

Paternity uncertainty overrides sex chromosome selection for preferential grandparenting

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Abstract

With respect to autosomal genes, a grandparent is equally related to male and female grandchildren. Because males are heterozygous for sex chromosomes, however, grandparents are asymmetrically related to male and female grandchildren via the sex chromosomes. For example, the Y chromosome from the paternal grandfather passes directly down to grandsons. This asymmetry leads to a prediction that genes on the sex chromosomes could drive differential grandparental care. Alternatively, the paternity uncertainty hypothesis for differential grandparent care brings about a different set of predictions. A grandfather, for example, has two degrees of uncertainty to his son's children but only one to his daughter's children. Thus, under high extra-pair paternity rates, paternity uncertainty predicts that a grandfather will favor his daughter's children over his son's children. A paternity uncertainty vs. a genetic relatedness hypothesis was tested using data from questionnaires asking adult grandchildren to rate the amount and quality of care of their various grandparents. We found no support for preferential care based on expected sex chromosome similarities. Instead, our data were in general accord with the predictions of the paternity uncertainty hypothesis of grandparental care. A model is presented to predict the rates of

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extra-pair paternity required in a population to have the effects of paternity uncertainty outweigh sex chromosome effects.

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1. Introduction

Using his (now) eponymous rule, Hamilton (1963, 1964) described the conditions necessary for seemingly altruistic acts to be evolutionarily beneficial: altruism is selectively advantageous when the fitness cost to the altruist is less than the benefit received by the recipient, devalued by the degree of relatedness between the interactors. Hamilton's rule, also called kin selection theory, is a pillar in the study of social behavior and has been foundational in the evolution-based study of human behavior (see Dugaktin, 1997; Getz, Page, & Starks, 2001). Here we use Hamilton's rule to make and test predictions regarding grandparental care.

Kin selection has previously been used to explain grandmother care and the evolution of menopause (Kaplan, Hill, Lancaster, & Hurtado, 2000; Lahdenpera et al., 2004; O'Connell, Hawkes, & Blurton Jones, 1999; Shanley & Kirkwood, 2001; Williams, 1957). The predictive power of kin selection, however, can be applied to all grandparents. If one considers only autosomal genes, biological grandparents are symmetrically related to all of their male and female grandchildren. The same cannot be said with respect to the sex chromosomes (see Fig. 1). Because males are heterozygous for the sex chromosomes, paternal grandparents are not symmetrically related to male and female grandchildren. Similarly, for the sex chromosomes, grandmothers are more related to granddaughters than grandsons, whereas grandfathers are on average more related to grandsons than granddaughters. By extension, paternal grandmothers (PGMs) are more closely related to

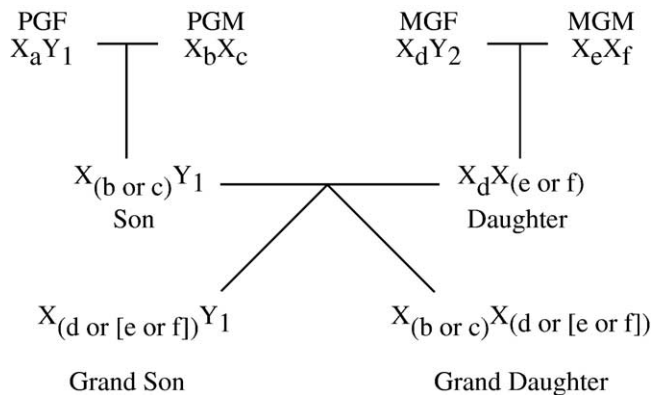


Fig. 1. Schematic representation of grandparent–grandchild lineage with respect to sex chromosomes. X and Y refer to sex chromosomes, and letters and numbers refer to different chromosomes, respectively.

granddaughters than are maternal grandmothers (MGMs), and paternal grandfathers (PGFs) are more closely related to grandsons than are maternal grandfathers (MGFs). Indeed, the Y chromosome from the PGF can be followed directly down to their grandsons. [It should be noted that a small region of the Y chromosome is known to exchange material with the X chromosome during meiosis (Graves, 2005); in this paper, we regard this region as part of the autosomal genome.] We propose that these sex-based asymmetries of relatedness that exist between different grandparent–grandchild dyads provide grounds for predicting kin-selective benefits of differential treatment of grandoffspring driven by genes residing on the sex chromosomes.

If one considers paternity assurance as the major factor in grandparental solicitude, a different set of predictions can be made. Because humans are internally gestating animals, the MGM has zero degrees of uncertainty regarding her biological relationship with her daughter's children (see Fig. 2). Maternal grandfathers and PGMs each have one degree of uncertainty, whereas PGFs have two degrees; for each male in the reproductive line, there exists one degree of uncertainty of him being the biological father. Given the paternity assurance asymmetries, one would predict that the MGM would provide relatively more care for grandoffspring, regardless of sex, than both the MGF and PGM, and all would provide relatively more care than the PGF (Euler & Weitzel, 1996; Laham, Gonsalkorale, & von Hippel, 2005; Smith, 1988). Here we test two hypotheses for grandparental care: the *paternity uncertainty hypothesis*, where differential investment in grandchildren is predicted according to the level of paternity uncertainty (see Fig. 2), and the *sex chromosome selection hypothesis*, where differential investment in grandchildren is predicted in accordance with the asymmetries of relatedness that exist between grandparents and grandchildren for the X and Y chromosomes (see Fig. 1).

