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Original Research Article

The Total Cost of Father Desertion

JEFFREY WINKING[1]* AND MICHAEL GURVEN[2]
[1]*Department of Anthropology, Texas A&M University, College Station, Texas 77843-4352*
[2]*Department of Anthropology, University of California, Santa Barbara, California 93106*

Objectives: The benefits of paternal investment have long been explored by assessing the impact of father's presence on child wellbeing. Previous studies, however, have only examined the average effect of father's presence on child survivorship. Here we assess the total fitness cost to men of deserting (or the benefit of staying), by considering effects on the entire progeny. We estimate the total number of children that a deserting father can expect to lose due to reduced survivorship over the life course in five populations, and compare this loss to the benefit gains from remarrying a younger wife.

Methods: We compiled the observed impacts of father's absence, as well as mortality and fertility schedules, for five foraging or foraging/horticultural populations. We calculate how many additional children a man can expect to lose due to father's absence throughout a marriage. We then calculate the minimum age difference between a first and second spouse that would be necessary to overcome this cost.

Results: Because child mortality rates drop so rapidly, the costs that men experience from desertion due to augmented child mortality are modest throughout marriage. Even hypothetically inflated father effects can be overcome with modest age differences between first and second spouses.

Conclusions: Returns to paternal investment in terms of increased child survival are not substantial compared to those received by successfully practicing a serial mating strategy. This suggests that factors other than the ability to enhance child survival, such as female choice, are important to the evolutionary history and continued adaptive functioning of men's unique reproductive strategies. Am. J. Hum. Biol. 23:755–763, 2011.

A hallmark of men's psychology and behavior is the evolved capacity for long-term pair-bonds and intensive paternal investment. The selective underpinnings that led to and maintain human marriage and investment patterns have been the subject of contentious debate (Gurven and Hill, 2009). As women age, their remaining reproductive value (sensu Fisher, 1930) declines, raising the conundrum: If men could gain fitness advantage from pairing with younger women of higher fertility, how could the romantic and paternal motivation to remain married to the same woman have been selected?

The provisioning model posits that the greater need of encephalized, altricial offspring provides large returns to familial investment, and that these more than make up for the opportunity costs to male fertility from remaining married to women of declining fecundity (Lancaster and Lancaster, 1987; Lovejoy, 1981; Winking, 2006). A major method for evaluating this model has been to evaluate differences in child survivorship or some other fitness-relevant outcome between those raised with and without fathers (Blurton Jones et al., 2000; Hurtado and Hill, 1992; Sear and Mace, 2008; Winking et al., 2011b). A substantial father effect presumably shows that men have the ability to enhance the wellbeing of their children, a hallmark criterion of the provisioning model. To date, these studies report mixed results concerning the effect of father's presence on the survivorship of children. To determine the overall fitness impact of desertion, however, the decrease in survivorship for all children in a father-absent family must be considered, not just the average effect per child. While average effects might be small, the cumulative effect over a large family may actually be quite substantial.

In this study, we apply the father-effect hazard ratio to baseline age-specific mortality rates for each child and sum the effects over the entire progeny for Tsimane forager-horticulturalists of Bolivia, as well as four hunter-gatherer populations originally discussed in Blurton Jones et al. (2000). These include the Ache of Paraguay, Hadza of Tanzania, !Kung of Botswana and Hiwi of Venezuela. For these populations, we calculate the total number of additional children expected to be lost to mortality due to father's absence. Such a sum varies across the life course of a marriage as the size and age structure of one's progeny changes.

The cost to desertion described above is weighed against the potential fertility increase from remarrying a younger wife. We calculate the minimum number of years younger a second spouse would have to be to overcome the loss of children due to the augmented mortality caused by desertion. This serves as a measure of the opportunity cost of remaining within a long-term relationship and not engaging in serial monogamy.

FATHERING IN HUMANS

Humans give birth to remarkably helpless infants who remain dependent for an extended period of time. Children are often born long before previous siblings are independent, resulting in large families that include children of varying levels of dependence. Men thus have a greater

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*Correspondence to: Jeffrey Winking, Department of Anthropology, Texas A&M University, College Station, TX 77843-4352.
E-mail: jwinking@tamu.edu

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opportunity than most other mammalian males to positively impact the wellbeing of offspring and the fertility of a mate (Hurtado et al., 1992; Marlowe, 2003). This line of reasoning, referred to as the provisioning model, posits that the greater need of women and children results in greater returns from family investment than could be obtained from alternative mating and investment strategies (Lancaster and Lancaster, 1983; Lovejoy, 1981). Furthermore, the universal practice of marriage facilitates the provisioning of biparental care by allowing men to invest in children they know to be theirs, and allowing couples to exploit the advantages of specialization and economies of scale (Lancaster and Lancaster, 1983).

