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Research Article

The Selfish Grandma Gene: The Roles of the X-Chromosome and Paternity Uncertainty in the Evolution of Grandmothering Behavior and Longevity

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When considering inclusive fitness, it is expected that individuals will provide more care towards those with whom they are more closely related. Thus, if a selfish X-linked genetic element influenced care giving, we would expect care giving to vary with X-relatedness. Recent studies have shown that X-chromosome inheritance patterns may influence selection of traits affecting behavior and life-history. Sexually antagonistic (SA) zygotic drive could encourage individuals to help those with whom they are more likely to share genetic material at the expense of other relatives. We reanalyze previously reported data in light of this new idea. We also evaluate the effects of paternity uncertainty on SA-zygotic drive. Our evidence suggests that human paternal discrepancy is relatively low. Using published models, we find the effects of paternal discrepancy do not override opportunity for selection based on X-relatedness. Based on these results, longevity and grandmothering behaviors, including favoritism, may be more heavily influenced by selection on the X-chromosome than by paternity uncertainty.

1. Introduction

Care giving between family members may be influenced by genes in ways that encourage people to treat relatives differently according to their degrees of relatedness [1, 2]. The importance of genetics in care giving behaviors within families is somewhat intuitive: one would expect a woman to care more for her son than for her nephew, and more for her sister than for her cousin. In other words, it is expected that people vary the amount of care they provide proportionally to their genetic relatedness with family members. It follows that a gene which encourages such a care giving pattern may also be adaptive, as those who carry it help others who are most likely to carry it.

The idea that differential relatedness encourages preferential behaviors is not new. Many publications have reported evidence supporting kin selection and several recent studies have explored the ways in which adopted children may be treated differently than biological children, how step-parents may invest less in step children than in biological children, and how the extent of paternal care may vary based on likelihood of paternity [3–7].

Along these same lines, grandmothering behavior has been implicated in our species' unique post-menopausal longevity. The advantages that grandmothers bestow upon certain grandchildren may create opportunity for the selection of selfish genetic elements that increase longevity. Beyond this, it has been suggested that sexually antagonistic zygotic drive (SA-zygotic drive) may contribute to the behavioral pattern of some grandmothers helping granddaughters at the expense of grandsons [8].

Recent research has shown how inheritance patterns of the X-chromosome may create opportunity for selection of traits affecting human behavior and life history. Here, we reanalyze previously published data in light of the SA-zygotic drive argument. We also re-evaluate data related to prehistoric rates of paternal discrepancy and consider how discrepancy would affect SA-zygotic drive. We present

models that examine how paternity uncertainty and X-linked selfish mutations may influence selection. We find that even the highest estimated rates of paternity uncertainty do not override models for selection on grandmothers based on X-chromosome relatedness. Therefore, the differential genetic relatedness between family members may explain the ways in which women treat their grandchildren, as well as the longevity of our species.

2. Grandmothering Behavior

2.1. X-Linked Grandmother Hypothesis. The grandmother hypothesis, originally formulated to account for menopause itself, has since often been utilized in discussions of postmenopausal longevity [9–11]. This view holds that postmenopausal longevity evolved in our species because women with genetic elements coding for increased lifespan experienced increased inclusive fitness, as they were able to increase their daughters' fertility and the survivorship of their grandchildren [9, 11]. Fox et al. [12] proposed an X-linked grandmother hypothesis, based on the fact that there is variation in X-chromosome sharing between grandmothers and grandchildren depending on the sex of the grandchild and whether the grandmother is from the matriline or patriline. This differential genetic relatedness creates differential incentives for grandmothers to invest in grandchildren. In Fox et al.'s analysis of seven populations, the variation in grandmothers' effect on grandchild likelihood of mortality correlated with their X-relatedness [12].

2.2. X-Linked Granddaughter Favoritism Hypothesis. The differential X-relatedness between grandmothers and grandchildren creates opportunity for genes that affect behaviors associated with grandparenting to cluster on the X-chromosome. When paternal grandmothers (PGMs) invest in granddaughters, there is a better return on that investment for the X-chromosome than for the autosomes, so X-linked alleles for grandparenting will be more strongly selected than autosomal alleles [13, 14].