Both the sex chromosome and paternity uncertainty hypotheses of differential grandparental care are influenced by the degree of extra-pair paternity in a population. If sex chromosome selection has an effect in differential grandparent care, a certain level of paternity assurance must exist for a PGF to reap fitness payoffs by caring for his grandsons

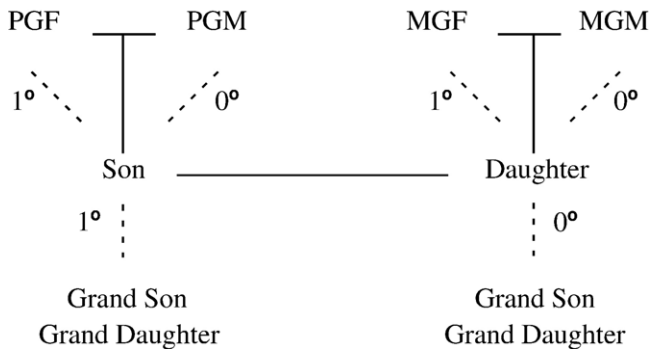


Fig. 2. Degree of paternity uncertainty. Schematic representation of grandparent–grandchild lineage with respect to paternity assurance. Solid lines indicate marital and parental relationships; dotted lines indicate paternity assurance. 1° indicates that the parent cannot be certain of the biological relationship, and 0° indicates complete certainty.

preferentially over granddaughters. At a level of paternity uncertainty calculated under a particular set of assumptions, however, the advantage of differential solicitude disappears because uncertainty of all the autosomal chromosomes, including that of the Y chromosome itself, outweighs the lineage of the one sex chromosome. Here we present a model to predict the point where paternity uncertainty outweighs sex chromosome selection in differential grandparent care.

2. Method

2.1. Collection of data

Studies in grandparent care have fallen into two major approaches, with positive and negative aspects of each. The first approach centers on the examination of historical records (Jamison et al., 2002; Lahdenpera et al., 2004; Ragsdale, 2004; Volland & Beise, 2002) and demographic information of current populations to gather anthropomorphic data that include, among other measurements, statistics on survivorship of grandoffspring in the presence of grandparents (Hawkes, 2003; Hill & Hurtado, 1996; Sear, Steele, McGregor, & Mace, 2002; see Clarke & Low, 2001, for a discussion of this technique). The second approach uses questionnaires to get information on modern living populations (e.g., Euler & Weitzel, 1996; Hartshorne & Manaster, 1982; Hoffman, 1979–1980; Kennedy, 1990; Matthews & Sprey, 1985). Historical populations are thought to more closely resemble the conditions of ancestral humans, without the use of modern medicine or contraceptive techniques. Use of historical and demographic information provides objective measures—life and death—to test the effects of a grandparent on the survivorship of their grandchildren. The measured effect is indirect, however, in that it only correlates the presence of the grandparent with the survival of the grandchild and only covers extreme cases of negative care (death of the grandchild). Use of living populations, on the other hand, provides room for more subtle differences in the levels of grandparental care. At the same time, the measure is more subjective, in that the subjects are asked to rate grandparent care based on their memories from childhood. This metric is more sensitive and, thus, more valid to detect preferential grandparental investment than questioning the grandparents themselves (Euler & Weitzel, 1996; Hoffman, 1979–1980) due to social expectations that grandparents ought to give equal care for all grandchildren. As we wanted to explore some of the more subtle differences in grandparental care, with a close examination of a few key dyads, we chose to use questionnaire data from two sources.

Analysis was done on a combination of previously published (Euler & Weitzel, 1996) and unpublished German data sets from one of the authors (H.A.E.). Questionnaires were collected from 1050 males and 1915 females (plus 3 unknown) for a total of 2968 participants. Participant ages ranged between ages 16 and 80 years. Those participants younger than 40 years were mostly enrolled in undergraduate courses at the University of Kassel, whereas those over 40 years were almost all members of the community recruited by the student participants; the community members generally filled out the questionnaires at

home. Return rates were 99% for the students and 60% for the community participants. Mean age for the participants was 25.6 years, with a median age of 21.5 years. Data are for those respondents who had all four grandparents alive until at least the age of 7 years. This sample consisted of 455 males and 889 females.