Despite the straightforward logic of the provisioning model, many have called into question the ultimate functions of men's investment decisions (Bleige Bird et al., 2001; Hawkes, 1991, 1993; van Schaik and Paul, 1996). One empirical trend that seems to be at odds with the provisioning model is that children from fatherless households do not always fare substantially worse than those from households with fathers. If men invest in their children, then commensurate costs should be detectable upon the loss of a father to death, divorce or desertion. Yet, such a father effect is not always observed. While all studies that have explored the impact of maternal absence on child survivorship among natural fertility populations report a significant effect, only 7 of 22 studies found a significant positive effect of father's presence on child survivorship (Sear and Mace, 2008). The father effects that are detected are often less substantial than those found for mother absence (e.g., Winking et al., 2011b). Fewer studies have explored continuous outcomes of child wellbeing in natural fertility populations, although no father effect was found on children's height among the Yanomamo (Hames et al., 2005) or a rural Gambian population (Sear et al., 2000), and while children of divorced Yanomamo parents were found to have a higher incidence of ectoparasite infection in one study (Hagen et al., 2001), no father effects were found in general health in a separate study from the same population (Hames et al., 2005).

Despite the fact that many detected effects are minor, these are simply the average effect that each child experiences. Even small effects might thus lead to a substantial impact when summed over the entire progeny. The magnitude of this potential cost should vary through time along with the size and age structure of a man's progeny. Finally, to determine whether any effects are indeed "substantial," they must be compared to the opportunity costs experienced by fathers who are constrained in their ability to seek alternative reproductive opportunities.

METHODS

Calculation of total progeny loss

Child mortality declines substantially after the age of 5 years in subsistence populations. Furthermore, there was no discernible effect of father's absence beyond this age on Tsimane (Winking et al., 2011b) or Ache children (Hurtado and Hill, 1992). We therefore only consider children less than 5 years to be at greater risk of dying due to father absence. We start with the assumption of stationary populations and later include population growth in the models. Therefore, in any given year, the number of children at risk of greater mortality risk as a consequence of father's absence is given by Eq. (1):

$$\sum_{y=D-4}^{D} m_y l_{D-y} \tag{1}$$

in which D is the wife's age in the year of husband loss, m_y is the age specific fertility rate and l_y is the proportion surviving to age y. We consider fertility attained in the year of desertion (m_D) to also have been sired by the father. Equation (1) sums the previous 5 years of fertility, discounting each child by the likelihood of survival to the year in which the mother is age D. Without husband loss, parents could have expected the following number to have survived to the age of 5 years:

$$\sum_{y=D-4}^{D} m_y l_5 \tag{2}$$

as all children have an equal chance of living to 5 years. With father loss, however, they can expect the following number to survive:

$$\sum_{y=D-4}^{D} \left(m_y l_{D-y} \cdot \prod_{x=D-y}^{4} 1 - fq_x \right) \tag{3}$$

in which q_x is the age-specific mortality and f is the yearly father-effect hazard ratio. The left-hand term in (3) is Eq. (1) and represents all children who are at risk of dying before 5 years after father's absence. The right hand term calculates the probability of each child living to age 5 years given the augmented mortality associated with father's absence. The father-absent mortality levels begin at the year of desertion (D). Therefore, the cost of father loss due to increased offspring mortality, C, at any wife's age, D, is the following:

$$C_D = \sum_{y=D-4}^{D} m_y l_5 - \sum_{y=D-4}^{D} \left(m_y l_{D-y} \cdot \prod_{x=D-y}^{4} 1 - fq_x \right) \tag{4}$$

Comparative spouse fertilities

If a man were to remarry a woman aged D immediately after deserting his first wife, he would gain no additional fertility benefits from remarriage, yet would suffer from the loss of C_D, in addition to having to potentially invest in nongenetic offspring belonging to his new wife. Because we consider women's fertility only as a function of age (the m_y schedule), fitness gains from remarriage therefore require marrying a second wife that is younger than the first one. Using age-specific fertility rates for women, we can calculate what the minimum age difference between a current and alternative wife would have to be to provide a reproductive benefit that is greater than the cost of desertion (C_D). If we assume that men are responsible for the wife's fertility, the year of desertion, the remaining fertility of the current wife lost to her deserting husband is:

$$\sum_{y=D+1}^{65} m_y \left(\frac{l_y}{l_D} \right) l_5 \tag{5}$$

This is the remaining reproductive value of the current wife (the next year), multiplied by the probability of each child living to the age of 5 years. We use the wife's age of 65 as an upper limit as men tend to be a few years older than their first wives in these populations, and male fertility is likely to be negligible beyond this age.

If we define A to be the difference in age between the current wife and an alternative wife (such that A is the current wife's age minus the alternative), the additional number of surviving children that is gained by the man from remarrying is equal to:

$$B_A = \left[\sum_{y=D-A}^{65-A} m_y \left(\frac{l_y}{l_{D-A}}\right) l_5\right] - \left[\sum_{y=D+1}^{65} m_y \left(\frac{l_y}{l_D}\right) l_5\right] \qquad (6)$$

This assumes that the husband marries the new partner immediately. Note that the upper limit of the alternative wife is 65-A years. This assumes that the original wife's 65th year is the upper limit of the man's reproductive career, regardless of how young his second wife is. Thus, if a 60-year-old man marries a 20-year-old, he will not sire any offspring after the first wife reaches 65. Ultimately, this does not have a large impact on the model, however, as it only impacts much older men.

