

Intergenerational conflicts may help explain parental absence effects on reproductive timing: A model of age at first birth in humans

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. Family members often help each other reproduce, meaning that parents and offspring may find themselves in competition over reproductive opportunities. In these intergenerational negotiations offspring will have less incentive to help the remaining parent rear future half-siblings relative to beginning reproduction themselves. **Method.** We illustrate this "intergenerational conflict hypothesis" with a formal game-theoretic model. **Results.** We show that when resources constrain reproductive opportunities within the family, parents will generally win reproductive conflicts with their offspring, i.e. they will produce more children of their own and therefore delay existing offsprings' reproduction. This is due to the asymmetric relatedness between grandparents and grandchildren ($r=.25$), compared to siblings ($r=0.5$), resulting in greater incentives for older siblings to help rear younger siblings than for grandparents to help rear grandchildren. 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.

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5 1 Introduction

6 Many social scientists have shown that children who experience parental absences due to di-
7 vorce or death consistently have earlier ages of puberty and first reproduction in post-industrial
8 societies (Surbey, 1990; Nettle et al., 2011; Ellis et al., 2003). This correlation is also seen in
9 some developing societies (Sheppard et al., 2014b; Birdthistle et al., 2008) although the effects
10 are less consistent in these contexts (Waynforth et al., 1998; Allal et al., 2004; Palermo and
11 Peterman, 2009; Leonetti and Nath, 2009; Shenk et al., 2013; Winking et al., 2011). While
12 much of this literature has focused on the influence of father absence on daughters' reproductive
13 maturity, some studies that have looked at other parent-offspring dyads have shown similar re-
14 sults (Sheppard and Sear, 2012; Bogaert, 2005; Sheppard et al., 2014a). These patterns seem to
15 contradict many evolutionary anthropological accounts that emphasize the importance of down-
16 ward intergenerational investments (Kaplan, 1996), including from fathers (Hill, 1993; Geary,
17 2000) and from grandmothers in helping raise dependent offspring (Hawkes, 1998) since one way
18 kin help can improve one's fitness is by expediting reproduction.

19 In this paper we suggest that models of intergenerational conflict within cooperatively breeding
20 kin groups can help explain why parental absences often expedite an adolescent's reproduction.
21 While intergenerational conflict can stem from several kinds of discrepancies between what
22 parents and offspring want, we focus on parent-offspring conflict over reproductive opportunities.
23 Humans' ability to cooperate in raising altricial and slow-developing young that are born in
24 relatively short succession has been proposed as part of the explanation for their success as a
25 species (Hrdy, 2009; Bell et al., 2014). This requires that some individuals invest in raising the
26 offspring of other individuals, at least at some points during their life course. We would expect,
27 therefore, that at least some individuals within the cooperative unit pay a short-term fitness
28 cost, but that the cooperative unit in general benefits long-term from this exchange of resources
29 or help. It should be noted that conflicts over public goods often occur within cooperative
30 systems, meaning that cooperation and conflict are not opposite strategies, as their common
31 usage implies. While "intergenerational negotiation" might be a better term for this phenomena,
32 we will stick to the commonly used terminology in the literature of "intergenerational conflict."
33 In many species of cooperative breeders older siblings help care for young, thus delaying their
34 own dispersal and possibly paying short-term costs in terms of their own reproduction (Jennions
35 and Macdonald, 1994). A similar intergenerational cooperative arrangement has been proposed
36 as a feature of many human societies given the extent of allocare that older siblings provide
37 (Kramer, 2005; Crognier and Baali, 2001).

38 Biologists have developed several models examining the allocation of reproductive opportu-
39 nities within cooperative interactions (Vehrencamp, 1983; Reeve and Keller, 1995; Reeve et al.,
40 1998), including the circumstances under which intergenerational conflicts are resolved in favor
41 of parents' versus offsprings' reproduction (Johnstone and Cant, 2010). If parents win such
42 reproductive conflicts, we would expect that offsprings' reproduction will be delayed if the older
43 generation uses up alloparental and household resources that the younger generation would also
44 need in order to reproduce. If the younger generation wins intergenerational reproductive ne-
45 gotiations over who breeds, we may instead see that parents forgo reproduction allowing their
46 offspring to commence their own reproductive careers. While biologists working with cooper-
47 atively breeding species have attempted to apply this logic to human family systems (Emlen,
48 1995), these insights have been neglected in the parental absence and human life history litera-
49 ture (see (Surbey, 1998) for a notable exception).

50 **1.1 Common explanations of parental absence effects**

51 **1.1.1 Parents as cues**

52 The most popular explanations of why parental presences delay first births focus on the pos-
53 sibility that these serve as cues to socio-ecological parameters. We will call these the “parents
54 as cues” accounts. One such explanation suggests that parental absences indicate high extrinsic
55 mortality risks in an environment, meaning that a developing child should reproduce sooner
56 to reduce their risk of dying childless (Chisholm, 1993). In such environments, delaying repro-
57 duction in favor of growth, development and skill acquisition may not yield sufficient long-term
58 fitness benefits because of mortality risks that the individual cannot easily control (Stearns,
59 1976). An alternative proposal is that parental — especially paternal — absences may indicate
60 that low investment in parenting, low partner selectivity, and earlier reproduction are adaptive
61 mating strategies in one’s environment (Draper and Harpending, 1982; Ellis, 2004). A problem
62 with this latter explanation is that it is ambiguous why a scarcity of highly investing partners
63 should necessarily lead to earlier ages at reproduction. A more general criticism of these pro-
64 posals that parents are cues to environmental circumstances is that they seldom make clear why
65 parents specifically, as opposed to a developing child’s broader social network, should be privi-
66 leged as informative about locally adaptive life history and mating strategies in their adulthood
67 (Nettle et al., 2012). In fact, whether children learn much from their parents rather than from
68 peers and non-kin is questionable (Harris, 1999).

69 Another version of the “parents as cues” explanation now treats parental absence as just
70 one of many stressors which result in rapid reproductive maturation. Psychosocial acceleration
71 accounts of life history development, first proposed to help explain why father absences should
72 expedite reproduction (Belsky et al., 1991), have been broadened to include any stressors that
73 might serve as indicators that one will live in a harsh environment and therefore should reproduce
74 sooner (Belsky, 2012). All of the “parents as cues” models have been critiqued given their
75 assumptions that environments are variable enough to merit developmental plasticity, but stable
76 enough for childhood environments to be predictive of adult ones. The extent to which early
77 childhood environments are predictive of future ones is an area of active debate (Wells, 2007;
78 Rickard et al., 2014).

79 **1.1.2 Parent-offspring interactions**

80 Two other kinds of explanations focus more directly on how parent-offspring interactions,
81 rather than parental absence as a cue to socio-ecology, should influence reproductive timing.
82 The first set of these “parent-offspring interaction” models focuses on parental investments.
83 Ellis (2004) has proposed that children growing up in households with high quality care stand to
84 benefit from capitalizing on this care by investing in their own growth (including skills), rather
85 than in early reproduction. This means that children with parents present in their households
86 would experience later ages of reproductive maturity, insofar as parental presence is a proxy for
87 quality of care. A related argument suggests that fathers invest in, and guard, their daughters in
88 ways that help them obtain high status and stable mates at the expense of earlier reproduction
89 (Flinn, 1988). These arguments seem functionally plausible, especially given the importance of
90 extended childhoods and slow life histories in humans (Kaplan et al., 2000), suggesting potential
91 long-term fitness benefits to delaying reproduction. However, these “parent-offspring interaction”
92 models focusing on the effects of parental investment deemphasize the possibility of parent-
93 offspring conflict regarding help allocations, and assume the importance of downward, rather
94 than upward, intergenerational transfers.

95 The second kind of “parent-offspring interaction” hypothesis focuses on inbreeding avoidance.
96 This one suggests that reaching sexual maturity in the presence of parents is poses a risk of
97 inbreeding depression (Matchock and Susman, 2006). While this model has been useful for
98 predicting reproductive strategies in cooperatively breeding species with small kin groups and
99 high reproductive skew (Cooney and Bennett, 2000), we are more skeptical that inbreeding
100 avoidance was an important selection pressure favoring delayed maturity in recent human evo-
101 lutionary history given that adolescents can find unrelated members of the opposite sex with
102 whom to reproduce even in small human social groups. Furthermore, in other primates with
103 similar multi-male multi-female groups, individuals manage to largely avoid parent-offspring
104 mating despite long alpha male tenures (Muniz et al., 2006).

105 An extension of the first “parents-offspring interaction” account suggests that parental deaths
106 or separations may have consequences for life history development, but only insofar as they
107 belong to a broader set of stressor that affect a child’s health outcomes. Several kinds of social
108 strains during childhood — e.g. residential moves (Nettle et al., 2011; Clutterbuck et al., 2014)
109 and chronic illnesses (Waynforth, 2012) — expedite maturation and reproduction. These kinds
110 of stressors may change a developing child’s physiological status in such a way that the child
111 becomes increasingly susceptible to age-specific extrinsic mortality and morbidity. This was
112 originally proposed as the “weathering hypothesis” (Geronimus et al., 1999). Individuals whose
113 health deteriorates rapidly with age need to get on with reproduction relatively early, in order to
114 ensure successful childbearing while still relatively healthy. A key assumption in this argument
115 is that developmental insults — including those resulting from lower parental investments —
116 change an individual’s physiological state in a way that the individual himself would not be able
117 to repair, or in a way that is not worth repairing (Rickard et al., 2014). If this were not the case
118 it is unclear why an unhealthy individual would not instead try to improve his physiological state
119 at the expense of earlier reproduction. Additionally, the effects of father absences on age at first
120 birth have been found to be larger than those of mother absences (Sheppard et al., 2014a). This
121 result is counter to the more straightforward prediction from a “weathering” model given that
122 mothers’ deaths tend to have more deleterious consequences for children than fathers’ deaths
123 (Sear and Mace, 2008).

124 1.1.3 A confounded relationship

125 It is worth considering that parental absences may not lie on any causal pathway affecting
126 reproductive timing. Rather parental absence effects may be confounded by other intergenera-
127 tionally correlated genetic or social factors that affect both parental availability and an individ-
128 ual’s mortality risks, especially in post-industrial societies with steep socio-economic gradients in
129 health outcomes . However, several studies have found robust parental absence effects on repro-
130 ductive acceleration when controlling for socio-economic confounds (Ellis et al., 2003; Michael
131 and Tuma, 1985; Kiernan, 1992; Vikat et al., 2002; Sheppard et al., 2014b), when controlling for
132 family-level effects (Ermisch et al., 2004; Tither and Ellis, 2008), when examining internationally
133 adopted children raised in well-off families (Teilmann et al., 2006), or when taking advantage of
134 natural experiments during which parental absences have more extrinsic causes such as war or
135 natural disaster (Pesonen et al., 2008; Cas et al., 2014). All of these studies suggest a unique
136 causal role of parental absence above and beyond the confounding effects of genetic or socio-
137 economic variables.

138
139 Here we resurrect the idea that intergenerational conflict may help explain parental influ-
140 ences on the timing of reproduction (Emlen, 1995), and suggest that models of intergenerational

141 conflict complement, and have several advantages over the more common accounts of parental
142 absence effects outlined above. First, unlike the “parents as cues” models, they can help account
143 for the primacy of parents’ presence in explaining children’s reproductive timing. Second, in-
144 tergenerational conflict models integrate the importance of conflict within cooperative systems
145 into the extant “parent-offspring interaction” models that emphasize downwards parental invest-
146 ments, skill acquisition, and delayed maturation as important phenomena throughout human
147 evolutionary history. Third, intergenerational conflict models allow us to make additional pre-
148 dictions about how parental effects on reproduction should vary cross-culturally within humans.