Participants were asked to respond using a scale from 1 (not at all) to 7 (very much) about how much each grandparent had cared for them until the age of 7 years. Other questions about grandparental life status (married, divorced, separated, widowed, or dead), socio-economic status of the family, and proximity of residence (in kilometers) were asked. The grandchildren were also asked how much they resembled each grandparent in both appearance and character or behavior. For the purposes of this study, we focus primarily on the question of amount of grandparental care. Although this approach may omit some early memories, it still provides a good measure of quantity of care from each grandparent relative to the other grandparents. Each of the eight dyads of grandparent–grandchild relationships were tested for mean rating of grandparental care. *t* tests were performed to test the interaction of grandparent and the sex of the grandchild. Additional *t* tests examined the differences between grandparents, with a focus on the comparison of the PGF–grandson dyad with the MGF–grandson dyad.

Additional data from an American sample were extracted from an unpublished PhD thesis (Shea, 1987) and analyzed for the interaction of the sex of the grandchild with the lineage and sex of the grandparent. Questionnaires were collected from 731 10th grade students (359 male, 372 female) in randomly chosen school districts in Virginia, with a 99% response rate. Questionnaires were then sent to all of the students' living parents and grandparents for whom addresses could be obtained. A total of 404 parent questionnaires and 492 grandparent questionnaires (168 male, 324 female) were completed and returned. The response rates for parents and grandparents were 33% and 51%, respectively. Median age of grandparents was 67.7 years (see Shea, 1987, for more demographic information).

Students were asked to check all of the adjectives from the following list that described time spent with each grandparent: enjoyable, satisfying, tense, stimulating, unpleasant, boring, interesting, and frustrating. Responses were tabulated with the following scale: 1—only negative descriptors checked; 2—more negative than positive descriptors; 3—equal number of positive and negative descriptors; 4—more positive than negative descriptors; 5—only positive descriptors. As an alternative approach to determining grandparental care, students were also asked to respond using a scale from 1 (*every day*) to 6 (*once a year*) to the question of how often they would choose to see each living grandparent if they had their way. Analysis was done on the grandparent–grandchild dyads using factorial analysis of variance with repeated measures. Dependent *t* tests were conducted to make pairwise comparisons of mean scores.

2.2. Model

2.2.1. Traits and relative fitness

In order for the effects of paternity uncertainty to outweigh the effects of sex chromosome selection, a certain amount of extra-pair paternity needs to be present in the

population. We have crafted a model to determine the point where extra-pair paternity becomes the dominant factor in differential care (see also Gaulin, McBurney, & Brakeman-Wartell, 1997; Russell & Wells, 1987). A model that can be used to assess the evolutionary consequences of different grandparental strategies requires that we first calculate the probabilities of alleles for grandparental strategy traits being passed on by descent to various grandchildren and then characterizing how implementation of these traits impacts the fitness of the grandchildren.

For notational convenience, rather than extending the mnemonic designators PGM, MGF, and the like, to include the gender of the grandchild, for the model, we use the more concise triplets GPC, where the genders of G (grandparent), P (parent), and C (child) can be F (female) or M (male), to represent the eight different types of grandparent/grandchild relationships that arise. Thus, for example, FMF is the PGM/granddaughter relationship, whereas MFM is the MGF/grandson relationship.

The probability of an allele being passed down by descent varies depending on whether the allele is at an autosomal (denoted by A) or sex-linked (X or Y as applicable) locus. We define P_{GPC}^B to be this probability, where G, P, or C is F or M, and B represents the locus for the allele, either A, X, or Y. Then, under random segregation of genes, the probabilities of alleles that are identical by descent (IBD) without and with extra-pair paternity are given in Table 1.

Our baseline assumption is that all individuals prior to consideration of grandparental investment are equally fit. We then assume that each grandparent has four units to invest in each of his or her four types of grandchildren but can distribute these evenly or unevenly. We use the notation r_{PC} to represent the relative investment of a grandparent in a grandchild arising from the lineage P, C, where P,C=F or M. Specifically, PC=FM is the maternal grandson, whereas PC=MF is the paternal granddaughter of the grandparent in question. Let the quadruplet $(r_{FF}, r_{FM}, r_{MF}, r_{MM})$ represent the distribution of a particular grandparent's investment, where $r_{FF} + r_{FM} + r_{MF} + r_{MM} = 4$.

Assume that if a grandparent invests r units in a particular grandchild, then the grandchild's fitness is increased from 1 to $1+r\phi$, where $\phi > 0$ is the "fitness value" of an investment of one unit. This grandchild fitness measure should be interpreted as the change in the proportional representation of alleles at low frequencies from the grandchildren's to the great-grandchildren's generation; that is, if the allele has a frequency of $k\%$ in the grandchildren's generation, it will have a frequency of $k(1+r\phi)\%$ in the great-grandchildren's generation, assuming k is less than a few percent. (Note, we make this low frequency assumption because the ensuing analysis is only valid for an allele invasion scenario, and we do not have to worry about saturation affects of allele frequencies as they approach fixation). This approach represents a linear-return-to-scale assumption, but one might well imagine situations where additional units of investment in a particular grandchild will yield either increasing or decreasing returns-to-scale. We now define $W_G^B(p, \phi; r_{FF}, r_{FM}, r_{MF}, r_{MM})$ to be the relative fitness of an allele at a B-type locus (B=A, X, or Y) in a grandparent (G=F or M) implementing investment trait $(r_{FF}, r_{FM}, r_{MF}, r_{MM})$ in a society that has an extra-pair paternity probability of p . This fitness measure should be interpreted as the change in the proportional representation of an allele from the grandparents to the great-grandchildren's generation, assuming low frequencies; that is, if