One pattern of grandparenting behavior observed in Fox et al.'s [12] meta-analysis is that of PGMs decreasing survivorship of grandsons. This phenomenon can be viewed in light of selfish genetic elements on the X-chromosome. SA-zygotic drive refers to selfish genetic material on the X or Y chromosomes that helps offspring who carry it and harms offspring who do not carry it [15]. Rice et al.'s [8] mathematical model reveals the circumstances under which natural selection would cause X-linked mutations that affect grandparenting behavior to persist. This can be thought of as an "X-Linked Granddaughter Favoritism Hypothesis." For a selfish X-linked mutation, the only relatedness that affects selection is X-chromosome relatedness. X-relatedness varies by line of descent and sex of grandchild, so an X-linked mutation in a woman has a 50% chance of being transmitted to her son's daughter, 0% chance of being transmitted to her son's son, and a 25% chance of being transmitted to her daughter's child of either sex. Using these values in Rice et al.'s [8] mathematical model shows that a dominant X-linked mutation causing all grandparents to help granddaughters at the expense of grandsons would increase in frequency as long as the magnitude of the cost to grandsons is no more than twice the benefit to granddaughters. What if the X-linked mutation were only expressed in certain grandparents (Table 1)? An X-linked mutation that causes only females (i.e., grandmothers and not grandfathers) to help granddaughters at the expense of grandsons would increase in frequency as long as the expense to grandsons is no more than three times the benefit to granddaughters. An X-linked mutation that is only expressed in PGMs would increase in frequency as long as there was a benefit to granddaughters, no matter what the effect on grandsons. This means that if an X-linked mutation arose which only affected how women treat their sons' children (in other words, the way paternal grandmothers treat their grandchildren) in terms of helping granddaughters at the expense of grandsons, there would be no hindrance to that mutation reaching fixation in the population. Overall, there are many opportunities for mutations to accumulate on the X-chromosome that cause granddaughters to be favored at the expense of grandsons. Although selection for this phenotype occurs only in PGMs, Rice et al.'s [8] model indicates that it can evolve in other grandparents as a correlated effect. Table 1 shows the predictions of the X-Linked Granddaughter Favoritism Hypothesis and the circumstances under which this phenotype would accumulate.

Table 1: The circumstances under which an X-linked gene coding for favoritism of granddaughters would persist in a population (based on Rice et al. [8] mathematical model).

When X-linked mutation helping granddaughters at expense of grandsons is expressed in:	It would increase in frequency provided the expense to grandsons is no more than (values below) times the benefit to granddaughters
All grandparents (dominant expression)	2
All grandparents (additive expression)	1.5
Grandmothers only (dom or add expression)	3
Paternal grandmothers only (dom or add expression)	no limit

The present study analyzes the data from Fox et al.'s [12] meta-analysis of seven geographically and temporally varied populations [16], in light of Rice et al.'s [8] discussion of SA-zygotic drive. Rice et al.'s [8] model suggests that granddaughters should be favored at the expense of grandsons. The predictions (Table 1) in order of increasing effect strength are that granddaughters are helped at the expense of grandsons by (1) and (2) All grandparents, (3) Grandmothers, and (4) Paternal grandmothers. The third prediction, that all grandmothers might favor granddaughters at the expense of grandsons, is not supported by the data, as the maternal grandmother (MGM) never exhibits this trend. However, in six of the seven populations PGMs have the predicted

Table 2: Data from Fox et al. [12] analyzed according to predictions based on SA-zygotic drive model (Rice et al. [8]). PGM: paternal grandmother; MGM: maternal grandmother; SA: sexually antagonistic; GD: granddaughter; GS: grandson. Check mark indicates that the population data in Fox et al. does conform to the Rice et al. prediction, and a dash indicates that it does not.

Population	PGM helps GD and harms GS	MGM helps GD and harms GS
Germany	✓	—
England	✓	—
Ethiopia	✓	—
Canada	✓	—
Japan	✓	—
Gambia	—	—
Malawi	✓	—

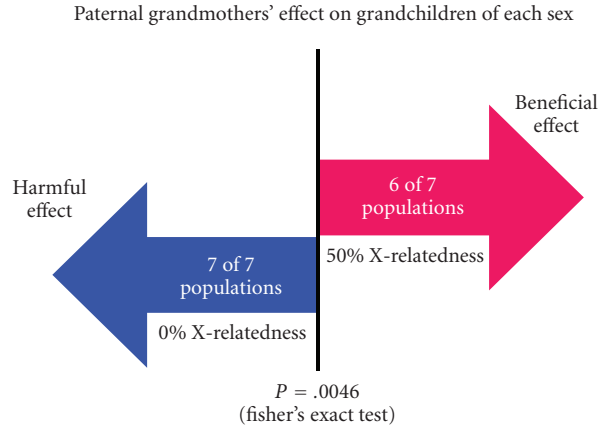


Figure 1: Analysis of the PGMs effect on grandchildren using data from Fox et al. [12]. Red (top) represents granddaughters, and blue (bottom) represents grandsons.

effect of helping granddaughters and harming grandsons, providing some support for the fourth prediction (Table 2).

