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# An intergenerational conflict model of age at first birth in humans

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## Abstract

**Background**. Parental absences in childhood are often associated with accelerated reproductive maturity in humans. These results are counterintuitive for evolutionary social scientists because reductions in parental investment should be detrimental for offspring, but earlier reproduction is generally associated with higher fitness. In this paper we discuss a neglected hypothesis that early reproduction is often associated with parental absence because it decreases the average relatedness of a developing child to her future siblings.

**Method**. We illustrate this "intergenerational conflict hypothesis" with a formal game-theoretic model.

**Results**. We show that parents will generally win reproductive conflicts with children when parents and children share limited household or kin resources, thus prioritizing their own reproduction and delaying offspring reproductive maturity. This is due to the asymmetric relatedness between grandparents and grandchildren (r=.25), compared to siblings (r=0.5) However, if a parent loses or replaces their partner, the conflict between the parent and offspring becomes symmetric since half siblings are as related to one another as grandparents are to grandchildren. This means that the offspring stand to gain more from earlier reproduction when their remaining parent would produce half, rather than full, siblings. We further show that if parents senesce in a way that decreases the quality of their infant relative to their offspring's infant, the intergenerational conflict can shift to favor the younger generation, suggesting that it is primarily younger parents who should delay their offspring's reproduction.

**Discussion**. We use insights from this model to discuss the father absence literature and develop predictions about how the effects of parental absences should vary cross-culturally.


**Keywords**: intergenerational conflict, cooperative breeding, life history theory, father absence, mother absence, helpers at the nest, senescence, reproductive decision-making, kin competition, parental investment

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# 1 Introduction

Many social scientists have shown that children who experience parental absences due to divorce or death consistently have earlier ages of puberty and first reproduction in post-industrial societies (Surbey, 1990; Nettle et al., 2011; Ellis et al., 2003). This correlation is also seen in some developing societies (Sheppard et al., 2014b; Shenk et al., 2013) although there is less consistency in the effect in these contexts (Waynforth et al., 1998; Winking et al., 2011). While much of this literature has focused on the influence of father absence on daughters' reproductive maturity, some studies that have looked at other parent-offspring dyads have shown similar results (Sheppard and Sear, 2012; Bogaert, 2005; Sheppard et al., 2014a). These patterns seem to contradict many evolutionary anthropological accounts that emphasize the importance of downward intergenerational investments (Kaplan, 1996), including of fathers (Hill, 1993; Geary, 2000) and of grandmothers in helping raise dependent offspring (Hawkes, 1998) since these kin resources may improve one's fitness by expediting reproduction.

In this paper we suggest that models of intergenerational conflict within cooperatively breeding kin groups can help explain why parental absences often expedite an adolescent's reproduction. While intergenerational conflict can stem from several kinds of discrepancies between what parents and offspring want, we focus on parent-offspring conflict over reproductive opportunities. Humans' ability to cooperate in raising altricial and slow-developing young that are born in relatively short succession has been proposed as part of the explanation for their success as a species (Hrdy, 2009). This cooperative problem may be solved at various levels including at the level of kin groups. As with any cooperative dilemma, we would expect that at least some individuals within the cooperative unit pay a short-term fitness cost, but that the cooperative unit in general benefits long-term from this exchange of resources or help. It should be noted that conflicts over public goods often occur within cooperative systems, meaning that cooperation and conflict are not opposite strategies, as their common usage implies. While "intergenerational negotiation" might be a better term for this phenomena, we will stick to the commonly used terminology in the literature of "intergenerational conflict." In many species of cooperative breeders older siblings help care for young, thus delaying their own dispersal and reproduction and possibly paying short term costs (Jennions and Macdonald, 1994). A similar intergenerational cooperative arrangement has been proposed as a feature of many human societies given the extent of allocare that older siblings provide (Kramer, 2005; Crognier and Baali, 2001).

Biologists have modeled the circumstances under which intergenerational conflicts are resolved in favor of parents' versus offsprings' reproduction (Reeve and Keller, 1995). If parents win such reproductive conflicts, we would expect that parental presences may delay their offsprings' reproduction if the older generation uses up alloparental and household resources that the younger generation would also need in order to reproduce. If the younger generation wins intergenerational reproductive negotiations over who breeds, we may instead see that parental presences would expedite their first births. While biologists working with cooperatively breeding species have attempted to apply this logic to human family systems (Emlen, 1995), these insights have been neglected in the parental absence and human life history literature (see (Surbey, 1998) for a notable exception).

Instead, the most popular explanations of why parental presences delay first births focus on the possibility that these serve as cues to socio-ecological parameters. We will call these the "parents as cues" models. One such account suggests that parental absences indicate high extrinsic mortality risks in an environment, meaning that a developing child should reproduce sooner to reduce their risk of dying childless (Chisholm, 1993). In such environments, delaying reproduction in favor of growth, development and skill acquisition would not yield sufficient long-term fitness benefits because of mortality risks beyond the control of the individual (Stearns, 1976). Alternately, the parental absences may indicate that low investment in parenting, low partner selectivity, and earlier reproduction are adaptive mating strategies in one's environment (Draper and Harpending, 1982). This account is ambiguous in explaining why a scarcity of highly investing partners should necessarily lead to earlier ages at reproduction. More generally, these proposals of parents as cues to environmental circumstances seldom make it clear why parents specifically, as opposed to a developing child's broader social network, should be privileged as informative about locally adaptive life history and mating strategies in their adulthood (Nettle et al., 2012). In fact, whether children learn much from their parents (Harris, 1999) and the extent to which early childhood environments are predictive of future ones (Wells and Stock, 2007) are both debated. The observation that a broader set of social disruptions during childhood e.g. residential moves (Nettle

et al., 2011) expedite reproduction may instead fit better with the psychosocial acceleration model first proposed to help explain why father absence should expedite reproduction (Belsky et al., 1991). This account suggests that childhood stressors more generally, favor reproductive and mating strategies that include earlier reproduction (Belsky, 2012). However, while the authors argue that fast life history responses to psychosocial stressors is an evolutionarily adaptive strategy, the functional logic behind this assertion is vague.