Thus for desertion and remarriage to result in a higher number of surviving children, the minimum age difference would be:

$$A_{\min} | B_A > C_D \qquad (7)$$

This inequality shows that desertion and remarriage will result in more surviving children when the additional fertility gained [Eq. (6)] is greater than the loss of children from the first marriage due to increased mortality [Eq. (4)].

Population data

Data were compiled from various sources to determine fertility and mortality profiles, as well as father effects and population growth rates for four foraging populations (the Ache of Paraguay, the Hiwi of Venezuela, the Hadza of Tanzania, the !Kung of southern Africa) and one forager-horticultural population (the Tsimane of Bolivia). For the Ache and Tsimane, survivorship for the first 5 years was estimated for children who resided with both parents. All other survivorship measures include all individuals. Father effects were calculated such that they equal the yearly hazard ratio in the first 5 years of life. For instance, if the reported measure equaled the hazard ratio over the first 5 years, Excel Solver was used to determine a standard yearly hazard ratio that resulted in the same 5-year hazard ratio after taking into account the population-specific mortality profile. The Tsimane father-effect measure is based on event-history analysis with numerous controls, while the others are simply calculated as a ratio of the mortality rates of children with and without fathers. Age specific mortality and fertility rates were smoothed using PROC LOESS in SAS with a smoothing parameter of 0.25. Below we provide a brief description of each population with an emphasis on marital and parental patterns. The ethnographic present is that during which the population-specific data were collected.

Ache

Ache data come from the pre-contact period during which they lived as foragers in the neotropical rainforest of eastern Paraguay (Hill and Hurtado, 1996; Hurtado and Hill, 1992). Ache men traditionally hunt nearly every day and acquire 87% of daily calories. Marriages are informal and fluid compared to the other populations, with women averaging 12.1 husbands throughout their lifetimes. The Ache believe that children can have multiple fathers. Approximately 63% of children had at least one secondary father, suggesting that marital sexual fidelity is not routinely practiced (Hill and Hurtado, 1996). The environment is such that mothers must dedicate substantial energy to protecting infants from numerous sources of danger. Infants are carried constantly and mothers must sleep while sitting up to ensure that infants are protected. Fathers have a significant impact on the survivorship of small children, although some of this effect is driven by lower rates of infanticide. This protection might simply be due to other individuals selecting fatherless children more often for ritual infanticide. While this might be indicative of a cultural understanding of the importance of paternal investment, it nevertheless exaggerates the apparent impact that paternal investment has.

Hiwi

The Hiwi are foragers who reside in the neotropical Savannas of Southwestern Venezuela. Demographic and behavioral data were collected by Hill and Hurtado in the late 1980s (Hurtado and Hill, 1990). The environment is marked by severe seasonality in rainfall, and foraging strategies vary throughout the year accordingly. Men produce the majority of daily calories, although women actually produce more during the wet season (Hurtado and Hill, 1990). Husbands engage mostly in hunting and women's collection is centered around roots, legumes and fruit, which are scarce for half of the year. Husbands and wives spend a great deal of time foraging together, and marriages are mostly monogamous and long-lasting. Women average 1.7 husbands throughout their lives (Hurtado and Hill, 1992). The environment offers relative safety for children and infants, particularly during the dry season, with few pests and cool temperatures.

!Kung

The !Kung are a well-known population that traditionally lived as foragers in the Kalahari desert of Southern Africa. The data presented here are based on research conducted by Howell and others from 1967 and 1969 (Howell, 1979). Marriages are moderately stable with women reporting an average of 2.45 husbands (ibid.). First marriages are typically arranged by parents and often end in divorce after a few weeks or months. Husbands and wives reside in a common dwelling with their children but typically separate during the day as men go off to hunt in groups and women forage for plant resources. There is debate concerning whether men or women produce more of the calories, depending on how the wage labor of men is considered. However, !Kung women produce more than the women in the three South American populations at almost all ages (Howell, 2010).

Hadza

Hadza foragers reside in the Savanna woodland of the Eastern Rift Valley in Tanzania (Marlowe, 2010). A typical day sees the men leaving to hunt and women leaving to

TABLE 1. Population parameters and sources of data

	Father effect ages 0–5	Father effect source	l_5	Survivorship source	TFR	Fertility source	r	r source
Ache	2.48	a	0.77	b	8.0	c	0.025	c
Hadza	1	d	0.63	e	6.2	f	0.013	g
Hiwi	1.12	h	0.66	i	5.1	j	0.009	k
!Kung	1.61	l	0.68	m	4.3	n	0.005	n
Tsimane	2.54	o	0.81	p	8.9	q	0.029	r