149 **1.2 Models of intergenerational conflict**

150 Other evolutionary scientists have fruitfully used intergenerational conflict models to illumi-
151 nate human family dynamics. For example, tug-of-war models, where actors expend resources
152 to compete over reproductive opportunities, have been developed to explain the evolution of
153 menopause (Cant and Johnstone, 2008; Johnstone and Cant, 2010) and the higher rates of in-
154 tergenerational male conflicts observed in polygynous societies (Ji et al., 2013). These particular
155 versions have treated genetic relatedness within populations as extrinsic features of the envi-
156 ronment resulting from sex-specific dispersal patterns or varying degrees of local reproduction.
157 They have also assumed that one sex controls reproductive decisions. For instance, in the model
158 of human menopause evolution (Cant and Johnstone, 2008), in order for reproductive cessation
159 to be favored among older women, mothers-in-law and daughters-in-law must compete with
160 each other and resolve this conflict over limited household resources, meaning that women are
161 controlling reproductive decision-making in a setting with substantial female-biased dispersal.
162 In such a context daughters-in-law win the conflict because they are less genetically related to
163 group members than the mother-in-law is, and thus suffer greater inclusive fitness opportunity
164 costs to not reproducing. Another recent model of intergenerational and sibling conflict over
165 parental resources suggests that parents may be more selective than their daughters over the
166 latter’s mate choice if parents have to compensate for non-investing sons-in-laws (van den Berg
167 et al., 2013). This dynamic implies that parents should pressure their children to be more se-
168 lective, and therefore possibly slower, to choose mates than they would otherwise be, although
169 the authors do not make predictions about parental effects on reproductive timing per se. Fur-
170 thermore, this model does not allow upward intergenerational transfers and does not examine
171 the tradeoff between a parent’s own and their offspring’s reproduction. Some other researchers
172 have suggested the importance of intergenerational conflict in negotiating young adults’ repro-
173 ductive strategies but have not modeled their hypotheses formally (Hoier, 2003; Surbey, 1998;
174 Waynforth, 2002; Apostolou, 2012). We therefore contribute a formal, but simple, model of
175 intergenerational conflict, and use it to predict the effect of family structure on reproductive
176 timing, and the cross-cultural variation in parental effects.

177 We describe a general framework for exploring reproductive timing decisions within individu-
178 als’ lifetime, which makes no assumption about dispersal patterns or about the sex that controls
179 reproductive decisions. More specifically, we examine under what circumstances a parent should
180 win potential intergenerational reproductive conflicts, and have another infant, and under what
181 circumstances their adolescent child should win the conflict and start their reproductive career.
182 This setup parallels that used in the animal dispersal literature where offspring have to choose
183 whether to leave their natal nest or territory (Koenig et al., 1992). We model the effects of 1)
184 parental continuity (i.e. the probability that a parent does not switch mates), 2) costs to repro-
185 ductive overlap, and 3) reproductive senescence (i.e. aging that results in the older generation
186 producing lower quality infants compared to the younger generation). We investigate these pa-

187 rameters because of their relevance to the human literature on life history and parental presence,
188 although they may speak to similar effects in, and across, other species. Mate-switching plays
189 a large role in explanations of father absence effects on reproductive timing in humans (Draper
190 and Harpending, 1982; Shenk et al., 2013), and varies significantly cross-culturally with mating
191 system. Additionally, reproductive senescence is a topic of much interest for evolutionary an-
192 thropologists given women's long post-menopausal lifespans (Hawkes and Coxworth, 2013), and
193 the possibility of comparable reproductive cessation for monogamous men. Reproductive senes-
194 cence for pre-menopausal women (Fretts et al., 1995) and men (Plas, 2000) has also been shown
195 to affect infant survivorship and health outcomes. In this model we treat reproductive senes-
196 cence as an extrinsic parameter that constrains reproductive decision-making. In other words
197 we do not allow senescence to evolve, although other models have examined the extent to which
198 sex-specific age and genetic structure in a population can select for reproductive senescence
199 (Johnstone and Cant, 2010).

200 Factors affecting mate stability, costs of intergenerational reproductive overlap, and reproduc-
201 tive senescence of a parent relative to an offspring are likely to vary both within, and between,
202 human populations, making this framework particularly useful for making predictions about
203 how parental effects on children's life history should vary cross-culturally.

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

215 **2 A simple model of intergenerational conflict**

216 **2.1 Actors**

217 In this model we assume there are two actors of reproductive age; a parent and her/his
218 adolescent offspring who has yet to reproduce. We do not explicitly model mate search costs,
219 instead assuming that the younger generation can acquire a reproductive partner should she want
220 to. However, for simplicity we assume that we do not have to consider the strategic interests
221 of the younger individual's potential partner. Not only does this simplification keep the model
222 tractable, we also believe that the decision to seek reproductive opportunities and mates should
223 be modeled in its own right since an adolescent can invest in physiological and behavioral
224 strategies that facilitate reproduction before marrying. This model is therefore analogous to
225 models of dispersal decisions in non-human animals. We also assume that the parents' other
226 children do not affect the payoff structures below. We will refer to the older generation as the
227 *parent*, or G_1 , and the younger generation as the *adolescent*, or G_2 . The sex of the actors does
228 not qualitatively change the results.

229 2.2 Setup

230 The parent and adolescent must each decide whether to reproduce at a given point in time.
231 Their decisions can result in one or two infants in the household. The payoffs to each actor of
232 reproducing will depend on the other's decision given that reproduction and infant survivorship
233 or quality are affected by access to resources that are shared within a household. If resources
234 were not shared within a family or household unit, then the actors would be competing with
235 all other group members when deciding whether to reproduce and therefore would have little
236 incentive to curtail their reproductive efforts even if their kin specifically had reproduced. The
237 limited household resources may include alloparenting or caloric production, for example.

238 We model independent sequential decision-making in Section 3.2, rather than synchronous
239 decision-making that is blind to the other's behavior. This is because parents and adolescents
240 are likely able to detect each other's reproductive effort and adjust their decisions accordingly,
241 and because they have some incentive to communicate their intentions to coordinate their re-
242 production in this game (Cant and Shen, 2006). We further assume that actors have equal
243 competitive abilities such that those who are willing to expend more competitive effort are more
244 likely to assure themselves the right to reproduce first. This suggests that those who stand
245 to lose more from forgoing reproduction should be more willing to compete for the right to
246 reproduce first.

247 2.3 Parameters

248 We model the effect of three parameters; infant survivorship when G_1 and G_2 both reproduce
249 relative to when only one reproduces (s), the relative fitness of an infant born to the younger
250 generation compared to the older parent (y), and parental continuity (c). We define s as the
251 ratio of survivorship of an infant who shares a household with another infant, relative to his
252 survivorship being the sole infant in the household. This can take values from 0 to 1, where 1
253 indicates equal survivorship whether or not the infant shares his household with another infant;
254 values less than 1 indicate lower survival if the infant shares his household relative to being the
255 only infant. We assume there are never benefits to infants sharing a household, because they
256 are competing for the same scarce resources. The parameter y (youth benefit) is the ratio of
257 the fitness of an infant born to the *adolescent* relative to the fitness of an infant born to the
258 older *parent*. We include this parameter in the model to allow reproductive senescence that can
259 switch the resolution of the intergenerational conflict to favoring the younger generation. While
260 y can take any positive value, we will primarily focus on values of $y \geq 1$, where 1 represents
261 equal fitness for the offspring of the older and younger generation, and $y > 1$ represents higher
262 fitness for the offspring of the younger generation relative to the offspring of the older generation.
263 While reproducing when very young can have detrimental effects (Chen et al., 2008; Fraser et al.,
264 1995), any fitness costs to infants of young parents (i.e. where $y < 1$) favor the older generation's
265 reproduction further and thus will only exaggerate the resolution of the conflict in favor of the
266 *parent*. Finally, parental continuity, c , is the probability that G_1 continues to reproduce with
267 the same person who produced G_2 . This parameter only affects the *adolescent's*, G_2 's, payoff
268 function. This continuity value, c , can also take values from 0 to 1, where $c = 1$ denotes that
269 G_2 will have a full sibling, and $c = 0$ denotes that G_2 will have a half sibling.

270 2.4 Payoffs

271 Each individual can choose to reproduce R , or not N . Variables subscripted 1 denote payoffs
 272 to the *parent*, G_1 , while those subscripted 2 denote payoffs to the *adolescent*, G_2 . We denote
 273 the payoffs to each actor, V , using conditional probability notation. In each equation the first
 274 term represents the contribution of the actor's own reproduction to her fitness and the second
 275 term refers to the other person's contribution the actor's inclusive fitness.

276

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

$$V_1(R|R) = 0.5s + 0.25sy \quad (1)$$

278

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

279 The payoffs for each individual when only the *parent*, G_1 , reproduces are:

$$V_1(R|N) = 0.5 \quad (3)$$

280

$$V_2(N|R) = 0.25(1 + c) \quad (4)$$

281 and when only the *adolescent*, G_2 , reproduces:

$$V_1(N|R) = 0.25y \quad (5)$$

282

$$V_2(R|N) = 0.5y \quad (6)$$

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

284

285 3 Results

286 3.1 What would each actor want given that the other one has reproduced?

287 Obviously, everyone wishes to avoid a household where neither actor reproduces. However, it
 288 is not always the case that both generations reproducing simultaneously maximizes each indi-
 289 vidual's inclusive fitness. Under these circumstances, the payoff structure described in equations
 290 1-6 suggests that, for some part of the parameter space at least, *parents* and *adolescents* are
 291 engaged in a hawk-dove game. That is, this decision-making requires coordination so that the
 292 household does not end up with too many or too few infants, but at least some of the time
 293 each actor prefers to be the one to reproduce. Here we address the question of how each indi-
 294 vidual would respond were the other actor to have reproduced. Below we also show whether
 295 each actor would want the other individual to reproduce given that they themselves had already
 296 reproduced.

