approx. 85%) on her fertility outcomes than those examining the effects of a woman's parents (approx. 50%) [21]. The pro-natal effects of patrilocalty has been documented at both the individual level in several societies [11,12,22–24] and at the community level [24,25]. Some have interpreted these individual-level findings as resulting from a woman's in-laws pressuring her to have more children than she might want [22]. Such logic might be extended to the group-level if patrilocal communities develop higher fertility norms that reflect the interests of coalitions of related men or of patrilineal lines that benefit from growth.

Polygyny tends to co-evolve with other institutions that limit female autonomy [13], but its relationship to fertility is harder to interpret since it reveals different patterns at the group and individual levels. Several studies have reported that women in polygynous households have lower fertility than their monogamous counterparts in the same society [26,27], but polygynous societies tend to have higher fertility

than monogamous ones [28]. Some evolutionary scholars interpret this higher fertility as being against women's interests, but are ambiguous whether it is specifically against her fitness interests [13]. It is worth noting that polygyny could empower women by increasing their mating options [27]—i.e. they can choose to be the only wife of a poorer man, or share a wealthier man with co-wives—and recent research questions the causal role of polygyny in lowering women's fitness outcomes like child health [29]. However, inter-male competition for wives in these contexts tends to lead to younger ages at marriage for women, and less autonomy for them in such relationships with larger age gaps [13]. This suggests that a woman's reproductive schedule may reflect her spouse's preferences more than her own.

Finally, some direct metrics of female autonomy and indirect measures, such as education, have been implicated as important predictors of fertility decline or lower desired fertility [30,31]. This has led some researchers to suggest that the nineteenth to twentieth century demographic transitions reflect female preferences for lower fertility [3,4], and furthermore that these preferences may reflect females' adaptive reproductive strategies for smaller family sizes [20,32–35]. This is a nascent field of inquiry among evolutionists and the arguments are not yet well fleshed-out, but the empirical association between female education and lower fertility is well documented at both the individual and group levels [36–39].

These patterns, and their interpretation in the literature, give the impression that women would have lower optimal fertility rates if they were not being coerced by husbands, in-laws or male mates into higher fertility strategies that only benefit the latter. Some authors are explicit in claiming that these reflect evolved adaptive strategies, while others are more ambiguous and may consider that currencies other than fitness (e.g. short-term health and economic status) affect decision-making. While some of the empirical findings reviewed above seem robust, we believe invoking adaptive universal female strategies for lower fertility to explain these effects is premature and does not take full advantage of the theoretical modelling work in this field. We next review some shortcomings of previous verbal arguments that rely on sexual conflict in reproductive decision-making to explain the above phenomena in humans.

### (b) Do differential costs of reproduction between the sexes result in sexual conflict over family size?

Several authors have argued that a man should favour larger families because the cost of producing each offspring is lower for him than for a woman [10,32]. However, differential costs do not mean that men and women necessarily have different optimal fertility strategies (but see the electronic supplementary material for how it can affect sexual conflicts of interest). For example, natural selection can favour the same optimal family size preference trait of six children in both males and females over evolutionary time, even if the asymmetric costs of reproduction weakens the strength of selection for six rather than five children in women, but not men. To our knowledge, no paper on humans shows that different reproductive rates within a relationship are optimal for men versus women. Penn *et al.* [32] purport to show greater fitness costs for women than for men of greater fertility in a pre-industrial North American population. However, the actual

consequence of reproduction reported is parity-specific parental mortality, rather than fitness [32]. Given the low parental mortality rates reported in this study, even the negative effect of dying on number of grandchildren and its effect on geometric mean fitness over evolutionary time do not seem to outweigh the fitness benefits of having an extra child in this population for both men and women, although these should be calculated more directly from the data. This suggests no clear conflicts of interest over offspring number in this population, as has been documented in other similar populations [40].

Further, men also suffer costs of reproduction, although these may be experienced differently. While women often experience higher physiological and parenting costs to reproduction, men pay reproductive costs in terms of acquiring and keeping mates, and may also engage in parenting. The last is associated with slight mortality increases after parenthood [32]. As further evidence that these are significant costs, it is worth noting that age-specific mortality is higher for males than females, and particularly higher for young men in part because they engage in high-risk forms of intra-sexual competition [41]. These costs to male reproduction cannot be neglected.

### (c) Can all males replace mates?

The argument that men should prefer higher fertility than women because women suffer higher costs of reproduction is typically associated with the assumption that a man can easily replace his spouse should the costs of reproduction prove too high for her—e.g. if she dies in childbirth. However, most males with such a strategy are statistically unlikely to be able to find another mate, or will pay considerable costs to do so. This is because acquiring mating opportunities entails competing with other males directly, or putting effort into attracting females. Fisherian sex ratios are constrained to be roughly equal in diploid organisms, because for most population structures daughters and sons will have equal fitness (though see [42] for an exception). This means that men and women will have the same number of mating opportunities on average [43], and thus any attempt by one male to acquire a new partner will reduce mating access for other men. This limit of reproductive opportunities for men is reflected in the nearly universal higher reproductive variance for men than for women, and the higher rates of never-married men than women [44]. Several features of human operational sex ratios exacerbate the costs of replacing female mates (see the electronic supplementary material).

Note that in all societies there are likely individual differences between men in quality, which will influence their attractiveness as mates and their likelihood of repartnering. Men who have been married once may have realistically high perceptions that they will be able to repartner. Marriage institutions and sexual mores also affect the ease of repartnering. Norms favouring large differences in age at marriage between men and women can change sex ratios in favour of men of marriageable age. Furthermore, variation in population-level wealth distributions and female preferences can affect how much a few men monopolize mating opportunities. This means that in some societies men deemed marriageable may have an easier time repartnering, at the expense of lifelong partner-free males. These caveats illustrate the importance of taking context and individual characteristics into account when

exploring sexual conflict. In §2, we build a formal model to illustrate the kinds of conditions under which sexual conflict over reproductive pace is likely if women, and then men, have at least some possibility of repartnering, and the direction of the conflict.