[a] Hurtado and Hill (1992). Yearly father effect was estimated from a hazard ratio of 2.13 for infancy and 2.75 for ages total mortality from 1 to 5.
[b] Baseline mortality for the first 5 years was estimated by estimating mortality rates of children whose parents did not divorce in Figure 2 of Hurtado and Hill (1992). For other years, mortality rates were taken from Hill and Hurtado (1996).
[c] Hill and Hurtado (1996).
[d] Blurton Jones et al. (2000).
[e] Blurton Jones et al. (2002).
[f] Hadza TFR of 6.2 (Dyson, 1977) was applied to the !Kung fertility profile from Howell (1979).
[g] Blurton Jones et al. (1992).
[h] Hurtado and Hill (1992). Yearly father effect was estimated from a hazard ratio of 1.1 for total mortality from 0 to 5.
[i] Hill et al. (2007).
[j] Hiwi TFR of 5.1 (Hurtado and Hill, 1987) was applied to the fertility profile of the similarly "fast" reproducing Agta (Early and Headland, 1998).
[k] Population growth estimate was based on l_{15} (Hill et al., 2007) and TFR (Hurtado and Hill, 1987) as outlined in Gurven and Kaplan (2007).
[l] Pennington and Harpending (1988). Father's absence was an inexact measure of the mother having more than one husband. It is unknown whether the child death succeeded the divorce. Father effect of 1.61 was based on a hazard ratio of 1.82 for infancy and 1.27 for childhood (ages 1 to 15). A yearly childhood hazard ratio of 1.33 was applied to years 1 to 5 to determine the over all father effect for <5.
[m] Mortality rates are based on 5-year estimates calculated by Gurven and Kaplan (2007), who used two sources of data detailed in Howell (1979). See Gurven and Kaplan for a description of the estimation process.
[n] Howell (1979).
[o] The odds ratio of 2.96 reported in Winking et al. (2011b) was applied to the base line mortality rates. This was roughly equivalent to a yearly hazard ratio of 2.54.
[p] Baseline mortality rates for ages 0 to 5 were calculated using only children whose fathers did not die or desert. For other years, mortality rates were taken from Gurven et al. (2007).
[q] McAllister L, Gurven M, Kaplan H. No date. Reproductive decision-making in the Bolivian Amazon: why do preferences not match outcomes?
[r] Unpublished data.

forage tubers early in the morning. Children often stay in camp with a caretaker, but can also accompany their mothers. The rolling landscape allows for easy observation and children are often able to forage plant foods near the camp, accounting for a substantial portion of their caloric intake (Hawkes et al., 1995a). Men and women contribute about equally to the diet, although men with small children contribute proportionally more (Marlowe, 2003). While their days are spent mostly separate, husbands and wives sleep in a common dwelling at night with their children, similar to the !Kung. Marital stability is estimated to be at a level between that of the !Kung and the Ache (Blurton Jones et al., 2000).

Tsimane

The Tsimane are a foraging/horticultural group who live in Amazonian rainforests of lowland Bolivia. The data reported here refer to data collected during the 2000s. Men produce approximately two-thirds of the calories (Kaplan et al., 2010), dividing their time roughly equally among hunting, fishing and garden labor (Gurven et al., 2009). Wage labor, an activity nearly exclusive to men, varies in importance depending on the proximity to the nearby town. Most of women's time spent in direct production consists of garden labor; women also account for the vast majority of food processing, childcare and domestic labor. After the first few years of marriage, divorce is extremely rare, and women average only around 1.4 spouses over their lifetimes (Winking, unpublished data). For 95% of men, the last birth of the wife (or wives) also marks the last child for the husband (Kaplan et al., 2010). Nuclear families typically reside in a common dwelling located close to those of other related families. While adults help other kin in garden labor, each family has its own identifiable horticultural fields.

RESULTS

Table 1 presents the effects of father's absence on the subsequent mortality of children, child survival to the age of 5 years, total fertility rate (TFR), population growth rates, and the sources of data for the five populations. These populations exhibit a great deal of variance in fertility and survivorship experience. The parameters exhibited by the five populations presented here encompass approximately 90% of the range in comparable fertility parameters and 60% of the range in survivorship parameters observed among 55 natural-fertility, subsistence-level populations (Gurven and Kaplan, 2007). This variance in demographic profiles is evident in Figures 1a, b, which show the age profiles of survivorship and fertility for each population. Differences are readily detectable between the low-mortality Tsimane (life expectancy at birth, $e_0 = 42$) and the high-mortality Hiwi ($e_0 = 27$), or the high-fertility Tsimane (TFR = 8.9) and the low-fertility !Kung (TFR = 4.2).

Figure 2 presents the total expected loss of children (C_D) by women's ages for the five study populations. Figure 2a uses the reported hazard ratio associated with father loss for each population (given in Table 1), whereas Figure 2b uses a hypothetical inflated hazard ratio of five, nearly twice that of the maximum observed father effect among these populations. Based on the observed effects, the maximum number of offspring expected to be lost due to father desertion is just above 0.2. Remarkably, the hypothetical hazard ratios still result in relatively minor losses from father desertion (maximum 0.70 for HR = 5). The cumulative father effect is small because child mortality rates drop to very low levels after the first 2 years, such that even high hazard ratios result in low absolute increases in mortality.