Table 1
The probabilities P_{GPC}^B of IBD alleles between grandparents and grandchildren

		No Extra-pair paternity			Extra-pair paternity probability p		
		B≡A	B≡X	B≡Y	B≡A	B≡X	B≡Y
Grandmother	P_{FFF}^B	1/4	1/4	0	1/4	1/4	0
	P_{FFM}^B	1/4	1/4	0	1/4	1/4	0
	P_{FMF}^B	1/4	1/2	0	$(1-p)/4$	$(1-p)/2$	0
	P_{FMM}^B	1/4	0	0	$(1-p)/4$	0	0
Grandfather	P_{MFF}^B	1/4	1/2	0	$(1-p)/4$	$(1-p)/2$	0
	P_{MFM}^B	1/4	1/2	0	$(1-p)/4$	$(1-p)/2$	0
	P_{MMF}^B	1/4	0	0	$(1-p)^2/4$	0	0
	P_{MMM}^B	1/4	0	1	$(1-p)^2/4$	0	$(1-p)^2$

the allele has a frequency of $kW_G^B\%$ in the grandparent’s generation, it will have a frequency of $k\%$ in the great-grandchildren’s generation. Then, among others, we can consider the following four investing strategies, with associated fitness functions calculated using Table 1. For example, a gene on an autosomal chromosome for an “equal investment in all grandchildren” trait (i.e., $r_{FF}=r_{FM}=r_{MF}=r_{MM}=1$) would have a fitness value (relative to 1) determined by the equation developed below. In the analysis that follows, we assume that the primary sex ratio in each generation is always 1:1. In this case, from Table 1 and the assumption that r units of investment in a particular grandchild increased its fitness from 1 to $1+r\phi$, it follows that

$$W_G^B(p, \phi; r_{FF}, r_{FM}, r_{MF}, r_{MM}) = \sum_{P=F,M} \sum_{G=F,M} P_{GPC} (1 + r_{PC}^B \phi)$$

2.2.1.1. *Equal investment trait at an autosomal locus (EQIT)*. This trait is defined as a grandparent investing equally in each type of grandchild, which corresponds to an investment strategy $(r_{FF}, r_{FM}, r_{MF}, r_{MM})^{EQIT} = (1, 1, 1, 1)$

$$\begin{aligned} W_F^{EQIT}(p, \phi) &= W_F^A(p, \phi; 1, 1, 1, 1) \\ &= \left(\frac{1+\phi}{4} + \frac{1+\phi}{4} + (1-p)\frac{1+\phi}{4} + (1-p)\frac{1+\phi}{4}\right) \\ &= \frac{(1+\phi)(2-p)}{2}. \end{aligned}$$

Similarly

$$W_M^{\text{EQIT}}(p, \phi) = \frac{(1-p)(1+\phi)(2-p)}{2}.$$

Thus, assuming this trait arises by chance in a population that has an equal sex ratio, the expected fitness of the allele itself is

$$W^{\text{EQIT}}(p, \phi) = \frac{1}{2} W_F^{\text{EQIT}}(p, \phi) + \frac{1}{2} W_M^{\text{EQIT}}(p, \phi) = \frac{(1+\phi)(2-p)^2}{4}. \quad (1)$$

2.2.1.2. Parental assurance investment trait at an autosomal locus (PAIT). This trait is defined as a grandparent investing equally in each type of maternal grandchild to the exclusion of paternal grandchildren, which corresponds to an investment strategy $(r_{FF}, r_{FM}, r_{MF}, r_{MM})^{\text{PAIT}} = (2, 2, 0, 0)$

$$\begin{aligned} W_F^{\text{PAIT}}(p, \phi) &= W_F^{\Lambda}(p, \phi; 2, 2, 0, 0) \\ &= \frac{1+2\phi}{4} + \frac{1+2\phi}{4} + \frac{1-p}{4} + \frac{1-p}{4} \\ &= \frac{2+2\phi-p}{2}. \end{aligned}$$

Similarly

$$W_M^{\text{PAIT}}(p, \phi) = \frac{(1-p)(2+2\phi-p)}{2}.$$

Thus, assuming this trait arises by chance in a population that has an equal sex ratio, the expected fitness of the allele itself is

$$W^{\text{PAIT}}(p, \phi) = \frac{1}{2} W_F^{\text{PAIT}}(p, \phi) + \frac{1}{2} W_M^{\text{PAIT}}(p, \phi) = \frac{(2-p)(2+2\phi-p)}{4}. \quad (2)$$