## 2. Formalizing sexual conflict over reproductive output: does multiple mating by women or men result in male preferences for faster reproduction?

Although the empirical literature focuses on total fertility because it is easy to measure, we model optimal birth spacing since it is easier to formalize the differences in the trade-offs for men and women using this outcome than using fertility. All else equal, reproductive pace should be a reasonable proxy for fertility. However, this assumes that people will use their full reproductive careers to optimize their reproductive success. Our framework also assumes that a woman's reproductive career can be cut short if she dies prematurely, and we allow this risk to be affected by her IBI. This is one way she can have a fast reproductive pace, but low lifetime fertility. We first describe a static model of sex differences in optimal birth interval given that women, and then men, can repartner. Then we consider a more complete demographic structure, individual variation in male mate quality, and constraints on repartnering using an agent-based model of reproductive pacing decisions. The agent-based model also allows us to track maternal mortality and therefore to measure the knock-on effect of reproductive pacing strategies on total fertility. Our two models are meant to be illustrative rather than full descriptions of the phenomenon. While it is not an exhaustive treatment, we discuss some other potential sources of sexual conflict in reproduction in the electronic supplementary material and suggest further readings. We also focus our models on serially monogamous conditions that are more likely to result in reproductive conflicts between spouses than contexts with lifelong pair bonds. For example, it is clear that there should not be sexual conflicts over number of offspring in purely monogamous contexts where a male's and female's reproduction are completely tied to that of their partner [45–47].

### (a) Modelling a single birth interval

To illustrate trade-offs in reproductive pace, we start by modelling the optimal IBI for a man and a woman following the birth of a child that is genetically related to both of them. Three parameters contribute to both the mother's and father's optimal IBI calculation (see parameter key in box 1). We assume that the survival of this first infant,  $I$ , increases with the IBI following its birth owing to lower sibling competition and greater parental investment, e.g. via breastfeeding [48]. Similarly maternal survivorship,  $M$ , increases if a woman waits at least some time after the first infant's birth [49] to reproduce again. On the other hand, the mother's residual reproductive value (i.e. how many future children she can produce times their quality),  $R$ , decreases the longer she waits because of senescence [50]. This means that a female's fitness,  $W_f$  (equation (2.1)) will be equal to the sum of the value of her current child and her residual reproduction

#### Box 1. Model parameter key.

$W_f$  = female fitness

$W_m$  = male fitness

##### Fitness sub-functions

—  $I$  = 1<sup>st</sup> infant's survival

$n$  = neonate mortality

$m$  = maturation rate = 1

—  $M$  = maternal survival

$p$  = perinatal maternal mortality

$r$  = recuperation rate

—  $R$  = residual reproductive value (woman's)

$s$  = starting residual reproductive value = 1

$a$  = ageing rate

—  $P$  = paternity probability

$d$  = when paternity decline begins

$f$  = how fast paternity declines

given that she survives to be able to reproduce.

$$W_f = I + M \times R. \quad (2.1)$$

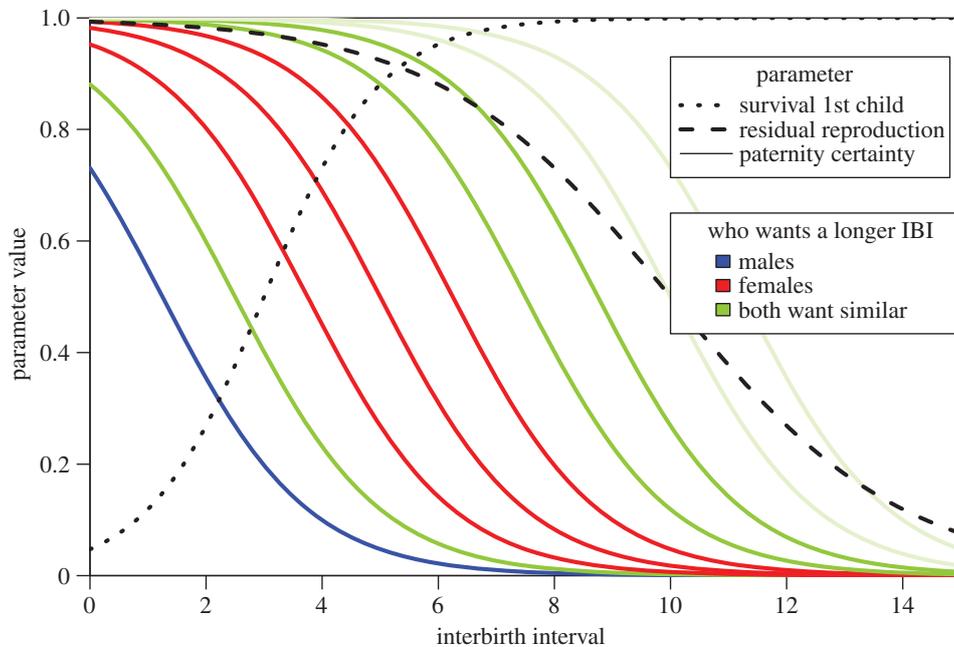
The male's fitness via this partner is additionally affected by his paternity through time (we consider his fitness via other partners later). We model the probability that the father sires the next child,  $P$ , as a decreasing function of IBI. This reflects that the longer a man waits to impregnate his partner again the more likely it is that he is not the father (e.g. either because of infidelity, divorce or his death). This parameter moderates the worth of a woman's residual reproductive value to the man, and only affects the father's (not the mother's) optimal birth spacing calculation. This means that a male's fitness,  $W_m$ , can be formalized using equation (2.2):

$$W_m = I + M \times R \times P. \quad (2.2)$$

Each of  $I$ ,  $M$ ,  $R$  and  $P$  can be modelled as functions of IBI. The first two functions, infant and maternal survivorship, increase with longer IBIs, whereas the last two functions—residual reproductive value and paternity—decline with longer IBIs. We use logistic functions because they can capture a range of monotonic shapes, and conveniently can asymptote at 0 and 1 thus constraining values that should be interpreted as probabilities. For simplicity, we only manipulate two parameters per logistic function at most.