Two other kinds of models focus more directly on how parent-offspring interactions, rather than parental absence as a cue to socio-ecology, should influence reproductive timing. We will refer to these as "parent-offspring interaction" models. The first set of models focus on parental investments. Ellis has proposed that children growing up in households with high quality care stand to benefit from capitalizing on this care by investing in their own growth (including skills), rather than in early reproduction (2004). This means that children with parents present in their households would experience later ages of reproductive maturity, insofar as parental presence is a proxy for quality of care. A related argument suggests that fathers invest in, and guard, their daughters in ways that help them obtain high status and stable mates at the expense of earlier reproduction (Flinn, 1988). These arguments seem functionally plausible, especially given the importance of extended childhoods and slow life histories in humans (Kaplan et al., 2000), suggesting potential long-term fitness benefits to delaying reproduction. However, this model deemphasizes the possibility of parent-offspring conflict regarding parental investments, and assumes the importance of downward rather than upward intergenerational transfers. The second parent-offspring model focuses on inbreeding avoidance. This one suggests that reaching sexual maturity in the presence of parents is not useful or poses a risk of inbreeding depression (Matchock and Susman, 2006). While this model has been useful for predicting reproductive strategies in cooperatively breeding species with small kin groups and high reproductive skew (Cooney and Bennett, 2000), we are more skeptical that inbreeding avoidance was an important selection pressure favoring delayed maturity in recent human evolutionary history given that adolescents can find unrelated members of the opposite sex with whom to reproduce even in small human social groups. Furthermore, in other primates with similar multi-male multi-female groups, individuals manage to largely avoid parent-offspring mating despite long alpha male tenures (Muniz et al., 2006).

Here we resurrect the idea that intergenerational conflict may help explain parental influences on the timing of reproduction (Emlen, 1995), and suggest that models of intergenerational conflict have several advantages over the more common accounts of parental absence effects outlined above. First, unlike the "parents as cues" models, they can help account for the primacy of parents' presence in explaining children's reproductive timing. Second, unlike the current "parent-offspring interaction" models described above, intergenerational conflict models integrate the importance of parental investments, skill acquisition, delayed maturation, and conflict within cooperative breeding systems throughout human evolutionary history. Third, intergenerational conflict models allow us to make predictions about how parental effects on reproduction should vary cross-culturally within humans. Other evolutionary scientists have fruitfully used intergenerational conflict models to illuminate human family dynamics. For example, tug-of-war models, where actors engage in costly competition over reproductive opportunities, have been developed to explain the evolution of menopause (Cant and Johnstone, 2008) and the higher rates of intergenerational male conflicts observed in polygynous societies (Ji et al., 2013). However, these particular versions have assumed the importance of specific post-marital residence norms and of one sex controlling reproductive decisions. For instance, the model of menopause assumes a patrilocal setting where mothers-in-law and daughters-in-law compete with each other over limited household resources (Cant and Johnstone, 2008). In such a context daughters-in-law win the conflict because they are less genetically related to group members than the mother-in-law is, and thus suffer greater inclusive fitness opportunity costs to not reproducing. While some researchers have suggested the importance of intergenerational conflict in negotiating young adults' reproductive strategies, they have failed to model it formally (Hoier, 2003; Surbey, 1998; Waynforth, 2002), have made additional assumptions in order to address more specific problems (van den Berg et al., 2013; Cant and Johnstone, 2008; Ji et al., 2013) or done both (Apostolou, 2012). Those theoretical proposals that relied on verbal arguments, have made predictions that only partially match predictions derived from our model and have seldom been leveraged for explaining cross- cultural variation in parental effects.

We describe a more general framework, which makes no assumption about dispersal patterns or about the sex that controls reproductive decisions. In other words, we explore under what circumstances a par-

ent should win potential intergenerational reproductive conflicts, and have another infant, and under what circumstances their adolescent child should win the conflict and start their reproductive career. We model the effects of 1) paternity uncertainty (or of a father switching mates), 2) costs to reproductive overlap, and 3) reproductive senescence (i.e. aging that results in the older generation producing lower quality infants compared to the younger generation). We investigate these parameters because of their relevance to the human literature on life history and parental presence, although they may speak to similar effects in, and across, other species. Mate-switching plays a large role in explanations of father absence effects on reproductive timing in humans (Draper and Harpending, 1982; Shenk et al., 2013), and varies significantly cross-culturally with mating system. Additionally, reproductive senescence is a topic of much interest for evolutionary anthropologists given women's long post-menopausal lifespans (Hawkes and Coxworth, 2013), and the possibility of comparable reproductive cessation for monogamous men. Reproductive senescence for pre-menopausal women (Fretts et al., 1995) and men (Plas, 2000) has also been shown to affect infant survivorship and health outcomes. Factors affecting paternity uncertainty, costs of intergenerational reproductive overlap, and reproductive senescence of a parent relative to an offspring are likely to vary both within, and between, human populations, making this framework particularly useful for making predictions about how parental effects on children's life history should vary cross-culturally.

We discuss how our model of intergenerational conflict can contribute to our understanding of why various forms of parental absence in childhood may expedite reproductive maturity in humans in Section 4. In this discussion we also develop several predictions regarding how cultural institutions may moderate these effects across human societies. However, first we describe the formal framework. In Section 2 we describe the setup for a simple game theoretic model including the payoffs to parents and their children of reproducing or not, given the other actor's reproductive behavior. In Section 3 we analyze the implications of the model in two stages. First, we model what each actor would do given that the other has reproduced (Section 3.1). Second, we use these results from the first stage to model how much each actor loses from not reproducing first (Section 3.2). The second stage allows us to determine under which circumstances parents or their adolescent children should win intergenerational conflict and reproduce first.