297 3.1.1 Given that the *parent*, G_1 , has reproduced

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

$$s > (1 + c)/(2y + 1 + c) \quad (7)$$

300 However, the *parent* will only want her offspring to reproduce when $V_1(R|R) > V_1(R|N)$. This
 301 is true when: :

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

302 **3.1.2 Given that the *adolescent*, G_2 , has reproduced**

303 On the other hand given that the *adolescent* has reproduced the *parent* will want to reproduce
 304 when $V_1(R|R) > V_1(N|R)$. This is true when:

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

305 whereas, the *adolescent* will want her *parent* to reproduce only when $V_2(R|R) > V_2(R|N)$. This
 306 is true when :

$$s > 2y/(2y + 1 + c) \tag{10}$$

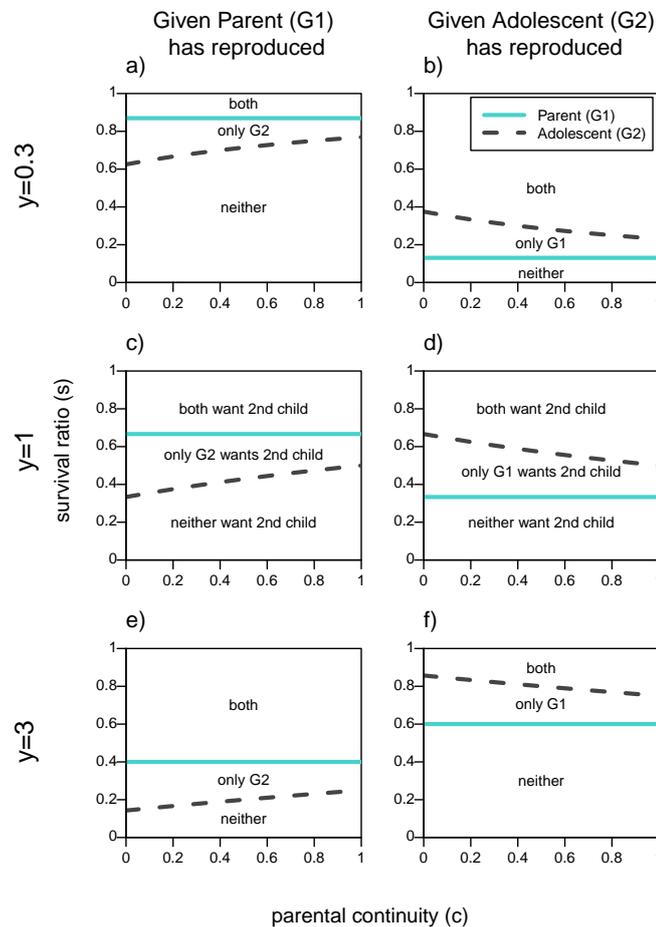


Figure 1: When actors should want a second infant in the household given one of them has already reproduced. Areas are plotted as a function of survival ratio (s), parental continuity (c), and youth benefit (y). Areas above each actors line denote when it is in their fitness interest to add the second infant to the family. The text within the plots denotes which actors want the second infant.

307 3.1.3 Summary of payoffs to adding a second infant to household

308 The first column of Figure 1 (a, c, and e) shows the parameter space over which actors want
 309 the *adolescent*, G_2 , to reproduce given that the *parent*, G_1 , has done so, assuming a reproductive
 310 benefit to the older generation ($y = 0.3$), no youth benefit ($y = 1$), and a threefold youth benefit
 311 ($y = 3$). These are represented by the areas above the line for each actor. First focusing on
 312 Figure 1 (c), when neither generation has a reproductive advantage ($y = 1$), if the survival ratio
 313 of 2 to 1 children in the household, s , is high enough there will be no conflict of interest as both
 314 actors will want the *adolescent* to reproduce. Similarly, if s is low enough neither actor will
 315 want the *adolescent* to reproduce because the additional infant will decrease the survival odds
 316 for both children too much. Disagreements between *parent* and *adolescent* in terms of adding
 317 a second infant to the household arise for intermediate values of s . The straight line for the
 318 *parent* shows that she has a higher threshold s for her to want her offspring to reproduce, and
 319 that this value does not depend on c since parental continuity does not affect a grandparent's
 320 relatedness to her grandchild. The *adolescent's* line on the other hand increases with c , that is
 321 the higher her relatedness to her new sibling the higher the survival ratio (s) has to be in order
 322 for her to benefit from reproducing as well.

323 Figure 1 (d) shows the same lines for each actor given that the *adolescent* has reproduced.
 324 Now the *adolescent* has a higher threshold of survival ratio for which she would want her *parent*
 325 to reproduce compared to the *parent's* own threshold. As her certainty that she will get a full
 326 sibling (c) increases, the *adolescent* becomes more tolerant of her *parent's* reproduction, that
 327 is, she benefits from a sibling for a wider range of costs to having two infants in the household
 328 (s). Still, even if the *adolescent* is a full sibling of the *parent's* child, there will be values of s
 329 for which she will not want her *parent* to reproduce even though the *parent* wants to.

330 By increasing the youth benefit, y (Figure 1 e and f) the *parent* has relatively more to gain
 331 from a grandchild. This reduces the size of the zone of conflicts of interests in both scenarios,
 332 but maintains the order of the lines in Figure 1. Both lines move down in the first column,
 333 and up in the second one. That is, both actors will want the *adolescent* to reproduce over a
 334 wider parameter space given that the *parent* has reproduced, whereas both actors will be more
 335 reticent to encourage the *parent's* reproduction once the *adolescent* has already reproduced.

336 Similarly, when the youth benefit is less than 1 (Figure 1 a and b), the *parent* has a repro-
 337 ductive advantage and the zone of conflict over the second child becomes smaller. The threshold
 338 lines in the first column of Figure 1 are higher when $y = 0.3$ meaning that both actors are less
 339 willing to have the *adolescent* reproduce given that she would produce a relatively lower quality
 340 infant. On the other hand if the *adolescent* has reproduced, both actors are more tolerant of
 341 the *parent* reproducing when the older generation's reproduction is more efficient as shown by
 342 the threshold lines being lower in (b) relative to (d). Given that values of $y < 1$ further favor
 343 the parent's reproduction we will not focus on this part of the parameter space.

344 It should be noted that even when both actors agree that a second child should not be added to
 345 the household, there may be conflict over whose child that should be. That is, for G_1 , $V_1(R|N)$
 346 is better than $V_1(N|R)$ so long as $y < 2$. In other words, if only one person is going to reproduce
 347 the *parent* prefers to be the one to do so, as long as the youth benefit is less than 2. Similarly,
 348 the *adolescent*, G_2 , prefers to be the one to reproduce much of the time. For example, when
 349 there is no reproductive benefit to the older parent reproducing ($y \geq 1$), $V_2(R|N)$ is strictly
 350 better than $V_2(N|R)$, so long as they are unsure that their parent will produce a full sibling
 351 — i.e. $c < 1$. Again, these hawk-dove dynamics suggest the importance of competition and
 352 coordination among the actors.

353 3.2 How much do actors lose from not reproducing first?

354 Section 3.1 shows that there are conflicts over who gets to reproduce, and that the actors
 355 will not always agree about adding a second infant to the household given that one of them is
 356 already giving birth. We now assess how much each actor stands to lose by not reproducing
 357 first. We assume that the actor who stands to gain more from reproducing first has more to
 358 gain from expending competitive effort to assure herself the first mover position, and thus her
 359 preferred reproductive outcome. It is worth noting that actors may exhibit negative fitness losses
 360 to reproducing first, meaning that they prefer to choose their strategy after the other actor has
 361 done so, and thus do not need to compete over the right to be the first mover.

362 We use payoffs from section 3.1 regarding what actors would do as second movers to calculate
 363 the payoffs to each actor were the *parent*, and subsequently were the *adolescent*, to reproduce
 364 first. We assume the second actor has full autonomy in their decision so that even though we
 365 plotted what both actors wanted in Figure 1, only the function for the second actor matters.

366 3.2.1 Payoffs to actors if the *parent*, G_1 , reproduces first:

367 The *adolescent*, G_2 , will be the second actor and will respond differently to G_1 's initial
 368 decision, depending on the values of s , y and c . Therefore, we need two different functions to
 369 determine the ultimate payoffs for each generation, depending on what the *adolescent* does.

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

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

370 3.2.2 Payoffs to actors if the *adolescent*, G_2 , reproduces first:

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

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

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

372 3.2.3 Summary of costs to not reproducing first

373 The *parent*, G_1 , will want to reproduce first when equation 11 > equation 13, and the
 374 *adolescent* will want her *parent* to reproduce first when equation 12 > equation 14. As a
 375 simple example, let's consider payoffs when $c = 0$ and $y = 1$. In this case, both actors will
 376 always want to be the first mover, or at worst be indifferent if $s > 1/3$ since both of them will
 377 reproduce when there are low costs to both reproducing. When $s < 1/3$, each actor will lose
 378 0.25 if she does not get her way. In other words the game is symmetric, and it is not obvious
 379 who will win the conflict. This is not surprising as when $c = 0$ both actors are equally related
 380 to the other actor's child. In much of the parameter space, however, the game is not symmetric,
 381 and one actor stands to lose more than the other by not reproducing first. Here, we can identify

382 the most likely winner of the conflict, namely the one who stands to gain more from being the
383 first reproducer.

384 Figure 2 illustrates the fitness losses to each actor as a function of whether they get to
385 reproduce first or choose their strategy after the second actor for a broader set of parameters.
386 In a tug-of-war model, the fitness losses would correspond to how much actors should be willing
387 to invest in competitive effort to win this conflict. This means that the higher an individual's
388 opportunity costs to not reproducing first relative to the other actor's opportunity costs, the
389 higher her likelihood of winning the conflict. The horizontal axes shows that these conflicts
390 will be resolved differently as a function of the costs to having two infants in the household, s
391 (note: s values have changed from being on the vertical axis in Figure 1). Each plot represents
392 a different combination of youth benefit, y , and parental continuity, c .

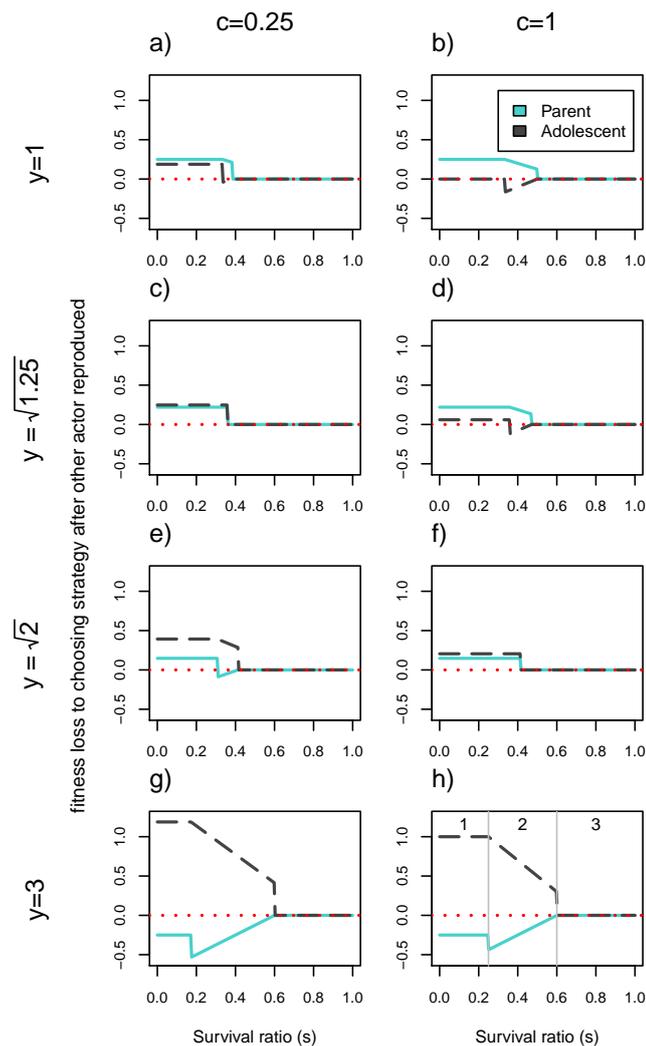


Figure 2: Cost of choosing strategy after the other actor has reproduced. Fitness losses are plotted as a function of the survival ratio, s , of 2 versus 1 infant in the household. The solid line denotes the older generation (i.e. the *parent*), and the dotted line denotes the younger generation (i.e. the *adolescent*). 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 parental continuity 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.