We assume that the first child's survival,  $I$ , asymptotes at a probability of 1 (see equation (2.3) and dotted line in figure 2). The initial rate of neonate mortality, reflected in  $n$ , and maturation,  $m$ , govern the shape of this survivorship curve and the extent to which there is a threshold-like effect of investment on their survival. The maternal survivorship curve,  $M$ , can be similarly modelled (equation (2.4)), with a parameter  $p$  affecting the perinatal mortality rate and  $r$  denoting the recuperation rate.

The mother's residual reproductive value,  $R$ , decreases the longer she waits (see equation (2.5) and dashed line in figure 2). Her residual reproductive value starts near  $s$  (where  $s > 0$ ) and asymptotes at 0, while the ageing parameter,  $a$ , affects the rate of this senescence (we fix the time at which senescence starts declining represented by the 5 in the denominator's exponent). This represents decreasing fecundity and time available to produce more children. How fast paternity declines,  $f$ , and when



**Figure 2.** Effect of women's sequential mating on sex differences in optimal IBI. How paternity certainty changes through time affects which parent wants a longer IBI. Line texture denotes different parameters, and line colour denotes the resulting form of sexual conflict. Each solid line represents a possible rate at which paternity certainty declines after having had a child ( $d = [1, 2, 3, 4, 5, 6, 7, 8, 9]$ ). Paternity certainty curves in blue (medium grey in print) indicate the father wants a longer IBI, those in red (dark grey in print) that the mother wants a longer IBI and those in green (light grey in print) that they want similar IBIs. The speed of paternity certainty decline was held constant ( $f = 0.8$ ). The dotted line represents the survival of the first child as a function of the succeeding IBI (survivorship function parameters are  $n = 3, m = 1$ ). The dashed line represents the residual reproductive value of the mother as a function of IBI (with an ageing parameter,  $a = 0.5$ ). Maternal survival rate,  $M$ , was held at 1. (Online version in colour.)

the decline begins,  $d$ , vary the shape of paternity uncertainty functions (see equation (2.6) and solid lines in figure 2).

$$\text{infant survivorship (1st child)} = I(\text{IBI}) = \frac{1}{1 + e^{n-m*\text{IBI}}} \quad (2.3)$$

$$\text{maternal survivorship} = M(\text{IBI}) = \frac{1}{1 + e^{p-r*\text{IBI}}} \quad (2.4)$$

$$\text{residual reproductive value} = R(\text{IBI}) = \frac{s}{1 + e^{d*\text{IBI}-5}} \quad (2.5)$$

$$\text{and paternity certainty} = P(\text{IBI}) = \frac{1}{1 + e^{f*\text{IBI}-d}} \quad (2.6)$$

For simplicity, we set maturation,  $m = 1$  (equation (2.3)), and the starting residual reproductive value,  $s = 1$  (equation (2.5)) for the remainder of the paper. We numerically solve for the values of IBI that maximize  $W_f$  and  $W_m$ . We can use this system of equations to investigate how variables like paternity certainty, maternal and infant survival can affect optimal birth spacing for men and women, and the extent of sexual conflict over reproductive pace—i.e. the sex difference in optimal IBI.

### (i) Women sequentially acquire new mates

One clear source of sexual conflict arises when a woman switches mates between reproductive events. If a woman acquires a new mate he will have no genetic interest in her previous children, a condition that is associated with infanticide in many species [51], and with higher rates of child homicide, at least in Western countries [52]. This motivation may lead to a woman's new partner preferring a shorter IBI than a woman would [53,54]. This conflict of interest between reproductive partners means that a father may want a woman to devote more of her reproductive resources towards a current child that the father knows is his, rather than to her future offspring whom he may or may not father. However,

it is unclear whether the father's optimal exploitation of maternal resources would entail her prolonging the IBI following their shared child, or whether it would entail encouraging her to have a shorter IBI in hopes of his being able to father her next child as well.

Here we use the model we specified above to investigate this issue. For now, we assume that only women can acquire new mates and ignore the role of maternal mortality, setting  $M = 1$  (i.e. assume  $p$  approaches 0 and  $r$  approaches infinity). Figure 2 shows that if paternity certainty decreases rapidly after the birth of the first child (left-most paternity certainty curve) the father should actually want *longer* IBIs than the mother (denoted as blue online or medium grey in print) as he values the first-born child relatively more than the mother's future offspring and wishes to buffer it from competition from siblings that are likely less related to him. If paternity certainty remains high for a longer period of time before decreasing (paternity certainty curves on the right-hand side of figure 2), the man's fitness interests resemble those of the woman so that they prefer an increasingly similar IBI (noted as green online, or light grey in print). Note that curves where paternity certainty remains high after the birth of the first child approach the effect of lifelong pair-bonding (either monogamous or polygamous). For intermediate paternity uncertainty curves women prefer a longer IBI than men do since men benefit from taking advantage of her reproductive resources at an intermediate time scale—i.e. men prefer to father a second child more rapidly in order to increase the odds of fathering the next child before his chances drop further. The electronic supplementary material shows the exact relative fitness values of different IBI strategies for men and women as paternity certainty curves change.