Considering Fox et al.'s [12] results, the PGM had a harmful effect on grandsons in all seven populations, and a helping effect on granddaughters in six of the seven populations (Figure 1). This trend was statistically significant: Fisher's exact test $P = .0046$. These results are consistent with the X-Linked Granddaughter Favoritism Hypothesis, which suggests that selfish genetic material on the X-chromosome coding for helping granddaughters at the expense of grandsons should be most strongly favored as it is only expressed in PGMs. This PGM-grandson harming behavior, first noticed by Jamison et al. [17] who described the effect in their own data as "startling to say the least," is consistent with the presence of X-linked mutations encoding sexually antagonistic phenotypes.

The aforementioned studies found evidence of PGMs favoring granddaughters, consistent with the fourth prediction of the X-Linked Granddaughter Favoritism Hypothesis (Table 1). But based on the limitations of the statistics and the number of study populations, this may not be the most sensitive method that could be employed to test the hypothesis. When each of the 28 effects measured in Fox et al.'s meta-analysis [12] are considered individually, only five were statistically significant, although the directionalities of the effects were highly significant (Figure 1). The conclusions of Jamison et al. [17] and Fox et al. [12], therefore, provide a limited amount of evidence for the fourth prediction of the X-Linked Granddaughter Favoritism Hypothesis. Further research is needed to verify a PGM-specific trend. Also, it is important to note that these studies only examine grandchild mortality rates, not behavior, health, or any other measure of favoritism. These studies were conducted not to analyze behaviors, but rather, as an opportunity to evaluate evidence related to the grandmother hypothesis. Therefore, if the specific predictions of Rice et al. [8] are to be tested rigorously, perhaps we should look at behavior, rather than mortality rates.

Evidence supporting favoritism of granddaughters via SA-zygotic drive comes from questionnaire studies in which grandparents and grandchildren are asked to evaluate their relationships with each other. Euler and Weitzel [18] found that grandparents provided more care to granddaughters than to grandsons. Participants were asked to rank amount of care on a scale from 1 to 7, and mean granddaughter care was 4.45 and grandson care was 4.23. These results support the first prediction of the X-Linked Granddaughter Favoritism Hypothesis (Table 1). Adding their own data to that of Euler and Weitzel, Chrastil et al. [14] found that granddaughters were favored over grandsons by both MGMs ($P < .0001$) and PGMs ($P = .003$). This favoritism of granddaughters over grandsons provides further support for the third prediction of the hypothesis (Table 1).

3. Longevity

3.1. Sexually Antagonistic Zygotic Drive and Grandmother Longevity. The X-Linked Granddaughter Favoritism Hypothesis can account for SA-zygotic drive causing some, or even all, grandparents (via side-effect of selection on PGM) to carry X-linked traits that induce favoritism of granddaughters at the expense of grandsons. By the same logic, SA-zygotic drive may cause perpetuation of an X-linked longevity gene.

If, as suggested by the evidence presented above, some grandmothers favor granddaughters, then those girls with grandmothers who live longer would have the greatest advantage, as they would experience the benefits of that favoritism longer. This effect may be tempered by costs associated with having a grandmother, which may increase as she ages. Additionally, the benefits of a grandmother may only benefit young grandchildren. Further research should explore these and other limits of grandmother benefits. Nonetheless, if a grandmother has X-linked genetic elements causing her to live longer to at least a certain extent, her granddaughters may disproportionately survive. The result might be that the X-linked genetic elements will increase in frequency in the population.

There may be natural selection for selfish X-linked alleles that help one sex of grandchild at the expense of the other. If presence of a PGM (i.e., surviving) for more years helps girls and harms boys, then there is opportunity for natural selection of X-linked alleles that increase longevity. Using Rice et al.'s [8] formula, in which relatedness (R) refers to X-relatedness because this hypothesis considers only X-linked traits, a selfish genetic element will be favored as long as the following condition is true:

$$R_{\text{Helped}} \times B_{\text{Helped}} > R_{\text{Harmed}} \times C_{\text{Harmed}}. \quad (1)$$

As described in Rice et al. [8], R_{Helped} is the relatedness to the individual helped, B_{Helped} is the benefit to the individual helped, R_{Harmed} is the relatedness to the individual harmed, and C_{Harmed} is the cost to the individual harmed. Therefore, if an allele encoding greater longevity is X-linked, it will increase in frequency as long as one of the conditions listed in Table 1 is met.

(1) The magnitude of grandparent longevity's harming effect on grandsons is no more than twice the magnitude of the helping effect on granddaughters.

(2) If an X-linked longevity allele is only expressed in females (i.e., grandmothers), it will increase in frequency as long as the magnitude of grandmother longevity's harming effect on grandsons is no more than three times its helping effect on granddaughters.