393 There are three areas of the parameter space that have functionally different outcomes for

394 the set of actors (illustrated in Figure 2 h). We will discuss these out of order from simplest to
395 most complicated (starting with zone 3, ending with 2) . Zone 3 corresponds to survival ratios,
396 s , that are high enough such that both actors will reproduce regardless of who acts first. This
397 means that both actors have zero fitness losses to choosing second in this zone, since everyone
398 will get to reproduce. This corresponds to the right hand side of each plot in Figure 2. On
399 the left hand side of each plot is zone 1 where the survivorship of two infants relative to one,
400 s , is so low that only one actor will reproduce. Finally, in zone 2 with intermediate survival
401 ratios, the number of people who reproduce will depends on who reproduces first. This area is
402 indicated by the sloping lines in Figure 2 and requires more explanation. This intermediate area
403 is bounded by $s = (1 + c)/(2y + 1 + c)$ and $s = y/(y + 2)$, as outlined in equations 11 through
404 14. Whether each of these expressions denotes the upper or lower limit of the intermediate
405 area depends on the values of y and c . For example, when there is no youth benefit, $y = 1$,
406 $(1 + c)/(2y + 1 + c) > y/(y + 2)$. This means that the younger generation has the higher
407 threshold s value at which they would produce a second child, and is therefore more reticent
408 to reproduce given that the other actor has already done so. However, this will flip when the
409 younger generation's reproduction is significantly more efficient — i.e. for large enough values
410 of y , specifically when $y > \sqrt{1 + c}$. Under these circumstances the *parent* will have a higher
411 threshold value for reproducing as a second mover than the *adolescent* does. When $y = \sqrt{1 + c}$
412 zone 2 disappears (e.g. Figure 2 c) and f), meaning that *parents* will not have a different
413 preferences for total infants from *adolescents* as second movers.

414 We first elaborate on the conflict dynamics using the simple case where there is no efficiency
415 benefit to the younger generation reproducing, $y = 1$. In this case, when the costs to synchronous
416 reproduction is low enough (e.g. $s > 1/2$ in Figure 2 b) both individuals will end up reproducing
417 meaning that order of decision-making is irrelevant. The lower c is, the larger this parameter
418 space, as indicated by the longer range of zero fitness losses (zone 3) of Figure 2 a) than b). This
419 means that with lower probabilities of parental continuity, the greater the range of survival ratios
420 under which the *adolescent* is willing to reproduce. If the costs of synchronous reproduction are
421 high enough (s is low), only the first actor will reproduce and the *parent* stands to lose more
422 than the *adolescent* from not being the one to do so (see zone 1 of Figure 2 a and b). In fact if
423 $c = 1$ the younger generation should be indifferent between reproducing or having their *parent*
424 produce a full sibling. This is indicated by the zero fitness loss to the *adolescent* of choosing
425 not to reproduce after the other individual has. For intermediate values of the survival ratio, s ,
426 the actors pursue different strategies as 2nd movers. In the case of $y = 1$, in this intermediate
427 range the *parent* will prefer to reproduce whether or not the *adolescent* has done so, whereas
428 the *adolescent* would want to reproduce only if the *parent* does not. This explains the negative
429 “losses” to going 2nd for the *adolescent*, who prefers to decide *not* to reproduce after having
430 seen the *parent* reproduce, than to reproduce herself first and then have the *parent* add a 2nd
431 child to the household. Under these circumstances (and whenever one actor suffers negative
432 losses from going second in Figure 2) the model exhibits endogenous timing, meaning that both
433 players agree about who should act first (Cant and Shen, 2006). Given the costs to pregnancy
434 termination and the mutual interests of kin, such contexts should favor signaling reproductive
435 intent.

436 Once we add large enough reproductive consequences to senescence (e.g. Figure 2 g and h
437 where $y = 3$), the younger generation wins out over the *parent* during contexts of reproductive
438 conflict. In the intermediate zone 2, if senescence is high enough ($y > \sqrt{1 + c}$) both actors prefer
439 the younger generation to reproduce alone, given that the *adolescent* would reproduce regardless
440 of the *parent's* reproductive decision in this range. For really severe resource constraints (zone

441 1) the bottom two rows of Figure 2 show that the younger generation will also lose more from
442 going second and not reproducing than the parent will. In fact, for very large youth benefits
443 (e.g. $y = 3$) even the *parent* prefers the *adolescent* to be the sole reproducer as indicated by her
444 fitness losses to going second being negative. This indicates that for this part of the parameter
445 space, even as first mover, the *parent* would forgo reproducing in favor of allowing her child
446 to do so. More generally this should be true when $y > 2$. However, in zone 1, the range of y
447 values for which the *adolescent* stands to lose more than *parent* is even broader. So long as
448 $y > (3 + c)/3$, the *parent* loses less than her child from forgoing reproduction when only one of
449 them is going to reproduce.

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

459 4 Discussion

460 Our model suggests that parents and their children will often agree about reproductive deci-
461 sions when there are low costs to synchronous reproduction, but that parents will generally have
462 the upper hand in negotiating intergenerational conflicts should these arise (i.e. when s is low
463 enough). However, this is contingent on the adolescent's expectation of her parent producing
464 a full-sibling. This means that biparental presence should favor the parents' reproduction over
465 their offsprings' reproduction and may thus delay the latter's age at first birth. This dynamic
466 is driven by the asymmetric relatedness of actors to the potential offspring being produced.
467 However, this game becomes fully symmetric if the parent cannot give birth to a full sibling,
468 meaning that if one parent is absent, offspring should be as likely as the remaining parent to win
469 intergenerational reproductive conflicts. It follows that relative to having two parents present,
470 an adolescent has more of an incentive to reproduce when one parent is absent since her future
471 siblings will be less related to her. Furthermore, the advantage can even shift to the younger
472 generation's reproduction if we incorporate physiological senescence that reduces the quality of
473 the older generation's child.

474 It is worth noting that these predictions hold only for species where parents and offspring
475 cooperate for reproductive purposes or rely on the same resources to reproduce. Similar facultative
476 helping-at-the-nest as a function of relatedness to siblings has been documented among
477 cooperatively breeding birds (Komdeur, 1994), suggesting these helpers also disperse and re-
478 produce at a later age. Furthermore, experiments with eusocial Damaraland mole rats show
479 that switching out a related dominant male from the family group induces physiological changes
480 and reproductive activity among the dominant pairs' daughters (Cooney and Bennett, 2000).
481 Although we do not argue that humans are similarly eusocial, this line of evidence suggests that
482 analogous physiological and behavioral pathways may help explain observed changes in human
483 menarche (Webster et al., 2014), adrenarche (but see Sheppard and Sear (2012) showing father
484 absences in late childhood may delay male puberty), and age of first reproduction when parents
485 are absent.

486 In the remainder of the discussion we develop predictions both about 1) factors that affect
487 the likelihood that offspring win intergenerational reproductive conflicts and therefore start
488 reproducing, and 2) factors that affect the size of the parental absence effect on offsprings'
489 reproduction. Figure 3 illustrates the difference between these two kinds of predictions. We
490 return to this distinction and explain it further in Section 4.2. First, we consider how our model
491 speaks to the effect of different kinds of parental absences on reproductive maturation. Then
492 we turn to the effects of sex, gender, age and other cultural institutions on intergenerational
493 relations.

494 4.1 Predicted differences in parental absence effects by type of absence

495 Our model does not explicitly differentiate between households with a stepparent from those
496 with a single parent. This is because we assumed that both generations could find a mate
497 at no cost and that other actors' interests did not matter. Table 1 shows how different kinds
498 of family compositions correspond to three parameters; parental continuity (c), the remaining
499 parent's mate search costs, and the presence of a non-kin actor in the household. The first
500 column shows that if we only consider parental continuity we should expect about equal effects
501 of parental absence due to divorce when there is a stepparent present as when the absence is
502 due to death. In contrast, a child raised in a single parent (non-widow) household should not
503 expedite their reproduction as much as children raised in other parent absent households given
504 there is some chance of parental continuity ($c > 0$). The child may rely on other cues to parental
505 continuity under such circumstances, such as degree to which the absent parent invests or visits,
506 to assess the probability of parental continuity. This may explain the fact that father absences
507 due to labor migration do not expedite adolescent's reproduction (Shenk et al., 2013), that tense
508 mother-father relations (Chisholm et al., 2005) and residential moves (Clutterbuck et al., 2014)
509 expedite maturation, and that the quality of paternal care matters more to pubertal timing than
510 mere presence (Ellis et al., 1999).

511 We can relax assumptions about mate search costs and other actor's interests in our model to
512 derive more predictions about family structure. If we incorporate mate search cost it is easy to
513 see that a *parent* and *adolescent* are in the most symmetric situation when neither has a partner
514 since both will have to pay the costs of finding a mate (see rightmost column of Table 1) and both
515 will produce infants that are 0.25 related to the other actor. While this symmetric relatedness
516 to infants is the same in a step-parent present household, asymmetries that favor the parent
517 arise when we incorporate mate search costs and the stepparent's interests. Relative to being a
518 single parent, a stepparent's presence more clearly indicates a parent's intention to reproduce.
519 Not only does the presence of a stepparent mean that only the younger generation has to pay
520 mate search costs, but it may also commit a parent to reproduce given that a stepparent has no
521 inclusive fitness interests in his stepchild's reproduction and therefore stands to lose a lot from
522 not reproducing himself. This leads to the prediction that parental absences due to death should
523 expedite an adolescent's reproduction the most since this gives the younger generation the most
524 leverage in family-level negotiations, especially in societies with large costs to marriage.

525 Previous accounts of how family structure affects intergenerational conflict over reproduction
526 and age at first birth have relied on verbal arguments and therefore made ambiguous predictions
527 that do not necessarily match those we have proposed above (Surbey, 1998; Apostolou, 2012).
528 For example, Hoier suggests that "the maternal reproductive interests model also predicts an
529 earlier menarche if the mother has children with the stepfather, but a less pronounced one
530 because half-siblings are not as closely related" (p. 214) 2003. The family structures being
531 compared are unclear in this formulation, but the author's expectation regarding the effect

532 of sibling relatedness on maturation seems contrary to our own. While her phrasing suggests
 533 that the lower relatedness among half-siblings would make parental absence effects smaller (i.e.
 534 expedite maturation less), we predict it is exactly because of this lower relatedness to half-
 535 siblings that stepfather presence should expedite adolescents' reproduction. In another example,
 536 Apostolou's verbal formulation suggests that parents should want their children to reproduce
 537 earlier than the children themselves would want to reproduce 2012 so that they can control the
 538 younger generation's reproductive decisions more effectively while the children are younger and
 539 more dependent on parents. In this account it is unclear why it is not in the fitness interest of
 540 adolescents to reproduce as early as they are reproductively mature as well, and how the older
 541 generation's political gains from controlling their children's reproduction trades off with their
 542 gains from using their children's labor and having healthy grandchildren.