This shows that the difference in optimal birth spacing for male and female partners can vary substantially. A woman's

switching mates can motivate her partner to want her to have a shorter IBI than she does so that he can capture more reproductive events, or a longer IBI so that his current child receives greater maternal investment at the expense of future offspring unrelated to him. This is true even without maternal mortality. So far, this means that men or women can prefer higher fertility strategies given that we have set maternal mortality to zero, meaning that the faster IBI strategies would be equivalent to higher fertility. Importantly, if paternity is constant through time the optimal IBI for men and women will not differ regardless of the baserate uncertainty levels. This suggests that polyandry, a rare form of pair-bonding where one woman is contemporaneously mated to two men, does not necessarily increase sexual conflicts over reproductive timing if it only increases baseline rates of paternity uncertainty, but paternity certainty does not change through time (see the electronic supplementary material for a formal justification). This framework also demonstrates the importance of knowing the exact effects of IBI on the rate of paternity decline, infant survivorship and the woman's residual reproductive value for determining the extent and direction of conflict. This variation and their dynamics are further explored in the electronic supplementary material.

It is worth noting that in this model male preferences for longer, and shorter, IBIs for their mate represent different avenues of exploitation, and both of these strategies would result in suboptimal fitness outcomes for the woman. This implies that a population where women switch mates often should have lower total fitness or population growth than one with less mate-switching, so long as women represent the limiting resource for population growth and optimal male strategies affect reproductive outcomes at either an evolutionary or behavioural time scale (for an empirical demonstration over evolutionary time in *Drosophila*, see [46]). Next, we consider the consequences of men being able to acquire multiple mates, even if mates are completely faithful to them.

## (ii) Men sequentially acquire new mates

We can now add the possibility that men, or at least some (e.g. high status) men, can acquire new mates in sequence. We analyse new mate acquisition after death, since verbal models of sexual conflict often assume that men can easily repartner after wearing a wife out with childbearing (see the electronic supplementary material for a model with repartnering after divorce).

Let us assume that a man can only repartner if his wife dies (thus maximizing sexual conflict). This happens with a probability equal to maternal mortality ( $1 - M$ ).

This means that men's fitness could be approximated as

$$W_m = I + M * R_1 * P_1 + (1 - M) * R_2 * P_2. \quad (2.7)$$

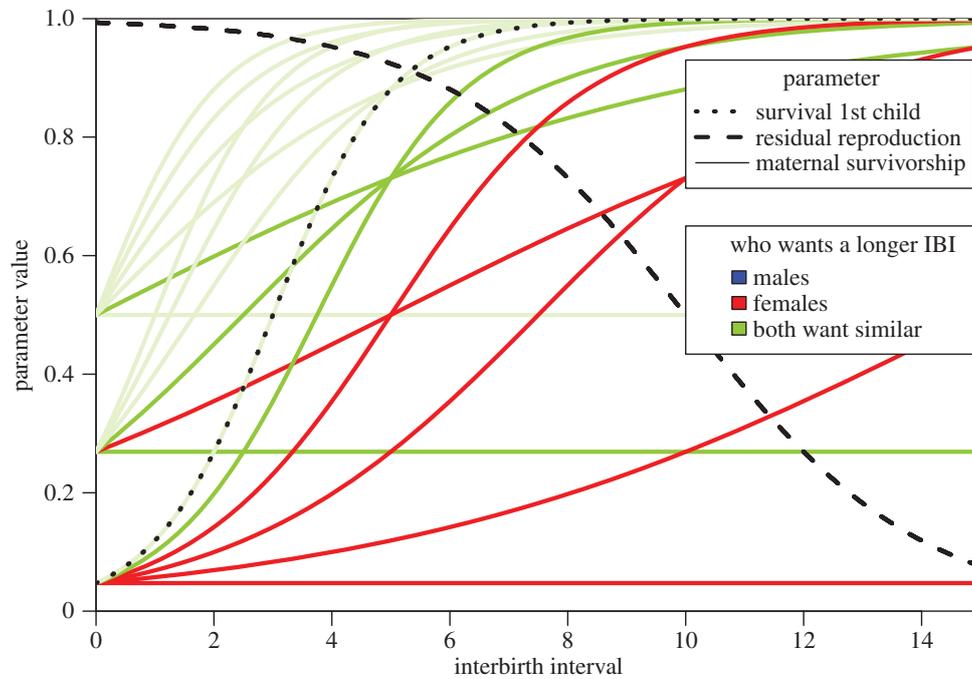
This is equivalent to the sum of three terms—the value of his first infant, the remainder of the first wife's reproduction weighted by her probability of survival,  $M$ , and the second wife's reproduction weighted by the probability of the first wife's death. If  $M = 1$  then the model is equivalent to the first one described above with only female sequential mating since the first wife never dies, meaning  $W_m = I + R_1 * P_1$ . Note, this assumes that the first infant's survivorship,  $I$ , is not directly affected by the death of its mother. This assumption is unrealistic, but increases the extent of conflict between the man and his first wife, since he does not need her to ensure the well-being of their joint infant.

If the two potential wives' values are equivalent ( $R_1 * P_1 = R_2 * P_2$ ), then  $W_m = I + R * P$ . Comparing this fitness function to that of a woman's in equation (2.1) ( $W_f = I + M * R$ ), we see that a man's and woman's fitness functions only differ in that the man's fitness is affected by paternity changes, while the woman's is affected by maternal survival. Let us assume that paternity is assured and constant through time,  $P = 1$ , approximating a society where a man controls a woman's full reproductive career. This means that  $W_m = I + R$  and  $W_f = I + M * R$ , so we investigate how the maternal survivorship function,  $M$ , produces sexual conflicts.

With increasing baseline rates of maternal mortality, a woman's optimal IBI increases, as does the extent of conflict over reproductive timing (see horizontal lines in figure 3 and the electronic supplementary material for formal justification). Moreover, if maternal survivorship increases with longer IBIs, this can further motivate women to lengthen their IBIs, while a man's decision is unaffected by this dynamic since we assumed he would have another mate to immediately replace his deceased one. This can also be seen in figure 3. For example, for an intermediate perinatal maternal mortality rate (e.g.  $p = 1$ , where the lines cross the  $y$ -axis at 0.27) the shallowest sloped line, when maternal survival improves most slowly, is red (or dark grey in print), indicating a much longer IBI preference for the woman than the man. Beyond a certain recuperation rate (as  $r$  increases) the woman's preferred IBI starts approaching the man's again as she needs less time to recover to get the benefits of increased survivorship. If the two wives are of different value—i.e.  $R_2 * P_2 \neq R_1 * P_1$ —then the male's reproductive decision-making starts being affected by the exact form of the maternal survivorship and residual reproductive value functions (see the electronic supplementary material for further analysis of these dynamics).