(3) If an X-linked longevity allele is only expressed in PGMs (in other words, only affects the way a woman treats her sons' children), then it will be favored without constraint.

In sum, SA-zygotic drive could contribute to our species' unique phenomenon of postmenopausal longevity, as a consequence of X-linked selfish genetic elements being favored in certain grandparents.

3.2. Grandmother Alloparenting and Longevity. Many proponents of the grandmother hypothesis have suggested that postmenopausal longevity has evolved in our species because grandmothers can bolster their inclusive fitness by reducing the weaning age of their grandchildren and thereby diminish the interbirth interval of their daughters and/or daughters-in-law and enhance the survivorship of their grandchildren especially as toddlers. Grandmothers may be in a unique position to increase their number of descendants and the likelihood of those descendants' survival without compromising their own fertility.

A recent study by Kachel and coworkers [19] set out to quantify whether grandmothering could actually be a strong enough selective force to account for the perpetuation of longevity. The authors ran three mathematical simulations to test if grandmothering could increase inclusive fitness enough to influence the evolution of human longevity and/or age at weaning and survival of grandchildren. While their results claimed to prove that grandmothering cannot account for longevity, in fact their results do not conflict with the new X-Linked Grandmother Hypothesis [8, 12]. This is because Kachel et al.'s [19] study only included maternal grandchildren. Their model did not consider the effects of the paternal line and assumed that grandmothers did not provide care for their sons' children. Their results contradict studies which suggest that maternal grandmothering accounts for our species' longevity [16, 20, 21], and they cite paternal discrepancy as the reason that only maternal grandmothers are relevant to the adaptive circumstances leading to postmenopausal longevity.

If, however, SA-zygotic drive is responsible for the evolution of grandmothering and longevity alleles, the asymmetry in genetic relatedness along the paternal line is an important consideration, despite potential problems of paternity uncertainty. The previous section of this article suggests that longevity could be a result of selection purely on the PGM, and recent work by Fox et al. [12] and Rice et al. [8] suggests that PGMs' care for granddaughters could be the key to selection for grandmother care (Tables 1 and 2). Thus, Kachel et al.'s [19] conclusion that maternal grandmothering cannot account for the selection of genetic factors affecting longevity is not in conflict with the possibility that the PGMs behavior drives selection for longevity. Further research should investigate the specific behaviors of grandmothers, and the particular ways in which granddaughters are helped and grandsons are harmed. Nevertheless, paternal relatives play an important role in the X-Linked Granddaughter Favoritism Hypothesis.

4. Paternity Uncertainty

Paternal discrepancy refers to cases in which a man raises a child as his own when unbeknownst to him, he is not the biological father. If this were often the case, there would be little incentive not only for men to invest in paternal care, but also for patrilineal kin to invest in caring for his children at all. With respect to the X-Linked Granddaughter Favoritism Hypothesis, high rates of paternal discrepancy would result in little selective pressure for women to engage in caretaking behaviors towards their sons' children.

Many previous studies of the grandmother hypothesis do not distinguish between MGMs and PGMs [22, 23], and those that do distinguish between matrilineal and patrilineal relatedness tend to frame their analysis around paternity uncertainty [16, 20, 21]. Prominent researchers have claimed that selection for grandmothering behaviors and postmenopausal longevity is a result of selection exclusively on the MGM. Some studies, such as the aforementioned paper by Kachel et al. [19], have even left PGMs out of their analysis entirely under the assumption that paternity uncertainty renders PGMs role immaterial in the evolution of human longevity. As described above, PGMs are integral to the bases of all X-linked grandmother hypotheses [8, 12, 14]. Therefore, two questions cannot be ignored: how prevalent has paternal discrepancy been throughout our species existence, and how prevalent would it have to be to refute X-linked theories of longevity selection?

We suggest that paternal discrepancy may not have been much different during pre-history than it is today, based

on studies of the Y-chromosome as well as anthropological information from modern hunter-gatherers (see Supplementary Material I available online at doi:10.4061/2011/165919). Based on an extensive literature review (see below), we suggest that this rate is 1.3–3.7%. We can reanalyze the likelihood of selfish X-linked genes accumulating using Rice et al.'s inequality equations [8] by taking into account paternal discrepancy. We find that the thresholds for the accumulation of X-linked mutations causing certain grandparents to favor granddaughters at the expense of grandsons are altered only slightly. The thresholds are reported below.