Table 1: Effects of different kinds of parental absences. Effect of family structures on parental continuity (c), the presence of a non-kin actor in the household, a parent's experiencing mate search costs, and an adolescent's predicted age at first birth (AFB). Note: When incorporating mate search costs, adolescents would always experience these as well.

| Family Household Structure | Parental continuity (c) | Non-kin actor | Marriage costs to parent | Adolescent's predicted AFB |
|---|-----------------------------|---------------|--------------------------|----------------------------|
| two genetic parents | ~ 1 | no | no | latest |
| parent and step-parent | ~ 0 | yes | no | intermediate |
| single parent (widow) | 0 | no | yes | earliest |
| ambiguous single parent (e.g. labor migrant or separated) | >0 | no | maybe | intermediate |

543 4.2 Predicted differences in parental absence effects by actors' sex and gender

544 While our model can apply to actors of either generation that are any sex, there are multiple
 545 reasons we might expect sons and daughters to be differentially affected by intergenerational
 546 conflict. We can conceptualize these sex and gender differences as changing the youth benefit.
 547 First, non-zero rate of paternity uncertainty will negatively affect a son's fitness through both
 548 his own reproduction and through that of his siblings; whereas it will only affect a daughters
 549 fitness through her siblings. This means that sons should favor their own reproduction less
 550 than daughters would, and thus that they are less likely to win intergenerational conflicts over
 551 reproduction. This would be mathematically equivalent to sons having a lower youth benefit, y ,
 552 than daughters. On the other hand, given that men tend to marry later than women do, their
 553 parents will be on average older when they commence reproductive negotiations, and thus more
 554 likely to lose reproductive conflicts given the larger physiological youth benefit, y , at these ages.

555 This means that sons should be *less* likely to win intergenerational reproductive conflicts than
556 daughters when there is high paternity uncertainty, and *more* likely to win intergenerational
557 conflicts when men marry late.

558 Additionally, while we haven't allowed parental coercion in our model, were we to do so it is
559 possible that parents would be more likely to delay daughters' or sons' reproduction, depending
560 on the relative contributions of each gender to the household. For example, if alloparental care
561 is a scarce resource then parents might delay daughters more given that they more commonly
562 help rear younger siblings cross-culturally, whereas if meat is a scarce resource, parents may
563 delay sons more given that men are usually more responsible for procuring animal protein.

564 So far we have focused on how actors' sex and gender roles can affect their likelihood of winning
565 intergenerational reproductive conflicts, but have said nothing regarding how sex changes the
566 size of parental absence effects. We can illustrate this interaction by considering more generally
567 how changes to the youth benefit (in this case, those resulting from sex differences) alter the
568 difference in the survival ratio at which an adolescent would be willing to reproduce when both
569 genetic parents are present relative to when one of them is absent. Although larger youth benefits
570 make it more likely that the younger generation wins intergenerational conflicts, this does not
571 mean that it translates into a smaller parent absence effect. Figure 3 shows the threshold survival
572 ratio value above which the *adolescent* will reproduce given that her *parent* has already done
573 so, in a parent absent versus both parents present household ($c = 0$ versus $c = 1$). Both of these
574 downward sloping curves show that the *adolescent* is willing to reproduce over a wider range
575 of survival costs, s , to having two infants in the household as the youth benefit, y , increases.
576 However, the dotted grey line shows that with larger youth benefits, the size of parental absence
577 effects increases. Specifically, the percent difference in the threshold value of s for parent absent
578 versus parent present households increases with y . Substituting in the relevant sex differences
579 for y , this implies that parental absence effects should be smaller for sons than daughters when
580 there is high paternity uncertainty ($y_{sons} < y_{daughters}$), but larger for sons than daughters when
581 ages at first birth are much later for men ($y_{sons} > y_{daughters}$).

582 It is worth noting that this model would also make similar predictions for mother and father
583 absences under conditions of little paternity uncertainty. If we incorporate paternity uncertainty,
584 the father's reproduction is of relatively less value to an *adolescent* than that of her mother.
585 This may help explain why helpers-at-the nest more often help mothers than fathers. It follows
586 that the younger generation is more likely to win intergenerational negotiations with a single
587 father than a single mother, and that mother absence effects should be larger than those of
588 father absence. The emphasis in the life history literature on the effects of father absence may
589 reflect the higher variance in paternal than maternal availability, both due to death and divorce.
590 However, contrary to our predictions, or to the predictions we would derive from models focusing
591 on parental investments, some data suggest that father absences have more expediting effects
592 on reproduction than mother absences (Sheppard et al., 2014a).

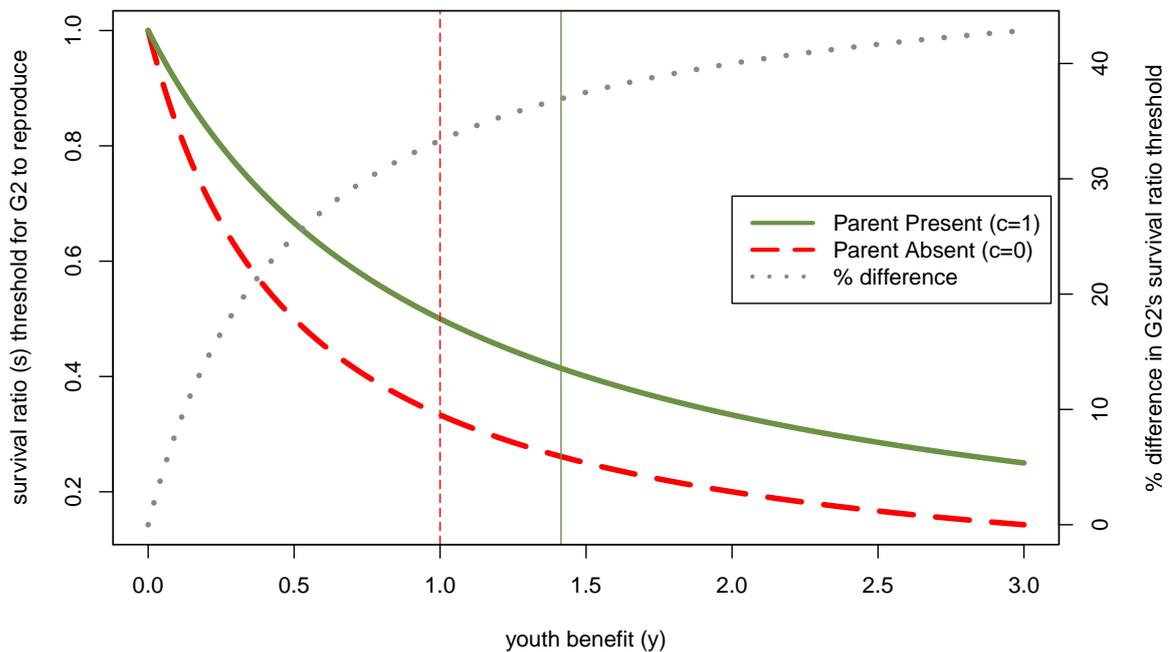


Figure 3: Effect of other parent's absence (parental continuity is 0 rather than 1) on *adolescent's* willingness to reproduce if her *parent* has done so, as a function of youth benefit. Green and red curves denote minimum survival ratios (s) at which *adolescent* will reproduce, derived from equation 7. When the second parent is absent, the *adolescent* will reproduce for a larger part of the parameter space. The dotted grey line (plotted on the right axis) shows that the relative size of the parental absence effect increases with the youth benefit (y) — i.e. the difference between these threshold levels of s when $c = 1$ relative to $c = 0$ as a percent of the effect when $c = 1$ increases with y . Vertical lines mark the y -values above which the *parent* becomes more reticent to add a 2nd infant to the household than the *adolescent* for the respective parental continuity values.

593 4.3 Predicted differences in parental absence effects by actors' ages

594 While we emphasized youth benefits greater than 1 — i.e. physiological senescence such that
 595 only the parent's infant could ever be lower quality than the offspring's infant — any process that
 596 makes one generation's infant higher quality than the other moves the resolution of the conflict
 597 in favor of that individual. Clearly, the older a parent is, the more likely the younger generation
 598 is to win this conflict, assuming that relatively elderly parents produce lower quality children
 599 (Fretts et al., 1995; Plas, 2000). Humans experience a particularly unusual pattern of senescence
 600 given that women's reproductive system declines, while they are still healthy and productive
 601 adults, thus allowing them to shift strategies to alloparenting even if they lose intergenerational
 602 conflicts. However, in the other direction, the more benefits to learning parenting skills or to
 603 delaying development for an adolescent, the more likely the older generation is to reproduce,
 604 and the smaller the scope for intergenerational conflict. This means that the more an adolescent
 605 gains from delaying reproduction (i.e. the farther below 1 y is), the less a parental absence should
 606 affect her developmental trajectory. We see this pattern in Figure 3 where the percent difference
 607 between parent absence and parent presence approaches 0 as the youth benefit approaches 0.

608 This dynamic might be particularly important in humans given the large repertoires of cultural
609 traits (including parenting skills) that they need to learn to become competent adults.

610 4.4 Predicted cross-cultural differences in parental absence effects

611 Here we develop predictions about how ages at first birth and how parental absences on age
612 at first birth may vary cross-culturally. Institutions can affect both how likely members of
613 the younger generation are to win intergenerational negotiations (corresponding to mean ages
614 at first birth), and the effect of parental absences on timing of first births (corresponding to
615 the difference between parent present and parent absent households). The effect that parental
616 *investments* have on age at first birth are likely to vary cross-culturally as well — for example,
617 father absences are likely to have smaller effects in societies where paternal investments are not
618 as important. However, here we focus on how the effect of parental absences on reproduction
619 should change cross-culturally due to the reduced relatedness of future siblings.

- 620 1. At the population level, in societies with less turnover between partners and less paternity
621 uncertainty we would expect greater alloparenting or provisioning of younger children by
622 older siblings or helpers-at-the-nest. This suggests there may be a group-level negative
623 association between repartnering rates and ages at first birth. This also means that the
624 presence of a father should delay reproductive maturity *less* in societies where mere pres-
625 ence is not a good indicator of his producing full siblings in the future, as might be the
626 case in societies with partible paternity institutions or high female sexual autonomy.
- 627 2. Polygamous contexts where future siblings are less likely to be full siblings should similarly
628 discourage the younger generation from investing in their natal household. Again this sug-
629 gests children being raised in polygamous households may experience earlier reproductive
630 maturity and that the presence of both parents may be a bad indicator of future returns to
631 investing in the natal household. By this logic we might expect smaller parental absence
632 effects in such households. It is also worth noting that a polygynous man can extend his
633 reproductive career by acquiring new wives. This puts him in direct competition with his
634 children — especially his sons — over household resources for bridewealth and over mates.
635 This should increase intergenerational conflict, but it is less clear who should win these
636 conflicts. If a polygynous father has some chance of reproducing with his son's mother
637 again, the father should retain more leverage in intergenerational negotiations, and thus
638 delay his son's reproduction, though less so than a monogamous man within a polygynous
639 society.
- 640 3. Societies with bridewealth or dowry increase the mate search costs for the younger gener-
641 ation. This means that there are relatively higher costs to the younger generation repro-
642 ducing with a given quality mate when bridewealth or dowry are expected. This should
643 result in delays to the average ages of first birth and smaller parent absent effects for the
644 affected gender, all else equal (see effect of smaller y -values in Figure 3).
- 645 4. Similarly, there is cross-cultural variation in the degree to which parental contributions are
646 needed to marry, set up a household (e.g. higher setup costs in neolocal societies than in
647 patri- or matri- local ones), or to become competent and skilled adult members of society.
648 Under these circumstances there is less intergenerational conflict over timing of first birth
649 given the benefits to adolescents of skill and material acquisition. We would expect later
650 mean ages of first birth under these circumstances. Again, the effect of parental presences

651 relative to absences should be smaller given the smaller youth benefit in the reproductive
652 domain. Importantly, this prediction is based on the assumption that the parental absence
653 only affects an adolescent's relatedness to future siblings, but not her other socio-economic
654 or health outcomes (i.e. education, resources or embodied capital).