Figure 3 presents $A_{\min}$ by age D of the first wife, given observed and hypothetical father effects from Figure 2. The plot shows that the fertility costs due to greater offspring mortality are overcome by only minor differences in the ages of first and second spouses for both reported and exaggerated effects. Even with a hypothetical father effect of HR = 5, the minimum age difference is only 1–3 years for the majority of the marriage span. Fertility declines rapidly throughout the forties, resulting in fewer

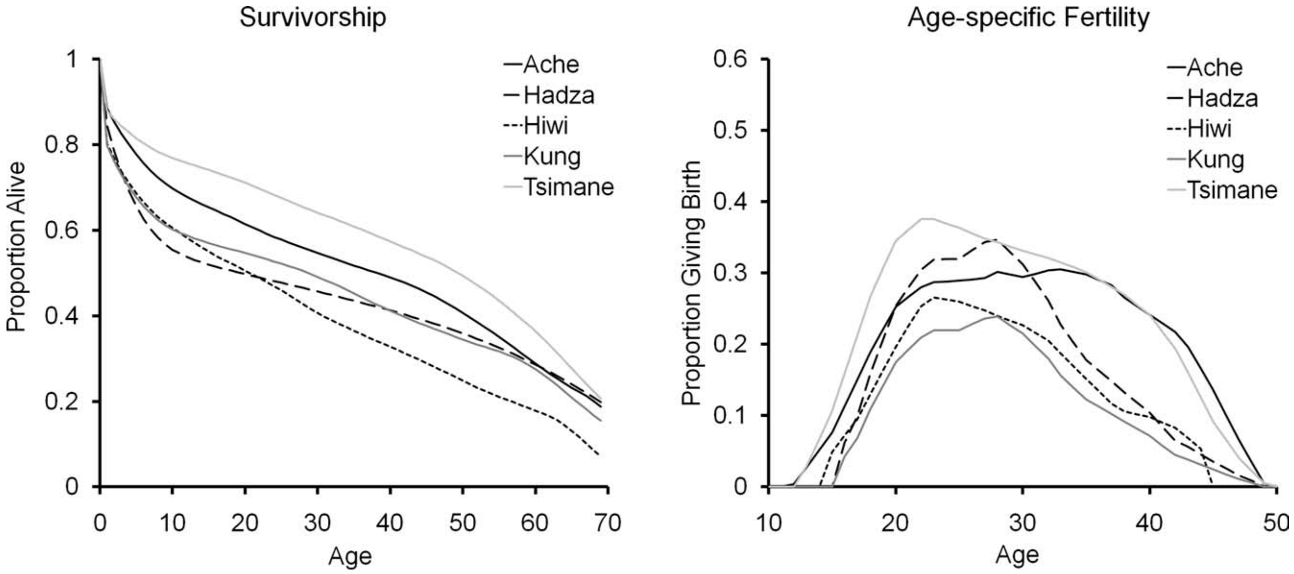

Fig. 1. Population survivorship and women's age-specific fertility of the five populations.

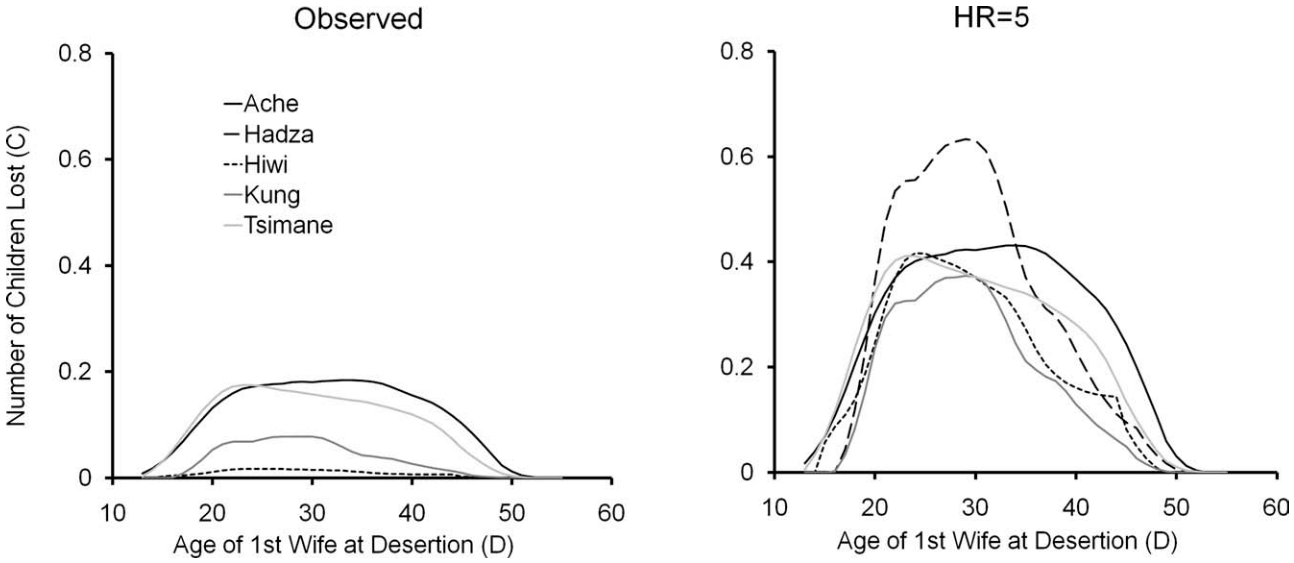

Fig. 2. Number of children lost to augmented mortality due to father loss by wife's age at loss.

young children, and smaller offspring mortality effects. Eventually, C_D becomes less than the last remaining year of non-zero fertility (the year before menopause), and $A_{\min}$ rises linearly with age, as it equals the age difference required to marry a second wife with non-zero fertility. To further explore the sensitivity of the model to the different parameters, we combined the most extreme child-mortality profile (Hadza) with the lowest fertility profile (!Kung), and the highest father-effect (Tsimane). The results remain largely unchanged. Of the 27 years prior to the linear increase associated with menopause, the minimum age difference was 1.0 for 19 of the years and 2.0 for 8 of the years.