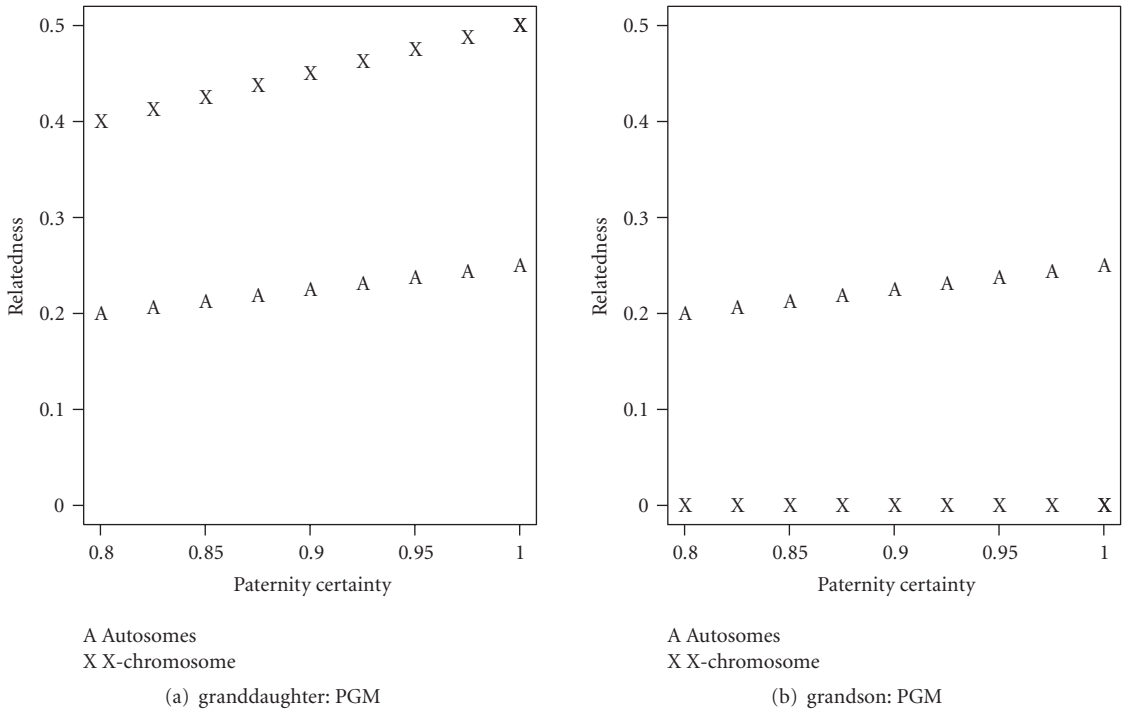
4.1. Prevalence of Paternal Discrepancy. Paternal discrepancy is often cited in academic literature as an unsubstantiated 10% in the modern human populations (e.g., [28–30]), but there is evidence that the actual rates are far lower. Bellis et al. [27] and Simmons et al. [25] performed meta-analyses on geographically varied samples of 20,871 people from 17 populations, and 16,523 people from 12 populations, respectively. All of these people underwent biological tests for purposes other than discovering paternity; therefore, the studies avoided bias towards discrepancy. Bellis et al. found that median paternal discrepancy was 3.7%, and Simmons et al. [25] reported the rate was 1.3%.

Two other studies analyzed the Y-chromosome to measure paternal discrepancy in ancient populations. Sykes and Irven [26] found a highly significant association between British men based on surnames and Y-chromosome haplotype, tracing back to a common paternal ancestor 700 years ago. Based on their data, Sykes and Irven [26] calculated a paternal discrepancy rate of 1.3%. A similar study analyzed the Y-chromosome similarities among modern "Cohanim" Jews, the supposed descendants of the biblical Moses [24]. Skorecki et al. [24] found that within this population, whose lineage dates back to 3,300 years ago, there is no evidence of paternal discrepancy from non-Cohanim Jews to complicate patterns of Y-chromosome inheritance. The authors show that paternity certainty is close to 100% with high probability. Although it is possible that extramarital paternity may have occurred with a man sharing the same surname, and thus discrepancy would not be detected, these estimates of paternal discrepancy are not only low but are also consistent with results published by Simmons et al. [25–27].

4.2. The Effect of Paternity Uncertainty on Selection for X-Linked Longevity Trait. Paternity uncertainty would surely change the likelihood of a PGM sharing an allele with her grandchild. Therefore, we have added paternal discrepancy into previously published calculations regarding the accumulation of X-linked mutations for grandmothering behavior and longevity. With this, we can show a range of PGM-grandchild relatedness given a generous variety of paternal discrepancy conditions. We use Rice et al's [8] equations to calculate the effect magnitudes for which an X-linked granddaughter favoritism trait would increase in frequency.