# 2   A simple model of intergenerational conflict

## 2.1   Actors

In this model we assume there are two actors of reproductive age; a parent and an adolescent offspring who has yet to reproduce. We do not explicitly model mate search costs, instead assuming that the younger generation can acquire a reproductive partner should they want to. However, for simplicity we assume that we do not have to consider the strategic interests of the younger individual's potential partner. Not only does this simplification keep the model tractable, we also believe that the decision to seek reproductive opportunities and mates should be modeled in its own right since an adolescent can make reproduction related physiological and behavioral decisions before marriage. We also assume that the parents' other children do not affect the payoff structures below. We will refer to the older generation as the mother, or $G_1$, and the younger generation as the daughter, or $G_2$. The sex of the actors does not qualitatively change the results, but modeling them as female simplifies the mathematics a little. Modeling the parent as a female provides a more general case since paternity certainty (i.e. the probability that her reproductive partner is the same across two time points) can take values between 0 and 1, whereas a child's assessment of whether they share the same mother as a sibling is likely to be more bimodally distributed around 0 and 1. Modeling the adolescent as female rather than male increases the value of the younger generation's reproduction given that she is assured of her relatedness to her own infant whereas a male would is not. We discuss this possibility a bit more below.

## 2.2   Setup

The mother and adolescent must each decide whether to reproduce at a given point in time. The payoffs to doing so will depend on the other's decision given that reproduction is resource limited and that resources that affect infant survivorship or quality are shared across a household. If resources were not shared within a family or household unit, then the actors would be competing with all other group

members when deciding whether to reproduce and therefore would have little incentive to curtail their reproductive efforts even if their kin specifically had reproduced. The limited household resources may include alloparenting or caloric production, for example. We model independent decision-making and do not include any opportunity for actors to engage in costly competition to acquire a greater share of these resources.

## 2.3 Parameters

We model the effect of three parameters; infant survivorship when $G_1$ and $G_2$ reproduce synchronously relative to non-synchronously ($s$), the relative fitness of an infant born to the younger generation compared to the older mother ($y$), and paternity certainty ($c$). We define $s$ as the ratio of survivorship of an infant who shares a household with another infant, relative to his survivorship being the sole infant in the household. This can take values from 0 to 1, where 1 indicates equal survivorship whether or not the infant shares his household with another infant; values less than 1 indicate lower survival if the infant shares his household relative to being the only infant. We assume there are never benefits to infants sharing a household, because they are competing for the same scarce resources. The parameter $y$ (youth benefit) is the ratio of the fitness of an infant born to the younger generation relative to the fitness of an infant born to the older mother. We include this parameter in the model to allow reproductive senescence that can switch the resolution of the intergenerational conflict to favoring the younger generation. Here we assume that $y \geq 1$, where 1 represents equal fitness for the offspring of the older and younger generation, and $y > 1$ represents higher fitness for the offspring of the younger generation relative to the offspring of the older generation. Any fitness costs to infants of young mothers (i.e. where $y \leq 1$) favor the older generation's reproduction further and thus do not qualitatively change the model. Finally, paternity certainty, $c$, is the probability that $G_1$'s next child has the same father as $G_2$. This parameter only affects $G_2$'s payoff function. This certainty value, $c$, can also take values from 0 to 1, where $c = 1$ denotes that $G_2$ will have a full sibling, and $c = 0$ denotes that $G_2$ will have a half sibling. Were $G_2$ to be a son we would have to incorporate additional paternity uncertainty into his and his mother's fitness function, but this does not qualitatively change the results so we ignore it in the remaining analyses.

## 2.4 Payoffs

Each individual can choose to reproduce $R$, or not $N$. Variables subscripted 1 denote payoffs to the mother, $G_1$, while those subscripted 2 denote payoffs to the daughter, $G_2$. We denote the payoffs to each actor, $V$, using conditional probability notation. In each equation the first term represents the contributions of their own reproduction, and the second term refers to the other actor's contributions, to their own inclusive fitness.

The payoffs for each individual - $G_1$ and $G_2$ in sequence - when both reproduce are:

$$V_1(R|R) = 0.5s + 0.25sy \tag{1}$$

$$V_2(R|R) = 0.5sy + 0.25s(1 + c) \tag{2}$$

The payoffs for each individual when only the mother, $G_1$, reproduces are:

$$V_1(R|N) = 0.5 \tag{3}$$

$$V_2(N|R) = 0.25(1 + c) \tag{4}$$

and when only the daughter, $G_2$, reproduces:

$$V_1(N|R) = 0.25y \tag{5}$$

$$V_2(R|N) = 0.5y \tag{6}$$

and, just for completeness, when no one reproduces: $V_1(N|N) = V_2(N|N) = 0$

Were $G_2$ male, a paternity certainty parameter, $c_2$, would have to be added to all of the fitness outputs for the younger generation. Paternity uncertainty negatively affects his relatedness to his own child, more

than it affects his relatedness to his sibling (assuming he can be assured of his relatedness to a sibling via his mother). More generally, for a given paternity uncertainty for the parental generation, $c_1$, a son would have to experience a certainty of $c_2 > 0.5(1 + c_1)$ in order to prefer to reproduce himself rather than have a sibling. In contrast, a daughter would prefer to reproduce so long as $1 > 0.5(1 + c_1)$. In other words, modeling $G_2$ as female provides a best case scenario for the younger generation's reproduction to be favoured.