Taken together this model suggests that maternal mortality can motivate sexual conflict in reproductive timing through several pathways, assuming that men can mate with multiple women at no cost, but only in sequence (see the electronic supplementary material for further discussion of these pathways). Generally, maternal mortality will result in the woman preferring a relatively longer IBI than the man. This is because we have only considered maternal survivorship functions,  $M$ , that increase or are stable with IBI. However, the extent to which mates disagree about birth timing will depend on several parameters like the baseline rates of maternal mortality, the effect that IBI has on maternal mortality and the relative qualities of the first and second wives. Furthermore, if we allow maternal survivorship,  $M$ , to decrease with IBI, for example because childbearing is more dangerous for older women, this can motivate a woman to reproduce sooner than would be optimal for her male partner, since he can repartner upon her death.

Another insight from these models is that there might be less spousal conflict over optimal IBIs in polygynous marriages than in serially monogamous ones [10]. This is because men who can afford additional mates can do so concurrently without having to forgo the future well-being of their current spouses in order to attain another mate. In fact, in the simplest scenario polygynous men are likely to optimize their own fitness by optimizing each of their spouse's fitness if they are monopolizing their partners' whole reproductive lives. This would be true if adding an  $n$ th child had the same kind of effect (positive or negative) on each wife's fitness. That is, under these simple conditions a polygynous man's fitness,



**Figure 3.** Effect of maternal survivorship on sex differences in optimal IBI when men can mate sequentially after the death of a mate. How maternal survival,  $M$ , changes through time affects the extent to which a woman wants a longer IBI. Each coloured line represents a possible maternal survivorship curve as a function of IBI. These represent different baseline perinatal survivorship rates for mothers ( $p = [0, 1, 3]$ ) and rates of recuperation ( $r = [0, 0.2, 0.4, 0.6, 0.8, 1]$ ). Maternal survivorship curves in red (dark grey in print) indicate that the mother wants a longer IBI, and those in green (light grey in print) that mothers and fathers want more similar IBIs. Note the absence of blue curves (medium grey in print) indicates that men never wanted longer IBIs than women did for these conditions where men could remarry an equivalent mate at no cost if his first mate died, maternal survivorship,  $M$ , increased with IBI, and paternity certainty,  $P$ , was held at 1. The dotted line represents the survival of the first child as a function of the succeeding IBI (survivorship function parameters are  $n = 3, m = 1$ ). The dashed line represents the residual reproductive value of the mother as a function of IBI (with an ageing parameter,  $a = 0.5$ ). (Online version in colour.)

$W_{mv}$ , equalling the sum of his wives' fitness,  $W_{w1} + W_{w2} \dots + W_{wn}$ , will be highest when each of his wives' fitness ( $W_{w1}, W_{w2}, \dots, W_{wn}$ ) is maximized. This would lead to similar fertility preferences between lifelong polygynous partners, much as we expect regarding lifelong monogamous pair bonds.

We made several assumptions in this model to maximize the potential for sexual conflicts over reproductive pace. For example, maternal mortality did not affect infant mortality, and men could acquire new wives at no cost. Next, we relax the latter assumption in an agent-based model.

### (b) Modelling a full reproductive span with constraints to repartnering

In this section, we use an agent-based model to analyse how IBIs evolve when wives are costly to acquire because of (i) Fisherian sex ratios (equal numbers of males and females), (ii) men having a longer reproductive career than women (25 years for men and 20 years for women) mirroring reproductive senescence in humans, and (iii) maternal mortality in childbirth. However, first we numerically calculate the optimal IBI for women, and for unconstrained men who can acquire a new mate for free using a parallel set of assumptions and functions to those that we will use for the agent-based model. We can then use these as benchmarks to compare the effects of constraints on repartnering and individual male differences in repartnering abilities on male IBIs and sex differences in optimal IBIs. Numerical calculations are with discrete IBIs, which means we use months in this section for greater resolution.

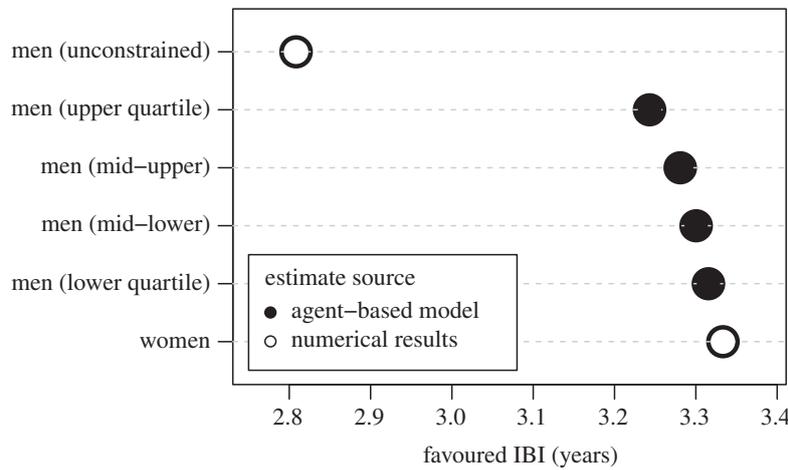
As before, we assume that infant and maternal survival improve with longer IBIs ( $n = 5, p = 4, m = r = 0.2$ ). This

means that infant survivorship starts near 0% and rises to nearly 100% by 4 years, while the mother's survivorship is about 10% for birth intervals of nine months and exceeds 96% by approximately 3 years. Short birth intervals are more detrimental to children than mothers, although mother's survival rate is unrealistically low to maximize sexual conflict.