Because these groups are not stationary but are undergoing population growth, $A_{\min}$ is also calculated after discounting future fertility by population growth rates (Fig. 4). As populations grow, fertility contributes proportionally less to the population and is therefore discounted by the inverse of population growth. This is done by multiplying age specific fertilities by e^{-rt}, with 4 years prior to D set to $t = 0$, as this is the first fertility that is included in any calculations. Age-specific fertilities are multiplied by this discounting factor in both the calculations of existing children (at time D) as well as the future fertility to be lost by the first wife and to be gained by the second wife. This increases $A_{\min}$ slightly as the future fertility of a second wife is discounted compared to earlier-born existing children. Despite this adjustment, $A_{\min}$ still hovers around one for observed levels. For the hypothetical father effect of $\text{HR} = 5$, $A_{\min}$ early in the marriage reaches

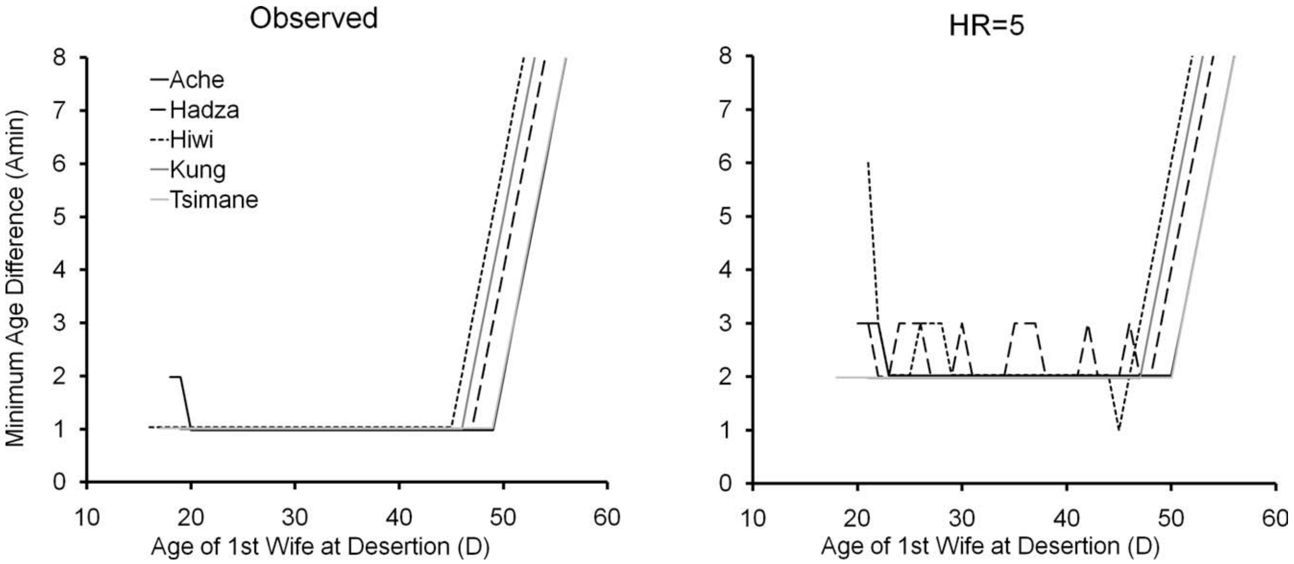

Fig. 3. Minimum age difference between first and second spouse in which fertility gained is greater than children lost due to father death (desertion).