While the varying relatedness between maternal and paternal grandmothers with granddaughters and grandsons has been reported before (e.g., [12, 14]), these predicted relatedness values can be re-evaluated by considering rates of paternal discrepancy. Paternal discrepancy changes some aspects of the X-chromosome and autosomal genetic relatedness between (a) PGMs and granddaughters, and (b) PGM and grandsons (Figure 2; see Supplementary Material Table S7 for mathematical methods available online at doi:10.4061/2011/165919). Previous authors have suggested that paternity uncertainty may result in PGMs being statistically unlikely to share genes with their grandchildren and, as a consequence, selection for grandmothering traits act only on MGMs. The best estimates of both current and ancient paternal discrepancy (see above and [24–27]) range from 1.3–3.7%, although literature and textbooks often claim an unfounded 10%. To consider the widest range of possible values, we have modeled PGM-grandchild relatedness with paternal discrepancy ranging from 0% to 20% (Figure 2). These graphs show that although paternal discrepancy has some impact upon genetic relatedness, the comparisons between grandmother-grandchild pairs remain largely the same. The X-relatedness between a PGM and grandson is always 0%, and so hypotheses related to behaviors associated with this relationship, based on sharing no X-linked genes, still hold no matter what the amount of paternity uncertainty. The X-relatedness between a PGM and granddaughter is 50% given total paternity certainty. Even when paternity uncertainty is as high as 20% (i.e., there is a 20% chance that the PGM's son is not the biological father of the granddaughter), the X-relatedness between the PGM and granddaughter is 40%. This is because Hamiltonian relatedness refers to the statistical likelihood that two individuals share a given gene, rather than the percent of genetic material two individuals share [1, 2]. Compared to the PGM-grandson relatedness of 0% and MGM-grandchild X-relatedness of 25% (which are all relationships unaffected by paternity uncertainty), PGM-granddaughter X-relatedness of 40% is still significantly higher than all other grandmother-grandchild X-relatedness. Even given an unlikely 20% rate of paternal discrepancy, the 40% chance of sharing X-linked genetic material between a PGM and granddaughter is still much higher than with a son's son (0%) and between a MGM and granddaughter (25%). Thus, there remains the same expected favoritism as Fox et al. [12] suggested (see Table 1 in Fox et al. [12]).

Rice et al. [8] calculated the circumstances under which an X-linked allele causing favoritism of granddaughters over grandsons would accumulate (Table 1). Using their inequality equations (see Table 2 of Rice et al. [8]), we have calculated new values to describe the circumstances under which the hypothetical X-linked granddaughter favoritism allele would increase in frequency, given varying degrees of paternal discrepancy (Table 3). Following Rice et al. [8], we calculate the likelihood that an X-linked mutation, which causes grandparents to help their granddaughters at the expense of their grandsons, would accumulate as long as the detriment to grandsons is not more than a calculable magnitude greater than the benefit to granddaughters. Given dominant allele expression and complete paternity certainty,



(a) granddaughter: PGM

(b) grandson: PGM

Figure 2: Hamiltonian r value for autosomal and X-relatedness between paternal grandmothers (PGM) and grandchildren; that is, the likelihood that any given autosomal or X-linked gene in the PGM will be present in her grandchild. These values are expressed in terms of a range of paternity certainty. (a) Shows the relatedness between a PGM and her granddaughter, and (b) shows the relatedness between a PGM and her grandson. For example, when paternal certainty is 100%, a granddaughter has a 50% chance of carrying any given X-linked allele of her PGMs', and a 25% chance of carrying any given autosomal allele of her PGMs'. See Supplementary Material Table S7 for mathematical methods available online at doi:10.4061/2011/165919.

Table 3: The circumstances under which an X-linked gene coding for favoritism of granddaughters would accumulate in a population using Rice et al. [8] model, given five rates of paternal discrepancy: 0% (as reported in Rice et al. [8], and consistent with Skorecki et al. [24]); 1.3% (estimate based on Simmons et al. [25] and Sykes and Irven [26]); 3.7% (estimate based on Bellis et al. [27]); 10% (popular unfounded figure included here to show range of possibility).

Rate of paternal discrepancy →	0%	1.30%	3.70%	10%
When X-linked mutation helping granddaughters at expense of grandsons is expressed in:	Its frequency would increase provided the expense to grandsons is no more than (values below) times the benefit to granddaughters			
All grandparents (dominant expression)	2	1.993457	1.98167	1.947368
All grandparents (additive expression)	1.5	1.331876	1.329235	1.321429
Grandmothers only (dom or add expression)	3	2.97400	2.9280	2.8000
Paternal grandmothers only (dom or add expression)	No limit	No limit	No limit	No limit

the threshold for selection is grandson harm at twice the expense of granddaughter help. Using the three rates of paternal discrepancy from the literature review above (0%; 1.3%; 3.7% [24–27]) and also the popular figure of 10%, this threshold remains above 1.9. In other words, even given the highest estimated rate of prehistoric paternal discrepancy (10%), a dominant X-linked mutation that causes grandparents to help granddaughters at the expense of grandsons would accumulate as long as the expense to grandsons were no more than 1.95 times the benefit to granddaughters. The figures for additive expression, sex-specific, and lineage-specific expression are given in Table 3. The paternity uncertainty induced changes in threshold appear to be minor enough that the possibility of SA-zygotic drive towards granddaughter favoritism and longevity is not compromised.