We numerically calculate the woman's fitness as the sum of the survivorship of her first offspring plus the survivorship of each subsequent offspring multiplied by the probability that she is alive to produce those offspring (equation (2.8)) and compare the fitness for each possible IBI (in number of months). Finally, the number of offspring can be calculated as the reproductive span divided by birth interval (in this case, we will assume a reproductive span of 240 months or 20 years).

$$\begin{aligned}
 W_w &= \sum_{n=1}^{\text{floor}(240/\text{IBI})} I * M^{n-1} \\
 &= I + I * M + I * M^2 + \dots \\
 &\quad + I * M^{\text{floor}(240/\text{IBI}) - 1}.
 \end{aligned} \tag{2.8}$$

By comparison, an unconstrained man's fitness is the product of the number of offspring he produces and the survivorship of children. In this example, we will assume (to maximize the conflict) that men can replace any wife who dies—so he is not constrained by the wife's mortality and this expression is not included in his fitness calculation. This also assumes that a man can acquire an additional wife and progress to the next birth in the allotted IBI. Figure 4 shows that the optimal IBI (illustrated as open circles) for women is 3.33 years, whereas it is 2.8 years for men under these circumstances. Reducing



**Figure 4.** Birth intervals selected for in women, unconstrained men and men of varying quality. The first two values (open circles) are from numerical solutions, while the male quality results are from the agent-based model (filled circles). The ABM results show the average IBI for the last 10 000 men who exit the model after 25 000 iterations. These men are divided by quality into quartiles.

women's survivorship would increase this sex difference in ideal birth interval, but women's survivorship is already unrealistically low.

Next we develop the agent-based model based on these functions, but add Fisherian sex ratios, longer male reproductive spans and sex ratio consequences from maternal mortality. We also introduce individual variation in male mate quality that affects their likelihood of repartnering. Once the population structure has been initialized (see the electronic supplementary material), we begin the evolutionary process in the agent-based model.

The life cycle—i.e. a generation for each cohort—includes: entering the population of reproductive-aged men, making decisions about reproductive strategies each year for 25 years, fathering the next generation of incoming men of reproductive age in proportion to their reproductive success, and finally death. First we describe the strategy decisions men make each year and then the way reproduction is allocated.

Each year men choose (i) whether to mate or switch mates (if there are available females) and (ii) whether to reproduce. Reproductive decisions are based on a man's inherited IBI preference and on the time since his and his partner's prior reproductive event. For example, men who have an IBI preference of 40 months wait until both they and their female partner have gone 40 months without a birth before choosing to reproduce.

Mate choices are made in order of the man's own quality, where higher-quality men get to choose mates first. Male quality is based on two factors: (i) age, where men's quality increases with age and then declines (mirroring resource acquisition abilities in many societies) and (ii) a random factor that is inherited from one's father. Male quality can be summarized as  $-(a/180 - 0.75)^2 + 1 + \xi$ , where  $a$  represents age (in months) and  $\xi$  represents the random factor. See the electronic supplementary material for more model details. Each year men have the option of leaving their wives, and make their decisions sequentially from the highest-quality to lowest-quality man. Each man opts to leave his wife if he expects to have higher fitness with a different available mate. This calculation is based on two factors: whether the potential new mate would be higher quality than his current one (the answer will always be yes if the man has no mate) and the cost of his leaving for his young children's survivorship. Female quality depends on the number of reproductive years she has left, and her recent

reproduction. A woman who recently reproduced is less desirable than a woman of the same age who has not recently reproduced. This reflects the constraint that a woman's and her next infant's survivorship are greater after long, compared with short, birth intervals. If the man leaves a mate, any offspring they have under age 5 will be of lower quality. Furthermore, each child's survivorship depends on his mother's IBI and has a likelihood:  $1/(1 + e^{(5-IBI/5)})$ . While maternal IBI affects child survivorship, in this model, women have no choice regarding divorce or when to reproduce. This is because the model was designed to examine men's optimal reproductive timing, meaning we only allowed these decisions to evolve.

At the end of 25 years of yearly decisions, we compare the relative lifetime fitness of males in the dying cohort in order to determine whose children will enter the population of reproductive-aged men. Dying men will father the next cohort of reproductive men in proportion to their lifetime fitness compared to cohort mates. Each man's lifetime fitness is calculated as the sum of the survivorship of each of the children he had, reduced by each child's quality loss owing to any early life paternal absences after divorce. This allows us to maintain a stable population size since the incoming group of men will have a fixed size equivalent to the number of males exiting the model.

There are equal numbers of males and females (20 each) entering reproductive age each month. Each incoming group of females is identical (the only difference between any two women in the model is their age, where younger women have greater reproductive value). Incoming men inherit the birth interval preference of their father plus some random value from a normal distribution ( $\mu = 0$ ,  $\sigma = 2$ ). Men also inherit the quality of their father, plus some random variation from a normal distribution ( $\mu = 0$ ,  $\sigma = 0.05$ ). We let this model run for 25 000 iterations to see how IBI preference evolves over time.

Results show that a male's optimal birth interval preference depends on his quality. If we examine birth intervals for the last 10 000 men who exit our model, we can see that men with higher quality are more likely to have a preference for shorter birth intervals (figure 4). Men of lower quality have birth interval preferences closer to women's optimal birth interval (mean of 3.32 years for the lowest quartile of quality), while

men with greater quality have shorter birth intervals (approx. 3.24 years for the highest quartile). Remember from our analytical solution that ideal birth interval should be approximately 3.3 years for women, and 2.8 years for men. So while men of higher quality are more likely to diverge from the woman's optimum, average or below-average men cannot afford to exploit their wives because they will not be able to replace her if she dies. On average, however, men can evolve shorter IBI preferences than women in this scenario because there are no advantages to any men of reproducing more slowly than is optimal for women. Even the low-quality men, whose preferences do not get expressed if they cannot acquire a mate, would not be able to do better than to express the optimal IBI for women. However, while some men may desire shorter IBIs, they will not be able to achieve a higher fertility per woman than she would want for herself since her reproductive career would be curtailed by premature death in this model.