655 5. Ambilocal post-marital residence patterns may afford families the option of moving ado-
656 lescents to contexts with less resource stress, effectively increasing the infant survival ratio
657 s , thus reducing intergenerational conflict and allowing earlier ages at first birth. Further-
658 more, the greater options afforded in societies with flexible residence norms may give the
659 younger generation more leverage in intergenerational negotiations. This may be true for
660 neolocal residence norms as well, assuming costs to setting up a household are low. Such
661 flexible residence norms should reduce the extent to which parents delay their children's
662 reproduction since both generations are likely to reproduce regardless of parental conti-
663 nuity rates when there are low costs to simultaneous reproduction (see high s values in
664 Figure 2).

665 It is worth discussing whether the intergenerational conflict model applies to low fertility,
666 post-industrial societies where most of the empirical research has been conducted. In these
667 societies several cultural norms reduce the extent to which we would expect intergenerational
668 reproductive conflict. First, reproductive overlaps between parents and offspring are relatively
669 rare in societies with late ages at first birth and early reproductive cessation. Second, cultural
670 norms limiting child labour and fertility reduce the usefulness of adolescents to their natal
671 household's economy. Relatedly, while perceptions of the costs associated with rearing a given
672 child may be increasing with expectations of high educational investment (Mace, 2008), these
673 same institutions effectively decrease the reproductive youth benefit. Third, perceptions of
674 household resource stress in most large-scale societies do not necessarily indicate an inability to
675 raise reproductively successful adult offspring given the relatively low rates of infant and child
676 mortality across socio-economic strata in modern economies.

677 This means that even if intergenerational reproductive conflicts do not account for parental
678 absence effects in post-industrial societies, they may well help explain the phenomena in other
679 cultural contexts. For example, it may be that in post-industrial societies parental absence
680 effects are better explained by socio-economic health differentials, whereas in pre-transition
681 societies intergenerational conflicts play more of a role. Alternately, it is possible that several
682 of the psychological mechanisms implied by this intergenerational conflict model systematically
683 misfire, even in low fertility societies, and result in maladaptive outcomes. If this were the
684 case we would posit that adolescents have an evolved expectation of reproductive conflict with
685 parents that does not accurately reflect reality in post-industrial settings. This misfiring account
686 would imply a relatively canalized, rather than plastic, set of psychological mechanisms. A cross-
687 cultural comparative approach may help disentangle some of the proposals on the table.

688 4.5 Limitations of the current model

689 While we made several simplifying assumptions to keep the project tractable future work can
690 develop other avenues of inquiry. For example, one might extend the two person game to include
691 the motivations of other potential actors, such as spouses for the younger generation. If the
692 younger individual is betrothed or partnered, their spouse will have no inclusive fitness incentives
693 to help raise their siblings-in-law. Such affinal ties only exist once the younger generation
694 has married, a state suggesting that the parental generation may have lost intergenerational

695 reproductive negotiations. This might help explain why the literature shows that a woman's
696 in-laws expedite first births more often than a woman's parents do (Sear et al., 2014). That
697 is, given that the older generation has lost this intergenerational conflict, and their child has
698 married, they may stand to gain from facilitating the production of grandchildren. Negotiations
699 between other older siblings might also be of importance when deciding how alloparental care is
700 provisioned, as has been shown in other cooperatively breeding species (Pasinelli and Walters,
701 2002).

702 It is also worth noting that the economic structure to the game we modeled might not reflect
703 real world contexts if there are efficiencies of scale to raising two children together rather than
704 two children apart. The extent to which intergenerational overlaps in reproduction are costly is
705 a question of much empirical debate that has yet to be resolved (Lahdenperä et al., 2012; Mace
706 and Alvergne, 2012; Skjærvø and Røskaft, 2013). We have also assumed that senescence is an
707 extrinsic process rather than one directly under selection. There is some evidence that female
708 reproductive physiology might be thus constrained (Robson et al., 2006), but this is debated
709 given the diversity of senescence rates both within (Thomas et al., 2001; Snopkowski et al., 2014)
710 and between (Jones et al., 2014) species.

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

722 While we have discussed this model in terms of intergenerational conflict, it is worth remem-
723 bering that these family dynamics are being played out in a larger population of less related
724 households. Bordered tug-of-war models incorporate pressures from between-group competi-
725 tion. These limit the extent to which group members (e.g. kin) engage in costly internal
726 conflicts (Reeve and Shen, 2006). Such models remind us that conflicts within cooperative units
727 occur within a larger population of competitors, meaning that selection should favor reduced
728 negotiation costs, and more efficient cooperative equilibria between parents and offspring. Cyrus
729 and Lee (2013) have proposed that the division of labor regarding alloparenting and calorie pro-
730 duction between the generations of human cooperative breeders is one such efficient equilibria
731 that can be modeled as a multi-stage evolutionary process.

732 5 Conclusion

733 The model proposed here provides an explanation for why family structure specifically can
734 result in different maturational rates and ages of first reproduction. We have argued that the
735 intergenerational conflict model is more plausible than the popular "parents as cues" models in
736 the literature, and a more complete account that complements the available "parent-offspring
737 interaction" models. To summarize, parental absences in childhood and adolescence may provide
738 cues of reduced inclusive fitness value to investing in future half-siblings rather than reproducing
739 on one's own. In contrast, if an adolescent perceives that her parents' relationship is stable, she

740 should be indifferent between reproducing on her own or helping rear any resulting full siblings.
741 This could shape a developing child's life history strategy, both physiologically (e.g. earlier
742 menarche when a parent is absent) and behaviorally (e.g. earlier mate seeking and reproduction).
743 This also provides a simple framework for devising predictions about how cultural and socio-
744 ecological parameters should interact with family structure in affecting adolescents' reproductive
745 decisions.

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749 **References**

- 750 Allal, N., Sear, R., Prentice, A., and Mace, R. (2004). An evolutionary model of stature, age at
751 first birth and reproductive success in Gambian women. *Proceedings of the Royal Society B*,
752 271(1538):465–470.
- 753 Apostolou, M. (2012). Parent-offspring conflict over the age of procreation: A life-history per-
754 spective. *Personality and Individual Differences*, 52(6):733–737.
- 755 Bell, A. V., Hinde, K., and Newson, L. (2014). Correction: Who Was Helping? The Scope for
756 Female Cooperative Breeding in Early Homo. *PLoS ONE*, 9(1).
- 757 Belsky, J. (2012). The Development of Human Reproductive Strategies Progress and Prospects.
758 *Current Directions in Psychological Science*.
- 759 Belsky, J., Steinberg, L., and Draper, P. (1991). Childhood experience, interpersonal develop-
760 ment, and reproductive strategy: An evolutionary theory of socialization. *Child development*,
761 62(4):647–670.
- 762 Birdthistle, I. J., Floyd, S., Machingura, A., Mudziwapasi, N., Gregson, S., and Glynn, J. R.
763 (2008). From affected to infected? Orphanhood and HIV risk among female adolescents in
764 urban Zimbabwe. *AIDS*, 22(6):759–66.
- 765 Bogaert, A. F. (2005). Age at puberty and father absence in a national probability sample.
766 *Journal of adolescence*, 28(4):541–6.
- 767 Cant, M. A. and Johnstone, R. A. (2008). Reproductive conflict and the separation of reproduc-
768 tive generations in humans. *Proceedings of the National Academy of Sciences of the United*
769 *States of America*, 105(14):5332–6.
- 770 Cant, M. A. and Shen, S.-F. (2006). Endogenous timing in competitive interactions among
771 relatives. *Proceedings. Biological sciences / The Royal Society*, 273(1583):171–8.
- 772 Cas, A. G., Frankenberg, E., Suriastini, W., and Thomas, D. (2014). The Impact of Parental
773 Death on Child Well-being: Evidence From the Indian Ocean Tsunami. *Demography*,
774 51(2):437–457.
- 775 Chen, X., Wen, S., Krewski, D., and Fleming, N. (2008). Paternal age and adverse birth
776 outcomes: teenager or 40+, who is at risk? *Human Reproduction*, 23(6):1290–96.
- 777 Chisholm, J. (1993). Death, Hope, and Sex: Life-History Theory and the Development of
778 Reproductive Strategies. *Current Anthropology*, 34(1):1–24.
- 779 Chisholm, J., Quinlivan, J., and Petersen, R. (2005). Early stress predicts age at menarche and
780 first birth, adult attachment, and expected lifespan. *Human Nature*, 16(3).
- 781 Clutterbuck, S., Adams, J., and Nettle, D. (2014). Frequent residential relocations cumulatively
782 accelerate menarcheal timing in a sample of english adolescent girls. *Journal of Biosocial*
783 *Science*.
- 784 Cooney, R. and Bennett, N. C. (2000). Inbreeding avoidance and reproductive skew in a coop-
785 erative mammal. *Proceedings of the Royal Society B*, 267(1445):801–6.

- 786 Crognier, E. and Baali, A. (2001). Do "helpers at the nest" increase their parents' reproductive
787 success? *American Journal of Human Biology*, 13(3):365–73.
- 788 Cyrus, C. C. Y. and Lee, R. D. (2013). On the evolution of intergenerational division of labor,
789 menopause and transfers among adults and offspring. *Journal of theoretical biology*, 332:171–
790 80.
- 791 Draper, P. and Harpending, H. (1982). Father absence and reproductive strategy: An evolu-
792 tionary perspective. *Journal of anthropological research*, 38(3):255–273.
- 793 Ellis, B. J. (2004). Timing of pubertal maturation in girls: an integrated life history approach.
794 *Psychological bulletin*, 130(6):920–58.
- 795 Ellis, B. J., Bates, J. E., Dodge, K. A., Fergusson, D. M., Horwood, L. J., Pettit, G. S., and
796 Woodward, L. (2003). Does father absence place daughters at special risk for early sexual
797 activity and teenage pregnancy? *Child development*, 74(3):801–21.
- 798 Ellis, B. J., McFadyen-Ketchum, S., Dodge, K. A., Pettit, G. S., and Bates, J. E. (1999). Quality
799 of early family relationships and individual differences in the timing of pubertal maturation
800 in girls: A longitudinal test of an evolutionary model. *Journal of Personality and Social
801 Psychology*, 77(2):387–401.
- 802 Emlen, S. (1995). An evolutionary theory of the family. *Proceedings of the National Academy
803 of Sciences*, 92:8092–8099.
- 804 Ermisch, J., Francesconi, M., and Pevalin, D. J. (2004). Parental partnership and joblessness
805 in childhood and their influence on young people's outcomes. *Journal of the Royal Statistical
806 Society: Series A (Statistics in Society)*, 167(1):69–101.
- 807 Flinn, M. (1988). Parent-offspring interactions in a Caribbean village: daughter guarding. In
808 Betzig, L., Borgerhoff Mulder, M., and Turke, P., editors, *Human reproductive behavior: A
809 Darwinian Perspective*, pages 189–200. Cambridge University Press, Cambridge.
- 810 Fraser, A., Brockert, J., and Ward, R. (1995). Association of young maternal age with adverse
811 reproductive outcomes. *New England Journal of Medicine*, 332:1113–1118.
- 812 Fretts, R., Schmittdiel, J., McLean, F., Usher, R., and Goldman, M. (1995). Increased maternal
813 age and the risk of fetal death. *The New England Journal of Medicine*, 333:953–957.
- 814 Geary, D. (2000). Evolution and proximate expression of human paternal investment. *Psycho-
815 logical bulletin*, 126(1):55–77.
- 816 Geronimus, A., Bound, J., and Waidmann, T. (1999). Health inequality and population variation
817 in fertility-timing. *Social science & medicine*.
- 818 Harris, J. (1999). *The Nurture Assumption: Why Children Turn Out the Way They Do*. Free
819 Press.
- 820 Hawkes, K. (1998). Grandmothering, menopause, and the evolution of human life histories.
821 *Proceedings of the National Academy of Sciences*, 95(3):1336–1339.
- 822 Hawkes, K. and Coxworth, J. E. (2013). Grandmothers and the evolution of human longevity:
823 A review of findings and future directions. *Evolutionary anthropology*, 22(6):294–302.