The most comprehensive analysis possible measures the circumstances under which an X-linked mutation would increase in frequency, given a rate of paternal discrepancy ranging from 0 (total certainty; all fathers identify their children accurately) to 1 (total discrepancy; all fathers identify their children inaccurately) (Figure 3). Although

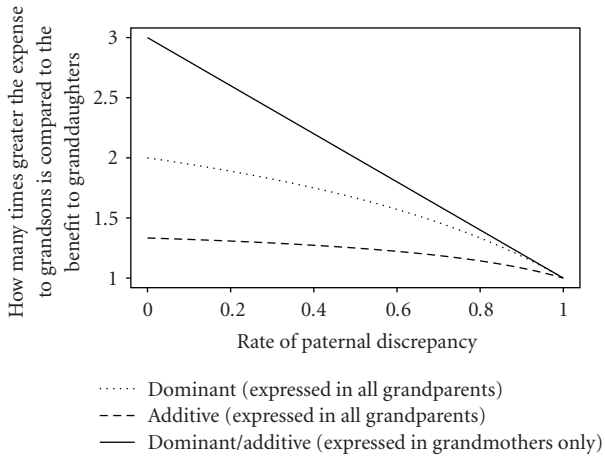


Figure 3: The threshold for an X-linked mutation causing grandparents (or grandmothers) to favor their granddaughters at the expense of their grandsons to accumulate. These curves represent the thresholds for which such a mutation would increase in frequency. The threshold can be described as the maximum number of times greater the expense of this mutation would be to grandsons, compared to the benefit of the mutation to granddaughters. These values were calculated using the mathematical model from Rice et al. [8, supplement]. We suggest that paternal discrepancy among our species would be approximately 1.3–3.7%. However, this graph shows a range of paternal discrepancy from 0% (all paternity is identified correctly) to 100% (all paternity is identified inaccurately).

total discrepancy is implausible, it is useful to visualize a curve that depicts the threshold for accumulation changes for the hypothetical X-linked mutation. A more specific analysis focuses on the curve where the threshold changes for allele frequency increase with rates of paternal discrepancy ranging from 0% to 10% (Figure 4). This segment of the larger threshold curve (Figure 3) displays the rate at which paternal discrepancy affects the threshold of the proportion benefit to granddaughters versus detriment to grandsons. This is the segment we consider to be the most likely range of paternal discrepancy rates among modern and ancient human populations. While increasing paternal discrepancy creates a stricter criterion for allele frequency increase (less detriment to grandsons compared to benefit to granddaughters), this effect is not strong (Table 3; Figure 4).

5. Conclusion

The asymmetrical inheritance pattern of the X-chromosome may influence selection among traits related to behavior and life history. The variation in X-relatedness between grandmothers and grandchildren, based on sex and lineage, may create opportunity for selection of genes that affect grandmothering strategy and longevity. Here, we have reanalyzed data from seven previously-studied populations, in light of Rice et al.'s [8] suggestion of SA-zygotic drive. The analysis explores the circumstances under which an X-linked mutation would persist, causing grandmothers to behave preferentially towards granddaughters at the expense of grandsons. The results show that six of the seven populations conform to a prediction of this hypothesis: that PGMs have a beneficial effect on granddaughters and a harmful effect on grandsons. Further research should explore how consistent this trend is between populations, and should see if this trend exists in modern industrialized populations. Additionally, future research should explore the behavioral mechanisms involved in this pattern.

Preferential grandmothering behavior may be present in other species as well. Johnstone and Cant [31] recently reported that whales represent another clade in which postmenopausal longevity is consistently observed. Among certain whales, as a female gets older, her genetic relatedness to the members of her local group increases. This suggests that it is increasingly advantageous for her to care for individuals in her social group because she is increasingly likely to be closely related to them. The benefits of this strategy may contribute to longevity in whales. Also, some whale species are known to favor sons over their daughters, and this may directly affect fitness of individuals. Further research into preferential behaviors within families should extend to other species, for the purposes of understanding our species in the context of others.