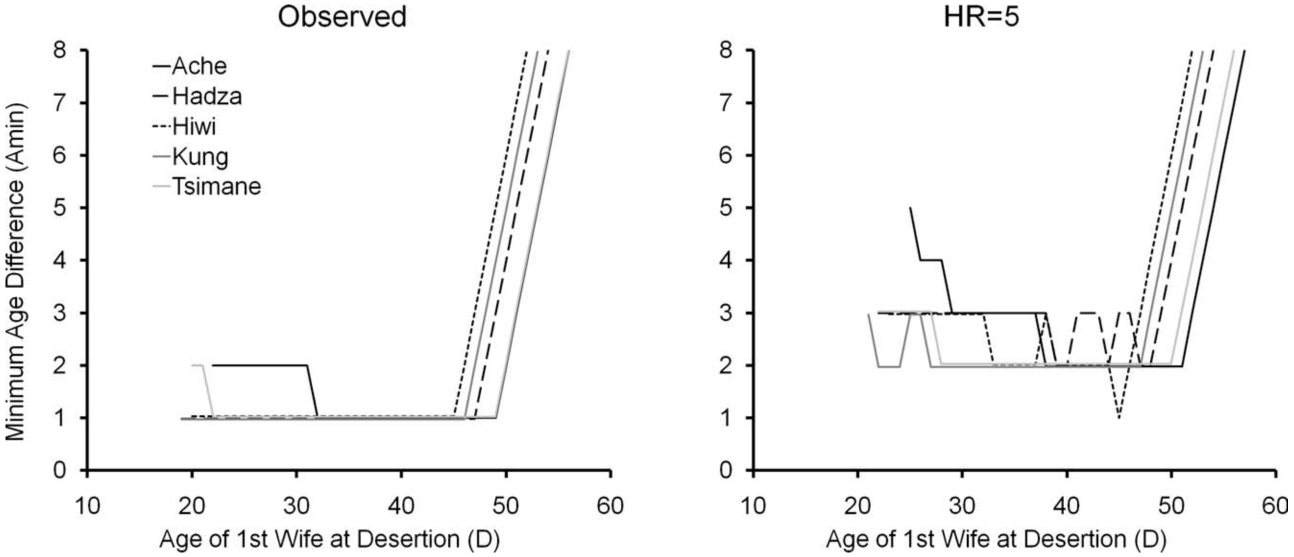

Fig. 4. Minimum age difference between first and second spouse in which fertility gained is greater than children lost due to father loss after discounting for population growth.

as high as five in some populations but remains between one and three for the majority of marriage.

DISCUSSION

We have considered a range of high to low fertility populations of foragers and horticulturalists whose demographic profiles may be the most representative of ancestral hunter-gatherer patterns. If ancestral population parameters throughout the selective history shaping men's capacities for long-term romantic attachment and paternal concern fell within the ranges presented here, our findings suggest that it is unlikely that these long-term pair bonding strategies were selected solely because of the greater benefits conferred via increased offspring survivorship. Based on the observed father effect affecting children from the first marriage, marrying a second wife who is younger by just 1 or 2 years would result in higher reproductive success. Thus, returns to paternal investment are not substantial compared to those received by successfully practicing a serial mating strategy at any point during the reproductive phase of the marriage. This suggests that either there are substantial costs or challenges to obtaining younger partners, and/or there are substantial benefits of staying within a marriage other than increasing the survival of children. We examine these two possibilities below.

Firstly, it should be noted that there are weaknesses to our modeling approach. To increase interpretability and deal with data limitations, we did not include the full range of relevant parameters, such as year-specific father effects, declines in father fecundity, and the additional potential cost of investing in step-offspring from the new wife's previous marriage. Nor did we include alternative scenarios, such as the possibility of men adding wives to form a polygynous union. However, the majority of family compositions in our sample, and of hunter-gatherers more generally, are monogamous (Kaplan and Lancaster, 2003), and we intended to explore why men might refrain from abandoning parental and marital responsibilities, which would also apply to polygynous unions. Determining under what circumstances it is beneficial to add an additional wife is a related, but separate problem. It is also possible that the father effects and demographic profiles observed in current populations may not reflect earlier patterns. The relatively minor impacts that fathers have in the five populations might be due to widespread resource pooling that is characteristic of the "cooperative breeding" or "pooled energy budgets" of human social systems (Hrdy, 2005; Kramer, 2010). Such redistribution and pooling acts to reduce the negative impact of father desertion on child survivorship and wellbeing. The fact that single mothers can recruit the investment of parents, siblings, and future husbands must diminish the negative impact of father desertion. When these avenues are lacking, as they might have been ancestrally, a father's aid might prove more valuable. Research focusing on Western populations, who more frequently lack access to such kinship networks, have identified numerous measures of wellbeing that are negatively impacted by father's absence (Lamb, 1997). Interestingly, the presence of a grandparent eliminates some of these effects (Deleire and Kalil, 2002). Future research will need to focus on disentangling the numerous predictors of within-population father effects.

There are many unaccounted-for benefits that potentially make staying more worthwhile, which might reconcile the results of the model with observed patterns of long-term pair-bonding. Having multiple children within a single family provides certain advantages compared to the step-families that are created by serial monogamy. There is less opportunity for conflict when husbands and wives share equal genetic relations to the progeny, and they might thus enjoy greater cooperative efficiency (Kaplan and Lancaster, 2003). Furthermore, the returns to nondepreciable paternal investment (e.g., protection, construction, clearing agricultural fields, etc.) increases with each additional biological child who benefits from such investment. Fathers might also improve the chances that their adult children marry and reproduce successfully, either by improving child skills on the marriage market, or by explicit aid in arranging marriages (Scelza, 2010; Winking et al., 2011a). By their late 30s, fathers may also be in a position to help support grandchildren.