# 3 Results

## 3.1 What would each actor want given that the other one has reproduced?

Obviously, everyone wishes to avoid a household where neither actor reproduces. However, it is not always the case that both generations reproducing simultaneously maximizes each individual's inclusive fitness. Under these circumstances, the payoff structure described in equations 1-6 suggests that, for some part of the parameter space at least, mothers and daughters are engaged in a hawk-dove game. That is, this decision-making requires coordination so that the household does not end up with too many or too few infants, but at least some of the time each actor prefers to be the one to reproduce. Here we address the question of how each individual would respond were the other actor to have reproduced. It is not always the case that the actor who decides second will want to reproduce themselves if the other actor has already done so, given the inclusive fitness costs of having two infants in a household. Below we also show what each actor would want the other individual to do given that they themselves have already reproduced.

### 3.1.1 Given that the mother, $G_1$, has reproduced

Under these circumstances the daughter will want to reproduce when $V_2(R|R) > V_2(N|R)$. This is true when:

$$s > (1 + c)/(2y + 1 + c) \tag{7}$$

However, the mother will only want her daughter to reproduce when $V_1(R|R) > V_1(R|N)$. This is true when: :

$$s > 2/(y + 2) \tag{8}$$

### 3.1.2 Given that the daughter, $G_2$, has reproduced

Now let's look at what each actor should want given that the daughter has reproduced. Under such circumstances the mother will want to reproduce when $V_1(R|R) > V_1(N|R)$. This is true when:

$$s > y/(y + 2) \tag{9}$$

whereas, the daughter will want her mother to reproduce only when $V_2(R|R) > V_2(R|N)$. This is true when :
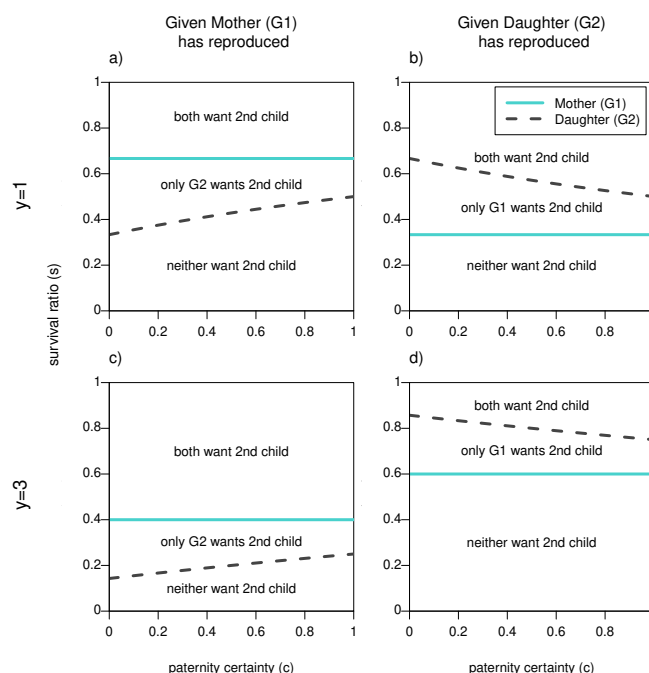
$$s > 2y/(2y + 1 + c) \tag{10}$$

Figure 1: When actors should want 2nd child given one of them has already reproduced as a function of $s, c$, and $y$. Areas above each actors line denote when it is in their fitness interest to add the 2nd child to the family.

### 3.1.3 Summary of payoffs to adding a second infant to household

The first column of Figure 1 (a and c) shows the parameter space over which actors want the daughter, $G_2$, to reproduce given that the mother, $G_1$, has done so, assuming no youth benefit ($y = 1$), and a threefold youth benefit ($y = 3$). These are represented by the areas above the line for each actor. First focusing on (a), when $y = 1$ if the survival ratio of 2 to 1 children in the household, $s$, is high enough there will be no conflict of interest as both actors will want the daughter to reproduce. Similarly, if $s$ is low enough neither actor will want the daughter to reproduce because the additional infant will decrease the survival odds for both children too much. Disagreements between mother and daughter in terms of adding a 2nd infant arise for intermediate values of $s$. The straight line for the mother shows that she has a higher threshold $s$ for her to want her daughter to reproduce, and that this value does not depend on $c$ since paternity certainty does not affect a grandmother's relatedness to her grandchild (at least via her daughter). The daughter's line on the other hand increases with $c$, that is the higher her relatedness to her current sibling the higher $s$ has to be in order for her to benefit from reproducing as well.

Figure 1 (b) and (d) show the same lines for each actor given that the daughter has reproduced. Now the daughter has a higher threshold of $s$ for which she would want her mother to reproduce compared to the mother's own threshold. As $c$ increases the daughter becomes more tolerant of her mother's reproduction, that is, she benefits from it for a wider range of values of $s$. Still, even if the daughter is a full sibling of the mother's child, there will be values of $s$ for which she will not want her mother to reproduce even though the mother wants to.

By increasing the youth benefit, $y$, the mother has relatively more to gain from a grandchild. This reduces the size of the zone of conflicts of interests in both scenarios, but maintains the order of the lines in Figure 1. Both lines move down in the first column, and up in the second one. That is, both actors will want the daughter to reproduce over a wider parameter space given that the mother has reproduced, whereas both actors will be more reticent to encourage the mothers reproduction once the daughter has already reproduced.

It should be noted that even when both actors agree that a second child should not be added to the household, there may be conflict over whose child that should be. That is, for $G_1$, $V_1(R|N)$ is better than $V_1(N|R)$ so long as $y < 2$. In other words, if only one person is going to reproduce the mother prefers

291 to be the one to do so, as long as the youth benefit is less than 2. Similarly, the younger generation, $G_2$,
292 prefers to be the one to reproduce since $V_2(R|N)$ is strictly better than $V_2(N|R)$, so long as $c < 1$, even if
293 there is no youth benefit. Again, these hawk-dove dynamics suggest the importance of competition and
294 coordination among the actors.

## 3.2 How much do actors lose from not reproducing first?

296 Section 3.1 shows that there are conflicts over who gets to reproduce, and that the actors will not
297 always agree about adding a second infant to the household given that one of them is already giving birth.
298 We now turn to deriving who is likely to win these conflicts over reproductive decisions by determining
299 how much each actor stands to lose from not reproducing first.