2.2.1.3. Sex chromosome investment trait at an X-Locus (SCIX). This trait is defined as a grandparent maximizing their investment in alleles passed on by descent through representations of their X chromosome in their grandchildren's generation. From Table 1, we see in the absence of extra-pair paternity (i.e., $p=0$) that a grandchild investment allele at a locus on the X chromosome maximizes its potential through an investment strategy in grandmothers and a $(r_{FF}, r_{FM}, r_{MF}, r_{MM})^{\text{SCIX:F}} = (2, 2, 0, 0)$ strategy in grandfathers. For $p>0$, the corresponding fitness functions are

$$\begin{aligned} W_M^{\text{SCIX}}(p, \phi) &= \frac{1}{4} + \frac{1}{4} + \frac{(1-p)(1+4\phi)}{2} \\ &= \frac{2-p+4\phi-4p\phi}{2} \end{aligned}$$

and

$$\begin{aligned} W_M^{\text{SCIX}}(p, \phi) &= (1-p) \left(\frac{(1+2\phi)}{2} + \frac{(1+2\phi)}{2} \right) \\ &= (1-p)(1+2\phi). \end{aligned}$$

Thus, assuming this trait arises by chance in a population that has an equal sex ratio and taking into account that females have two X chromosomes while males have one, the expected fitness of the allele itself is

$$W^{\text{SCIX}}(p, \phi) = \frac{2}{3} W_F^{\text{SCIX}}(p, \phi) + \frac{1}{3} W_M^{\text{SCIX}}(p, \phi) = \frac{3+6\phi-2p-6p\phi}{3}. \quad (3)$$

2.2.1.4. Sex chromosome investment trait at a Y locus (SCIY). This trait is defined as a grandfather maximizing his investment in alleles passed on by descent through his Y chromosome. Thus, an allele for this trait is only found in males and is only passed down to paternal grandsons, which implies that the only heritable investment strategy is $(r_{FF}, r_{FM}, r_{MF}, r_{MM}) = (0, 0, 0, 4)$. The corresponding fitness function is

$$W^{\text{SCIY}}(p, \phi) = (1-p)^2(1+4\phi). \quad (4)$$

2.2.2. Model: allele competition at low frequencies

We use functions presented in Eqs. (1–4) to compare the relative fitness of the various traits EQIT, PAIT, SCIX, and SCIY for the scenario where each of the alleles is at a very low density. In essence, we evaluate which alleles will increase in frequency, and for those that do increase, which of them increases most rapidly. For this scenario, our assumption is that each of the alleles is at a sufficiently low frequency so that interactions among alleles at the different loci are negligible second order effects. For an invasion scenario, where one of the alleles is established at moderate to high frequencies and the question is addressed of whether a second allele can then invade (i.e., an evolutionarily stable strategy analysis), second order effects are important. In this case, some assumptions regarding interaction effects are needed. The simplest assumption is codominance or linear averaging with respect to both allele dose and location. In this case, for example, a grandmother who is homozygous for PAIT and heterozygous for SCIX (the allele at the other SCIX locus is assumed to have no effect) would express the investment trait

$$(r_{FF}, r_{FM}, r_{MF}, r_{MM}) = \frac{2}{3}(2, 2, 0, 0) + \frac{1}{3}(0, 0, 4, 0) = \left(\frac{4}{3}, \frac{4}{3}, \frac{4}{3}, 0 \right);$$

that is, to not invest in her son's sons, but invest equally in the remaining grandchildren. Note that under the assumption of a nonlinear decreasing-return-to-scale investment function, we might expect a grandmother to invest in her sons' sons as well. Here we will not consider the dynamics of genes at moderate to high frequencies competing among one another, but focus

purely on relative fitness when all alleles are at low frequencies as a first cut at understanding the tradeoffs among genes for parental care at loci on different chromosomes in an environment where extra-pair paternity plays a role.

3. Results

3.1. Data

The German data suggest no significant difference in the care of PGM for their grandsons vs. their granddaughters. The only significant effect of sex of the grandchild on grandparental solicitude was in the MGM, with granddaughters favored over grandsons ($p < .0001$, Fig. 3). When looking at the entire sample, not just those who rated all four grandparents, there is also a significant difference in amount of care by the PGM, favoring granddaughters over grandsons ($p = .003$). Comparisons between grandparents for each sex of grandoffspring revealed that MGM cared for granddaughters significantly more than MGF ($p < .0001$), who showed significantly greater care than PGM ($p < .0005$), who showed significantly more care than PGF ($p < .0001$). For grandsons, the same effect was found, with the same order of care, MGM > MGF > PGM > PGF, with all relationships (all $p < .0001$) except MGF–PGM significantly different. These findings are specifically predicted by the paternity assurance hypothesis of grandparental care.