### 3. Re-evaluating the empirical literature

The models described above illustrate several important features of sexual antagonism over reproductive pace. First, lifelong pair bonds should favour the same reproductive pace optima for men and women. Second, men and women can differ in their optimal IBI, however if decreases in paternity certainty are motivating this conflict, either men or women may prefer the longer IBI. Third, if men can only partner with wives sequentially they may favour faster IBIs than a woman because of higher maternal than paternal mortality rates. However, such a strategy would only be optimal for a minority of high-quality men who can afford to replace their wives. How can we make sense of the empirical literature about sexual conflicts of interest in light of these insights?

#### (a) Gender differences in ideal family size

While gender discrepancies in IFS seem a clear indication of men's higher fertility preferences, the empirical patterns may reflect male preferences for more children over multiple partners, rather than per woman. In contexts where polygyny is common, such as sub-Saharan Africa, we may expect larger differences in ideal male and female fertility because men may hope to obtain more mates in the future. The larger gender discrepancies in ideal fertility in studies conducted in Africa lends some support to this argument (figure 1). Further, a cross-cultural study of unmarried youths also found that women reported desiring fewer children than men did [6], perhaps because unmarried men may imagine their fertility over several partners, whereas married men may envisage future reproduction only with their current partner and thus report more similar IFSs to women. While men's potential reproductive rate is higher than women's and they tend to benefit more from multiple matings [55], this does not necessarily translate into a conflict within a particular couple over the ideal number of children that they should have together. One might expect that a minority of high-status men for whom multiple mates is an option may be driving these results, whereas the majority of men who could only expect a single partner may report more similar IFSs to women's.

It is also possible that IFS questions tap into different psychological biases from those that evolved for reproductive decision-making. Questions about ideals may motivate optimistic responses, including preferences in a world without constraints or trade-offs. Men are often more overconfident

than women [56], which may translate into an inaccurately high assessment of their ability to acquire multiple mates or afford resources for multiple children. This highlights the importance of distinguishing an individual preference from a strategy that is selected for in the context of real-world trade-offs and demographic structure. Furthermore, asking about fertility preferences may highlight the health and opportunity costs of reproduction for women, rather than the costs for men in the domain of mating competition and later parenting or provisioning.

#### (b) Institutions affecting female autonomy and fertility: patrilocality

The positive effects of in-laws on a woman's fertility and reproductive pace have often been interpreted as coercive reflections of her male partner's fitness interests [11,12]. These arguments are particularly surprising given that higher fertility and shorter IBIs are often used as indicators of higher fitness. For example, in much of the cooperative breeding literature higher fertility, and probabilities of progressing to a next birth, are interpreted as evidence that kin presence is helpful—presumably because it increases fitness [57–59]. This inconsistency means the same empirical association of kin presence with higher fertility is often interpreted as evidence of altruism, or of coercion, depending on whether the family member is a woman's mother [57,59] or mother-in-law [11,60], respectively. In fact, in most places where anthropologists have tried to measure the relationship between fertility and fitness, including in high fertility contexts with limited effective contraception, these are positively and monotonically related [61–64]. This does not necessarily mean that one or both arguments must be incorrect: a woman's costs to shorter IBIs can be lowered by supportive social relations, and she can be coerced into a shorter (or longer) IBI by a mate unsure about his future paternity. However, we should be devising better predictions for differentiating the hypothesized mechanisms of influence on reproduction. This problem of multiple interpretations parallels inconsistencies in the development literature where both high *and* low fertility outcomes can be interpreted as signs of women's disenfranchisement or as poor health outcomes [65].

In-laws' pro-natal effects on women's reproduction are often interpreted as coercive in part because of ethnographic information about strains in such relationships [66,67]. Our models suggest that men, and their kin, can benefit from a faster reproductive pace than the woman herself would benefit from, in the case where he is high status and can replace his wife, or she is likely to repartner. However, the mechanisms suggested by our models mean that if women were thus being coerced in these patrilocal contexts their total fertility should be lower (e.g. because of premature death or wear on her reproductive system). This suggests that if the in-law effects are evidence of evolved sexually antagonist strategies, we would see more pro-natal in-law effects on IBIs than on total fertility. One possible reason why it has been difficult to detect trade-offs between fertility and fitness is that we may be under-sampling deceased women representing victims of such coercion. Alternatively, we may be underestimating the fitness consequences to fast reproduction over evolutionary time by looking at modern societies, but see the electronic supplementary material for reasons to be skeptical of the relevance of such evolutionary lag.

An alternative adaptationist interpretation of the patrilocal effect is that women act in their own self-interest by reproducing *more* in patrilocal than matrilocal contexts. This is because they benefit less from helping other household members reproduce when they are living among less related people than when they are living with more related individuals matrilocally [68]. On the other hand the fact that the stated fertility preferences of daughters-in-law are lower than those of mothers-in-law in at least one such patrilocal context [69] casts doubt on higher fertility outcomes necessarily reflecting a woman's true preferences. In such monogamous patrilocal contexts where women have explicitly lower fertility preferences than in-laws, currencies other than fitness (e.g. health, pleasure, economic status) may be motivating the discrepancies in preferences between unrelated household members.

Our models suggest that much closer attention needs to be paid to both the context in which men and women are making fertility decisions, and individual differences between men and women. There may be some limited circumstances under which men benefit from coercing women into higher fertility—e.g. a relative surplus of women over men, and men being of high quality—but there are alternative explanations for why women should reproduce faster in patrilocal contexts. Future research should focus on testing between these alternative hypotheses, for example, by examining whether birth intervals are particularly short in patrilocal contexts where women are in relatively plentiful supply.