300 We use payoffs from section 3.1 regarding what actors would do as second movers to calculate the
301 payoffs to each actor were the mother, and subsequently were the daughter, to reproduce first. We assume
302 the second actor has full autonomy in their decision so that even though we plotted what both actors
303 wanted in Figure 1, only the function for the second actor matters.

### 3.2.1 Payoffs to actors if the mother, $G_1$, reproduces first:

305 The daughter, $G_2$, will be the second actor and will respond differently to $G_1$'s initial decision,
306 depending on the values of $s$, $y$ and $c$. Therefore, we need two different functions to determine the
307 ultimate payoffs for each generation, depending on what the daughter does.

$$V_1 = \begin{cases} V_1(R|R) = 0.5s + 0.25sy & \text{if } s > (1+c)/(2y+1+c), \\ V_1(R|N) = 0.5 & \text{if } s < (1+c)/(2y+1+c). \end{cases} \tag{11}$$

$$V_2 = \begin{cases} V_2(R|R) = 0.5sy + 0.25s(1+c) & \text{if } s > (1+c)/(2y+1+c), \\ V_2(N|R) = 0.25(1+c) & \text{if } s < (1+c)/(2y+1+c). \end{cases} \tag{12}$$

### 3.2.2 Payoffs to actors if the daughter, $G_2$, reproduces first:

309 The mother, $G_1$, will act differently depending on whether $s$ is greater or less than $y/(y+2)$.

$$V_1 = \begin{cases} V_1(R|R) = 0.5s + 0.25sy & \text{if } s > y/(y+2), \\ V_1(N|R) = 0.25y & \text{if } s < y/(y+2). \end{cases} \tag{13}$$

$$V_2 = \begin{cases} V_2(R|R) = 0.5sy + 0.25s(1+c) & \text{if } s > y/(y+2), \\ V_2(R|N) = 0.5y & \text{if } s < y/(y+2). \end{cases} \tag{14}$$

### 3.2.3 Summary of costs to not reproducing first

311 The mother, $G_1$, will want to reproduce first when equation 11 > equation 13, and the daughter will
312 want her mother to reproduce first when equation 12 > equation 14. As a simple example, let's consider
313 payoffs when $c = 0$ and $y = 1$. In this case, $G_1$ and $G_2$ will always want to be the first mover, or at
314 worst be indifferent if $s > 1/3$ when both actors will reproduce. When $s < 1/3$, each actor will lose 0.25
315 if she does not get her way. In other words the game is symmetric, and it is not obvious who will win
316 the conflict. This is not surprising as when $c = 0$ both actors are equally related to the other actor's
317 child. In much of the parameter space, however, the game is not symmetric, and one actor stands to lose
318 more than the other by not reproducing first. Here, we can identify the most likely winner of the conflict,
319 namely the one who stands to gain more from being the first reproducer.

320 Figure 2 illustrates the fitness losses to each actor as a function of whether they get to reproduce first
321 or choose their strategy after the second actor for a broader set of parameters. In a tug-of-war model,
322 the fitness losses would correspond to how much actors should be willing to invest in competitive effort
323 to win this conflict. This means that the higher an individual's opportunity costs to not reproducing
324 first relative to the other actor's opportunity costs, the higher her likelihood of winning the conflict. The
325 horizontal axes shows that these conflicts will be resolved differently as a function of the costs to having

two infants in the household, $s$ (note: $s$ values have changed from being on the vertical axis in Figure 1).
Each plot represents a different combination of youth benefit, $y$, and paternity certainty, $c$.
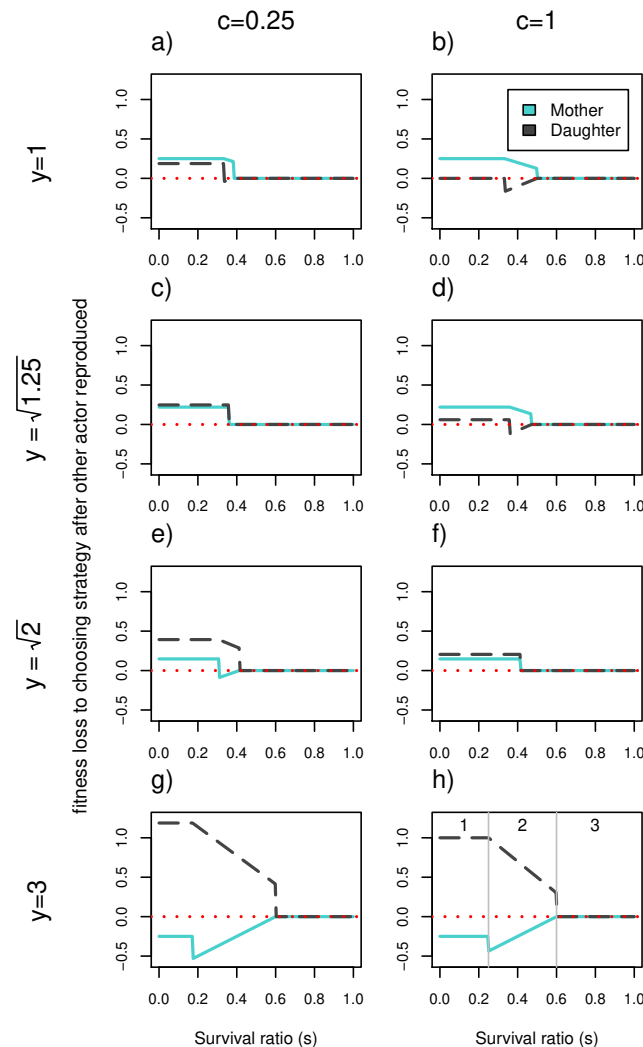


Figure 2: Cost of choosing strategy after other actor has reproduced as a function of the survival ratio, $s$, of 2 versus 1 infant in the household. The solid line denotes the older generation (mother), and the dotted line denotes the younger generation (e.g. daughter). The larger the fitness losses from not reproducing first, the more likely the actor is to win the conflict. Values of $c = 0.25$ and $c = 1$ represent low and high paternity certainty respectively, and increasing values of $y$ represent higher fitness of the younger generation's infant. When $y = 1$ there is no senescence. Intermediate $y$ values correspond to values of $y = \sqrt{1+c}$ for $c = .25$ and $c = 1$ respectively. At these values the payoffs work out such that the actors never disagree about whether there should be two or one infant in the household. Plot h) shows the limits of three functionally different zones; zone (1) where only one actor will reproduce, (2) where the number of infants produced will depend on who reproduces first, and (3) where both actors will reproduce. The corresponding zones can be found in all other plots except for c) and f) where zone 2 disappears.