Examination of the American data indicate a trend in the care of PGF ($p = .060$) and PGM ($p = .062$) for grandsons over granddaughters, but no significant difference between the care of MGF and PGF for grandsons. For granddaughters, there was a significant difference between the care of the MGF and PGF ($p = .010$), which was not found for grandsons. The general trend in quality of care for both granddaughters and grandsons was

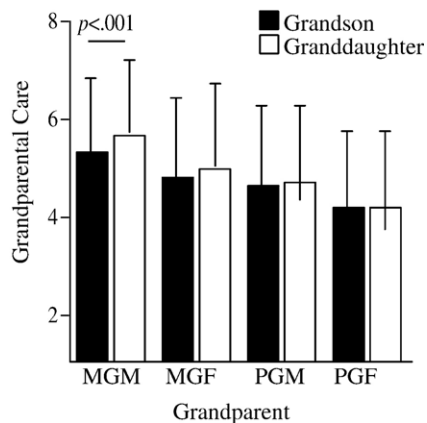


Fig. 3. Grandparental care (German data). Amount of care provided to grandsons and granddaughters by grandparents. Columns are means and error bars are S.D.'s. A value of 1 indicates no care; a value of 7 indicates a lot of care. All data were collected from questionnaires.

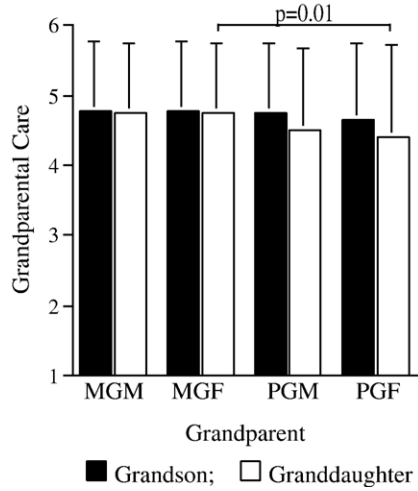


Fig. 4. Grandparental care (American data). Quality of care provided to grandsons and granddaughters by grandparents. Columns are means and error bars are S.D.'s. A value of 1 indicates low (or negative) quality; a value of 5 indicates high (or positive) quality. All data were collected from questionnaires (drawn from *Shea, 1987*).

MGM>MGF>PGM>PGF (Fig. 4). These findings are also in general accord with predictions of the paternity assurance hypothesis.

The results for amount of contact desired indicate that grandsons desire more contact with grandmothers, whereas granddaughters desire more contact with maternal grandparents, regardless of the sex of the grandparent. Grandsons overall desired contact with PGM>MGM>MGF>PGF, whereas granddaughters desired MGM>MGF>PGM>PGF. These findings are also in general accord with predictions of the paternity assurance

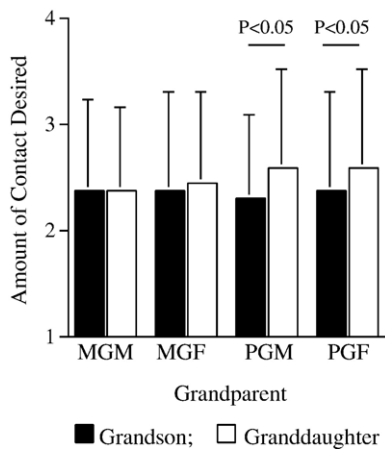


Fig. 5. Amount of contact desired by grandchildren (American data). Amount of contact with grandparents wanted by grandsons and granddaughters. Columns are means and error bars are S.D.'s. A value of 1 indicates contact desired every day; a value of 6 indicates contact desired once a year. All data were collected from questionnaires (drawn from *Shea, 1987*).

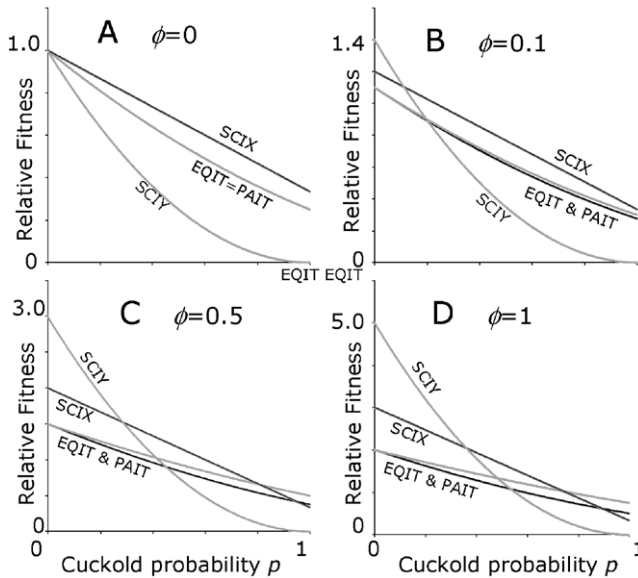


Fig. 6. Relative fitness of four parental care traits. The relative fitness of EQIT, PAIT, SCIX, and SCIY traits are plotted as functions of the extra-pair paternity probability parameter p ($0 \leq p \leq 1$) for the four investment value cases, $\phi=0.0$ (A), 0.1 (B), 0.5 (C), and 1.0 (D).

hypothesis. Grandsons also desired significantly more contact than granddaughters for both PGF ($p=.032$) and PGM ($p=.017$) (Fig. 5). This result provides weak support for the sex-chromosome selection hypothesis.