### (c) Institutions affecting female autonomy and fertility: polygyny

While our models would not predict any difference in fertility between polygynously and monogamously pair-bonded women all else equal, the empirical evidence suggests otherwise. At the individual level, polygynously married women tend to have lower fertility, but these effects may be driven by self-selection effects [70]—i.e. women in worse condition become later wives to polygynous men [71,72]. This may help explain why we see the opposite effect at the group level; polygynous societies have higher total fertility rates than monogamous ones [28]. These differences seem to be driven primarily by the higher demand for women, which reduces the number of unmarried women and pushes their age at first birth down, thus extending women's reproductive lifespan [73].

Higher fertility through younger marriage has both fitness costs and benefits to women. Women who start reproduction too early tend to experience greater infant mortality risks throughout adulthood [74]. Optimal age at first birth models fit with data from pre-demographic transition populations show that intermediate ages maximize a woman's reproductive success, usually in the late teens, meaning that lowering the age at first birth beyond that was predicted to reduce women's fitness [63,74]. This sets up a potential sexual conflict of interest between men needing to compete for younger wives, and women having a later optimal age at first birth. On the other hand, earlier ages at first birth are often empirically associated with higher number of surviving children [63,75–78]. The net effect of this lower age at first birth in polygynous societies seems to be positive for fitness and has tended to promote their spread—e.g. of nineteenth century Mormons [79]. This suggests we should flip the question around and ask why women in monogamous societies tend to wait so

long to start having children when they could increase their reproductive success by starting younger.

An additional source of sexual conflict may arise from spousal age differences in polygynous societies because they increase the likelihood that a husband dies before the end of his wife's reproductive lifespan. As shown in our first model, this means an older husband may devalue a woman's future reproduction if he is unlikely to father her children in the distant future. This prediction can be tested by checking whether women married to older husbands reproduce sooner upon marriage than women with younger spouses, and have different IBIs. Furthermore, this effect should be particularly strong in societies with high adult male mortality.

### (d) Institutions affecting female autonomy and fertility: patriarchal norms

A few researchers have suggested that evolved female strategies for lower fertility are expressed in societies with more female autonomy and can help explain the demographic transition [20,35]. There is a broader social science literature that makes parallel proposals that patriarchal norms or women's low social status kept fertility high until recent centuries [2]. Although the latter literature is not committed to evolutionary accounts, and therefore has no interest in whether the actors were pursuing fitness-maximizing strategies, their argument hinges on a rather unlikely assumption that women have little autonomy in any society pre-demographic transition. In fact, empirical evidence from high-fertility societies on reproductive decision-making refutes this [7]. Furthermore, when considering the strategic interests of individual actors it is difficult to imagine circumstances under which all men have similar reproductive agendas, as illustrated in our agent-based model, and where gender categories constitute coalitions.

Our models provide additional reasons to be skeptical of the role of universal male preferences for higher fertility keeping reproductive rates high in pre-transition societies. The fact that the optimal reproductive pace for men and women, and the sex difference in optimal strategies depend on factors that vary both between- and within-population suggests the importance of conditional and flexible strategies. Furthermore, any resolution of sexual conflicts that favours male strategies over female ones in our models leads to suboptimal fitness outcomes for females. This can be either because she reproduces more quickly or more slowly than would be optimal for her. Because population growth is usually limited by the abundance of females, rather than the availability of males—i.e. all women can reproduce with a few men—anything that reduces female fitness will likely reduce population growth. This suggests that increases in female autonomy, power or leverage in mating systems should increase the sum of individual women's fitness, and therefore population growth. And yet the demographic transitions of the past two centuries from high- to low-fertility strategies have been accompanied by some of the largest increases in female economic and reproductive autonomy and led to the first populations known to have below-replacement reproduction despite no resource scarcity. At the individual level, most of the evidence to date suggests that adopters of these lower fertility strategies in fact ended with lower lineage fitness—i.e. they had fewer descendants up to five generations down the line [80,81].

A more nuanced examination of the evolution of male control of female reproduction reveals the importance of

considering diverse interests on the part of males [82]. There are many other proposed pathways whereby improving the social capital of women can motivate lower fertility (e.g. changing sources of social information or the status benefits to other behaviour) [36,37,83]. These explanations do not rely on a commitment to the fertility reduction itself reflecting a fitness-maximizing strategy.

## 4. Conclusion

We should be clear that we are not arguing for the absence of sexual conflicts of interests in human mating systems. Rather, we have shown that the presence of sexual conflicts of interest critically depends on the mating system and a man's ability to acquire more mates. Both of these vary substantially cross-culturally (e.g. with marriage system), and the latter varies within populations as well. Furthermore, our models illustrate that sexual conflicts can result in men benefiting from longer or shorter IBIs than are optimal for women. This makes it problematic to make proposals about average sex differences in optimal reproductive strategies.

We also show that several lines of evidence used to argue that women evolved preferences for lower fertility strategies than men did require more careful analysis. Resolving conflicts of interest in favour of female rather than male strategies should increase population growth [84]. This means that empowering women to pursue fitness-relevant goals is unlikely to explain demographic transitions towards lower fertility if these reproductive strategies are associated with lower long-term fitness [80,81]. Similarly, the fact that polygyny and patrilocality are associated with population growth or higher fertility, without

a commensurate decrement in infant or maternal mortality, speaks against their being detrimental to women's fitness or their resulting in the maladaptive coercion of women.

We do not dispute that cultural practices that disenfranchise women are often associated with higher fertility. However, we discuss how institutions like higher education, polygyny and patrilocality can have these effects through different pathways. Furthermore, we believe these phenomena will benefit from evolutionary explanations beyond those that we can derive from individual-level fitness-maximizing logic. For example, norms prioritizing status-striving over reproduction may influence women's reproductive preferences more than men's, given that women usually experience greater opportunity costs when reproducing. More detailed theoretical work and linked empirical analyses that consider both ultimate fitness consequences and proximate mechanisms can help elucidate the forms and extent of sexual conflict in different socio-ecological contexts.

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