The extent of care giving behaviors among the paternal line in our own species is often analyzed in terms of degree of paternity certainty. Many assumptions are made regarding the prevalence and importance of paternity uncertainty in the evolution of grandmothering behaviors and longevity. A review of the relevant literature ranging from cultural anthropology to genetics suggests that paternal discrepancy may be 1.3–3.7%, and there is evidence that rates today are similar to rates in prehistoric times, although more research needs to be done to confirm this. By evaluating a wide range of rates of paternal discrepancy, our models (adapted from Rice et al. [8]) suggest that the thresholds for selection of X-linked grandmothering traits are not dramatically influenced by paternal discrepancy, even when the rates are extremely high. Thus, there is opportunity for selection based on asymmetrical genetic relatedness, such as differential inheritance of sex chromosomes.

SA-zygotic drive may contribute to the evolution of human longevity. If the benefits of having a living grandmother are sufficiently advantageous for certain individuals, then this could lead to selection for longevity on a larger scale. Further research should probe the mechanisms by which paternal grandmothers have a beneficial effect on granddaughters and a detrimental effect on grandsons, in light of incentives for longevity. Additionally, as our understanding of functional genetics increases, finding X-linked traits influencing longevity and care giving would provide support for the hypotheses described herein.

Researchers should also further investigate the magnitude of the effects grandmothers have on different grandchildren. Finally, although attention has primarily focused on grandmothers and the X-chromosome, we think the roles of grandfathers and the Y-chromosome should also be explored in light of SA-zygotic drive.

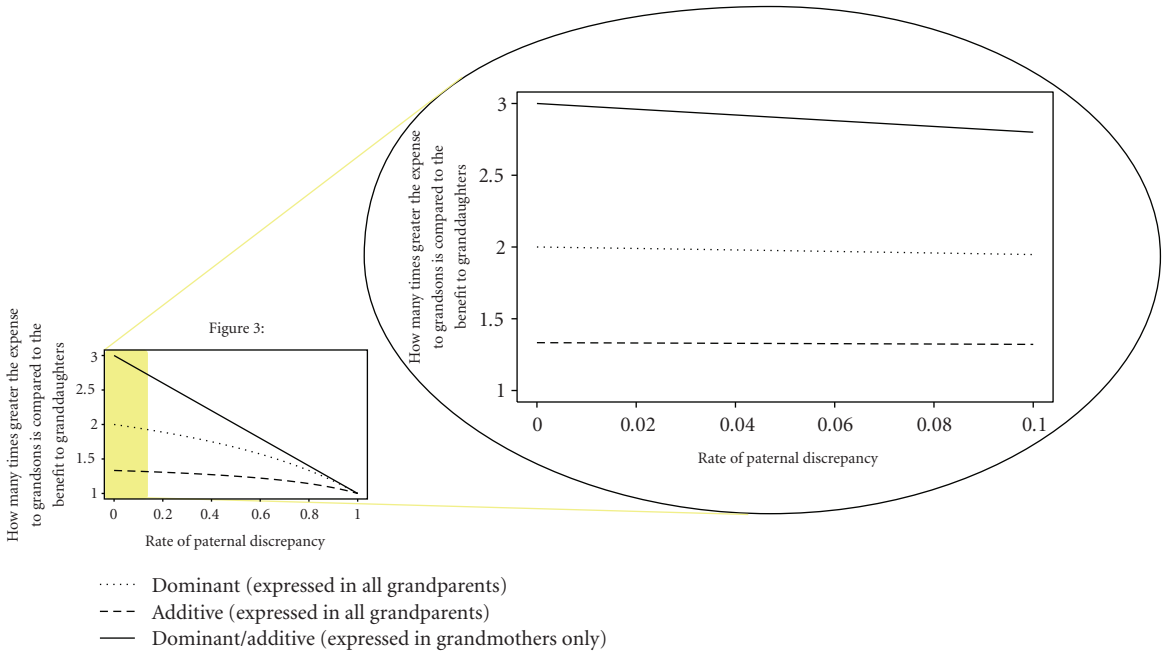


Figure 4: The threshold for an X-linked mutation causing grandparents (or grandmothers) to favor their granddaughters at the expense of their grandsons to accumulate. The threshold can be described as the maximum number of times greater the expense of this mutation would be to grandsons, compared to the benefit of the mutation to granddaughters. These values were calculated using the mathematical model from Rice et al. [8, supplement]. The range of paternal discrepancy is 0% (all paternity is identified accurately) and 10% (1 in 10 instances paternity is identified inaccurately). This range was chosen because previous studies suggest that our species' normal rates of paternal discrepancy may range from 1.3% to 3.7%, although many sources claim an unsubstantiated rate of 10%. Therefore, the range in this graph is meant to be inclusive and show a more sensitive scale of invasion threshold than Figure 3.

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