3.2. Model

In the baseline case $\phi=0$ (i.e., grandparental investment is worthless), the EQIT and PAIT fitness functions have identical values as a function of the extra-pair paternity parameter $0 \leq p \leq 1$ (Fig. 6A). Both of these fitness functions are dominated by the SCIX fitness function and, in turn, dominate the SCIY fitness functions. This situation changes when a unit of grandparental investment has a modest effect. In the case $\phi=0.1$ (Fig. 6B), SCIY dominates for extra-pair paternity rates below 0.11 ($p \leq .11$), whereas SCIX dominates the other three for rates higher than 0.11 . Now, PAIT marginally dominates EQIT for all $p > 0$, but both dominate SCIY for $p > .2$. As the value of a unit invest ϕ increases, the pattern changes (Fig. 6C) so that for large values of p PAIT now begins to dominate SCIX, although PAIT continues to dominate EQIT for all p . This result becomes accentuated as ϕ increases. For example, when $\phi=1$, PAIT dominates SCIX for all $p \geq .75$.

4. Discussion

We have proposed an alternative hypothesis to the paternity uncertainty explanation for differential grandparent care. This alternative—sex chromosome selection—would manifest

itself in differential care by PGFs favoring grandsons over granddaughters. We have also presented a model with four scenarios of differential grandparent care: equal investment (EQIT), paternity assurance investment (PAIT), sex chromosome investment favoring the X chromosome (SCIX), and sex chromosome investment favoring the Y chromosome (SCIY). Our results do not support the hypothesis of sex chromosome selection, but rather are in accord with the paternity uncertainty model (PAIT) of differential grandparental solicitude.

The only significant differences in care between grandsons and granddaughters were in the German data, which indicate that PGM favor females over males. Of the four investment strategies presented in the model, these data fit most closely into PAIT or SCIX. There is a trend in the American data indicating that PGF (as well as PGM) favor grandsons over granddaughters, but the same trend does not exist in the German data. We also see a difference in care by the PGM favoring granddaughters over grandsons in the German data when considering all of the responses, not just those who rated all four grandparents. This result is not seen in the more strictly defined sample and thus is not strong enough to provide support for the SCIX model. Accordingly, a preference by PGM for males (in support of SCIY) is not identified, and neither is a preference by PGM for females (in support of SCIX). If trends for these alternative models exist, we have found no evidence that they overtake paternity uncertainty as the major factor in differential grandparental care (see Figs 3–5). Thus, the PAIT investment strategy is supported by the data in this study.

The model suggests that if the value of a unit of grandparental investment is modest—that is, it increases the relative fitness of a grandchild by 10% or less ($\phi=0.1$)—then the SCIX strategy dominates whenever extra-pair paternity is a significant factor (i.e., above 10%) (Fig. 6B). The paternity discrepancy in current populations seems to be low, mostly around 1% to 4% (Anderson, 2005; Euler, 2004). Alternatively, when considering the differences of investment between matrilineal and patrilineal offspring, Gaulin et al. (1997) and Hoier, Euler, & Hänze (2001) estimated that in ancestral populations the paternity discrepancy clustered around 10% to 15%. The rates of extra-pair paternity may have decreased recently due to options for contraception and less restricted choice of long-term heterosexual partners. Given this ancestral rate of extra-pair paternity, and a ϕ of 0.1 or less, a strategy of SCIX should dominate.

As the relative value of a unit investment ϕ increases, the more advantageous SCIY becomes, dominating the other strategies whenever extra-pair paternity is a minor (Fig. 6B) to moderate (Fig. 6C) factor. Parental uncertainty (PAIT) only comes into play when both investment values ϕ and extra-pair paternity p are relatively large (Fig. 6D). The data in this study suggest that these conditions may be the most prevalent, as grandparents favored more certain kin and no significant preference by the PGF for grandsons over granddaughters was detected.

Using data to discriminate between SCIX and PAIT is complicated by the fact that both traits imply identical behavior for grandfathers—that is, preferential investment in the maternal line. Thus, the only way to discriminate between pure SCIX and pure PAIT is through grandmothers who, in the former, will preferentially invest in paternal granddaughters. As the data in this study show no support for this preference, our results suggest that PAIT is the dominant investment strategy. We would expect complications to arise if the

investment strategies of grandparents are not independent of one another, but rather are in conflict. These complications may result in a compromise between investment strategies, which should be explored further in future studies.

Our results in support of the paternity assurance model of differential grandparent care are in agreement with previous literature. Although much research has focused on investment at the parental level (e.g., Clutton-Brock, 1991; Trivers, 1972), investigations at the grandparental level are relatively new. Some of the first studies in differential grandparent care explored the expected roles and interactions, from both the perspective of the grandparent and the grandchild (Fischer, 1983; Hartshorne & Manaster, 1982; Kahana & Kahana, 1970; Kennedy, 1990; Robertson, 1976). These studies were the first to notice the relationship between sex of the grandparent and the effects on the grandchild, with a particular closeness between grandchildren and their MGM (Eisenberg, 1988; Hoffman, 1979–1980; Matthews & Sprey, 1985). Studies that have examined differential grandparent care have shown that the presence of a MGM generally increase the probability of survival for grandoffspring, with PGMs having a lesser effect (Hawkes, 2003; Hawkes, 2004; Jamison et al., 2002; Lahdenpera et al. 2004; O'Connell et al., 1999) or even decreasing the offspring's probability of survival (Voland & Beise, 2002).