- 824 Hill, K. (1993). Life history theory and evolutionary anthropology. *Evolutionary Anthropology:*
825 *Issues, News, and Reviews*.
- 826 Hobcraft, J., McDonald, J., and Rutstein, S. (1985). Demographic Determinants of Infant and
827 Early Child Mortality: A Comparative Analysis. *Population Studies*, 39(3):363–385.
- 828 Hoier, S. (2003). Father absence and age at menarche. *Human Nature*, 14(3):2003.
- 829 Hrdy, S. (2009). *Mothers and others: the evolutionary origins of mutual understanding*. Harvard
830 University Press, Cambridge, MA.
- 831 Jennions, M. and Macdonald, D. (1994). Cooperative breeding in mammals. *Trends in Ecology*
832 *& Evolution*, 9(3):89–93.
- 833 Ji, T., Xu, J., and Mace, R. (2013). Intergenerational and Sibling Conflict Under Patrilocality.
834 *Human Nature*.
- 835 Johnstone, R. A. and Cant, M. A. (2010). The evolution of menopause in cetaceans and humans:
836 the role of demography. *Proceedings of the Royal Society B*, 277(1701):3765–71.
- 837 Jones, O. R., Scheuerlein, A., Salguero-Gómez, R., Camarda, C. G., Schaible, R., Casper, B. B.,
838 Dahlgren, J. P., Ehrlén, J., García, M. B., Menges, E. S., Quintana-Ascencio, P. F., Caswell,
839 H., Baudisch, A., and Vaupel, J. W. (2014). Diversity of ageing across the tree of life. *Nature*,
840 505(7482):169–73.
- 841 Kaplan, H. (1996). A theory of fertility and parental investment in traditional and modern
842 human societies. *American journal of physical anthropology*, 39:91–135.
- 843 Kaplan, H., Hill, K., Lancaster, J., and Hurtado, A. (2000). A theory of human life history
844 evolution: diet, intelligence, and longevity. *Evolutionary Anthropology*, 9(4):156–85.
- 845 Kiernan, K. E. (1992). The Impact of Family Disruption in Childhood on Transitions Made in
846 Young Adult Life. *Population Studies*, 46(2):213–234.
- 847 Koenig, W., Pitelka, F., Carmen, W., Mumme, R., and Stanback, M. (1992). The evolution of
848 delayed dispersal in cooperative breeders. *The Quarterly Review of Biology*, 67(2):111–150.
- 849 Komdeur, J. (1994). The effect of kinship on helping in the cooperative breeding Seychelles
850 warbler (*Acrocephalus sechellensis*). *Proceedings of the Royal Society of London. Series B:*
851 *Biological Sciences*, 256:47–52.
- 852 Kramer, K. (2005). Children’s help and the pace of reproduction: cooperative breeding in
853 humans. *Evolutionary Anthropology*, 14(6):224–237.
- 854 Lahdenperä, M., Gillespie, D. O. S., Lummaa, V., Russell, A. F., and Sorci, G. (2012). Severe
855 intergenerational reproductive conflict and the evolution of menopause. *Ecology letters*.
- 856 Leonetti, D. L. and Nath, D. C. (2009). Age at first reproduction and economic change in the
857 context of differing kinship ecologies. *American journal of human biology : the official journal*
858 *of the Human Biology Council*, 21(4):438–47.
- 859 Mace, R. (2008). Reproducing in cities. *Science (New York, N.Y.)*, 319(5864):764–6.

- 860 Mace, R. and Alvergne, A. (2012). Female reproductive competition within families in rural
861 Gambia. *Proceedings of the Royal Society B*, 279(1736):2219–2227.
- 862 Matchock, R. L. and Susman, E. J. (2006). Family composition and menarcheal age: anti-
863 inbreeding strategies. *American journal of human biology : the official journal of the Human*
864 *Biology Council*, 18(4):481–91.
- 865 Michael, R. T. and Tuma, N. B. (1985). Entry into marriage and parenthood by young men
866 and women: the influence of family background. *Demography*, 22(4):515–44.
- 867 Muniz, L., Perry, S., Manson, J. H., Gilkenson, H., Gros-Louis, J., and Vigilant, L. (2006).
868 Father-daughter inbreeding avoidance in a wild primate population. *Current biology*,
869 16(5):R156–7.
- 870 Nettle, D., Coall, D. a., and Dickins, T. E. (2011). Early-life conditions and age at first pregnancy
871 in British women. *Proceedings. Biological sciences / The Royal Society*, 278(1712):1721–7.
- 872 Nettle, D., Frankenhuus, W. E., and Rickard, I. J. (2012). The adaptive basis of psychosocial
873 acceleration: Comment on Beyond Mental Health, Life History Strategies articles. *Develop-*
874 *mental Psychology*, 48(3):718–721.
- 875 Palermo, T. and Peterman, A. (2009). Are female orphans at risk for early marriage, early sexual
876 debut, and teen pregnancy? Evidence from sub-Saharan Africa. *Studies in family planning*,
877 40(2):101–12.
- 878 Pasinelli, G. and Walters, J. (2002). Social and environmental factors affect natal dispersal and
879 philopatry of male red-cockaded woodpeckers. *Ecology*, 83(8):2229–2239.
- 880 Pesonen, A.-K., Rääkkönen, K., Heinonen, K., Kajantie, E., Forsén, T., and Eriksson, J. G.
881 (2008). Reproductive traits following a parent-child separation trauma during childhood: a
882 natural experiment during World War II. *American journal of human biology : the official*
883 *journal of the Human Biology Council*, 20(3):345–51.
- 884 Plas, E. (2000). Effects of aging on male fertility? *Experimental Gerontology*, 35(5):543–551.
- 885 Reeve, H., Emlen, S., and Keller, L. (1998). Reproductive sharing in animal societies: reproduc-
886 tive incentives or incomplete control by dominant breeders? *Behavioral Ecology*, 9(3):267–78.
- 887 Reeve, H. and Keller, L. (1995). Partitioning of reproduction in mother-daughter versus sibling
888 associations: a test of optimal skew theory. *American Naturalist*, 145(1):119–132.
- 889 Reeve, H. K. and Shen, S.-F. (2006). A missing model in reproductive skew theory: the bordered
890 tug-of-war. *Proceedings of the National Academy of Sciences of the United States of America*,
891 103(22):8430–4.
- 892 Rickard, I., Frankenhuus, W., and Nettle, D. (2014). Why Are Childhood Family Factors Asso-
893 ciated With Timing of Maturation? A Role for Internal Prediction. *Perspectives on Psycho-*
894 *logical Science*, 9(1):3–15.
- 895 Robson, S., van Schaik, C., and Hawkes, K. (2006). The derived features of human life history.
896 In Hawkes, K. and Paine, R., editors, *The Evolution of Human Life History*, pages 17–44.
897 School of American Research Press, Santa Fe.