328    There are three areas of the parameter space that have functionally different outcomes for the set of
329 actors (illustrated in Figure 2 h). We will discuss these out of order from simplest to most complicated
330 (starting with zone 3, ending with 2) . Zone 3 corresponds to survival ratios, $s$, that are high enough such
331 that both actors will reproduce regardless of who acts first. This means that both actors have zero fitness
332 losses to choosing second in this zone. This corresponds to the right hand side of each plot in Figure 2.

On the left hand side of each plot is the zone 1 where the survivorship of two infants relative to one, $s$, is so low that only one actor will reproduce. Finally, in zone 2 with intermediate survival ratios, the number of people who reproduce will depends on who reproduces first. This area is indicated by the sloping lines in Figure 2 and requires more explanation. This intermediate area is bounded by $s = (1+c)/(2y+1+c)$ and $s = y/(y+2)$, as outlined in equations 11 through 14. Whether each of these expressions denotes the upper or lower limit of the intermediate area depends on the values of $y$ and $c$. For example, when there is no youth benefit, $y = 1$, $(1+c)/(2y+1+c) > y/(y+2)$. This means that the younger generation has the higher threshold $s$ value at which they would produce a second child, and is therefore more reticent to reproduce given that the other actor has already done so. However, this will flip for large enough values of $y$, specifically when $y > \sqrt{1+c}$. Under these circumstances the mother will have a higher threshold value for reproducing as a second mover than the daughter does. When $y = \sqrt{1+c}$ zone 2 disappears (e.g. Figure 2 c) and f), meaning that mothers will not have different strategies from daughters as second movers.

We first elaborate on the conflict dynamics using the simple case where there is no benefit to the younger generation reproducing, $y = 1$. In this case, when the costs to synchronous reproduction is low enough (e.g. $s > 1/2$ in Figure 2 b) both individuals will end up reproducing meaning that order of decision-making is irrelevant. The lower $c$ is, the larger this parameter space, as indicated by the longer range of zero fitness losses (zone 3) of Figure 2 b) than a). This means that with greater paternity uncertainty, the greater the range of survival ratios under which the daughter is willing to reproduce. If the costs of synchronous reproduction are high enough ($s$ is low), only the first actor will reproduce and the mother stands to lose more than the daughter from not being the one to do so (see zone 1 of Figure 2 a and b). In fact if $c = 1$ the younger generation should be indifferent between reproducing or having their mother produce a full sibling. This is indicated by the zero fitness loss to the daughter of choosing not to reproduce after the other individual has. For intermediate values of the survival ratio, $s$, the actors pursue different strategies as 2nd movers. In the case of $y = 1$, in this intermediate range the mother will prefer to reproduce whether or not the daughter has done so, whereas the daughter would want to reproduce only if the mother does not. This explains the negative "losses" to going 2nd for the daughter, who prefers to decide *not* to reproduce after having seen the mother reproduce, than to reproduce herself first and then have the mother add a 2nd child to the household.

Once we add large enough reproductive consequences to senescence (e.g. Figure 2 g and h where $y = 3$), the younger generation wins out over the mother during contexts of reproductive conflict. In the intermediate zone 2, if senescence is high enough ($y > \sqrt{1+c}$) both actors prefer the younger generation to reproduce alone, given that the daughter would reproduce regardless of the mother's reproductive decision in this range. For really severe resource constraints (zone 1) the bottom two rows of Figure 2 show that the younger generation will also lose more from going second and not reproducing than the parent will. In fact, for very large youth benefits (e.g. $y = 3$) even the mother prefers the daughter to be the sole reproducer as indicated by her fitness losses to going second being negative. This indicates that for this part of the parameter space, even as first mover, the mother would forgo reproducing in favor of allowing her child to do so. More generally this should be true when $y > 2$. However, in zone 1, the range of $y$ values for which the daughter stands to lose more than mother is even broader. So long as $y > (3+c)/3$, the mother loses less than her child from forgoing reproduction when only one of them is going to reproduce.

Generally, the model shows that the higher the paternity certainty $c$, the easier it is for the mother to win the intergenerational conflict, while it is more likely that the younger generation wins the conflict as $y$ increases. For parts of the parameter space (i.e. when the lines fall below zero) it is even to an actor's advantage to allow the other individual to reproduce first and forgo reproducing themselves. For intermediate values of the survival ratio, $s$, this is because the "losing" actor (e.g. the mother in Figure 2 e-h) would not reproduce were there an infant in the household already, whereas the other actor would reproduce regardless. For low enough $s$ both actors agree that only one individual should reproduce, which creates the discontinuities in fitness loss values.