Additional benefits to marriage may be in forms other than increased child wellbeing. For instance, pair-bonds are common in nonhuman primates even in the absence of paternal care, suggesting they often develop to serve other functions or as a response to socio-ecological constraints. Such pair-bonds might be predicated on the distribution of females (Cluttonbrock, 1989), the dynamics of male-male competition and mate guarding (Hawkes et al., 1995b), low variance and high lethality in male competitiveness (Chapais, 2008; Preuschoft and Paul, 1999), or the need for male protectors of females and infants (Mesnick, 1997; Palombit, 1999). If pair-bonding provides other forms of benefits, or if the arrangement becomes established as the most common strategy (a system which might be resistant to invasion by alternative strategies), the investment pathways for men's surplus production might be limited, and paternal investment may be the most beneficial avenue, despite a seemingly low return (Chapais, 2008).

Our model assumes that men switch immediately to an alternative spouse, and this might characterize a substantial proportion of opportunistic desertions by husbands. However, remarriage is not an available option for all men. For instance, among the Tsimane, the death of a wife had a substantial negative impact on the probability of the husband reproducing within the subsequent 10 years, suggesting that finding a spouse later in life is not something that can be done with great ease (Winking et al., 2011a). The ability to marry a second spouse will be affected by the availability of marital partners and is thus dependent on the age and sex distribution of the adult population, existing divorce rate, adult mortality rate, mate choice criteria, and the willingness of younger never-been-married women to marry older men. There is undoubtedly a great deal of variance in this willingness of young women to accept an older spouse. While such arrangements were traditionally the norm in numerous Australian populations (e.g., Burbank, 1988), among the Tsimane, for example, 85% of married couples were within 10 years of age of one another. In developing countries, median age differences range from 2.5 in the Philippines to 9.8 in Mauritania (Casterline et al., 1986). The fact that $A_{\min}$ tends to be very low suggests that the minimum age difference between men and potential second wives (i.e., 1 or 2 years greater than that between men and their first wives) would not be great enough to deter women from accepting these men; however, many of these women might not be available for marriage. In many populations, therefore, men simply do not have many options even if they wish to remarry. Below, we explore why men might experience greater constraints in their abilities to find additional partners.

While the modeling approach taken in this article is admittedly androcentric, a corollary study needs to explore the impact of a husband's investments on a woman's reproduction and child survival, compared to the opportunity costs imposed on pair-bonded women. Many models have been proposed to explain why men may have been motivated to forgo alternative mating strategies to pursue long-term pair-bonds; however, women are often viewed as passive beneficiaries of this development. Yet, despite the valuable contribution of men's investments to the economics of reproduction, there are clearly costs incurred by women from tying their reproduction to a single man. These are largely in the form of reduced genetic diversity of one's progeny and restricted choice imposed by the need to consider a suitor's resource potential and willingness to invest (Quinlan, 2008). Indeed, Gangestad and Thornhill (2008) argue that the loss of conspicuous estrus in humans was selected to mediate these costs by allowing women to surreptitiously pursue extra-pair sires. If so, illegitimate children of unknowingly cuckolded men should fare better in survival or reproduction, given that their mothers were not subject to such constraints when choosing the biological fathers of their children as lovers.

The fact that women in most cultures seem to prefer to reproduce within biparental unions suggests that the tradeoff is typically worthwhile. Not only do the children of married women benefit from the additional care of men, but, perhaps more importantly, women's fertility is boosted by their partners' investments (Marlowe, 2001). Instead of questioning what factors led pair-bonding and parental provisioning to be a more effective strategy for men compared to more mating-effort based strategies (e.g., Chapais, 2011; Hawkes et al., 1995b; Hurtado and Hill, 1992), it would be equally as fruitful to explore what factors led pair-bonding to be preferable to women. Such a preference may have been selected as the evolution of increasingly encephalized and altricial children placed such a reproductive burden on women that it became worthwhile to trade-off the genetic quality of children for additional investment. Female preference for high-investing men may have led to a demand for costly indicators of long-term intent (e.g., courtships, celebrations, love). This would simultaneously increase the incentive for men to offer investment and reduce the gains from pursuing additional partners. Additionally, if women sought similarly-aged men to assure long-term investment, men would eventually be constrained in their ability to remarry as they aged.

The early evolutionary arguments concerning long-term pair bonds and nuclear family formation, while clear and logical, now seem in need of modification. Blurton Jones et al. (2000) noted some time ago that the impact of fathers on offspring wellbeing was not a good predictor of pair-bond stability among the four foraging populations reviewed in their study and in this article. Accounting for the entire progeny effect and the addition of a fifth population did not improve this association. The ranking of average total progeny loss due to father desertion (from highest to lowest: Ache, Tsimane, Kung, Hiwi, Hadza) is not associated with pair-bond stability (from highest to lowest: Tsimane, Hiwi, Kung, Hadza, Ache). However, we do not believe that the benefits of paternal investment conferred to children are unimportant to this story. It is clear that fathers exhibit paternal investment and have the capacity for genuine paternal concern (Gray and Anderson, 2010; Hewlett, 1992; Winking et al., 2009), although the benefits of such investment might be mostly in the form of higher partner fertility. Fathers frequently continue to offer parental support after the death of or divorce from the mother, and continue to do so after the mother has reached menopause. Despite the ubiquity and the importance of fathering, however, adaptive models must take into account the constraints faced by men, particularly those imposed by women's preferences (and those of their families), how these constraints impact the relative returns to different strategies available to men, and how these interactions ultimately shape human reproductive patterns.

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