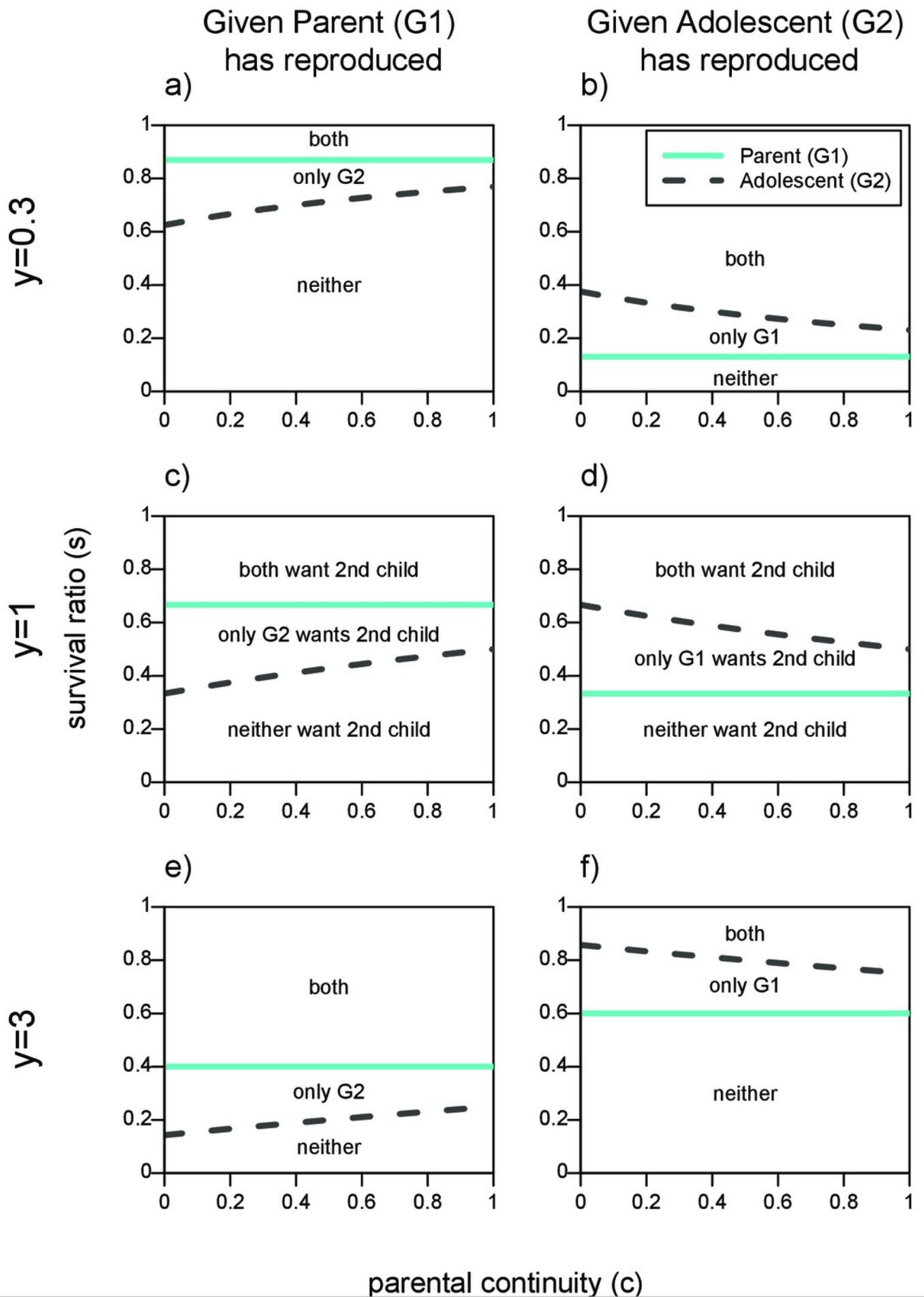
- 898 Sear, R. and Mace, R. (2008). Who keeps children alive? A review of the effects of kin on child
899 survival. *Evolution and Human Behavior*, 29(1):1–18.
- 900 Sear, R., Moya, C., and Mathews, P. (2014). The impact of kin on female fertility: a systematic
901 review. *Working Paper*, page 24.
- 902 Shenk, M. K., Starkweather, K., Kress, H. C., and Alam, N. (2013). Does absence matter? : a
903 comparison of three types of father absence in rural bangladesh. *Human Nature*, 24(1):76–110.
- 904 Sheppard, P., Garcia, J. R., and Sear, R. (2014a). A not-so-grim tale: how childhood family
905 structure influences reproductive and risk-taking outcomes in a historical u.s. Population.
906 *PloS one*, 9(3):e89539.
- 907 Sheppard, P. and Sear, R. (2012). Father absence predicts age at sexual maturity and repro-
908 ductive timing in British men. *Biology letters*, 8(2):237–40.
- 909 Sheppard, P., Snopkowski, K., and Sear, R. (2014b). Father absence and reproduction-related
910 outcomes in Malaysia, a transitional fertility population. *Human Nature*, 25(2):213–34.
- 911 Skjærvø, G. R. and Røskaft, E. (2013). Menopause: no support for an evolutionary explanation
912 among historical Norwegians. *Experimental gerontology*, 48(4):408–13.
- 913 Snopkowski, K., Moya, C., and Sear, R. (2014). A test of the intergenerational conflict model
914 in Indonesia shows no evidence of earlier menopause in female-dispersing groups. *Proceedings
915 of the Royal Society B*.
- 916 Stearns, S. (1976). Life-history tactics: a review of the ideas. *Quarterly review of biology*,
917 51(1):3–47.
- 918 Surbey, M. (1990). Family composition, stress, and the timing of human menarche. In Ziegler, T.
919 and Bercovitch, F., editors, *Socioendocrinology of primate reproduction*, pages 11–32. Wiley-
920 Liss, New York.
- 921 Surbey, M. (1998). Parent and offspring strategies in the transition at adolescence. *Human
922 Nature*, 9(1):67–94.
- 923 Teilmann, G., Pedersen, C. B., Skakkebaek, N. E., and Jensen, T. K. (2006). Increased risk of
924 precocious puberty in internationally adopted children in Denmark. *Pediatrics*, 118(2):e391–9.
- 925 Thomas, F., Renaud, F., Benefice, E., de Meeüs, T., and Guegan, J. F. (2001). International
926 variability of ages at menarche and menopause: patterns and main determinants. *Human
927 biology*, 73(2):271–90.
- 928 Tither, J. and Ellis, B. (2008). Impact of fathers on daughters' age at menarche: a genetically
929 and environmentally controlled sibling study. *Developmental psychology*, 44(5):1409–20.
- 930 van den Berg, P., Fawcett, T. W., Buunk, A. P., and Weissing, F. J. (2013). The evolution of
931 parentoffspring conflict over mate choice. *Evolution and Human Behavior*, 34(6):405–411.
- 932 Vehrencamp, S. (1983). Optimal degree of skew in cooperative societies. *American Zoologist*,
933 23:327–35.

- 934 Vikat, A., Rimpelä, A., Kosunen, E., and Rimpelä, M. (2002). Sociodemographic differences in
935 the occurrence of teenage pregnancies in Finland in 1987/1998: a follow up study. *Journal of*
936 *Epidemiology & Community Health*, 56:659–668.
- 937 Waynforth, D. (2002). Evolutionary theory and reproductive responses to father absence: Im-
938 plications of kin selection and the reproductive returns to mating and parenting effort. In
939 Tamis-Lemonda, C. and Cabrera, N., editors, *Handbook of father involvement*, pages 337–357.
940 Lawrence Erlbaum Associates: Mahwah, NJ, 1st edition.
- 941 Waynforth, D. (2012). Life-history theory, chronic childhood illness and the timing of first
942 reproduction in a British birth cohort. *Proceedings of the Royal Society B*, 279(1740):2998–
943 3002.
- 944 Waynforth, D., Hurtado, A., and Hill, K. (1998). Environmentally Contingent Reproductive
945 Strategies in Mayan and Ache Males. *Evolution and Human Behavior*, 19(6):369–385.
- 946 Webster, G. D., Graber, J., Gesselman, A., Crosier, B., and Orozco Schember, T. (2014). A Life
947 History Theory of Father Absence and Menarche : A Meta-Analysis. *Evolutionary Psychology*,
948 12(2):273–294.
- 949 Wells, J. (2007). Flaws in the theory of predictive adaptive responses. *Trends in Endocrinology*
950 *& Metabolism*, 18(9):331–7.
- 951 Winking, J., Gurven, M., and Kaplan, H. (2011). Father Death and Adult Success among the
952 Tsimane: Implications for Marriage and Divorce. *Evolution and Human Behavior*, 32(2):79–
953 89.

Figure 1

When actors should want a second infant in the household given one of them has already reproduced.

Areas are plotted as a function of survival ratio (s), parental continuity (c), and youth benefit (y). Areas above each actors line denote when it is in their fitness interest to add the second infant to the family. The text within the plots denotes which actors want the second infant.



parental continuity (c)

Figure 2

Cost of choosing strategy after the other actor has reproduced.

Fitness losses are plotted as a function of the survival ratio, s , of 2 versus 1 infant in the household. The solid line denotes the older generation (i.e. the *parent*), and the dotted line denotes the younger generation (i.e. the *adolescent*). 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 parental continuity 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 $c=0.25$ 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.

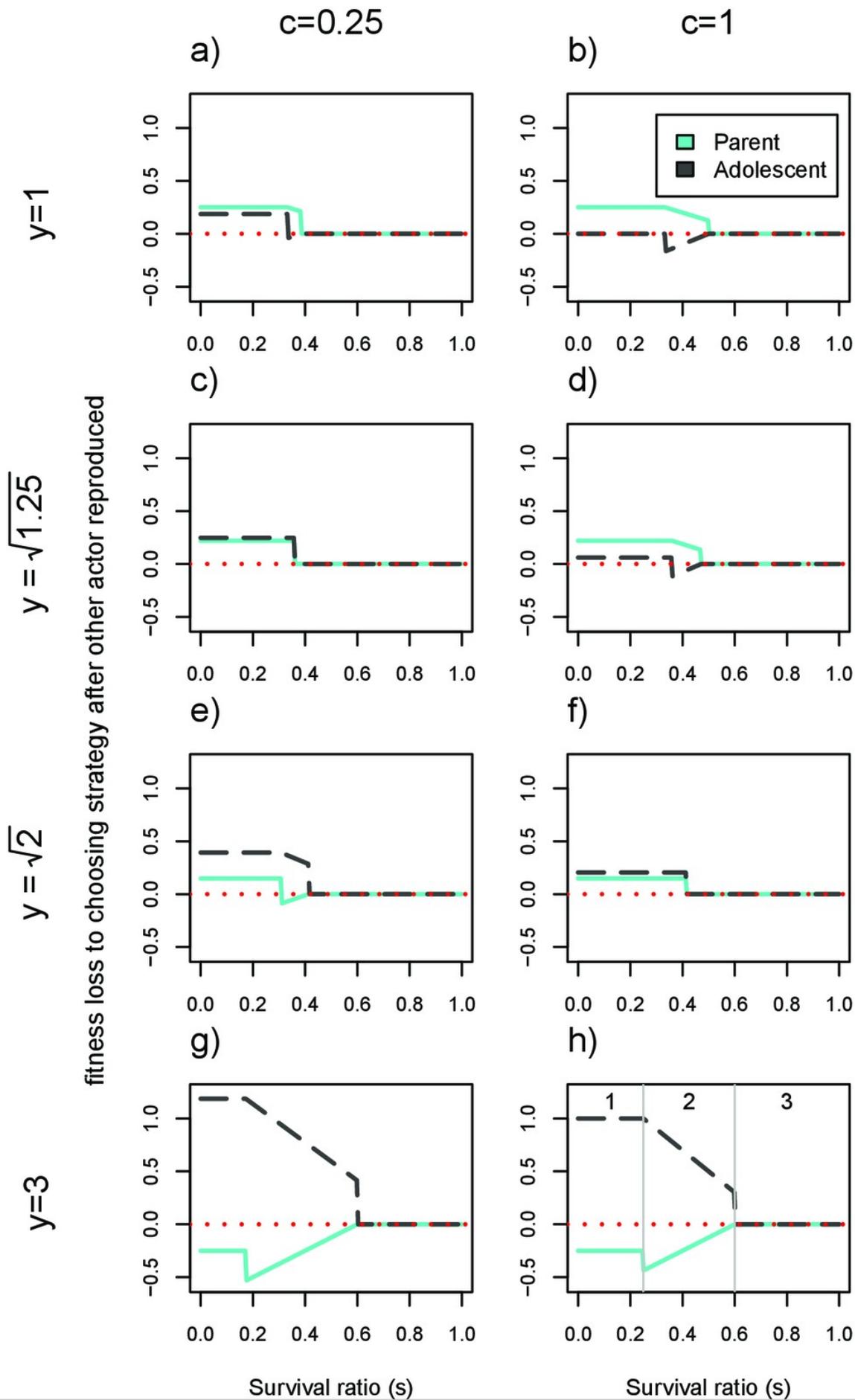


Table 1 (on next page)

Effects of different kinds of parental absences.

Effect of family structures on parental continuity (*c*), the presence of a non-kin actor in the household, a parent's experiencing mate search costs, and an adolescent's predicted age at first birth (AFB). Note: When incorporating mate search costs, adolescents would always experience these as well.

| Family Household Structure | Parental continuity (c) | Non-kin actor present | Marriage costs to parent | Adolescent's predicted AFB |
|---|--------------------------------|------------------------------|---------------------------------|-----------------------------------|
| Two genetic parents | ~ 1 | no | no | latest |
| Parent and step-parent | ~ 0 | yes | no | intermediate |
| Widowed single parent | 0 | no | yes | earliest |
| Other single parent (e.g. labor migrant or separated) | > 0 | no | maybe | intermediate |

Figure 3

Effect of other parent's absence (parental continuity, c , is 0 rather than 1) on *adolescent's* willingness to reproduce if her *parent* has done so, as a function of youth benefit.

Green and red curves denote minimum survival ratios (s) at which *adolescent* will reproduce, derived from equation 7. When the second parent is absent, the *adolescent* will reproduce for a larger part of the parameter space. The dotted grey line (plotted on the right axis) shows that the relative size of the parental absence effect increases with the youth benefit (y) --- i.e. the difference between these threshold levels of s when $c=1$ relative to $c=0$ as a percent of the effect when $c=1$ increases with y . Vertical lines mark the y -values above which the *parent* becomes more reticent to add a 2nd infant to the household than the *adolescent* for the respective parental continuity values.