# 4   Discussion

Our model suggests that parents and their children will often agree about reproductive decisions when there are low costs to synchronous reproduction, but that parents will generally have the upper hand in

negotiating intergenerational conflicts should these arise (i.e. when $s$ is low enough). This means that biparental presence should favor the parents' reproduction over their offsprings' reproduction and may thus delay the latter's age at first birth. This dynamic is driven by the asymmetric relatedness of actors to the potential offspring being produced. However, this game becomes fully symmetric if the parent cannot give birth to a full sibling, meaning that if one parent is absent offspring should be as likely as the remaining parent to win intergenerational reproductive conflicts. In other words, relative to having two parents present, an adolescent has more of an incentive to reproduce when one parent is absent since her future siblings will be less related to her. Furthermore, the advantage can even shift to the younger generation's reproduction if we incorporate physiological senescence that reduces the quality of the older generation's child. This means that parental delays to an offspring's reproduction should be largest for young parents, or first born children.

It is worth noting that these predictions hold only for species where parents and offspring cooperate for reproductive purposes or rely on the same resources to reproduce. Similar facultative helping-at the nest as a function of relatedness to siblings has been documented among cooperatively breeding birds (Komdeur, 1994), suggesting the commensurate delayed dispersal in biparental nests is likely. Furthermore, experiments with eusocial Damaraland mole rats show that switching out a related dominant male from the family group induces physiological changes and reproductive activity among the dominant pairs' daughters (Cooney and Bennett, 2000). Although we do not argue that humans are similarly eusocial, this line of evidence suggests that analogous physiological and behavioral pathways may help explain changes in adrenarche, menarche, and age of first reproduction when parents are absent.

Because our model did not specify any mate search costs, it does not make different predictions for parental presence relative to step-parent presence. However, we can imagine that a mother and daughter are in the most symmetric situation when neither has a reproductive partner and will therefore experience the same mate search costs. Relative to this situation a stepfather's presence can act as a commitment device for the parent, signaling the mother's intention to reproduce. This may be a particularly honest signal given that a stepfather has no inclusive fitness interests in his stepchild's reproduction and therefore stands to lose a lot from not reproducing himself. If we include mate search costs in the model, we also see that the presence of a stepfather lowers mating costs for the parent relative to the offspring. This means that when we incorporate mate search costs, going from a father absent to a stepfather present household should favor the mother's reproduction, and therefore expedite an adolescent's reproduction less, than the absence of father figures altogether. Alternately, the presence of a stepparent may be a better cue that one's future siblings are going to be half siblings, than the absence of a father given that there are many reasons fathers may not be in a household. By this account stepfather presence and clear cues to a father's death should expedite adolescents' reproduction more than a father's absence from other causes, since in the last scenario future full siblings may still be an option. It is worth noting that this model would make similar predictions for mother and father absence, although the base rates of offspring helping a father's reproductive efforts might be lower given lower certainty about genetic relationships.

While our model can apply to members of the younger generation that are any sex, there are multiple reasons we might expect sons and daughters to be differentially affected by intergenerational conflict. First, a given rate of paternity uncertainty will negatively affect a son's fitness through his own reproduction more than through his maternal siblings since he can be relatively assured of a 0.25 relatedness to a sibling via his mother. This means that sons should favor their own reproduction less than a daughter will, and thus that they are less likely to win intergenerational conflicts over reproduction. This means they may also be less affected by parental absences, especially in contexts with high paternity uncertainty for young men. Second, given that men tend to marry later than women do, their parents will be on average older and thus more likely to lose the conflict when reproductive decisions are being made. Third, given gendered division of labor and developmental trajectories in productivity, parents might be more likely to delay daughters' or sons' reproduction, depending on their relative contributions to the household. For example, if alloparental care is a scarce resource then parents might delay daughters more given that they more commonly help rear younger siblings, whereas if meat protein is a scarce resource, parents may delay sons more given that men are often more responsible for procuring animal protein.

Finally, while we modeled senescence such that only the parent's infant could ever be lower quality than the offspring's infant, any process that makes one generation's infant high quality than the other moves the resolution of the conflict in favor of that individual. Clearly, the older a parent is, the more likely the younger generation is to win this conflict, assuming that relatively elderly parents produce lower

quality children (Fretts et al., 1995; Plas, 2000). Humans experience a particularly unusual pattern of senescence given that women's reproductive system declines, while they are still healthy and productive adults, thus allowing them to shift strategies to alloparenting even if they lose intergenerational conflicts. However, in the other direction, the more benefits to learning parenting skills or to delaying development for an adolescent, the more likely the older generation is to reproduce, and the lower the scope for intergenerational conflict. This means that the more an adolescent gains from delaying reproduction, the less a parental absence should affect her developmental trajectory, except insofar as deviations from biparental care decrease the quality of parental investments (see (Ellis, 2004)). This dynamic might be particularly important in humans given the large repertoires of skills (including with respect to parenting) that they need to learn to become competent adults. Several of these parameters, such as the difficulty of becoming a competent parent, may vary cross-culturally. We next turn to developing more specific predictions about how cultural variation may interact with parental absence to affect timing of reproduction. In other words, how do we expect the effect of parental absences to vary cross culturally?

## 4.1 Predictions of how cultural institutions interact with parental presence

Many of the parameters that we modeled as species-typical can also vary across populations. These can either be sums of individual behaviors (e.g. mate switching rates are the sum of individual level remarriage rates), or emergent institutions that cannot be boiled down to individual-level properties (e.g. a single individual cannot have a bridewealth property, rather this is a property of the marriage market).

1. At the population level, in societies with less turnover between partners and less paternity uncertainty we would expect greater alloparenting or provisioning of younger children by older siblings or helpers at the nest. Polygamous contexts where future siblings are less likely to be full siblings should similarly discourage the younger generation from investing in their natal household.

2. While we did not explicitly model costs to acquiring a mate, these dynamics should parallel the effects of the youth benefit to infant quality. For example, we may assume that in societies with bridewealth or dowry the younger generation may have a harder time acquiring a high quality mate for whom they would have to make such a payment. This means that there are relatively higher costs to the younger generation reproducing for a given quality of mate when bridewealth or dowry are expected. Under these circumstances, we would expect parents to be more likely to delay children's reproduction.