From these first observations on grandmothers and the roles and expectations of grandparents, research has focused on paternity assurance as the main factor in the differential solicitude between MGM and PGM (Smith, 1988, 1991). Euler and Weitzel (1996) explicitly tested the hypothesis of paternity uncertainty as an explanation for differential grandparental care. Looking at historical populations, Jamison et al. (2002), Ragsdale (2004), and Voland & Beise (2002) found significant differences between care given by MGMs and PGMs as measured by the survival of grandchildren. Others have confirmed the matrilineal bias when examining other extended family members (Gaulin et al., 1997; Hoier et al., 2001; McBurney, Simon, Gaulin, & Geliebter, 2002), non-Western cultures (Holden, Sear, & Mace, 2003; Sear et al., 2002), as well as other modern populations (Euler, Hoier, & Rohde, 2001; Laham et al., 2005; Pashos, 2000).

Although much of the current literature focuses on care provided by grandmothers, only a few researchers have studied the differences in care provided by grandfathers (Eisenberg, 1988; Pashos, 2000) or the sex of the grandchild (Salmon, 1999). A few authors mention that PGFs generally favor grandsons through care or through inheritance (Cherlin & Furstenberg, 1986; Hagestad, 1985; Hill, 1970; Smith, Kish, & Crawford, 1987; Troll, Miller, & Atchley, 1979), but do not go into much detail on this topic. In general, grandfathers provide less care than grandmothers (Pashos, 2000) and may have a negative or neutral effect on survival for their grandchildren (Jamison et al, 2001; Sear et al, 2002). Jamison et al. (2002) examined the effects of the presence of grandparents on the odds of a child's survival in preindustrial Japan: of all grandfather–grandoffspring relationships, the only one that did not increase the likelihood of death for the grandchild was the PGF and grandson. Interestingly, this finding is expected under the sex-chromosome hypothesis.

More evidence in support for the paternity uncertainty hypothesis is found by looking at extended families. Gaulin et al. (1997) and Hoier et al. (2001) found a matrilineal bias in care by aunts and uncles, indicating that paternity assurance effected quality of care. McBurney

et al. (2002) conducted a differential care study in a population considered to have a high degree of paternity certainty. They found that the population with a high degree of paternity certainty did not have a significantly lower matrilineal bias than the population studied by Gaulin et al. (1997). McBurney et al. (2002) concluded that the lack of difference was due to the upper bound of paternity uncertainty in ancestral environments with the cultural effects of high paternity certainty having little effect. Laham et al. (2005) explored other factors involved in paternity assurance looking at cousins. Specifically, they explored the discrepancy between care of MGF and PGM, who both have one degree of uncertainty, but MGF consistently show a higher level of care (Euler & Weitzel, 1996; Rossi & Rossi, 1990; Smith, 1988, 1991). Laham et al. (2005) discovered a significant difference in care only when the PGM (and to a lesser extent, PGF) has other grandchildren through a daughter, thus, utilizing her resources on more certain kin. Paternity uncertainty may thus play a role in both direct (through degree of uncertainty to grandchildren) and indirect (through resources diverted toward more certain kin) means.

Previous work has shown that paternity uncertainty plays a major role in differential grandparental care, even in indirect ways. It is not surprising, then, that it overrides consideration of sex chromosomes in this study. Although there are some hints of differences in care by PGF between grandsons and granddaughters (in support of SCY), both in this study and others, these differences are not significant and are not strong enough to alter the main effect of paternity assurance. In this study, we have focused on paternity uncertainty as the main explanation for why there is no preference by the PGF for grandsons. An alternative account is that Y chromosome selection may not evidence itself through other factors such as selection for silencing a sex chromosome bias (Hamilton, 1967). In order to prevent a mutant strain on the Y chromosome from having adverse effects, the effects of that chromosome may have been buffered or silenced (Hamilton, 1967). Thus, it may not even be possible for such a preferential strategy to develop in the PGF.

In our model, we found the rates of investment and extra-pair paternity necessary for paternity uncertainty to dominate over X or Y chromosome selection. Given relatively high amounts of investment ($\phi=0.5$, see Fig. 6C) and extra-pair paternity in the population (greater than 0.11), the paternity uncertainty hypothesis of grandparental solicitude will take precedence. As the rates of extra-pair paternity in a variety of human populations, as well as the expected ancestral rate, exceed this level, the model is in accord with the paternity uncertainty hypothesis. With little or no support for the alternative models of differential grandparent care and support for the paternity uncertainty model from the collected data, we suggest that paternity uncertainty is the dominant factor involved in differential grandparental care.

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Appendix A. Assumptions of model

1. Random segregation of genes
2. Equal fitness of grandoffspring before grandparent investment
3. Linear return-to-scale
4. Equal sex ratio
5. Interactions among alleles at different loci are negligible in the context of both epistatic effects and at the population dynamics level as well.

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