3. Similarly, if greater parental contributions are needed to marry and set up a household (e.g. higher setup costs in neolocal societies than in patri- or matri- local ones), parents may delay children's reproduction more since producing children for them is relatively cheaper than it is for the younger generation.

4. Ambilocal post-marital residence patterns may allow children to choose contexts with less resource stress, and gives the younger generation more leverage in intergenerational conflicts. This may be true for neolocal residence norms as well, assuming costs to setting up a household are low. Such flexible residence norms should reduce the delaying impact that parents have.

## 4.2 Limitations of the current model

While we made several simplifying assumptions to keep the project tractable future work can develop other avenues of inquiry. For example, one might extend the two person game to include the motivations of other potential actors, such as spouses for the younger generation. If the younger individual is betrothed or partnered, their spouse will have no inclusive fitness incentives to help raise their siblings-in-law. Such affinal ties only exist once the younger generation has married, a state suggesting that the parental generation may have lost intergenerational reproductive negotiations. This might help explain why the literature shows that a woman's in-laws expedite first births more often than a woman's parents do (Sear et al., 2014). That is, given that the older generation has lost this intergenerational conflict, and their child has married, they may stand to gain from facilitating the production of grandchildren. Negotiations between other older siblings might also be of importance when deciding how alloparental care is provisioned, as has been shown in other cooperatively breeding species (Pasinelli and Walters,

2002). It is also worth noting that the economic structure to the game we modeled might not reflect real world contexts if there were efficiencies of scale to raising two children together rather than two children apart. The extent to which intergenerational overlaps in reproduction are costly is a question of much empirical debate, without yet full resolution (Lahdenperä et al., 2012; Mace and Alvergne, 2012; Skjæ rvøand Rø skaft, 2013). We have also assumed that senescence is an extrinsic process rather than one directly under selection. There is some evidence that female reproductive physiology might be thus constrained (Robson et al., 2006), but this is much debated given the diversity of senescence rates both within (Thomas et al., 2001) and between (Jones et al., 2014) species.

There are also several reasons to believe that this model might underestimate the upper hand that the older generation has in this hawk-dove game. For one, we assume autonomous decisions, whereas cross-culturally parents tend to have some coercive power over their offspring. This coercion may go beyond the asymmetries arising from the dynamics illustrated by our model. In any case it is likely that either group-level adaptive or non-adaptive cultural institutions play a role in the evolution of such norms. Second, caring for children, especially in humans, takes some specialized skills and the younger generation may stand to gain from the learning opportunities afforded by taking care of a child under the supervision of an experienced mother with a higher vested interest in the wellbeing of the infant. In fact, first born children are often at higher risk of mortality, both because of younger mother's physiological development and relative inexperience (Hobcraft et al., 1985).

While we have discussed this model in terms of intergenerational conflict, it is worth remembering that these family dynamics are being played out in a larger population of less related households. Bordered tug-of-war models that incorporate pressures from between-group competition limiting costly internal conflicts (Reeve and Shen, 2006), remind us that conflicts within cooperative units occur within a larger population of competitors, meaning that selection should favor reduced negotiation costs, and more efficient cooperative equilibria between parents and offspring. Cyrus and Lee (2013) have proposed that the division of labor regarding alloparenting and calorie production between the generations of human cooperative breeders is one such efficient equilibria that can be modeled as a multi-stage evolutionary process.

# 5 Conclusion

While several authors have proposed reasons that family disruptions in early childhood may affect reproductive development (Chisholm, 1993; Ellis, 2004; Draper and Harpending, 1982) many of these proposals rely on the assumption that parental presence is a cue to some feature of the larger socio- ecological setting (either the mortality or mating context). It is unclear why parents, rather than the larger social group, should be particularly useful cue to the broader environmental setting. Furthermore, these frameworks suggest mechanisms whereby children adjust their life history strategies to fit local socio-ecological conditions, but they do not make clear predictions about how parental effects on life history should vary across cultures since they imply that parental presences are equally good cues to environmental conditions across contexts. Other verbal models of parent-offspring relations influencing reproductive strategies are unclear about the extent to which these result in conflict, and how the negotiations should be resolved (Flinn, 1989; Surbey, 1990; Hoier, 2003; Apostolou, 2012). These have suggested predictions that are counter to our own, such as the reduced effect of a stepfather's presence on accelerating menarche "because half-siblings are not as closely related" (p214) (Hoier, 2003) and that parents should want their children to reproduce earlier than the children themselves would want to reproduce (Apostolou, 2012).

It is worth noting that several of the psychological mechanisms implied by this intergenerational conflict model may be systematically resulting in maladaptive outcomes in low fertility societies. For example, reproductive overlaps between parents and offspring are relatively rare in societies with late ages at first birth and early cessation. In such contexts, if adolescents have any evolved expectations of reproductive conflict with parents, these may not accurately reflect reality. Similarly, perceptions of household resource stress in most large-scale societies do not necessarily indicate an inability to raise reproductively successful adult offspring given the relatively low rates of infant and child mortality across socio-economic strata in modern economies. The fact that so many of the empirical tests of parental absence effects have been conducted in low fertility contexts, where parental deaths and extended families are rare, and where people are not clearly following fitness maximizing reproductive strategies makes it

particularly difficult to draw broad conclusions about the meaning of such effects. A cross-cultural comparative approach may help disentangle some of the proposals on the table.

The model proposed here provides a more plausible explanation for why family structure specifically can result in different maturational rates and ages of first reproduction than the more popular models in the literature. In other words, parental instabilities in early childhood may provide cues to the relative inclusive fitness value of alloparenting siblings rather than reproducing on one's own in the future. This should shape a developing child's life history strategy, both physiologically (e.g. earlier menarche) and behaviorally (e.g. earlier mate seeking and reproduction). This also provides a simple framework for devising predictions about how cultural and socio-ecological parameters should interact with family structure in affecting adolescents' reproductive decisions.

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